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Rock-colonizing plants: abundance of the endemic cactus *Mammillaria fraileana* related to rock type in the southern Sonoran Desert

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Abstract Establishment, colonization, and permanence of plants affect biogenic and physical processes leading to development of soil. Rockiness, temperature, and humidity are accepted explanations to the influence and the presence of rock-dwelling plants, but the relationship between mineral and chemical composition of rocks with plant abundance is unknown in some regions. This study documents plant species growing on rocks, their capacity as rock colonizers measured by the Importance Index, and the relationships between the chemical composition of rocks and the abundance of the dominant plant. The community is composed of eight species and is dominated by the small cactus *Mammillaria fraileana*. Sites with low abundance of this species contain volcanic breccias, high amounts Ca, Fe, Mg, Ti, Al, and Mn as part of moderately weatherable minerals, such as plagioclase and pyroxene. Sites with higher abundance contain rhyodacite, rhyolite, and andesite rocks rich in more weatherable minerals, such as volcanic glass and minerals containing Si, K, and Na. K and Na were present in equal proportions only at the site with more plants. Since Na is toxic for most plants, an experiment was carried out to assess its effect on the survival of *M. fraileana* seedlings. Decreased survival occurred as the concentration of Na increased. Even in the treatment without Na, survival decreased slightly. In summary, presence and abundance of plants is related to the type of bedrock, their weathering characteristics, and proportion of elements. The interactions among elements, rather than the isolated effect of specific elements, could be the most reliable explanation for local variations in the abundance and dominance of *Mammillaria fraileana* in rocky habitat in the southern Sonoran Desert.

Keywords Cactus nutrition · Colonization · Rock weathering · Saxicolous desert plants

Introduction

Rocky environments constitute a suitable location for study of ecological phenomena, such as colonization (Ryti 1984), plant succession (Martinez 1999), and rock weathering (Adams et al. 1992; Puente et al. 2004a). Colonization by plants can occur on primary

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sites (newly created) or secondary sites (previously vegetated) and participate in rock weathering through the establishment and persistence of species (Glenn-Lewin et al. 1992). Rock and mineral weathering by physical and biochemical processes eventually lead to formation of soils (Barber 1995). Biological weathering is the result of metabolic activity of bacteria, cyanobacteria, fungi, lichens, and vascular plants releasing organic acids and chelating compounds that completely or selectively extract mineral components from rocks and exploit them for their own use (Hinsinger 1998; Belnap and Lange 2003; Schulze et al. 2005). Plant roots enhance the rate of soil formation as a result of changes in the physico-chemical environment of the rhizosphere, for example, by increasing substrate porosity (Gibbs and Reid 1988) and rhizhosphere acidity, the latter by production of root exudates and protons that modify the nutrient concentration and availability of nutritional elements for plants and microorganisms (Hinsinger 1998; Jones 1998; Carrillo et al. 2002; Akter and Akagi 2005).

Saxicolous plants (plants inhabiting rocks) occur in many ecosystems, temperate (Franklin and Dyrness 1973), semi-arid (Zwieniecki and Newton 1995), and very arid (Bashan et al. 2002) environments. Saxicolous plant communities share similar limiting environmental conditions, such as shallow soil or bare rocks, low soil moisture and nutrients, and exposure on slopes (Martinez 1999; Nobel and Zutta 2007).

In hot, dry deserts, colonization of rocks by plants is an additional challenge that requires adaptations to this harsh environment. Even so, perennials, succulents, cacti, and shrubs are common on rocky substrates in the Sonoran Desert of northwestern Mexico and southwestern USA (Turner et al. 1995; Nobel and Loik 1999; Anderson 2001; Chadwick and Steinmetz 2006; Nobel and Zutta 2007). Rock-colonizing plants become established on bare rock, that is, without the benefit of soil (Bashan et al. 2002, 2006). Apparently, the key to their outstanding performance in harsh environments lies in their association with microorganisms (Puente et al. 2004a, b; Bashan et al. 2007). However, the relationship between environmental factors, such as specific plants colonizing rocks and the composition of the rocks are almost unknown.

This study assessed the capabilities of the small cylindrical cactus *Mammillaria fraileana* (Britt. & Rose) Boedeker, which is endemic in the State of Baja California Sur, Mexico, to colonize rocky areas within the desert. This cactus is common in rocky habitats and many individuals grow in fissures or directly on the rock surface (Wiggins 1980; Bashan et al. 2002). The hypotheses of this study were that rock-dwelling cacti, even small species, are major colonizers of rocks in the desert and that rocks are a suitable habitat for pioneering desert plants. This study attempted to (1) determine the importance of the population of *M. fraileana* compared to other plant species growing on representative rocky habitats and (2) evaluate whether abundance of *M. fraileana* can be explained by the composition and weatherability of the rocks in its habitat. This was done by combining quantitative field surveys, chemical and mineralogical analyses, a plant growth experiment, and comprehensive statistical analyses of the data from these sources. This is the first study specifically intended to understand patterns of abundance of cacti and environmental factors related to rock composition.

Materials and methods

Plant species

Mammillaria fraileana (Britt. & Rose 1923) Boedeker (common local name 'viejito' or 'small old man') is an endemic cactus from Baja California Sur, Mexico. Its main habitat is rocky hillsides and desert islands, where it is found in large populations that dominate the habitat, despite the small size of individual plants. Its range is about 250 km along the east coast of the Baja California Peninsula from Isla Catalina (25°36′ N, 110°48′ W) southward to the city of La Paz (Wiggins 1980). *M. fraileana* grows in clusters, 10–15 cm high, 3 cm average diameter with narrow cylindrical stems, pink flowers, red fruit, and small black seeds (Anderson 2001). The biology of this species has not been studied (JL Leon de la Luz, pers. comm.). Field observations suggest similarities to other *Mammillaria* that it strongly resembles phenologically, that is, the flowering periods are associated with the oncoming rainy season and fruit maturation often occurs inward toward the stem, between the tubercles (Bravo-Hollis and Sanchez-Mejorada 1991; Zavala-Hurtado and Valverde 2003).

Study area

We studied three sites about 2 km north of the city of La Paz, Baja California Sur, Mexico (24°11′15″ N, 110°17′50″ W) (Fig. 1). Sampling sites A, B, and C were located on adjacent hills landward of the first ridge of hills bordering the coastal plain. The vegetation of the study area is sarcocaulescent or desert scrub vegetation. The overstory is dominated by several shrubs, *Jatropha cuneata* Wigg. & Rollis, *Fouquieria burragei* Rose, *Bursera microphylla* A. Gray, *Bursera epinnata* (Rose) Engler, *Agave sobria* Brandegee, *Aeschynome vigil* Brandegee, and the treelike cactus *Pachycereus pringlei* (S. Wats.) Britt. & Rose. The lower story is composed primarily of the small cacti, *Mammillaria fraileana* (Britt. & Rose) Boedeker, *Echinocereus brandegeii* (J.M. Coulter) K. Schumann. Among herbaceous plants, only *Euphorbia leucophyhlla* Benth. is common (JL Leon de la Luz, pers. obs.).

The climate is subtropical, mostly hot and dry. The multi-year average rainfall is 180 mm ranging from 35 mm in dry years to 424 mm in the mountainous areas. The rainfall is usually associated with Eastern Pacific hurricanes and tropical storms that occur from August through October. Winter rain is likely, but uncommon, and is usually about 10% of annual precipitation. Data from the CIBNOR meteorological station near La Paz indicates that average monthly temperature ranges from 14.8°C in January to 32.4°C in the three summer months, with several hours each day reaching 38–42°C. The 6-year average insolation during the hottest period of the day may reach 2,300–2,500 μmol photons m^{-2} s^{-1} for several hours.

The lithology is interbedded sandstones and conglomerates derived from rhyolite-based ash-flow and tuff and andesite-based lahars and lava flows. The soils are immature, brown to gray in color, composed of fragmental debris (Hausback 1984).

Field methods

This area was chosen because the hillsides display perceptible differences in rock substrate, different plant densities occur on the rocks, and the vegetation seems undisturbed.

To avoid effects of coastal salt spray, prevailing high winds, and variable humidity in an east-west direction, only south-facing slopes were chosen. The sample plots at each site covered about 1,000 m^2 at

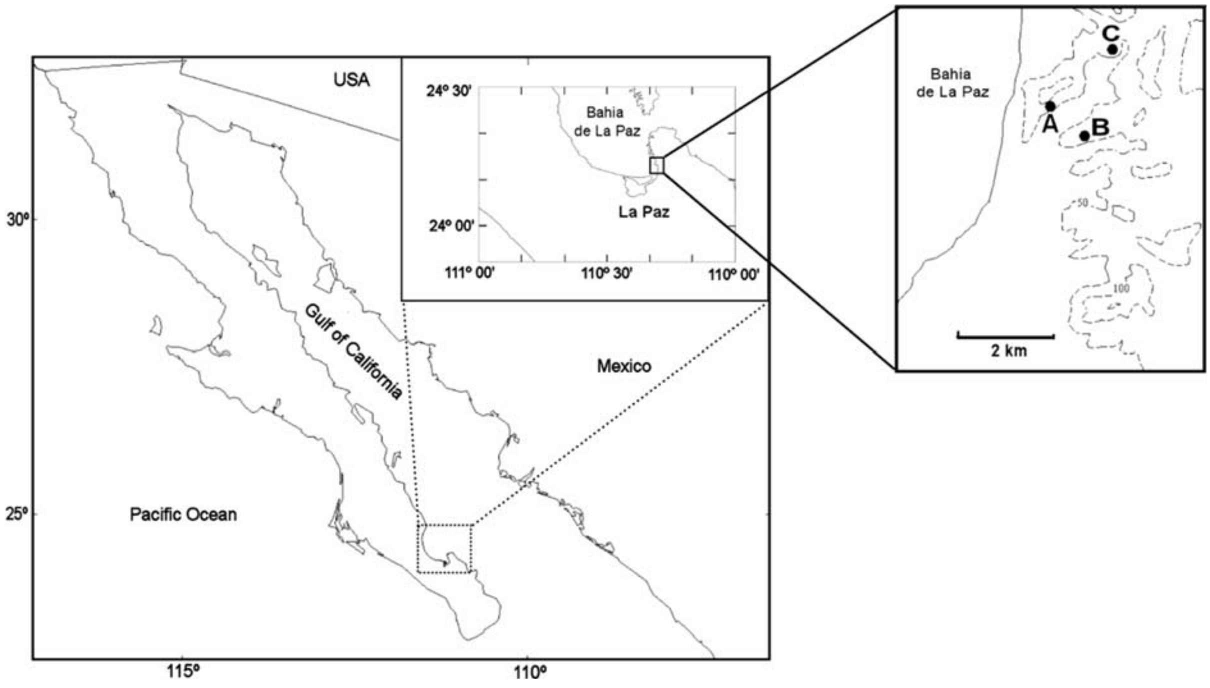

Fig. 1 Location of the study area and sampling Sites A, B, and C on three hillsides. Contours represent 50 and 100 m

an elevation between 50 and 100 m. At Sites A and B, the surface of the sample plots were boulder-sized rocks. At Site C, the surface of the sample plots was massive sedimentary rock consisting of angular or sub-angular breccias larger than 2 mm. Each site consists of 10 sample plots ranging from 0.1 to 19 m^2.

Measurement of plant abundance and volume

To measure plant species abundance in each sample unit, the volume of individual plants and the frequency of occurrence were calculated. Volume is a measurement calculated from the plant cover and its height. Plant species, their height, number of stems, and stem diameter were recorded for each individual growing on the sampled rocks. Most desert plants located in the sampled area did not have leaves at the time of sampling. Volume is usually used to reflect the size of the plant and is an essential growth parameter for cacti growth related in general to survival in the wild (Gibson and Nobel 1986; Bashan et al. 1999). For woody and herbaceous species that were measured, the volume denotes stems and branches without leaves; for cacti, this attribute indicates stem volume; and for agaves, this indicates the volume of the fleshy leaves. The volume of cacti stems were calculated from the volume equation for a cylinder; the volume of each agave leaf was calculated by estimating a pyramid using the height from the base to the terminal spine, the width at the base, and the thickness of the leaf, expressed as cm^3 of plant per m^2 of rock.

Identification of rock types

One composite sample was collected from each rock; some fragments were taken from the vicinity of the plants but without any fragments smaller than cobble size. Representative samples were identified by J. Hirales at the Department of Geology of the Universidad Autonoma de Baja California Sur, La Paz, B.C.S., Mexico.

Mineralogical analysis

Because most of the rock fragments available for this analysis was gravel, the relative composition of the minerals were analyzed with a microscopic thin section method used in soils and sediment analyses (Murphy 1986). Analysis was performed at the GeoAnalytical Laboratory at Washington State University, Pullman, WA. In this case, the gravels were glued with a special epoxy resin (Epon 815C, Hexion Specialty Chemicals, Columbus, OH) and ten parts of triethylenetetramine (Sigma-Aldrich, #13,209-8) on a round, 5-cm diameter aluminum tray and dried for two days at room temperature. The flat-bottom side of the solidified samples was polished into a thin section by standard methods. The minerals were identified and counted under a petrography microscope.

Analysis of elements in rock minerals

The samples were analyzed at the GeoAnalytical Laboratory of the Washington State University for common and trace element abundances with X-ray fluorescence spectrometer (XRF; ThermoARL Advant'XP+ sequential X-ray, Thermo Fisher Scientific, Lausanne, Switzerland), following the procedure of Johnson et al. (1999). This low-dilution fusion method is reliable and robust with high analytical precision (Johnson et al. 1999). During XRF analyses, elements in the unknown samples are measured by comparing the X-ray intensity of each element with the intensity of United States Geological Survey standard samples and pure vein quartz as blanks for all elements except Si. The elemental concentrations are expressed as wt%, volatile-free, with iron expressed as FeO.

Effect of NaCl on survival of *Mammillaria fraileana* seedlings

Since sodium was abundant at all the sites, and it is frequently referred as toxic for plants, we evaluated the effect of Na on the survival of *M. fraileana*. Using concentrations of Na similar to those found at the study sites, batches of about 100 seeds were rinsed with de-ionized water and then placed in plastic cups (5 cm diameter × 3 cm height) containing 6 g perlite (Supreme Perlite, Portland, OR) and 4 g of 0.2-mm diameter white quartz sand. The medium was kept at saturation by adding 9 ml de-ionized water until 80% germination occurred (~5 days). Four salinities were tested (0, 1.5%, 2.5%, 3% wt/v of analytical grade NaCl) in nine replicates, where each replicate consisted of 50 seedlings (450 seedlings per treatment). Young, 20-day-old seedlings were watered with 10 ml of the corresponding salt treatment and later watered daily with 4 ml of de-ionized water to keep saturation level constant. The experiment was conducted in an incubator (model 815, Precision Scientific, Chicago, IL) under the conditions considered optimal in previous experiments: 30 ± 1°C and 31 ± 2 μmol photon m^{-2} s^{-1} for an 8-h light period during a 24-h cycle. Survival of seedlings was recorded weekly for 1 month.

Statistical analysis

Statistical analyses were related to the type of experiment and the measured parameters.

(1) *Importance of rock-colonizing plants*: The importance of rock-colonizing plants was evaluated with the Importance Value Index (IVI). This index indicates the contribution of a species within the community (Barbour et al. 1999); in this case, to the plant community growing only on the rocks. The IVI is calculated by adding the separate values of relative density, relative frequency, and relative dominance of each species reaching maximum values of 300 or 200 (expressed without units) (Mueller-Dombois and Ellenberg 1974), depending on the components used for its calculation. In this study, we calculated the IVI as the sum of the relative volume (as the parameter of relative dominance) plus relative frequency, so that the maximum possible value is 200. Relative frequency was the frequency of one species as a percentage of total number of plants at a site (Barbour et al. 1999). Plant density was estimated, rather than measured, because of the difficulty of precisely counting individual, caespitose cacti (arranged in clusters). Therefore, plant density is used as a complementary value and not for statistical comparisons.

(2) *Spatial variations in abundance of M. fraileana*: The volume of *M. fraileana* plants was not normally distributed. The differences between sites were analyzed first by Kruskal-Wallis ANOVA by rank and then by Dunn's test to determine which sites have significant differences. Based on the number of groups and their size, Dunn's test compared the sum of ranks between two groups with the expected average difference (Zar 1999).

(3) *Spatial variation of elements at the study sites*: Principal Component Analysis (PCA) was used to explore spatial variability based on the correlation matrix of concentration of the major elements determined by X-ray fluorescence. The PCA multivariate analyses were performed with Multivariate Statistical Package (MVSP 3.1; Kovach 1998). Standardization and centering of the matrix seemed appropriate to perform the PCA eigenanalysis to reduce extreme variation among variables (Kovach 1998). The measure of the relative importance (load) for each element on the extracted PCA axes was given by the PCA loadings. To detect differences among sites, elements with higher PCA loadings were compared with one-way ANOVA and Tukey's HSD test at $P < 0.05$ with statistical software (JMP v. 5.1.2; SAS Institute 1989).

(4) *Correlation of abundance of plants and chemical composition*: The chemical elements that contributed to differences among sites were tested to seek statistical correlation between the concentrations of chemical elements and plant volume. The correlation matrix was constructed with standardized data of the concentration of major and trace elements and *ln* of plant volume.

(5) *Effect of NaCl on survival of M. fraileana seedlings*: Survival was calculated as the proportion of the starting number of cacti surviving to the next week (Barbour et al. 1999). Survival of seedlings under different concentrations of NaCl was tested by one-way ANOVA and Tukey's HSD at $P \leq 0.05$ with statistical software (JMP v. 5.1.2; SAS Institute 1989).

Results

Relative importance of rock-colonizing plants

Species richness of saxicolous plants at the three sites was low. Of eight species identified, five were succulents (four cacti, *Mammillaria fraileana*, *M. brandegeei*, *Echinocereus brandegeei*, *Pachycereus pringlei*, and one agave *Agave* sp.); two were small herbaceous plants *Euphorbia leucophylla* and *Comelina* sp., and one was a woody species (*Fouquieria burrageei*). The eight species are common in the surrounding area. The relative importance of the

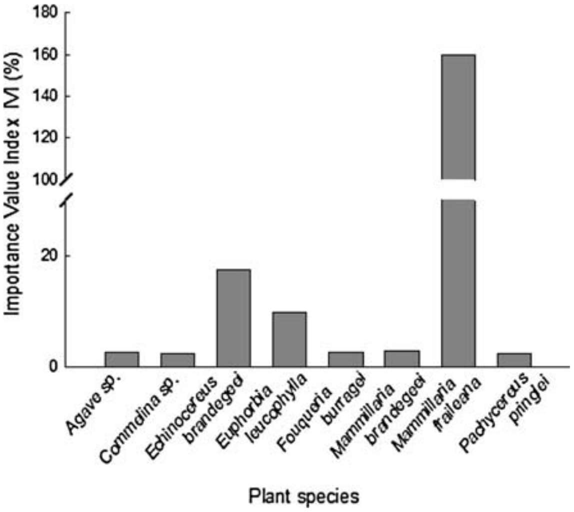

Fig. 2 Importance Value Index (IVI) for the plants growing among 30 rocks. IVI is an additive value calculated as the sum of 'relative dominance' plus 'relative frequency,' so that the maximum possible value is 200

species at each site was measured by the IVI index as the sum of two parameters: relative volume of plants and relative frequency. Each parameter can reach a maximum of 100% (Fig. 2). Therefore, the maximum value for the IVI of one species would be 200 (value without units) in strongly dominated communities.

The IVI for *M. fraileana* was 159.70; the second species was the cactus *Echinocactus brandegeei* with 17.46, which was present only at site A. About 63% of the eight species were found only once growing on rocks (*Fouquieria burragei* IVI = 2.64, *Agave* sp. IVI = 2.57, and *Pachycereus pringlei* IVI = 2.48), even though they were abundant in the surrounding vegetation (Fig. 3a). Only *M. fraileana* grew on 100% of the sampled rocks; therefore, this species was considered dominant (Fig. 3a, b). In general, the population of *M. fraileana* looked healthy, ranging in size from seedlings of 5 mm in height to adults up to 15 cm high and 5 cm across. Plants usually grow in cracks or fissures that are deeply penetrated by the root system (Fig. 3c). Seedlings (<5 mm high) were more frequently found in deep cracks, protected from direct solar radiation and reflected light.

Spatial variations in abundance of *M. fraileana*

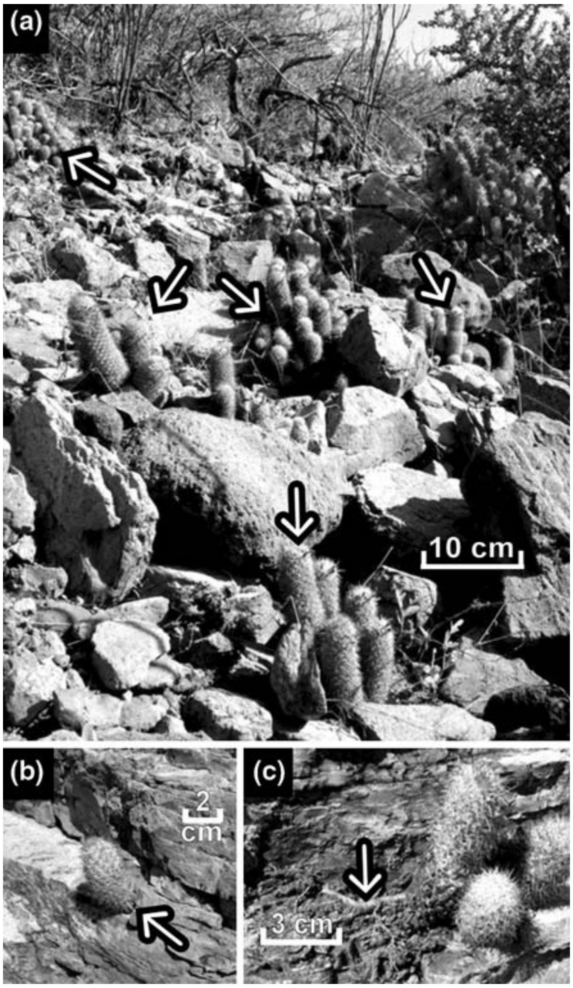

Fig. 3 **a** Plant community at Site A in the study area (arrows indicate clusters of *Mammillaria fraileana*), **b** *M. fraileana* growing on andesite, **c** *M. fraileana* with roots exposed after removing rock fragments surrounding the plant

The plant volume of this species varied among sites. The maximum volume occurred at Site B (744.3 cm^3 m^{-2}) and the minimum (5.6 cm^3 m^{-2}) at Site C. Even though volume was not normally distributed, for a better understanding, average of plant volume and its corresponding plant density were calculated for each sampled plot. In ascending degree, Site C had 19.0 cm^3 m^{-2} (~0.38 plants m^{-2}), Site A had 110.7 cm^3 m^{-2} (~4.17 plants m^{-2}), and Site B had 350.3 cm^3 m^{-2} (~9.91 plants m^{-2}). Kruskal-Wallis ANOVA by ranks, showed significant differences in the volume of *M. fraileana* between sites ($H = 18.56$, $P \leq 0.0001$). Dunn's Test showed significant differences between sites A and C ($Q = 2.936$; $P \leq 0.05$), and C and B ($Q = 4.165$; $P \leq 0.05$), but no differences were found between sites A and B ($Q = 1.397$;

Table 1 Dunn's nonparametric test for multiple comparisons of volume of *Mammillaria fraileana* at the three sites at $P \leq 0.05$

Site comparisons	Ranks difference	Standard error	Q	$Q_{0.05,3}$	Conclusion concerning hypothesis[a]
B vs. A	5.45	3.902	1.397	2.394	Accept
B vs. C	16.25	3.902	4.165	2.394	Reject
C vs. A	10.8	3.679	2.936	2.394	Reject
Sites grouping					
A	a				
B	a				
C	b				

$Q_{0.05,3}$ = one-tailed hypotheses, 3 df

[a] Hypothesis that volume of *Mammillaria fraileana* is the same at Sites B and A

$P \leq 0.05$). Therefore, the A–B group had the highest volume and the C group had the lowest plant volume per m^2 (Table 1).

Lithology and mineralogy

The rocks from the three sites were part of the Comondu Formation (Hausback 1984). Sites A and B (Fig. 4a, b) are volcanic rocks called Providencia rhyodacites (gray flow-laminated lava), ranging in composition from rhyodacite to rhyolite and andesite containing horizontal fissures and vertical fractures. Site C is composed of rhyolite breccias that are more massive-like and with much fewer crevices and fractures (Fig. 4c). In our field observations, cracks, which are numerous at Sites A and B, provide a firm anchor for the roots that grow in intimate association with the parallel surfaces of fissures or penetrate deeply into rock fractures of the solidified andesite breccia at Site C. Data on fracture density is not available.

Microscopically, the ratio of plagioclase, pyroxene, and volcanic glass were identified and characterized. The mineralogy at Sites A and B was significantly different from Site C. Sites A and B had less plagioclase (general formula (Na, Ca)[$Al_2Si_2O_8$]), pyroxene (general formula (Ca, Mg, Fe, Al, Na)$_2$[Al,Si]$_2$O$_6$) and a high percentage of volcanic glass (combination of several minerals). Site C had the least volcanic glass and the highest percentage of plagioclase and pyroxene (Table 2). Rocks at the three sites contained felsic minerals, that is, high amounts of silicon, oxygen, aluminum, sodium, and potassium. Site C had a distinctly more mafic composition, that is, enriched with magnesium and

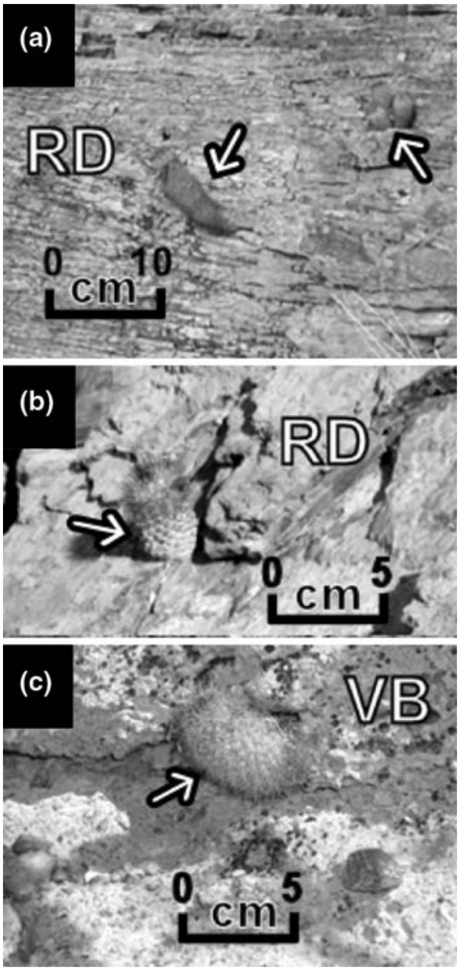

Fig. 4 Typical volcanic rocks in the study sites. *Arrows* indicate *Mammillaria fraileana*. **a** Site A composed of Providencia rhyodacite. **b** Site B composed of Providencia rhyodacite. **c** Site C composed largely of andesitic breccia. RD = Providencia rhyodacite, VB = Volcanic brecchias

Table 2 Mineral composition of rocks at the three study sites

Minerals	Site		
	A	B	C
Volcanic glass[a]	~96%	~90%	~60%
Plagioclase	1–2%	5–8%	25–40%
Pyroxene	1–2%	2–5%	~5%
Other	Hornblende	<1% magnetite, trace of calcite, weathered hornblende	~2% magnetite, 2% weathered olivine

Source: GeoAnalytical Laboratory, Washington State University, Pullman, WA, USA

[a] Combination of several minerals, mostly related to rhyolite, dacite, and possibly andesite

iron and less silicon, yet still somewhat felsic. In general, the study area had very low phosphorus, while sulfur was close to the limit of detection and chlorine was insignificant (Table 3).

Spatial variation of elements at the study sites

PCA analysis of elements showed that along the first variation axis PCA 1 (70.66% of total variance), there is a clear separation of conditions at Site C (Number 1 on the left side in Fig. 5a) from conditions at Site A and Site B (on the right side in Fig. 5a). Although the second variation axis PCA 2 (10.35% of total variance) seems to separate Site A and Site B, its explained variance is much lower that the variance explained by PCA 1, such that the distance is not comparable to the distance from Site C to Site A–Site B. Consequently, Site A and Site B were considered a single group. Site C is predominantly related to the abundance of the major elements Ca, Fe, Mg, Ti, Al, and Mn (PCA loadings −0.209, −0.209, −0.208, −0.207, −0.206, and −0.202, respectively); Site C was also partly explained by the trace elements Sc, V, Sr, Cr, and Ni (PCA loadings −0.208, −0.204, −0.201, −0.189, and −0.174, respectively). Site A and Site B were primarily associated with high concentrations of three major elements Si, K, and Na (PCA loadings 0.209, 0.208, and 0.187, respectively), and the trace elements Zr, La, Pb, Rb, Ce, Nd, U, Nb, and Th (PCA loadings 0.197, 0.193, 0.190, 0.188, 0.187, 0.181, 0.171, 0.165, and 0.160, respectively).

Table 3 Elemental content of rocks at the three study sites based on X-ray fluorescence analyses

Element	Site		
	A	B	C
Major elements (mg element g rock^{-1} ± SE)			
Al	137.6 ± 0.7	135.1 ± 3.1	180.8 ± 1.9
Ca	9.1 ± 0.2	10.7 ± 1.0	69.8 ± 1.4
Fe	25.3 ± 0.2	23.8 ± 0.8	70.4 ± 1.1
K	45.5 ± 0.2	48.2 ± 1.0	14.3 ± 0.5
Mg	1.9 ± 0.1	2.7 ± 0.3	30.5 ± 0.9
Mn	0.5 ± 0.0	0.5 ± 0.0	1.3 ± 0.0
Na	37.6 ± 0.5	36.9 ± 0.7	29.4 ± 0.5
P	0.9 ± 0.1	1.6 ± 0.3	2.3 ± 0.2
S	0.1 ± 0.0	0.3 ± 0.2	0.4 ± 0.2
Si	704.6 ± 1.2	707.4 ± 5.7	566.1 ± 4.1
Ti	4.5 ± 0.0	3.8 ± 0.3	9.0 ± 0.2
Trace elements (mg kg-rock^{-1})			
As	16.0 ± 1.0	16.2 ± 3.4	3.0 ± 1.0
Ba	1700.7 ± 67.6	1330.4 ± 158.1	946.6 ± 138.8
Ce	94.8 ± 3.0	126.2 ± 9.3	44.9 ± 1.7
Cr	2.6 ± 0.3	4.0 ± 0.6	17.7 ± 1.8
Cs	4.3 ± 0.4	10.1 ± 1.1	5.4 ± 0.6
Cu	5.8 ± 0.3	8.8 ± 1.2	12.1 ± 0.8
Ga	21.2 ± 0.2	22.8 ± 1.0	26.0 ± 0.4
La	45.9 ± 1.3	59.7 ± 3.3	20.9 ± 0.9
Nb	23.5 ± 0.3	34.6 ± 5.5	7.6 ± 0.3
Nd	44.1 ± 1.5	53.9 ± 4.5	23.1 ± 1.2
Ni	2.5 ± 0.4	4.4 ± 0.4	9.1 ± 0.7
Pb	24.4 ± 1.6	21.7 ± 0.8	8.2 ± 0.5
Rb	176.8 ± 0.8	238.2 ± 18.6	59.2 ± 3.5
Sc	12.4 ± 0.2	9.4 ± 0.8	31.1 ± 2.8
Sr	181.7 ± 3.4	210.6 ± 23.9	472.7 ± 9.8
Th	17.5 ± 0.3	31.2 ± 4.2	4.3 ± 0.3
U	5.4 ± 0.3	7.6 ± 1.0	1.2 ± 0.4
V	28.5 ± 1.2	49.7 ± 5.3	234.4 ± 9.5
Y	47.0 ± 1.8	53.8 ± 5.9	35.0 ± 1.3
Zn	72.0 ± 1.8	76.4 ± 8.4	108.9 ± 1.5
Zr	493.6 ± 2.9	534.9 ± 44.9	172.1 ± 3.2

Data were calculated by converting wt% to wt/wt units

Source: GeoAnalytical Laboratory, Washington State University, Pullman, WA, USA

From PCA, all elements associated with the described pattern were analyzed first by ANOVA and then by Tukey's HSD test to find the most important variables related to the ordination pattern and to confirm differences between Site C and Sites A-B. Significant differences ($P < 0.001$, 2/26 df) between sites were found for all the elements related to the ordination pattern. Tukey's HSD test at $P < 0.05$ showed similarities between Sites A and B for seven of the major elements: Si, Al, Fe, Mn, Ca, Mg, and Na (Figs. 6a–f, 7a).

Essential nutrients for plant growth, such as K and P, were significantly different among sites but there was no consistent grouping of sites (Fig. 7b, c). Nevertheless, when the cumulative amount of K and P was calculated, significant differences between sites and groupings were displayed ($F = 684.86$, $P < 0.0001$, 2/26 df), which indicates higher cumulative K + P at Sites A and B (Fig. 7e). In general, significant differences ($F = 1475.22$, $P < 0.0001$, 2/26 df) occurred when the combination of Fe + Mn + Ca + Mg was higher at Site C and lower at Sites A and B (Fig. 7f). Titanium showed significant differences between sites and was higher at Site C, which had fewer plants.

Regarding noxious trace elements (Taiz and Zeiger 2006), Zn was lower at Sites A and B ($F = 18.65$, $P < 0.0001$, 2/26 df) and higher at Site C ($F = 14.58$, $P < 0.0001$, 2/26 df), but Cu and Ni did not show a pattern ($F = 14.67$, $P < 0.0001$, 2/26 df, and $F = 40.47$, $P < 0.0001$, 2/26 df, respectively). When the combination of Al + Zn + Cu + Ni was compared between sites, significant differences occurred ($F = 182.24$, $P < 0.0001$, 2/26 df). Sites A and B had less of these elements (Fig. 7g). Other significant findings involved the ratio Na:K, which was lower at Sites A and B (Na:K = 1:1), meaning that Na and K were present in equal amounts at these two sites. Site C was depleted in K and the ratio of Na:K was about 2:1.

Correlations between abundance of *M. fraileana* and chemical composition of rocks

About 70% of the major elements were strongly correlated to the abundance of *M. fraileana* and 40% of the trace elements showed strong and mostly positive correlations. Positive significant correlations ($P < 0.001$) were found only for three major elements: K, Si, Na, and seven trace elements, Nd, La, Ce, Zr, Nb, Y, and Rb. Negative correlations were found for Al, Ca, Fe, Mn, Mg, and Ti (Table 4).

Table 4 Correlation coefficient between abundance of *Mammillaria fraileana* and concentration of elements in rocks at the three sites

Major elements		Trace elements			
Al	**−0.74**	As	0.42	Pb	0.56
Ca	**−0.67**	Ba	0.52	Rb	**0.60**
Fe	**−0.65**	Ce	**0.75**	Sc	**−0.69**
K	**0.68**	Cr	0.15	Sr	−0.45
Mg	**−0.60**	Cs	0.25	Th	0.49
Mn	**−0.63**	Cu	−0.02	U	0.53
Na	**0.62**	Ga	−0.31	V	**−0.63**
P	−0.25	La	**0.76**	Y	**0.61**
S	−0.16	Nb	**0.64**	Zn	−0.32
Si	**0.66**	Nd	**0.78**	Zr	**0.72**
Ti	−0.59	Ni	0.14		

Bold letters indicate significant correlations ($P < 0.001$)

Effect of NaCl on survival of *M. fraileana* seedlings

With time, survival rate of seedlings decreased in all treatments; control seedlings, watered only with deionized water, showed some 'natural' mortality. Survival rates declined with increasing NaCl concentrations (Fig. 8a). Statistical differences among treatments ($P < 0.0001$, $F = 140.01$) and Tukey's HSD comparison ($P < 0.05$) indicated that the effect on survival at the end of the experiment is similar at a 1.5% and 2.5% NaCl solution (survival = 19.77% ± 2.32 and 19.3% ± 2.73), but very different from seedling growing at 0% NaCl solution (survival 79.5% ± 4.11) and 3.0% NaCl solution 5.55% ± 1.19) (Fig. 8b).

Discussion

Plants colonizing barren desert rocks have a significant ecological advantage over species incapable of handling extreme substrate conditions (Bashan et al. 2002, 2006). In this study, the saxicolous community contains only eight plant species, mostly cacti *M. fraileana*, *E. brandegeei*, *M. brandegeei*, and *P. pringeli*. This result agrees with other studies describing cacti often growing on rocky substrates in Mexico (Valverde et al. 2004; Bashan et al. 2002). Particularly in our study, these cacti were observed growing in nearby vegetation in soil patches among

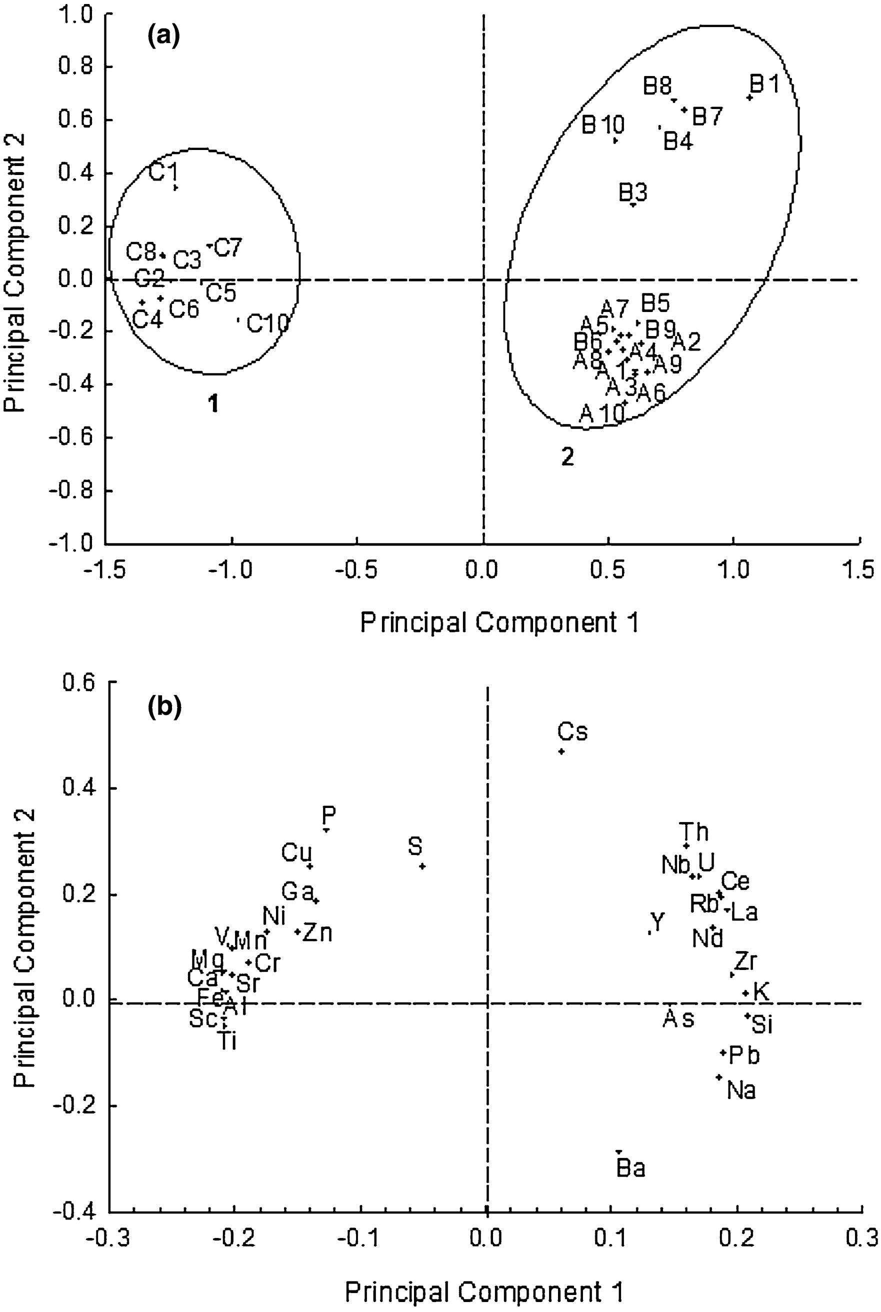

Fig. 5 Principal Components plots. **a** Ordination of sites. Large ovals represent Groups 1 and 2, A1 to A10, B1 to B10, or C1 to C10 indicate sampling units (•) at Sites A, B, or C, respectively. **b** Ordination of elements based on loading values

the rocks, but despite their abundance in rocky soil, colonization of barren rocks was almost exclusively *M. fraileana*. Taken together, a restricted number of species and high dominance of one species represent a plant community of low diversity (Crawley 1986). This usually occurs in stressful environments; in this case, the rocky habitat represents a limiting habitat characterized by extremely high temperatures, high insolation, low availability of water, and a highly impervious substrate for roots, limited soil volume and scarce nutrients (Nagy and Proctor 1997; Bashan et al. 2002, 2006).

For desert plants inhabiting rocky soils, plant development is related to physical factors, such as reflected light, rock hardness, rock and sediment porosity, water-holding capacity of the substratum

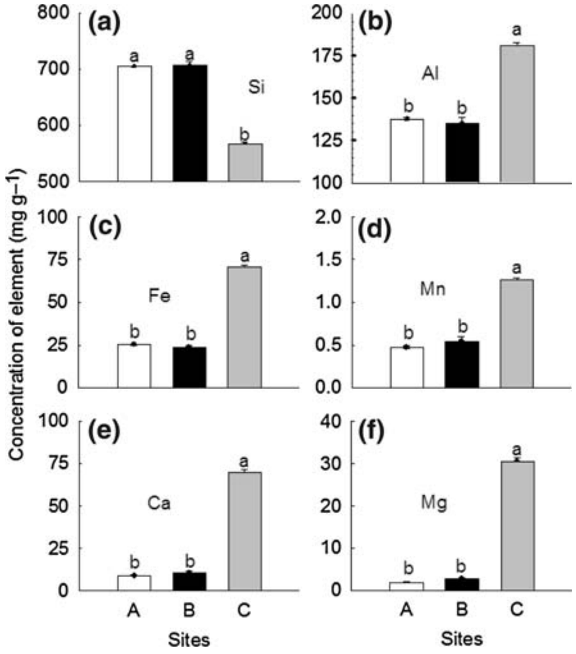

Fig. 6 Tukey's HSD test for concentration of elements at Sites A, B, and C with comparisons for: **a** Silicon, **b** aluminum, **c** iron, **d** manganese, **e** calcium, and **f** magnesium. Columns denoted with a different lower case letter differ significantly at $P < 0.05$. Whisker bars indicate standard error (SE). Absence of a bar indicates negligible SE

(Martre et al. 2002; Nobel and Zutta 2007). However, very little is known about physical factors controlling the abundance of rock colonizers. In our study, *M. fraileana*, like other saxicolous plants, exploit cracks and crevices as do other cacti and arid-zone plants (Zwieniecki and Newton 1995; Bashan et al. 2002). In fact, the numerous fissures and crevices in rhyodacites (Hausback 1984) were related to the abundance of *M. fraileana* at Site A and Site B, although it was not statistically demonstrated. Fissure density, fracture depth, and other microenvironmental conditions will be important to evaluate in further studies. We observed that cracks provide microsites that are safe against herbivores and protected from extreme environmental conditions, such as direct radiation.

In addition to physical factors, it is known that the presence and concentration of specific minerals (Nobel and Zutta 2007), the rate of weathering of rock minerals to clay minerals and salts (Nagy and Proctor 1997), and availability of plant nutrients may be crucial factors affecting rock colonizers. We hypothesized that such factors, specifically mineralogy and the chemical composition of the rocks, contribute to the ecological success of *M. fraileana* and possibly control its local distribution.

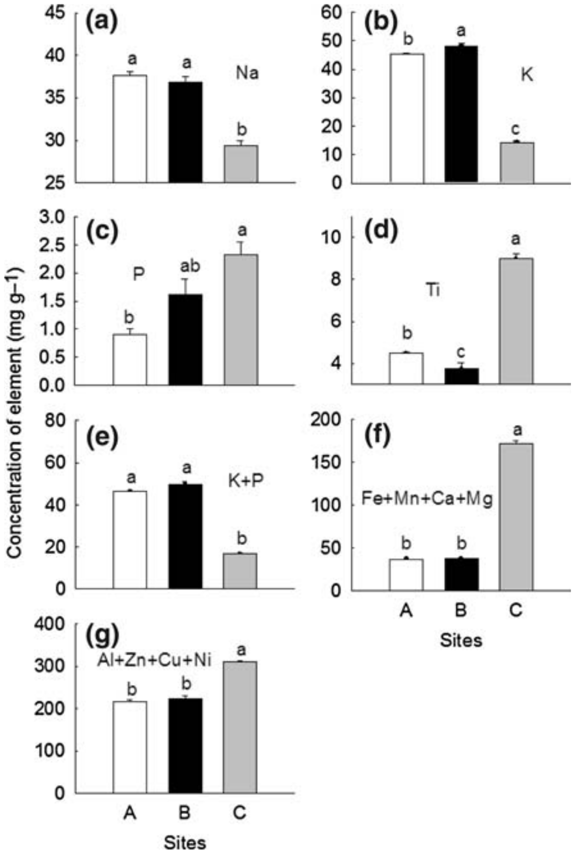

Fig. 7 Tukey's HSD test for concentration of elements at Sites A, B, and C with comparisons for **a** Sodium, **b** Potassium, **c** Phosphorous, **d** Titanium, **e** cumulative amount of macronutrients potassium + phosphorous, **f** cumulative amount of iron + manganese + calcium + magnesium, and **g** cumulative amount of toxic elements: aluminum + zinc + copper + nickel. Columns denoted with a different lower case letter differ significantly at $P < 0.05$. Whisker bars indicate standard error (SE). Absence of a bar indicates negligible SE

The mineral analysis of the rocks in our study area was similar to earlier reports of these rock types (Hausback 1984), generally, andesite and rhyolite outcrops and breccias. We found higher abundance and volume of *M. fraileana* at Sites A and B associated with larger amounts of volcanic glass. This mineral is more susceptible to weathering according to the following scale; volcanic glass > plagioclase > pyroxene (Colman 1982). Site C, with the smallest

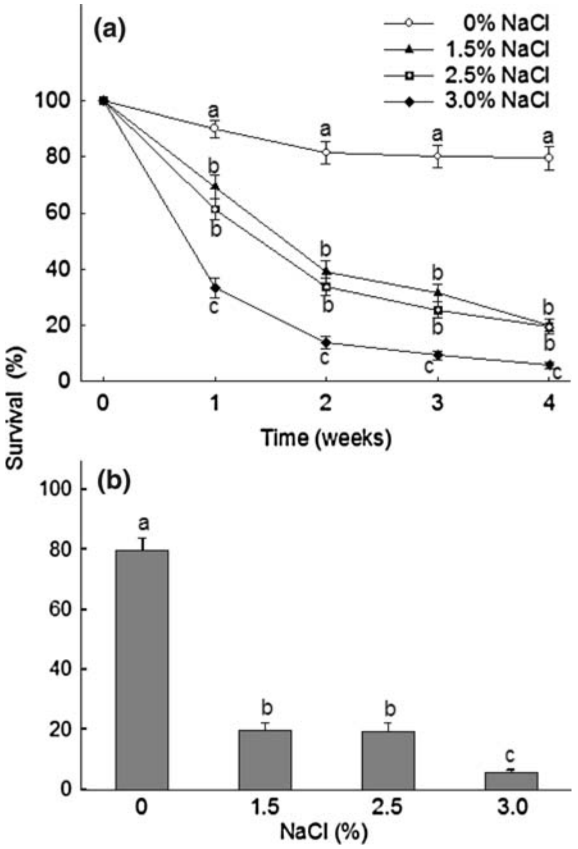

Fig. 8 Effect of NaCl on survival of *Mammillaria fraileana*. **a** Survival curves, **b** Tukey's HSD test comparison of survival at end of experiment. Values of survival at each incubation time (**a**) denoted with a different lower case letter differ significantly by one-way ANOVA and Tukey's HSD post hoc analysis at $P < 0.05$. Columns denoted with a different lower case letter differ significantly by one-way ANOVA and Tukey's HSD post hoc analysis at $P < 0.05$. Whisker bars indicate standard error

population of *M. fraileana*, has more slowly weathering minerals (plagioclase and pyroxene).

Since *M. fraileana* colonizes barren rocks, we analyzed the elements present in the rock and their availability as the rocks weather to determine if this has relevance in accounting for the abundance of plants. We found that sites with low abundance of this species contain high amounts Ca, Fe, Mg, Ti, Al, and Mn, whereas sites with higher abundance were rich in Si, K, and Na. While weathering of rocks was not directly determined, it is known that weathering of andesite, characteristic of our study sites, initially releases Ca, Mg, K, and Na, but metals (i.e., Al and Fe) are less mobile (Mulyanto et al. 1999); however, certain plants can enhance dissolution of Si, Mn, Al, and Fe (Akter and Akagi 2005). Given the negative correlation with Ca, Mg, Fe, and Mn, it is likely that these cations are available, perhaps in excessive amounts, and therefore limiting the abundance of *M. fraileana* at Site C.

Contrary to expectations, positive correlations between Na and Si and abundance of *M. fraileana* at Site A and Site B hinted at a possible advantage for *M. fraileana*, although both elements are not considered essential for plants (Raven 2003). Na is even toxic to most plant species at moderate concentrations and Si forms cellular deposits that help plants keep their cell structure or it can lessen the toxicity of metals, including Al and Mn (Taiz and Zeiger 2006). According to the weathering sequence of rocks described above, Na at sites rich in *M. fraileana* is likely to affect plants; however, in the field, Na would be easily dissolved and washed away during rainfall. We tested the hypothesis that resistance to NaCl gives an environmental advantage to *M. fraileana* over other plants at these sites that are colonizers of rocks. In general, the negative effect of NaCl could be associated with the sensitivity of terrestrial plants to moderate concentrations of Na and Cl. The higher concentrations of NaCl in the growth medium (256–513 mM) was related to lower survival, except that *M. fraileana* has higher resistance to NaCl than other cacti. In this study, *M. fraileana* seedlings tolerated higher concentrations of NaCl than seedlings of other cacti, *Ferocactus acanthodes*, *Trichocereus chilensis*, and *Carnegia gigantea*, which can survive NaCl to 130 mM (Nobel 1983). Despite significant mortality of *M. fraileana* seedlings on high saline treatments, the decrease in survival with the nonsaline treatment suggests that *M. fraileana* may require low levels of Na^+ for growth, perhaps lower than the levels tested in this study. This is a likely possibility because Na is considered essential in some C_4 plants and plants with crassulacean acid metabolism (CAM; Winter and Ziegler 1992; Winter and Holtum 2005). Indeed the response to Na in plants with CAM varies, depending on the age of plants; it may also be influenced by drought conditions (Winter and Ziegler 1992; Winter and Holtum 2005).

Another explanation for the advantage of *M. fraileana* in colonizing bare rocks and rock crevices might be related to the amount of K and its relations with other elements. Although relative low levels of K were found in the rocks, high populations of *M. fraileana* were positively correlated with higher K levels. When the effect of K + P is measured, the sites with greater abundance have larger amounts of these two elements than sites with lower abundance. Potassium may play an important role because, under saline conditions, K can counteract toxic levels of Na and the K:Na ratio could represent an indicator of balanced ions (Poole 1971; Cramer et al. 1987). Analysis showed a ratio of about 1:1 K:Na at Sites A and B, which had an abundance of *M. fraileana.* Site C, with a small population of *M. fraileana* contained about twice as much Na as K. It is likely that an imbalance in the K:Na ratio in the rocks and the weathered products in the crevices influenced the lesser abundance of *M. fraileana* at Site C. Regarding other major plant nutrients, the source of nitrogen that supported colonization of rocks by *M. fraileana*, was not studied. Past studies have shown that rock-dwelling cacti have large populations of nitrogen-fixing bacteria on their roots (Puente et al. 2004a, unpubl. data); hence, we accepted that nitrogen would be generally available.

In summary, our results highlighted the importance of *M. fraileana* in rocky habitats and showed that local variations in its abundance are based on the interaction of several elements, rather than the effect of single elements. We have provided evidence of relationships between chemical composition of rocks and the abundance of *M. fraileana*. However, it is necessary to explore physical and biological factors to elucidate their relative contribution and the relations among them.

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