Primary Colonization of Volcanic Rocks by Plants in Arid Baja California, Mexico

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Abstract: **In an arid region of Baja California Sur, Mexico, field observations, combined with chemical and physical analyses, mineral analysis and scanning electron microscopy of unweathered and weathered volcanic rocks, revealed the presence of rock-colonizing plants (most are tree-shaped cacti, possibly rock weathering), growing in volcanic rocks without benefit of soil. Many are at the seedling stage. At least four cactus species (*Pachycereus pringlei* [S. Wats] Britt. and Ross, *Stenocereus thurberi* [Engelm.] Buxb. subsp. *thurberi, Mamillaria fraileana* [Britt. and Rose] Boed., *Opuntia cholla* F. A. C. Weber), and one tree (wild fig, *Ficus palmeri* [S. Wats]) were capable of cracking, growing in and colonizing cliffs and rocks formed from ancient lava flows and, consequently, forming soil for succession by other plant species. This study shows that plant colonization of volcanic rocks may assist soil formation, which eventually leads to accumulation of soil, water and nutrients in a desert terrestrial ecosystem that otherwise lacks these essential plant-growth variables.**

Key words: Rock colonization, rock weathering, soil formation, rock-weathering cacti.

Introduction

The weathering (physical and chemical breakdown) of stones and rocks is caused not only by weather conditions (Goudie and Parker, 1999[19]), but also by acid rain and air pollution, plants and microbial activities (Hirsch et al., 1995[23]). In hot desert climates, soil formation solely by abiotic processes (extreme temperatures, wind and limited rain) may take several hundred thousand to millions of years, depending on variations in environmental forces, erosion and deposition processes and rock type. Plants may accelerate soil formation from rock and improve soil structure by root penetration, production of weathering agents, such as organic acids, biogenic minerals and biocycling of cations (Angers and Caron, 1998[2]; Gregory and Hinsinger, 1999[20]; Kelly et al., 1998[27]; Sagoe et al., 1998[32]). Biological weathering of rock by roots and microorganisms plays an indispensable role in maintaining a continuous supply of inorganic nutrients for plants (Berthelin et al., 1991[7]; Chang and Li, 1998[12]; Gobran et al., 1998[18]; Hinsinger and Gilkes, 1993[21], 1995[22]; Illmer et al., 1995 a[24]; Illmer and Schinner, 1995 b[25]; Leyval et al., 1990[28]; Phillips and FitzPatrick, 1999[31]; Vazquez et al., 2000[35]).

In temperate regions, several tree species have been found growing in soilless environments. Lodgepole pine *(Pinus contorta)* and ponderosa pine *(P. ponderosa)* commonly occur in lava beds in central Oregon (USA) (Franklin and Dyrness, 1973[16]), while Scots pine *(Pinus sylvestris)* and Norway spruce *(Picea abies)* are commonly found on granitic bedrock in Sweden and Denmark (Lundstrom et al., 2000[29]).

Because of the aridity of the Peninsula of Baja California, desert plants are concentrated in areas that have some water for prolonged periods, such as in dry arroyos or where an aquifer is close to the surface (Garcia-Carreño et al., 1992[17]). In these places, many plants are green year-round. In all other parts of the peninsula, plants grow only during the short summer wet season. Cacti are an exception. They are evergreen and grow everywhere, regardless of water availability, because they can tolerate drought and high temperatures of air and soil, the latter often exceeding 50 °C at the surface (Carrillo-Garcia et al., 2000 a[10]).

In these hot deserts, there are at least two types of vegetative colonization by cacti. In lowland alluvial soils, cacti initially establish under the canopy of a mature mesquite tree *(Prosopis articulata)* (Bashan et al., 2000[4]; Carrillo-Garcia et al., 1999[9]). Nurse trees modify soil structure, increase nutritional value and provide a soil rich in mycorrhizal hyphae with increased water-holding capacity (Bashan et al., 2000[4]; Carrillo-Garcia et al., 2000 a[10], b[11]). In the mountainous highlands, we have observed several species of desert plants growing on cliffs, rocks and ancient lava flows in the absence of soil (Bashan et al., 2001[5]). Many of these plants are cacti endemic to Baja California. To the naked eye, cacti growing under such conditions were healthy and showed no signs of nutritional deficiencies, suggesting that these plants are able to obtain nutrients from the weathering rocks, although they potentially may receive nutrients from dry deposition.

This study was designed to document the novel phenomenon of primary colonizing of volcanic rock by desert plants. The magnitude of the population of plants living in rocks in Baja

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California provides an opportunity to determine if plant-induced rock weathering occurs in arid climates. The study presented herein is a first stage in understanding soil formation by vegetation processes in arid zones.

Materials and Methods

Site description

The central mountain range in the State of Baja California Sur (Sierra de La Gigante) was surveyed four times during the wet (one time) and dry (three times) seasons of 1998 – 2000, using survey techniques described earlier (Bashan et al., 1995[6]). Specifically, large parts of the Peninsula of Baja California are virgin wilderness, lacking paved roads. Surveys were restricted to areas with dirt roads or rancher's trails, as long as they could be negotiated with a rugged off-road vehicle. After arriving at a location where plants were growing in rocks, the following survey method was adopted. Out of 15 locations surveyed, five sites were evaluated in detail. Once such a site was chosen, the field team created five ad-hoc evaluating stations. We surveyed the site's boundaries on foot and estimated the intervals where evaluating stations could be placed. Station one was usually placed in the approximate centre of each site and the other four stations were located at nearly regular distances from each other. Distances between stations were constant, usually between 100 – 300 m, depending on the natural terrain and accessibility. At each station, a circular section of terrain, having a diameter of 100 m, was selected. All the cacti growing in rocks at each station were counted. Special attention was paid to the volcanic areas south and west of Loreto, between parallels 25° to 26°N. Each survey lasted 1 – 2 days and was largely done on foot over exposed rocks, which were ancient lava flows formed 12 – 24 million years ago (Flores, 1998[15]). The sites are in canyons and on mountain slopes of exposed rocks lacking soil. The rocks found in the study area formed during the late stages of volcanic eruption. The rocks are composed of more plagioclase feldspar and less ferro-magnesian minerals like olivine, than basalt (Best, 1982[8]). Three additional surveys were made in the 1998, 1999 and 2001 dry seasons on eroded mountain slopes in the Sierra de La Paz, at the northern outskirts of the city (Fig. **1**).

Both areas are arid, rainfall seldom exceeds 200 mm/year and some years are without rain. The average temperature is 33 °C in summer and 21 °C in winter. However, daytime summer temperatures, like any hot desert region, are extreme, frequently reaching over 40 °C. Almost no natural shade exists on these rock exposures, and the rocks and small plants growing in them are subjected to direct solar radiation of up to 2000 μmole/m^2/s.

Samples of young cacti growing in rocks on volcanic slopes were taken from areas 10 – 20 km northeast of the village of San Isidro-Purisima, 130 km northeast of Ciudad Constitucion, and 60 km northwest of Loreto in Sierra de La Gigante, Baja California Sur, Mexico.

Sampling techniques, size and design

The cactus species sampled were the arborescent (tree-shape) giant cardon *(P. pringlei),* pitaya dulce *(S. thurberi),* the small Mamilaria *(M. fraileana)* and Choya *(O. cholla).* The number of plants in a sample varied, but was never smaller than 10 plants per species. Only small plants (5 – 20 cm height) growing on rocks lacking any direct connection to soil were collected. Usually, the rocks holding the plants were carefully broken open by hammer and chisel to expose the rock-cavity in which the plant roots were growing. The entire plant and its root system were removed by hand and stored in a cooler for the 6-h drive to the laboratory near La Paz. All samples were processed after being kept overnight at 4 ± 1 °C.

Chemical and physical analyses of rocks

Rocks with and without plants were collected (5 samples from each of the five locations) from the same bluff outcrop where the plants grew. They were labelled and transported to the laboratory. Large rocks were broken into fragments lighter than 1 kg and transported to the laboratory. There, the rocks were thoroughly surface-washed with distilled water to remove dirt, roots and soil particles. Measuring dissolved minerals within the rock was performed after each rock was separately crushed and ground to pass through a 100-μm screen. The rock powder was digested by concentrated HNO_3 and HF acid in a pressured-controlled microwave oven and analyzed both by inductively coupled plasma emission spectroscopy (ICP) at the Central Analytical Laboratory at Oregon State University and by atomic absorption at CIB. The latter according to the method of van Loon (1985[34]), using the certified standard BCSS-1 of the National Research Council of Canada for marine sediments. Minerals were identified by field emission scanning electron microscopy (FESEM) on root segments, based on the morphology of crystals, according to Welton (1984[37]), or by normal and cross-polarized light microscopy of thin sections of the rocks, as described for porosity analysis. The porosity of the rock samples was calculated as follows: samples were cut squarely (2 × 2 × 1 cm, using a tile saw with a diamond blade) from about 3 cm below the surface of the rock, where the rock would not have had contact with roots. Volume of each sample was calculated by measuring the dimensions of the samples. Each sample was weighed, and the bulk density of the samples was calculated by dividing the weight by the volume. Each sample was then measured in a helium pyconometer to calculate average grain density. Porosity was then calculated by the common equation P(%) = (Grain density – Bulk density/ Grain density) × 100. All analyses were performed in triplicate; one fraction of rock (up to 500 g) was one replicate.

Plants growing in rocks were counted in five locations, five sites per location, and each site had an approximate area of 7850 m^2. Results were pooled and were transformed to number of plants per hectare. Rocks were sampled in five replicates from each of the five locations. One sample contained a piece of rock weighing less than 1 kg. Mineral analyses were performed on triplicate pieces of rocks from the sampling sites, after grinding each sample. All data were analyzed by one-way ANOVA at $p < 0.05$ or by Student's t-test.

Results

Survey of desert plants growing in rocks

Surveys in the volcanic areas of part of Baja California Sur (Fig. **1**) reveal cacti were growing in rocks without any physical connection to soil. Most plants associated solely with rocks

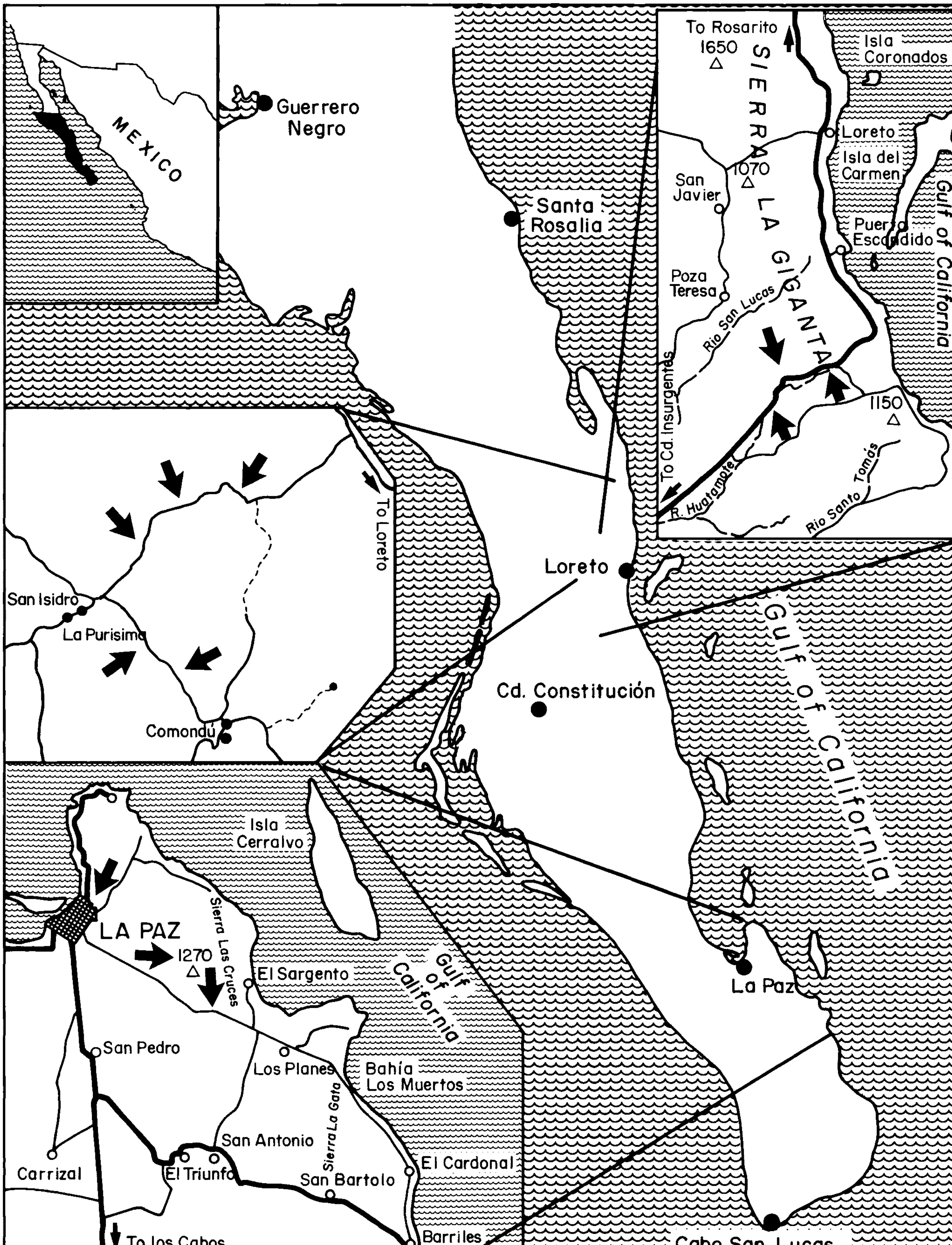


Fig. 1 Locations in Baja California Sur, Mexico, where desert plants were found growing in rocks (thick arrows). The map scale is 1:1000000.

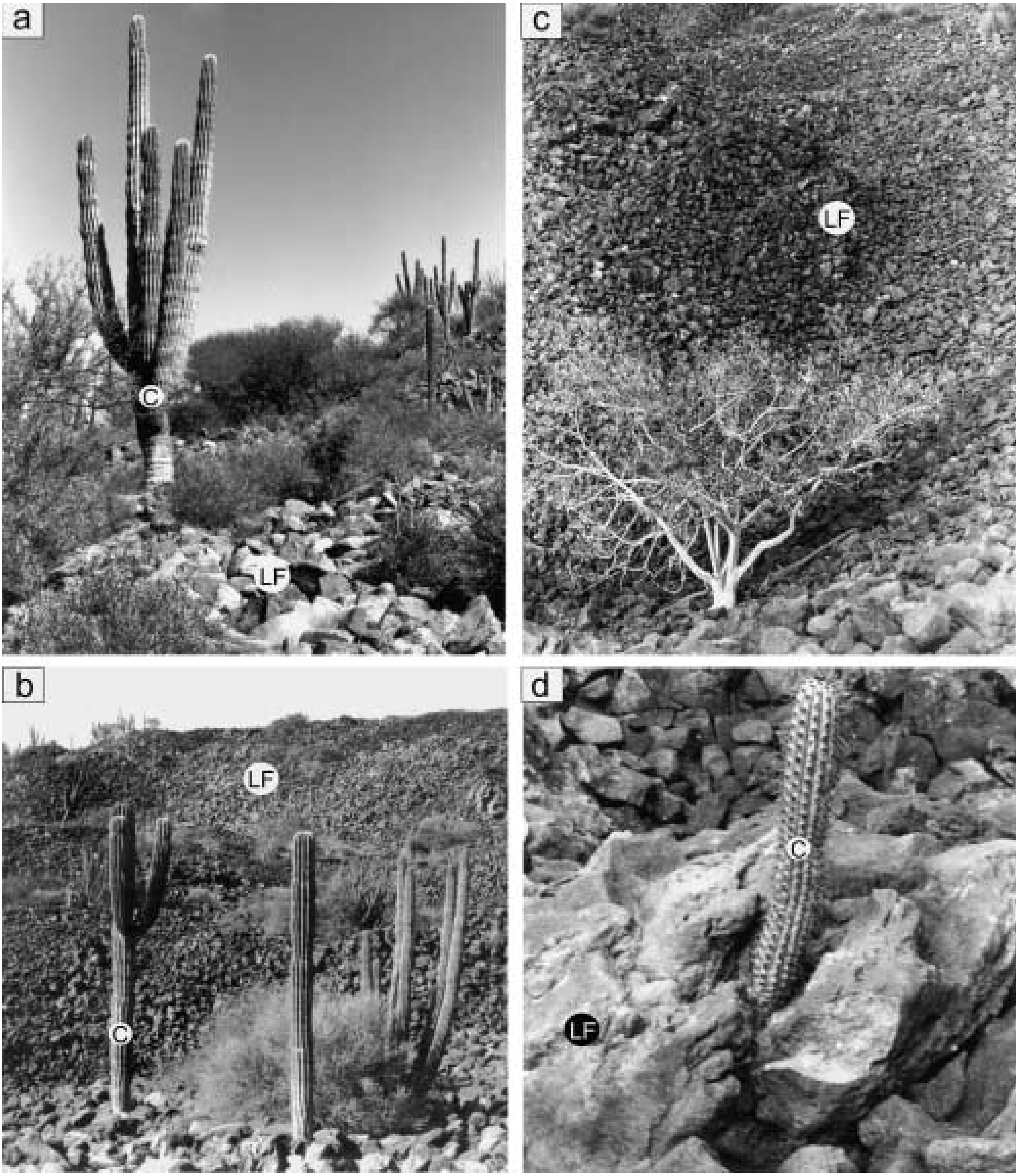


Fig. 2 Cacti growing in rocks in ancient lava flows in La Purisima area. (**a**) Mature cardon *(Pachycereus pringlei)* surrounded by secondary succession of plants growing in "soil islands" within the lava flow. (**b**) Younger cardon cacti growing almost exclusively inside an old volcanic crater. (**c**) Wild fig tree *(Ficus palmeri)* growing alone at the bottom of a volcanic crater. (**d**) Young cardon cactus growing inside lava rock. Abbreviations: C – Cardon cactus; LF – lava flow. Cardon in **a** is 4.5 m high, in **b** 2.5 m high and in **d** 40 cm high. Fig tree in **c** is 5.5 m high.

were at the seedling stage. These include cardon, pitaya dulce, mamilaria and choya (Fig. **2**). Other desert plant species growing on volcanic rocks were always associated with soil deposits (islands). These plants could potentially be rock-degrading as well, but could not be used to study the direct effect of plants on rock colonization and weathering.

Cacti associated with rock degradation were randomly distributed in the rocks. There were always more specimens of the small mamilaria cacti (maximum 10 cm tall as adult) than the other mature columnar cacti (*P. pringlei* and *S. thurberi*), which reach 3 – 6 m in this area. These rock-based plants are a small fraction of the cacti population in the area (not analyzed in this study), mostly growing in "islands" of soil deposits on the volcanic rocks. In the Sierra de La Paz, where the rocks were mostly weathered on the surface, only small mamilaria cacti were associated with rocks. Occasionally, between 20 – 40 small plants were found per 10 m^2 of rock (Table **1**). The other two cactus species growing in rock cavities had extended their roots to nearby soil deposits.

Table 1 Rock-degrading cacti in the volcanic rock of the Purisima-San Isidro area and in the Sierra de La Paz

Cactus species	Average number of plants/hectare*	
	Purisima-San Isidro	Sierra de La Paz
Pachycereus pringlei	6.4 ± 2.1 a	0
Stenocereus thurberi	5.1 ± 1.7 a	0
Mamilaria fraileana	48.6 ± 21 bA	973 ± 284 B

* Number denoted by a different lower case letter differs significantly at $p \leq 0.05$ by one-way ANOVA. Numbers in *M. fraileana* denoted by different capital letter differ significantly at $p \leq 0.05$ in Student's *t*-test. ± = SE.

Wild fig trees are commonly associated with degradation of cliffs of both volcanic and sedimentary origin in Baja California. Large mature trees fracture (root wedging) huge blocks of stone during their growth, but their roots also extend to pockets of soil. We failed to locate young fig trees associated exclusively with rocks. Therefore, it is unknown whether young fig trees are associated with initial volcanic rock colonization and

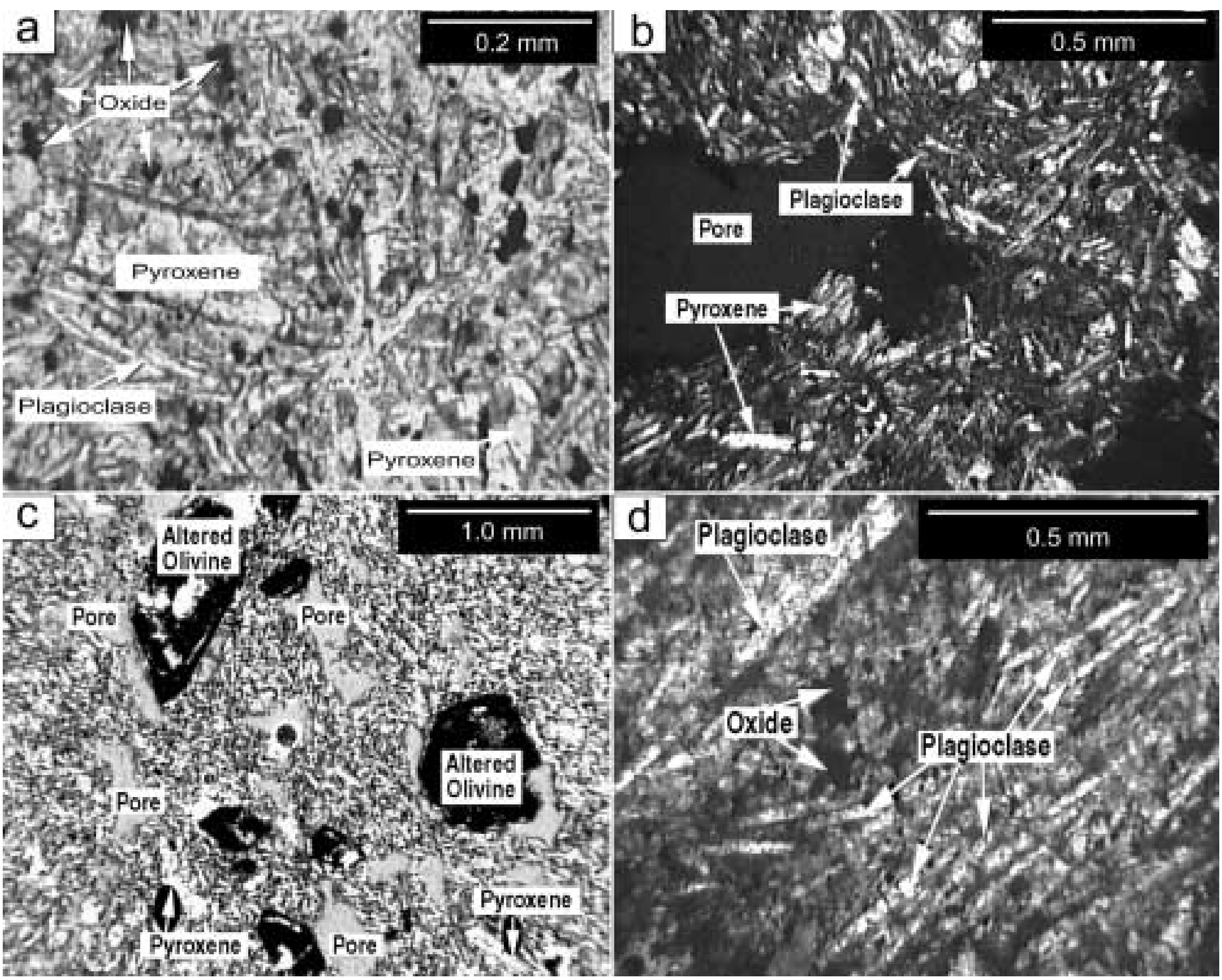


Fig. 3 Prevention of natural alteration (oxidation) of rock minerals by cacti and pore type in these rocks. Thin sections of rock chips were observed under light microscopy with plane and polarized light.

Table 2 Porosity and chemical composition of cactus-colonized rocks

Plant species	P (%)	K (%)	Ca (%)	Mg (%)	Na (%)	Mn (%)	Fe (%)	Cu (ppm)	Zn (ppm)	Porosity[a] (%)
M. fraileana	0.45 ± 0.02 b	1.36 ± 0.03 a	5.16 ± 0.12 b	2.57 ± 0.13 a	2.11 ± 0.02 c	0.07 ± 0.01 a	4.16 ± 0.14 b	72 ± 3 c	102 ± 6 c	19.6 c
O. cholla	0.42 ± 0.01 b	1.27 ± 0.03 a	4.71 ± 0.14 ab	2.54 ± 0.34 a	2.06 ± 0.01 c	0.09 ± 0.01 a	4.14 ± 0.09 b	73 ± 4 c	97 ± 2 b	ND[b]
P. pringlei	0.45 ± 0.03 b	1.24 ± 0.02 a	4.84 ± 0.16 ab	2.43 ± 0.21 a	1.79 ± 0.03 b	0.06 ± 0.02 a	4.33 ± 0.07 b	64 ± 3 b	94 ± 4 b	12 a
S. thurberi	0.92 ± 0.06 c	1.24 ± 0.03 a	4.79 ± 0.23 ab	3.26 ± 0.14 b	1.63 ± 0.02 a	0.08 ± 0.01 a	5.93 ± 0.22 c	67 ± 2 b	124 ± 5 d	ND[b]
No plant	0.30 ± 0.01 a	1.27 ± 0.04 a	4.25 ± 0.31 a	2.91 ± 0.33 ab	1.83 ± 0.02 b	0.06 ± 0.02 a	3.73 ± 0.03 a	53 ± 1 a	79 ± 2 a	14.6 b

Results are the average of 3 independent analyses on 3 different rock samples per plant species done by two different analytical services using different analytical methods. Chemical composition was determined by acid digestion followed by the ICP emission spectroscopy at the Central Analytical Laboratory, Oregon State University, Oregon, and by atomic absorption at CIB, Mexico. No detectable nitrogen and organic matter were presented in the rocks. Number in each column denoted by a different letter significantly differs at $p \leq 0.05$ by one-way ANOVA. ± = SE.

[a] Porosity was determined by Comparative Sedimentology, University of Miami, Florida, using plane- and cross-polarized light microscopy.

[b] ND – not determined.

weathering. Only one large fig tree was found growing at the bottom of a stony volcanic crater that lacked soil (Fig. **2c**).

Mineral analyses

All rocks collected for this study were of the same rock type, a porous basaltic-like andesite (composed mainly of plagioclase and oxides). Mineral composition place it between the characteristic basalts and andesites. Thin sections show these rocks are rich in plagioclase ($CaAl_2Si_2O_8$-$NaAlSi_3O_8$) and magnetite (Fe_3O_4), with less abundant mafic phases of yellow pyroxene ($[Mg,Fe,Ca]_2Si_2O_6$) and olivine (Mg_2SiO_4-Fe_2SiO_4) (Fig. **3**). The yellow tint in the pyroxenes (a more Fe-rich pyroxene) suggest a more weathered rock than common basalts. The most obvious difference between rocks harboring plants and rocks without plants was the degree of alteration. The unaltered rocks (with plants) were blacker and the iron in the rocks was less oxidized. The altered rocks were redder, resulting from oxidation of iron in the rock minerals.

Mineral analyses revealed that rocks harboring cacti were relatively richer in P, Fe, Cu and Zn than bare rocks, with few exceptions. All rock specimens had high levels of Na (about 2%). No nitrogen or organic matter was present (Table **2**). Porosity of the rock specimens ranged from 12 – 19.6%, whether or not they harbored plants; the pores were typically elongated in the direction of the lava flow. Fractures varied greatly among the rocks. Whereas rocks without plants were smooth (due to a long erosion time of 20 million years [Flores, 1998[15]]), the rocks harboring plants were densely fractured and pitted with numerous small cavities, which were 1 – 5 cm in diameter and depth (resembling a moonlike structure) (Fig. **4**).

Description of root system of cacti growing in rocks

Seedlings usually emerge from a tiny crack in the rock (Fig. **5**). Most seedlings showed no signs of stress and were similar in appearance to cacti growing in nearby soil deposits. When a rock containing a seedling was cracked open, a cavity was revealed. This cavity contained the entire root system of the seedling. Most roots were attached to the rock surface, and a few were suspended in air space of the cavity (Fig. **5**). A small amount of "soil", possibly a mixture of weathered minerals and organic matter formed from degraded roots, was sometimes attached to the root system. However, most of the sub-

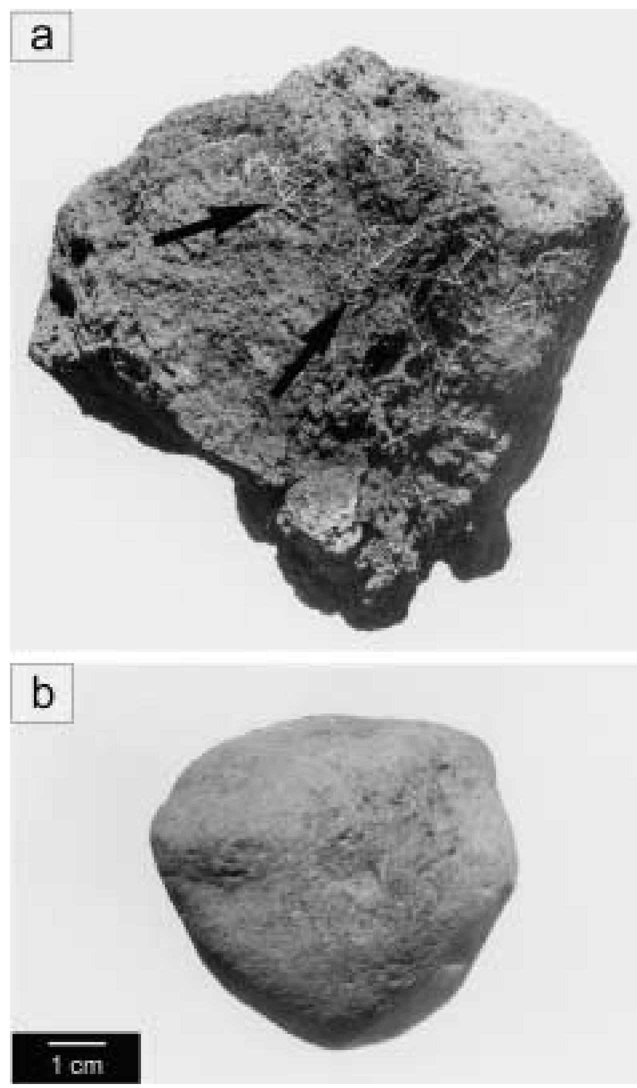
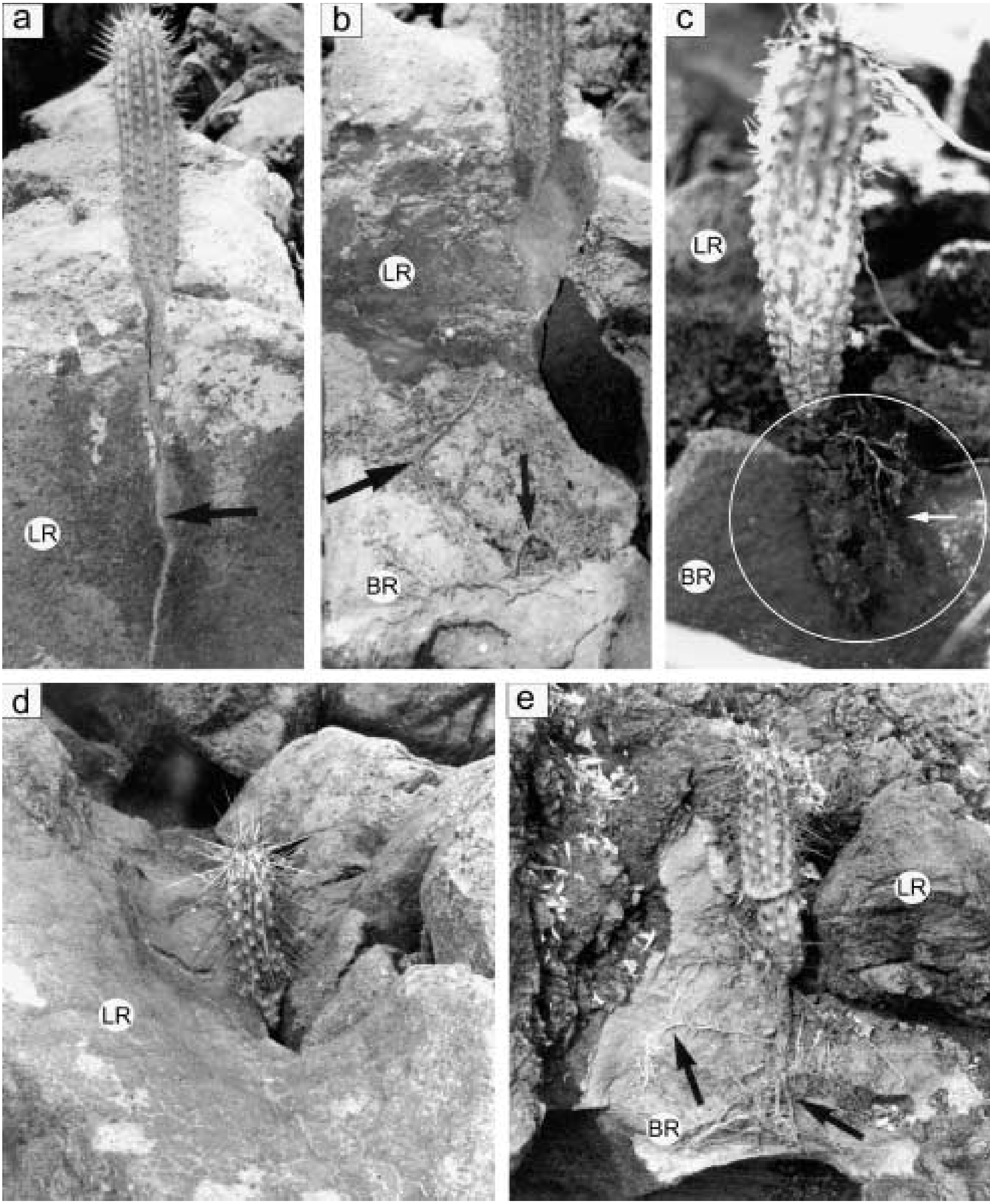


Fig. 4 Weathering of volcanic rock by growth of cactus (from the growth cavity of cardon cactus) (**a**) vs. intact volcanic stone from the same lava flow less than 1 m away (**b**). Note the numerous fractures and pitting on the former. Arrows indicate roots attached to the bare rock.



Figs. 5 a–e

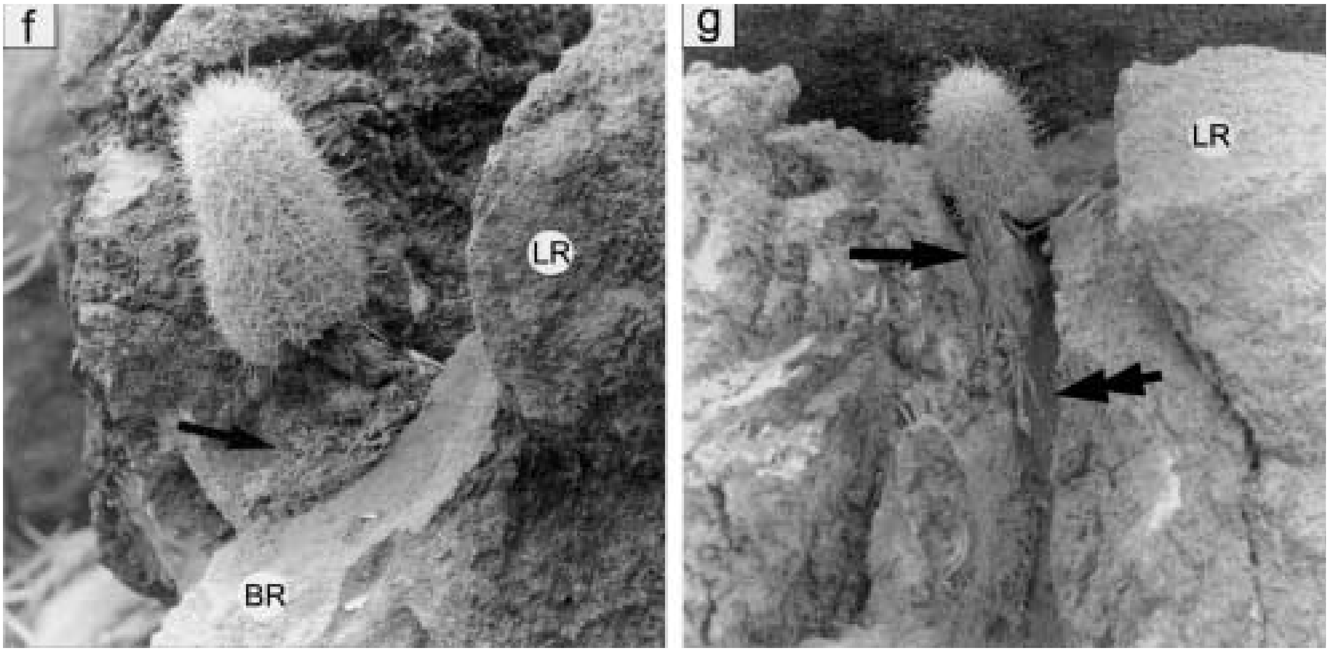


Fig. 5 Primary colonization of lava rocks by seedlings of the giant cardon cactus *(Pachycereus pringlei)* in a volcanic lava flow in La Purisima-San Isidro area. (**a**) Cardon seedling cracking volcanic rock. An arrow indicates the crack. (**b**) Same plant after the rock was broken by hammer and chisel, exposing the root system (arrows) of the plant attached to the bare rock. No soil is present. (**c**) Cardon seedling growing inside a small cavity in the rock after half of the rock was broken. A small amount of soil, presumably from the degradation of the rock, is present. Arrow indicates root system and the produced soil and the circle encompasses the entire root system of this plant. (**d**) Cardon cactus growing in a large rock; the rock is not cracked. (**e**) Same plant after the rock was broken, exposing the root system (arrows) attached to the rock. No soil is present. (**f**) Mamilaria cacti growing inside a volcanic rock without cracking it. Arrow indicates the entire root system of the plant growing without soil. (**g**) Mamilaria cactus *(Mamillaria fraileana)* cracking a small volcanic rock. Double arrow shows the crack enlarged by a chisel and hammer for photography. Single arrow shows the roots of the plant penetrating the rock. Abbreviations: LR – volcanic rock; BR – rock broken with chisel and hammer. Size of plants: **a, b** 2.6 cm; **c** 51 cm; **d, e** 18 cm; **f, g** 3 cm.

strate that would have been generated during cavity formation was absent. The secondary minerals found attached to the surface of roots and root-colonized microorganisms formed from degradation or weathering processes of the primary minerals in the rock. Secondary minerals found were calcite ($CaCO_3$) and cristobalite (SiO_2, a polymorph of quartz) (Fig. **6**).

Discussion

We surveyed barren areas of ancient lava flows, and detected rock-colonizing cacti. Almost all locations where these young cacti seedlings were growing were soilless. Despite the very long time (perhaps hundreds of thousands of years) needed for basalt to erode in the desert (Flores, 1998[15]) and the absence of soil, our survey could not rule out the possibility that seeds germinated in cavities filling with rain water. These rocks may have been weathered by the elements and soil may not have been dispersed, as is common in desert rocks thoroughly washed by the occasional torrential rains. However, considering the large number of rock-colonizing cactus seedlings growing in this area and surveyed in this study, it is more likely that the small amount of soil and secondary minerals commonly detected in small root cavities within the rocks were produced by weathering of the rocks by roots and associated microorganisms that always were found on their surfaces (Fig. **6** and Puente M. E., personal communication). Larger cacti (1 m or taller) were mostly associated with significant amounts of soil that accumulated around the plant. Eventually, the small plant breaks up the rock, and this soil is dispersed. The actual amount of soil formed from weathering of the rocks by the root system and its associated microorganisms cannot be measured. Rock-degrading, phosphate-solubilizing and nitrogen-fixing bacteria are associated with cacti colonizing rocks (Puente M. E., personal communication). All of the possible ingredients in a small rock cavity are subject to rare episodes of torrential rains, the outcome of summer hurricanes. These soil ingredients may be the source of material for soil in the “islands” in the lava flows. Soil material washed downhill could accumulate in lower spots in the lava flow, providing a growth substrate for other plant species. This soil is the sole substrate for most of the vegetation in this area.

Plants may greatly hasten rock weathering and soil formation and subsequent erosion in barren areas, breaking up small and large rocks in a matter of several years. They can solubilize rock by excreting acidic compounds in root exudates. However, it is not known whether these less-studied tree-shaped cacti have this capacity. Many microorganisms use similar mechanisms to solubilize minerals, for example, fungi that grow in sandstone (Hirsch et al., 1995[23]; Palmer et al., 1991[30]), mycorrhizae fungi (Jongmans et al., 1997[26]; Van Breeman et al., 2000[33]), bacteria that solubilize otherwise insoluble Fe(III) oxides and oxyhydroxides from rocks (Adams et al., 1992[1]), or the ectomycorrhizal fungus *(Laccaria laccata)* and phos-

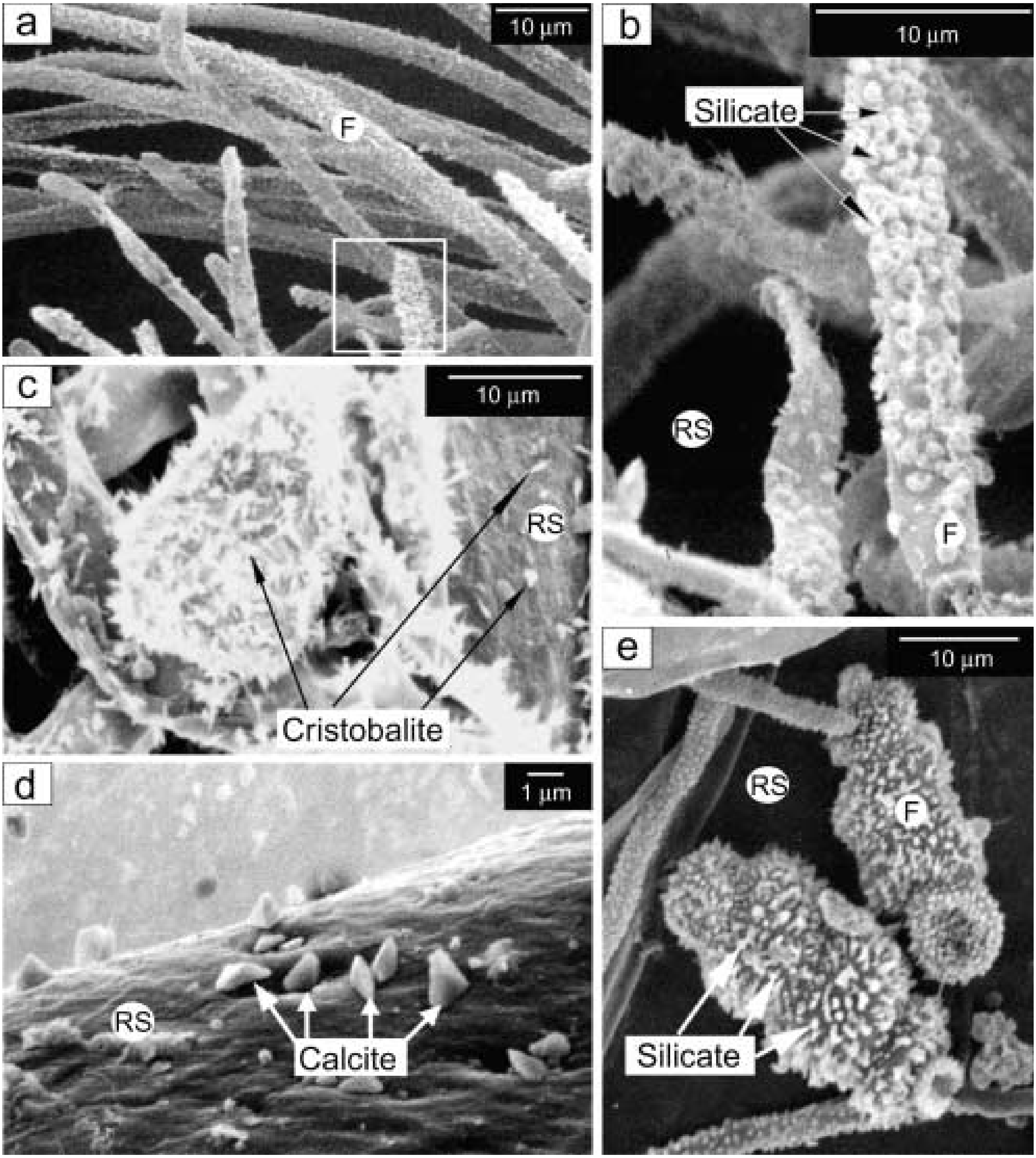


Fig. 6 Minerals from the volcanic rock on the root surface of a cardon growing in rock (**d**) and on microorganisms associated with the roots (**a–c, e**). Panel **b** is an enlargement of the frame in panel **a**. Abbreviations: F – fungal material; RS – root surface.

phate-dissolving bacteria (*Agrobacterium radiobacter* and *Achromobacter* sp.) that inhabit the rhizospheres of pine and beech (Leyval et al., 1990[28]). It is conceivable that some of the rock-solubilizing activity can be attributed to root-colonized microorganisms (Puente M. E., personal communication). The presence of cristobalite and calcite in plant-bearing rocks, not found in the parent bedrock, indicates biomineralization processes that may be attributable to microbes residing on the roots. The host cactus plant is the major immediate beneficiary of this activity. However, further solubilization would increase soil formation from rock material that, in turn, would benefit other plant species.

Roots of maize, rice and pine trees can solubilize rock phosphates and phyllosilicates (biotite, phlogopite), thereby releasing mineral elements, such as P and K, for uptake by plants (Berthelin et al., 1991[7]). Our study shows that cactus roots modified the volcanic rock in which they grew. For example, iron in rocks that contain plants was less oxidized than iron in barren rocks. Root microenvironments may have less oxygen because intense respiration of plant roots and associated microbial activity in the rhizosphere consume available oxygen, despite the large pore size after rock. Hence, the alteration (weathering or oxidation process) that would normally occur in the regular weathering of rocks is greatly reduced. Probably the plants, even small ones, protect the rock surface from somewhat acidic rain water. Additionally, the rocks colonized by cacti were highly fractured and pitted, to a large extent, as is often seen in stone and marble monuments (Danin and Caneva, 1990[14]) and deterioration of limestone in soil (Verges, 1985[36]). Some lichens weather volcanic rock and alter minerals in the rock on which they grow, similarly to the phenomenon observed in this study (Ascaso et al., 1990[3]; Chen et al., 2000[13]).

In summary, volcanic rocks in hot and arid regions of northwest Mexico are colonized by some species of large and small cacti and possibly contribute to soil formation in an otherwise barren landscape.

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