Rock–Soil Preferences of Three *Cephalocereus* (Cactaceae) Species of Tropical Dry Forests

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We examined rock–soil–plant relationships of three endemic Cactaceae species [*Cephalocereus apicicephalium* E.Y. Dawson, *C. nizandensis* (Bravo & T. MacDoug.) Buxb., and *C. totolapensis* (Bravo & T. MacDoug.) Buxb.] from the tropical deciduous forest of the Tehuantepec River basin, Mexico. The goal was to explain the relationships between the species, rock, soil, and calcium oxalate. The x-ray diffraction patterns from the rock and soil analyses showed that the species do not share either a rock or a soil type. *Cephalocereus apicicephalium* grew exclusively on outcrops of limestone with quartz on the summit to backslope of the hill and *C. nizandensis* grew in metalimestone outcrops on the summit and shoulder of the hill, while *C. totolapensis* preferred acid soils from andesite, growing also on siltstones or on mica schist on the shoulder to toeslope of the hill. Although only insignificant quantities of soluble Ca were found in the soil, weddellite is abundant in the plant tissue. This suggests that the plants take up the Ca they need and that weddellite is a genetically fixed characteristic related to deflection of excess radiation or an herbivore deterrent. Energy dispersive x-ray analysis showed that calcium oxalate crystals contained other elements (Si, Mg, Na, K, Cl, and Fe) and that these impurities modified the crystal shape, as for bipyramids in *C. totolapensis*. Biominerals did not change the mineral composition of the soil. The three species are distributed as edaphic or rocky islands, giving rise to their allopatric and patchy distribution across the landscape. Finally, the endemicity of the three *Cephalocereus* species is promoted by the parent material and the particular soil conditions in the area in which each one grows.

Abbreviations: EDX, energy dispersive x-ray.

Plant distribution is not random but rather tends to follow environmental patterns (McAuliffe, 1994). In the Cactaceae family, these patterns are not completely understood, particularly the ones related to soil (Parker, 1991). Together, great soil heterogeneity (Ruedas et al., 2006) and specific edaphic conditions (Parker, 1988; Valiente et al., 1995; Contreras and Valverde, 2002; Zavala-Hurtado and Valverde, 2003; Lopez et al., 2009) appear to contribute to the high level of rarity of cacti species. While information on soil properties is not always available, edaphic factors are commonly used to draw links between environments and the endemicity of taxa (Kruckeberg and Rabinowitz, 1985). Despite the *Cephalocereus* species endemicity, the factors that determine their distribution in discontinuous patches have not yet been determined (Dávila-Aranda et al., 2002).

Cephalocereus Pfeiff. is a monophyletic genus of five species (Bárcenas-Argüello, 2006). Two of these are endemic to the southern part of the Chihuahuan Desert, *C. columna-trajani* (Karw. ex Pfeiff.) K. Schum. and *C. senilis* (Haw.) Pfeiff. in the arid tropical scrub, while *C. apicicephalium*, *C. nizandensis*, and *C. totolapensis* are endemic to the Tehuantepec River basin in Oaxaca State. These three species grow in xerophytic scrub or tropical deciduous forests (Pérez-García and Meave, 2004). In this region, these three species are allopatrically distributed, growing on calcareous sedimentary rocks (Bravo-Hollis, 1978; Pérez-García et al., 2009); however, no detailed information about parental material, soils, or biominerals exists for these species. The Tehuantepec River basin is characterized by a range of igneous,

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sedimentary, and metamorphic rocks (Santana et al., 2009). Therefore, our hypothesis was that the allopatric and patchy distribution of the *Cephalocereus* species in the Tehuantepec River basin is restricted to the inclusion of calcareous rocks, where each species develops under specific edaphic conditions defined by texture, moisture, or depth. Thus, we expected that, if Ca is abundant in the soils, then calcium oxalate crystals will be also abundant in the tissues of the plants.

Calcium oxalate crystals have been reported in the tissue of Cactaceae (Rivera and Smith, 1979; Hartl et al., 2007). Predominantly, druses occur in the cortical tissue (Terrazas and Mauseth, 2002; Hartl et al., 2007); however, prisms in the epidermis and hypodermis distinguish *Cephalocereus*, *Neobuxbaumia*, and *Pseudomitrocereus* (Terrazas and Loza-Cornejo, 2002). The crystals produced by species of the same genus share the same crystalline system, but their shapes may vary at the level of the crystal class due to internal factors such as ions and organic acid composition (De Yoreo and Dove, 2004). According to Garvie (2003), these crystals are released as a result of plant decay after death, incorporating the biominerals into the soil where they are subsequently solubilized and remobilized. The Ca precipitates out as caliche on the soil surface or may be redistributed by the wind (Garvie, 2003), causing restrictions to plant establishment (McAuliffe, 1994). An analysis to quantify and identify biominerals in the sandy fraction on the soil surface is missing for sites where cacti grow. This would be an important link because it makes it possible to relate biominerals provided by the plant to those that remain in the soil environment. Our second hypothesis was that the studied columnar cacti would be able to change the mineral composition of the soil where they grow.

The objectives of this study were to determine the bedrock and soil properties in the Tehuantepec River basin where three species of *Cephalocereus* develop, to quantify and identify calcium oxalate types present in their stems and in the soil, and to relate the bedrock and soil properties with the crystals in their stems.

MATERIALS AND METHODS

Study Area

The study area is located in the southeastern portion of Oaxaca State, Mexico, including parts of the Central Valley, Sierra Madre del Sur, and the Isthmus of Tehuantepec (Fig. 1). The region is complex: there are different geological strata including metamorphic rocks from the Precambrian to the Cenozoic, intrusive and extrusive igneous rocks from the Paleozoic and Cenozoic, and sedimentary deposits from the Paleozoic to the Quaternary (Instituto Nacional de Estadística, Geografía e Informática, 2003; Santana et al., 2009). The climate varies from hot and dry in the Central Valley to tropical, subhumid, and highly seasonal in the Isthmus of Tehuantepec (Vidal, 2005). Vegetation is mainly tropical deciduous forest (Rzedowski, 1978). In this region, the populations of the three species are rare but distinct from the surrounding vegetation. Based on the literature (Bravo-Hollis, 1978; Torres, 1989; Pérez-García et al., 2001), herbaria data (Colegio de Postgraduados, Chapingo, Mexico [CHAPA]; Universidad Nacional Autónoma de México [MEXU]; and the Missouri Botanical Garden [MO]), and our own field observations, we selected 11 populations that represent the whole endemic area of Oaxaca. These populations varied in size and in number of individuals per species (Fig. 1; Table 1).

Fig. 1. Location of the studied sites in the Tehuantepec River basin in Oaxaca State, México.

Study Species

The three studied species have a columnar habit branching from the base, with an apical pseudocephalium (Fig. 2). *Cephalocereus apicicephalium* reaches a height of 1 to 2 m, with a diameter <8 cm, 5 to 10 branches and 24 to 26 ribs (Fig. 2C). *Cephalocereus nizandensis* is 1 to 2 m high, with a diameter of 8 to 10 cm, >20 branches, and 21 to 23 ribs (Fig. 2G). *Cephalocereus totolapensis* grows 3 to 5 m tall and has a diameter of 12 to 15 cm with <5 branches per individual; one

Table 1. Site characteristics for the *Cephalocereus* species studied.

Species and site	Elevation	Area	Individuals	Slope	Exposure	Geomorphic position†	Rock type	Not present on adjacent soil or rock	Substrate or soil texture
	m	~m^2	no.	%					
C. apicicephalium									
Guiengola‡	300	50	>20	100	west	1,2,3	limestone outcrops, cracks	soil	debris
Mixtequilla‡	163	150	>20	top	NA§	1	limestone outcrops, cracks	soil	debris
C. nizandensis									
Nizanda‡	206	50	>20	67	west	1,2	metalimestone outcrops, cavities	soil	debris
La Mata‡	200	150	>20	100	west	1,2	metalimestone outcrops, cavities	soil	debris
C. totolapensis									
Las Margaritas	1000	100	>20	44	north	2,3	colluvial material from andesite	breccia	soil <10 cm, sandy clay loam
Boquerón‡	822	35	10–20	26	north	2,3	andesite bedrock	metaandesite	interrock soil, sandy loam
Km. 123‡	830	25	5–10	55	north	2	colluvial material from andesite	polymictic conglomerate	soil with stones, clay loam
El Gramal	680	15	3–5	22	north	2	andesite bedrock	sandstone and polymictic conglomerate	soil <10 cm, not determined
San Bartolo‡	675	400	10–20	44	north	2,3,4	siltstone folds	andesite	soil >30 cm, sandy clay loam
Tlacolulita	434	400	10–20	27	north	2,3,4	andesite bedrock	granite–granodiorite	soil <10 cm, loam
San Miguel Ecatepec	386	9	1–3	22	north	2	mica schist bedrock	granite–granodiorite	soil >30 cm, loam

† 1 = summit, 2 = shoulder, 3 = backslope, 4 = toeslope of the hill.
‡ Sampled for soils.
§ NA= not applicable.

of the branches is always higher and has 24 to 28 ribs, and remnants of reproductive events remain on the stem as rings (Fig. 2J).

Collection Sites and Field Work

At each site, the species' spatial distribution was described with respect to geomorphic position, slope, and and sun exposure; soil and bedrock reactions to HCl were tested as a measure of their calcareousness. We recorded the soil properties of depth, stoniness, root distribution, H_2O_2 reaction, structure, and Munsell color. The rock dissolution processes caused by roots and the organic debris characteristics in cracks and cavities were also recorded. We estimated drainage conditions near the roots during plant establishment based on crack size, cavity depth, slope, and soil depth. Three bulk or rhizosphere soil and rock samples were collected along the geomorphic position per site (Table 1). In the cases where there was no soil, organic debris was collected. Four young branches were selected at each site. Two were placed in liquid N_2, and the other two were kept alive. All of them were used in the mineralogical analyses.

Laboratory Analysis
Rocks

Rock fragments were pulverized with a porcelain mortar and pestle and sieved to obtain particles <50 μm. Rock powder mounts were examined with an x-ray diffractometer using Cu Kα radiation at 35 kV and 25 mA. Mineral species were determined using ICDD software, version 2002 (International Centre for Diffraction Data, Newtown Square, PA).

Soils

The particle size, pH (water/soil ratio of 2:1), and organic matter procedures used were according to van Reeuwijk (1995), and soluble Ca^{2+}, Mg^{2+}, Mn^{2+}, and Fe^{2+} were measured by inductively coupled plasma diffractometry, K^+ and Na^+ by flame emission spectroscopy, and Cl^- by volumetric analysis. The same procedure was followed for organic debris, except the particle size analysis.

Mineralogical Analyses
Sandy Fraction

The bulk soil or rhizosphere soil samples were passed through a 0.025 mm (300-mesh) sieve. A 1-g subsample was taken after sifting and washed with distilled water to remove the clay fraction. Hydrogen peroxide (w/w 30%) was used to eliminate any organic material. Three hundred grains from the sandy fraction were counted on a grain mount by line counting methods using an Olympus (B52) petrographic microscope.

Dry Plant Tissue

The plant tissue was removed from the liquid N_2, freeze-dried, ground, and sieved. The fine fraction (<2 μm) was analyzed by x-ray diffraction (Cu Kα radiation at 35 kV and 25 mA) using a random powder mount. The isolated crystals were fixed on a microscope slide and photographed with a Canon digital camera mounted on an Olympus (B52) petrographic microscope.

Fresh Plant Tissue

The spines were removed from the collected branches and the branches were cut up and ground in a manual blender. The material was passed through a sieve to separate the dense tissue. The crystals and water were collected in flasks, which were then decanted and washed with distilled water (Al-Rais et al., 1971). The crystals were mounted onto an aluminum specimen holder with double-sided tape and coated with Au. They were photographed and their morphology described through a Hitachi S-2460N scanning electron microscope. The elemental composition of these crystals was quantified using a JEOL JSM-35C element analyzer (JEOL Ltd., Tokyo), in addition to an energy dispersive x-ray (EDX) analysis (Tracor Northern).

RESULTS
Species Distribution Pattern According to Parent Materials, Rocks, and Soils

Cephalocereus apicicephalium grew on limestone outcrops with quartz (Fig. 2A–2C; Tables 1 and 2) on the summit to

Fig. 2. ***Cephalocereus*** **plant habit and soil features for the different sites where the species grow: *C. apicicephalium* at (A and B) Mixtequilla and (C) Guiengola; *C. nizandensis* at (D and F) Nizanda and (E and G) La Mata; and *C. totolapensis* at (H and J) Tlacolulita and (I) San Bartolo.**

Table 2. X-ray diffraction pattern of rocks where *Cephalocereus* species grow.

C. apicicephalium		*C. nizandensis*		*C. totolapensis*			
d_{hkl}†	Card 5-586 synthetic calcite	d_{hkl}	Card 24-27 calcite	d_{hkl}	Card 20-572 Albite	d_{hkl}	Card 5-586 low quartz
Å		Å		Å		Å	
3.04 (100)‡	3.04 (100)	3.03 (100)	3.03 (100)	3.21 (100)	3.21 (100	3.36 (100)	3.34 (100)
2.29 (30)	2.29 (20)	2.09 (20)	2.09 (30)	3.18 (100)	3.18 (90)	4.24 (40)	4.26 (40)
2.09 (20)	2.10 (20)	3.84 (10)	3.85 (30)	4.04 (30)	4.03 (80)	1.81 (20)	1.82 (20)
1.91 (20)	1.91 (20)	1.87 (30)	1.87 (30)	3.75 (60)	3.75 (60)	–	–

† d-spacing.

‡ Relative intensity (%) in parentheses.

backslope of the hill. Organic debris accumulated in rocky cracks; the color of this material was dark brown (10YR3/3) when dry and very dark grayish brown (10YR3/2) when wet, the pH was between 5.7 and 6.8, and the soluble Ca content varied from 4.6 to 10.6 cmol kg^{-1} of organic debris (Table 3). The roots grew near the surface and only penetrated deeper where there were cracks in the rocks. The roots were joined to the rock and generated channels by dissolution processes. Drainage was good without water accumulation. Although there were areas with soil at the site (Table 1), this species did not grow in these places but only on outcrops (Fig. 2C).

The outcrops on which *C. nizandensis* grew were metalimestone (Tables 1 and 2) on the summit and shoulder of the hill. These rocks showed dissolution processes forming cavities up to 10 cm deep (Fig. 2D–2F). The bare rock cavities accumulated organic debris at different stages of decomposition (Fig. 2E), together with water (Fig. 2F), in which the plants were established and grew (Fig. 2G). The soluble Ca content in the substrate varied from 4.2 to 5.2 cmol kg^{-1} of organic debris, and the pH ranged from 6.6 to 7.1 (Table 3). This species only grew in the cavities formed in the outcrops.

Cephalocereus totolapensis was distributed in more diverse substrates on the shoulder to toeslope but not on the summit of the hill. For example, at five sites they grew on soils formed from andesite (Tables 1 and 2; Fig. 2H), at one site on siltstone (Fig. 2I), and at other on mica schist. None of these rocks reacted with HCl. The soil depth varied from 10 to 60 cm (Fig. 2I). These soils showed a dark brown color (10YR3/3) when dry and varied from very dark gray (10YR3/1) to dark yellowish brown (10YR4/4) when wet, including a site that was brown when wet (7.5YR4/4). The organic matter content of the soil was variable (1–10%); soluble Ca was low and varied from 0.9 to 3.6 cmol kg^{-1} of soil. Magnesium, Mn, K, and Na were present in quantities <2 cmol kg^{-1} of soil (Table 3). The pH level varied from 6.5 to 6.7. Although this species grew on fine soils, it did not exhibit drainage problems because there were various combinations of texture with slopes >50% or its roots grew on stony soils. Because of this, the microhabitat of *C. totolapensis* was restricted to noncalcareous rock, fine-textured soil, and steep slopes (Table 1) having abrupt distribution limits depending on the underlying rock.

Mineralogical Analyses

The sandy fraction of the sampled soils contained a low proportion of biominerals (Table 4). There was a higher proportion of calcite in the substrate on which *C. nizandensis* grew, at about 1%. In addition, 1.1% of calcium oxalate was found in the same site. The proportions of these minerals were lower in the soils in which *C. apicicephalium* and *C. totolapensis* grew (<0.3% calcite and <0.2% calcium oxalate).

Polyhydrate calcium oxalate crystals were observed in the dry plant tissue samples. The weddellite found in *C. apicicephalium* and *C. nizandensis* corresponded to the 14-0704 card in the ICDD software included with the x-ray diffraction equipment, and its chemical formula was $CaC_2O_4{\cdot}2.5H_2O$ (Table 5). The weddellite in *C. totolapensis*, on the other hand, corresponded to the 4-0702 card, and its formula was $CaC_2O_4{\cdot}2H_2O$ (Table 5).

Table 3. Soil and organic debris (OD) parameters for the sites of the *Cephalocereus* species (*n* = 3 per site).

Species and site	Sample	Sand	Silt	Clay	Organic matter	pH	Ca	Fe	Mg	Mn	K	Cl	Na
		%			g kg^{-1}	2:1	cmol kg^{-1}						
C. apicicephalium													
Guiengola	OD	NA†	NA	NA	136.2	6.8	4.67	0	0.87	0.01	0.30	1.07	0.10
Mixtequilla	OD	NA	NA	NA	233.5	5.7	10.67	0	0.99	0.34	0.32	8.88	0.17
C. nizandensis													
Nizanda	OD	NA	NA	NA	1000	7.1	5.22	ND‡	0.88	0.01	0.31	1.07	0.34
La Mata	OD	NA	NA	NA	272.4	6.6	4.23	ND	1.80	0.01	0.63	1.74	0.69
C. totolapensis													
Las Margaritas	soil	49.68	16.77	33.54	38.9	6.9	3.36	0	1.25	0.00	0.32	0.90	0.24
Boquerón	soil	53.16	28.10	18.73	109.0	6.5	1.96	ND	0.98	0.01	1.01	0.90	0.57
Km. 123	soil	40.22	20.79	38.98	54.4	6.7	0.94	ND	0.45	0.00	0.28	0.61	0.58
San Bartolo	soil	51.13	26.88	21.99	12.4	6.5	3.62	ND	0.56	0.01	0.31	0.95	0.43
Tlacolulita	soil	39.43	34.23	26.33	101.2	6.0	7.87	ND	5.54	0.03	1.86	5.13	0.34

† NA = not applicable.

‡ ND = not detected.

Table 4. Percentages of calcite and calcium oxalate in the sand fraction for the sites of the *Cephalocereus* species (n = 900 grains per site).

Species	Site	Sample†	Calcite	Calcium oxalate
			%	
C. apicicephalium	Guiengola	OD	0.02	0.00
	Mixtequilla	OD	0.30	0.12
C. nizandensis	Nizanda	OD	0.90	1.14
	La Mata	OD	0.06	0.14
C. totolapensis	Boquerón	soil	0.15	0.01
	Km. 123	soil	0.00	0.00

† OD = organic debris.

Table 6. Percentage of elements detected by energy dispersive x-ray diffraction in the different crystals present in the *Cephalocereus* species (*C. apicicephalium*, n = 22; *C. nizandensis*, n = 95; *C. totolapensis*, n = 62).

Element	*C. apicicephalium*	*C. nizandensis*	*C. totolapensis*
		%	
Si	2.14 ± 1.46†	1.85 ± 1.42	1.62 ± 1.17
Mg	2.07 ± 2.56	0.94 ± 0.73	0.93 ± 0.76
Na	2.69 ± 2.22	1.73 ± 1.19	1.84 ± 1.66
K	0.77 ± 0.87	0.35 ± 0.40	0.50 ± 0.47
Cl	1.41 ± 1.98	0.55 ± 0.37	0.60 ± 0.46
Fe	0.77 ± 0.68	0.56 ± 0.46	1.17 ± 0.88

† Mean ± standard deviation.

The EDX analysis showed a wide range of Ca concentrations, as well as other elements such as Si, Mg, Na, K, Cl, and Fe (Table 6). Weddellite crystals were composites of several individual crystals; However, the scanning electron microscope analysis showed that weddellite had different shapes according to the species; such as *C. apicicephalium* (conglomerated crystal sands), *C. nizandensis* (typical druses), and *C. totolapensis* (bipyramids) (Fig. 3).

DISCUSSION

Species Distribution Pattern According to Parent Materials, Rocks, and Soils

According to Meyrán (1970), members of the family Cactaceae prefer calcareous soils or limestone. Our results showed that, in addition to calcareous soils, there was more than one parent material without soluble or precipitated Ca. In either case, the three species are distributed as edaphic and rocky islands with different geomorphic position preferences (Table 1). For instance, *C. totolapensis* did not show specificity for a calcareous substrate, growing instead in an acid soil (pH 5.5–6.9). Furthermore, *C. totolapensis* showed a high specificity for fine-textured soils developed only on andesite, siltstone, or mica schist (Table 1), even though these rocks were associated with other igneous, sedimentary, and metamorphic rocks (Instituto Nacional de Estadística, Geografía e Informática, 2003). *Cephalocereus apicicephalium* and *C. nizandensis* grew only on inclusions of calcareous rocks but under different edaphic conditions. The first preferred rocky cracks where water drainage was good, and the second developed in cavities on bare rock where organic debris and water accumulated. In either case, the substrate in the root influence area had a pH between 5.7 and 7.1. The roots of these plants probably have the ability to exude low-molecular-weight organic acids that produce changes in the availability of nutrients (Bar-Yosef, 1996; Brady and Weil, 1999) as well as the ability to participate actively in $CaCO_3$ dissolution. Among such organic acids, oxalic acid is abundant in the rhizosphere (Ström et al., 1994, 2005; Ström, 1997), and *C. apicicephalium* and *C. nizandensis* had calcium oxalate crystals in their tissues, suggesting that oxalic acid is present. This ability to successfully grow on outcrops with high temperatures and low nutrient availability has promoted the endemism of these two species. Endemicity found on rocky outcrops, either calcareous or otherwise, has been reported by several researchers (Jeffries, 1985; Collins et al., 1989; Pérez-García et al., 2001, 2009; Searcy et al., 2003; Müller, 2007; Lopez et al., 2009).

Our results showed that *C. apicicephalium* and *C. nizandensis* are examples of endemism strongly associated with inclusions of limestone with quartz or metalimestone outcrops surrounded by a complex of rocks (Table 1; Fig. 4A), and the two are separated by the available moisture. These factors may also promote other endemisms at the same sites, such as *Agave nizandensis* Cutak, *Barkeria whartoniana* (C. Schweinf.) Soto Arenas, *Brongniartia guiengolensis* O. Dorado & L. Torres-Colín, *Encyclia nizandensis* Pérez-García & Hágsater, *Eupatorium guiengolense* L. Torres & Villaseñor, and *Solandra nizandensis* Matuda (Torres, 1989; Pérez-García et al., 2001). On the other hand, *C. totolapensis* is the species with the widest distribution, but it requires soils with particular conditions, such as depth and a fine texture, that provide sufficient moisture and that are related to specific parent materials like andesite, siltstone, or mica schist (Fig. 4B). Other researchers have also recorded high edaphogenic specificity related to the distribution of Cactaceae species (Bashan et al., 2002; Contreras and Valverde, 2002; Zavala-Hurtado and Valverde, 2003; Lopez et al., 2009).

Mineralogical Analyses

Despite the weddellite abundance in the plant tissues of the three species studied, the amount of this mineral incorporated into the soil is not enough to promote calcification, as was reported for *Carnegiea gigantea* Britton & Rose by Garvie (2003) or other cacti (Garvie, 2006). Although the *C. nizandensis* substrate contained up to 2% biominerals (counted from 300 grains), this does not represent a considerable contribution to form surface horizons made up of caliche. Probably the decay of dead

Table 5. X-ray diffraction pattern of biominerals in *Cephalocereus* species.

C. apicicephalium		*C. nizandensis*		*C. totolapensis*	
d_{hkl}†	Card 14-0704	d_{hkl}	Card 14-0704	d_{hkl}	Card 4-0702
Å		Å		Å	
6.15 (86)‡	6.17 (100)	6.17 (58)	6.17 (100)	6.26 (54)	6.23 (90)
2.77 (100)	2.78 (100)	2.77 (100)	2.77 (100)	2.78 (88)	2.78 (100)
2.24 (57)	2.24 (60)	2.24 (38)	2.24 (160)	2.24 (100)	2.24 (60)

† d-spacing.

‡ Relative intensity (%) in parentheses.

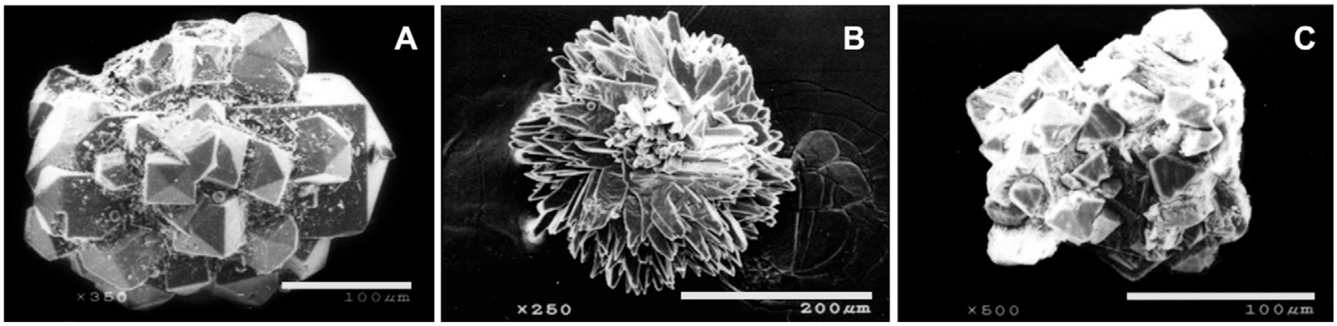

Fig. 3. Weddellite forms in *Cephalocereus*: (A) conglomerated crystal sand in *C. apicicephalium*; (B) typical druse in *C. nizandensis*; and (C) bipyramid druse in *C. totolapensis*.

individuals of the *Cephalocereus* species studied is more rapid because humidity and rains are higher than in the Sonoran Desert (Vidal, 2005). Moreover, the bare rocks and persistent winds in this area (Romero-Centeno et al., 2003) prevent the accumulation of biominerals that has been observed in the Sonoran and Chihuahuan deserts (Garvie, 2006).

When the soil is rich in Ca, an element that is essential for the plant's vital functions, the root absorption area may be saturated with this element. This microenvironment could promote plants incorporating large quantities of Ca into their tissue, although it may also generate mechanisms to precipitate the Ca as oxalate (Franceschi and Horner, 1980; Webb, 1999; White and Broadley, 2003). It has also been reported that some species can concentrate an element in their tissues even when it is only available in low amounts in the solution soil or when other species are competing for the elements (Golley, 1986). Both regulatory mechanisms operate under genetic control (Ruiz and Mansfield, 1994; Horner and Wagner, 1995). The presence of calcium oxalate crystals has been reported in *Cephalocereus* species (Gibson and Horak, 1978; Terrazas and Loza-Cornejo, 2002; Vázquez-Sánchez et al., 2005, 2007), and x-ray diffraction analysis has measured their composition. Nevertheless, it cannot be claimed that the abundance of calcium oxalate in the plant tissue is caused by Ca abundance in the soil in which the *Cephalocereus* species develop. These findings indicate that *C. totolapensis* grows in environments with low Ca content (0.94–3.62 cmol kg^{-1}) and acid pH soils. While *C. apicicephalium* and *C. nizandensis* grow on calcareous rocks, the Ca present in the substrate is only soluble in low amounts (4.23–10.67 cmol kg^{-1}). This means that species included in the genus *Cephalocereus* solubilize and take up the Ca they need and that calcium oxalate crystal formation is a genetically fixed characteristic that may be related to the deflection of excess radiation (Darling, 1989) or an herbivore deterrent (Franceschi and Nakata, 2005). These traits are shared with other species of the tribe Pachycereeae

Hartl et al. (2007) recorded that *C. apicicephalium*, the only *Cephalocereus* species they studied, forms whewellite. This hydration form was not found in our study; weddellite crystals were identified in the three analyzed species. The occurrence of weddellite crystals is shared with most members of the Pachycereeae tribe studied by Hartl et al. (2007). The calcium oxalate crystal morphologies in several members of Cactaceae have been documented since at least 50 yr ago (Metcalfe and Chalk, 1950; Bailey, 1961), and more recently, their chemical compositions were determined (Rivera and Smith, 1979; Monje and Baran, 2002; Hartl et al., 2007). The calcium oxalate crystals show druses in the *Cephalocereus* species. According to Franceschi and Horner (1980), a *druse* is defined as a "spherical aggregate of individual crystals." The scanning electron microscope showed that druses are composed of bipyramids or layers. This mineral shape is related to impurities in its chemical composition (De Yoreo and Dove, 2004). The EDX analysis indicated an important presence of some elements like Si, Mg, Na, K, Cl, and Fe (up to 5%) in the studied *Cephalocereus* species. For instance, bipyramidal druses were found in *C. totolapensis*, druses with sharp points growing around the core were observed in *C. nizandensis*, and conglomerated crystal sands were present in *C. apicicephalium*. Thus, the

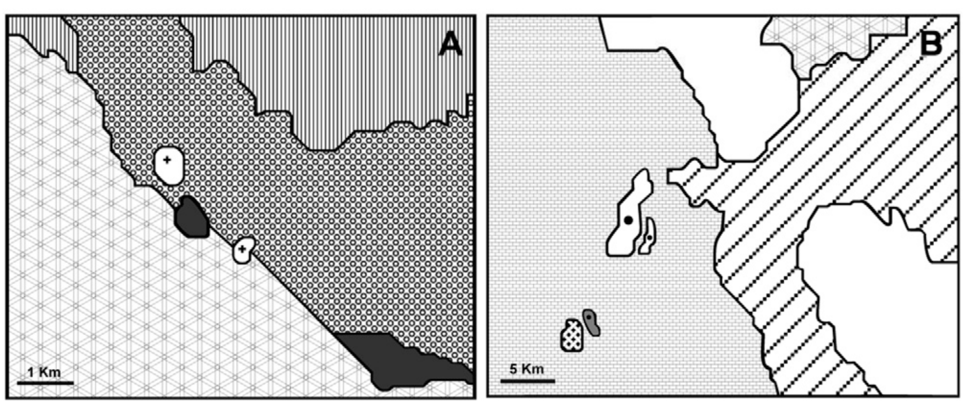

Fig. 4. Rocky islands for some sites of *Cephalocereus* species (modified from SGM, 2000, 2007). (A) *C. nizandensis*. + white = dolomite-limestone La Mata and Nizanda, connected diamonds = sand-silt, black = travertine-polymictic-conglomerate, white dots = metalimestone, vertical lines = metasedimentary. (B) *C. totolapensis*. * white = andesite Las Margaritas and Km 123, * gray = siltstone San Bartolo, solid diamonds = granite-granodiorite, oblique lines = granodiorite, connected diamonds = sand-silt, bricks = volcano-sedimentary.

crystal form could follow a close relationship between the species and the soil mineral content.

CONCLUSIONS

The discontinuous distribution of three *Cephalocereus* species is not restricted to a calcareous environment. This distribution pattern is related to rocky inclusions that are specific for each species acting as rocky and edaphic islands. All studied species accumulate biominerals in their tissue, but this does not impact the soil mineral composition. The weddellite crystalline forms present in the species do not belong to the same system, and the wide variety of forms should be studied to understand their taxonomic value. Due to the association between parent material and soil preference in the three *Cephalocereus* species studied, we claim that these factors have promoted their endemicity. To entirely understand the endemicity of the Cactaceae, it is essential to take into account the parent material and soil preference associations.

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