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SURFICIAL INJURIES OF SEVERAL CACTI OF SOUTH AMERICA

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Evans L. S., McKenna C., Ginocchio R., Montenegro G. and Kiesling R. *Surficial injuries of several cacti of South America.* Environmental and Experimental Botany **34**, 285–292, 1994.—Analyses of several species of long-lived columnar cacti in Argentina and Chile show that an accumulation of epicuticular waxes is occurring on many species and that these accumulations obscure stomata. This accumulation leads to visible surficial maladies such as scaling and barking on crests and troughs of ribs similar to those that occur on saguaros, *Carnegiea gigantea* (giant saguaro) of North America, which results in premature death of individual saguaros. Scaling is the appearance of tan to red-orange discoloration of surfaces. Barking refers to a larger buildup of materials on the surfaces than scaling that appears dark brown to black. Equatorial facing surfaces showed more injuries on stems of *Trichocereus pasacana* and *T. terscheckii* in Argentina, and *Echinopsis chilensis* and *E. scotsbergii* in Chile, than on polar surfaces. Crest barking was as much as five times greater on equatorial-facing sides compared with polar-facing sides. Spine retention was up to three times greater on equatorial- vs polar-facing sides. The two troughs of a crest were evaluated separately. Results show that injury to one trough of a crest facing the equator was as much as twice that of the second trough facing the south pole. These results show that surficial injuries were greater on equatorial than on polar surfaces, and are related to total incident irradiance on these surfaces.

Key words: *Trichocereus, Echinopsis*, cacti, scaling, barking.

INTRODUCTION

Recent evidence has shown that epidermal browning is correlated with several surface and tissue characteristics of saguaros [*Carnegiea gigantea* (Engelm.), Britt. and Rose; giant saguaro] in the Sonoran Desert of North America.[1] Specifically, brown-stemmed cacti have obscured stomata concomitant with an epicuticular wax buildup on the epidermis which is associated with a deterioration of other surface characteristics. Epidermal browning has been shown to be associated with premature senescence of *C. gigantea* at Saguaro National Monument, Arizona.[1] In addition, research has shown that epidermal browning occurs predominantly on southern (equatorial) surfaces of *C. gigantea* and that this injury has increased over the past several decades.[2]

Because of the above information, the following questions were asked: does this same type of surficial injury occur to long-lived columnar cacti in other areas of the world? If these surficial injuries occur to long-lived cacti in other regions, what is the predominant azimuth direction of injury? If exposure to solar irradiance is a factor in surficial injuries, should cacti in the Southern Hemisphere have more injuries on equatorial (northern) than on polar (southern) surfaces? The following hypotheses were tested: (1) long-lived columnar cacti of Argentina and Chile will have surficial injuries similar to those of *C. gigantea*; and (2) cacti in the Southern Hemisphere will exhibit these surficial injuries predominantly on the equatorial (northern) surfaces.

MATERIALS AND METHODS

Plant materials

In December 1991 and January 1992, surficial observations and tissues of *Trichocereus pasacana* (Web.) Britt. and Rose [= *Echinopsis pasacana* Fried. and Rowley] and *T. terscheckii* (Parm.) Britt. and Rose = [*Echinopsis terscheckii* Friedr. and Rowley] were completed. One hundred specimens of *T. pasacana* were observed at Humahuaca Valley near Humahuaca at 3000–3100 m elevation (23°15′S, 65°20′W) and near the road from Humahuaca to Costaca. One hundred specimens of *T. terscheckii* were observed. Thirteen were observed near Cafayate (26°12′S, 65°50′W, 1500 m elevation) and the remainder were observed in the mountains 10 km southeast of Andagala (27°30′S, 66°20′W; 1000 m elevation) near the road to Catamarca.

In November 1991 through January 1992, surficial observations and tissue samples of *Echinopsis chilensis* (Cholla) Friedr. and Row. [= *Trichocereus chilensis* (Cholla) Br. and Rose] and *E. scotsbergii* (Backbg.) Friedr. and Rowl. [= *T. scotsbergii* (Backbg.) Britt. and Rose] were procured. Fifty specimens of *E. chilensis* were observed at Curacavi (33°24′S, 71°08′W) and at Til Til (33°06′S, 70°56′W). In a similar manner, 50 specimens of *E. scotsbergii* were observed each from two distinct populations near Parque Nacional Fray Jorge (30°40′S, 71°22′W). Population No. 1 was 1 km inside the eastern boundary of Parque Nacional Fray Jorge, population No. 2 was 2 km east of the boundary of the refuge. Thus, the two populations were 3 km apart.

Sampling design

Observed cacti were not selected randomly. Rather, an attempt was made to sample cacti with a wide range of phenologies. Namely, phenologies ranging from young cacti with few epidermal injuries to older specimens with many surficial injuries. However, the only cacti excluded from this study were cacti with no apparent epidermal problems and those that exhibited extensive injuries on all rib crest and troughs, neither of which would provide useful information to determine the predominant azimuth direction of injury.

Cacti were evaluated for many stem surface parameters, as described previously.[2] For each cactus, the azimuth directions of all rib crests were recorded. Rib crests (protrusions on stems where tubercles are present[4] and rib troughs (indentations on stems) were evaluated. The rib crest was considered to be the area among areoles and to include 2 mm to each side of each areole. The rib trough area was considered to be from the crest area to the indentation between two troughs, so there was a rib trough on each side of a rib crest (= ridge)[4]. Troughs of each rib crest were designated left and right troughs. Surfaces were characterized as being apparently healthy, scaling or barking. Scaling is a visible appearance of epicuticular wax buildup.[1,2] Barking refers to a more extensive buildup of epicuticular waxes.[1,2] Generally, the epicuticular waxes on barked surfaces have a color distinctly different from the normal green color. Normally, the wax surface color is species specific and ranges from white, yellow, orange, tan, brown or black. For example, barking on *E. chilensis* was whitish, while that for *T. terscheckii* was orange to brown. For each rib crest and trough observed, the percentage of surface area exhibiting scaling and barking was recorded. Observations were also made of the degree to which a full complement of spines was present at an areole. Specifically, each rib crest was characterized as having only one of two conditions. Either a full complement of spines was present or many spines were missing. A full complement of spines was determined as the number of spines present at areoles of young plants. The criteria of many spines missing would indicate that at least 30% of the full complement of spines of an areole were not present. For each cactus, a score of 1 was given 'a full complement' of spines; a score of 0 for 'many spines missing'.

Before evaluations began, standardization procedures were performed. For randomly selected cacti, all researchers involved in Chile and Argentina agreed on the criteria and the degree or extent of the appearance of the surface characteristics. In Argentina and Chile, two persons (evaluators) evaluated the two cactus species in each country. Standardization procedures were concluded when all values from both evaluators were within 10% for each characteristic evaluated.

Once standardization procedures were completed, evaluators worked in pairs. One person was primarily responsible for the visual evaluation, while a second person was responsible for recording values on data sheets. For each cactus, the azimuth directions of all rib crests were recorded. Troughs on each side (denoted left and right sides) of each crest were also evaluated individually. For each crest, the complement of spines was recorded. For crests and troughs, the percentage coverage of scaling and barking was estimated. The second evaluator provided an independent evaluation when requested. In addition, the second evaluator provided an independent evaluation on several preselected rib crests and troughs for each cactus sampled. The roles of the evaluator and recorder changed after each 10 cacti. Observations of characteristics of each crest and trough were taken at 1.5 m above ground level.

After all the data were accumulated, the numbers or rib crests were determined for each species. The mean number of rib crests for all cactus samples of *T. pasacana*, *E. chilensis*, *E. scottsberii* and *T. terscheckii* was 20.1, 13.5, 14.1 and 11.9, respectively. As a result, all azimuth directions of rib crests were changed to the nearest 20 degrees for *T. pasacana*, 24 degrees for both *E. chilensis* and *E. scotsbergii*, and 30 degrees for *T. terscheckii*, starting with 0 degrees. In order to standardize the database, all compass directions of rib crests of individual cacti were changed for each species. For example, since *T. pasacana* had 20 crests on average, the crests were moved to the nearest 20-degree azimuth so the 'standard' cactus for *T. pasacana* had crests at 0, 20, 40, 60, 80 degrees, *etc*. For *T. terscheckii* with an average of 11.9 rib crests, the crests were moved to the nearest 30-degrees azimuth so the 'standard' cactus for *T. terscheckii* had crests at 0, 30, 60, 90, 120 degrees, *etc*. Such a standardization was done previously for *Carnegiea gigantea*.[2] An analysis of variance followed by the Student–Newman–Keuls test was performed to determine if samples for the various angles were statistically significant at $P < 0.05$.[6]

Microscopic analyses of surface characteristics

For each of the four species, tissue samples were removed from a portion of the cacti evaluated above. One tissue sample (2 × 2 × 2 cm) was taken from the trough closest to north and one from the trough closest to south.

Archived photographs were taken of the surface and internal characteristics of each tissue sample and tissues were immediately fixed in formalin, alcohol, acetic acid (FAA).[5] The epidermis and hypodermis (EH) of each tissue sampled were removed from tissue samples and was affixed to a microscope slide with 5-min drying epoxy glue. These EHs were viewed with a microscope at 100 × magnification. Five randomly selected views of each EH were used to evaluate cuticular characteristics. Flaking, pitting, sheeting and buildup of epicuticular waxes were observed. Stomatal densities of each of the five views were determined. These parameters have been defined previously[1] but will be described briefly here. Microscopically, flaking is defined as the presence of epicuticular waxes on EH surfaces but all stomata are clearly visible. Pitting is characterized by an accumulation of epicuticular waxes except over most stomata providing a pitted appearance. Stomata may be visible with pitting. Sheeting is characterized as the same as pitting except pits are not present. Stomata may be visible with sheeting. Buildup is a condition in which epicuticular waxes accumulate so that no stomata are visible. Data were placed on spread sheets according to species and surface observed (equatorial or polar). Chi-square analysis was performed for samples of each species to determine if there were statistically significant differences of *P* value of between equatorial and polar surfaces for each of the parameters measured.[7]

RESULTS

Directional studies—rib ridges

The percentages of crest barking on surfaces of *Trichocereus pasacana* and *T. terscheckii* are shown in Fig. 1. For *T. pasacana*, values ranged from 18% on polar surfaces (180°) to above 30% on equatorial surfaces (360°). In a similar manner, *T. terscheckii* exhibited 12% barking on polar surfaces (180°) to above 24% barking on equatorial surfaces (360°) and about 27% at 30°. Although *T. pasacana* had more crest barking, *T. terscheckii* exhibited the largest

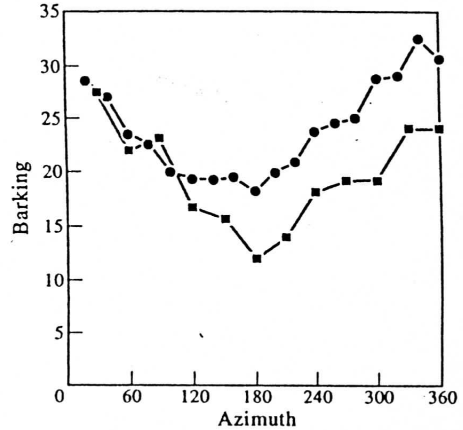

Fig. . . Relationships between azimuth and percentage of crest barking for 100 cacti each of *Trichocereus pasacana* (circles) and *T. terschekii* (squares). The standard errors of the measurement means were 0.84 and 1.01, respectively, for the two species. Means separated by more than 6 and 5 units are significantly different at $P \leqslant 0.05$ for the two species, respectively.

differential between equatorial and polar facing surfaces for these two Argentine species. Similar results for crest barking were obtained for the two Chilean cactus species observed (Fig. 2). For *E. chilensis* at Til Til, barking was above 50% (nearly 60% at 24°) on equatorial surfaces while below 20% on polar surfaces (14% at 204°). In contrast, *E. chilensis* at Curacavi exhibited a smaller differential between equator and polar surfaces in which significantly higher barking occurred on equatorial surfaces (28% at 350° and 33% at 14°) than on polar surfaces (12% at 180°). Similar differences occurred with *E. scotsbergii* (data not shown).

Directional studies—loss of spines

Trichocereus pasacana and *T. terscheckii* showed above 17% missing spines on equatorial surfaces while fewer spines were present (less than 10%) on polar surfaces (Fig. 3). Surfaces of *E. chilensis* and *E. scotsbergii* showed no effects of azimuth direction on the loss of spines (data not shown).

Directional studies—rib trough barking

Data were also taken for barking on individual troughs. If azimuth direction is an important determinant for surficial injuries to cacti, in which equatorial surfaces show more injuries than polar surfaces, then cacti of the Southern Hemisphere should have more barking on right troughs than on left troughs of ribs at 90° and more barking should occur on left troughs than on right troughs of ribs

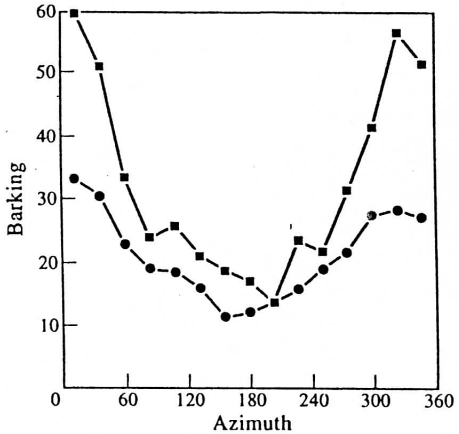

Fig. 2. Relationships between azimuth and percentage of crest barking for *Echinopsis chilensis* at the Curacavi (circles; lower line) and the Til Til (squares; upper line) sites (50 cacti per site). The standard errors of the measurement means were 0.91 and 1.41, respectively, for the two sites. Means separated by more than 12 and 11 units are significantly different at $P \leqslant 0.05$ for the two sites, respectively.

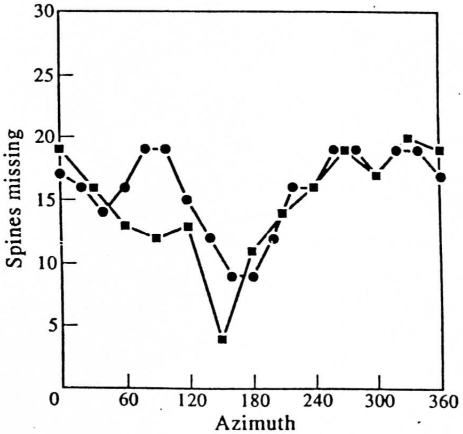

Fig. 3. Relationships between azimuth and percentage of spines missing on surfaces of 100 cacti each of *Trichocereus pasacana* (circles) and *T. terschekii* (squares). The standard errors of the measurement means were 0.55 and 0.30, respectively, for the two species. Mean values separated by more than 8 and 6 units are significantly different at $P \leqslant 0.05$ for the two species, respectively.

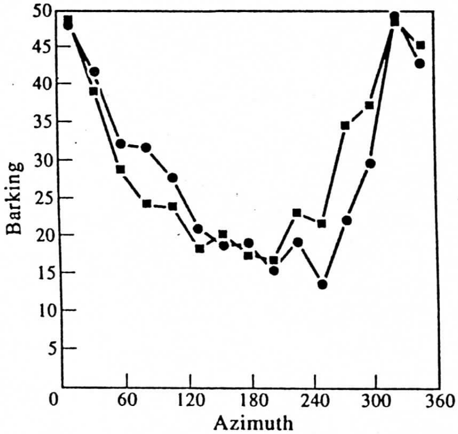

Fig. 4. Relationship between azimuth with percentage of trough area exhibiting barking for *Echinopsis chilensis* at Til Til. Right trough (circles) and left trough (squares) were considered separately. The standard error of the measurement mean was 1.25 for the 50 cacti, and means separated by more than 7 units are significantly different at $P \leqslant 0.05$.

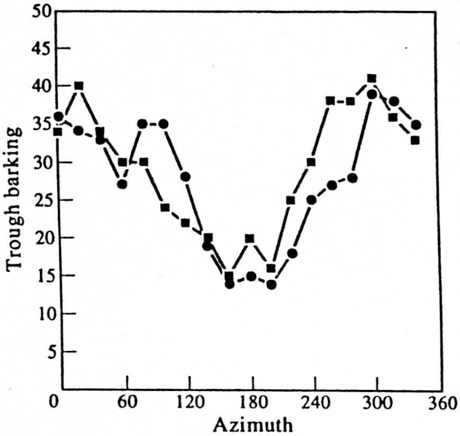

Fig. 5. Relationship between azimuth with percentage of trough area exhibiting barking for *Echinopsis chilensis* at Curacavi. Right trough (circles) and left trough (squares) were considered separately. The standard error of the measurement mean was 0.93 for 50 cacti, and means separated by more than 6 units are significantly different at $P \leqslant 0.05$.

at 270°. This hypothesis was supported by several cactus species of this study. For *T. pasacana* (Fig. 4), right troughs showed 32% barking compared with 24% barking on left troughs at 80° and left troughs exhibited 34% barking compared with 22% barking on right troughs at 280°. The same relationship was observed in *T. terscheckii* (data not shown). Among the Chilean cacti sampled, no strong differences occurred for barking between right and left troughs except for *E. chilensis* at Til Til (Fig. 5). At 84° barking on right troughs was 35% compared with 30% on left troughs. In addition, at 276°, left troughs had 38% barking compared with 26% on right troughs. *Echinopsis chilensis* did not exhibit this same pattern at Curacavi (data not shown). Moreover, this pattern was not exhibited by either population No. 1 or population No. 2 of *E. scotsbergii* at Fray Jorge (data not shown).

Microscopic analyses of surface characteristics

A limited number of cactus surface samples were collected to observe surface characteristics for a buildup of epicuticular waxes. Previous results[1] show that apparently healthy cacti have little or no accumulation of epicuticular waxes, stomata are clearly visible as waxes flake off. However, an accumulation of epicuticular waxes can occur so that stomata are not clearly visible and thus the density of visible stomata decreases to nil. Results in Table 1 show a buildup of epicuticular waxes for all species. For *T. pasacana*, equatorial surfaces had pits on 23% of all samples, while the remainder exhibited buildup. No stomata were visible on any equatorial facing surface samples of *T. pasacana*. On polar-facing surface samples, less buildup was present so that stomata were clearly visible on some surfaces.

At the microscopic level, *T. terscheckii* exhibited less severe epicuticular wax sheeting than *T. pasacana*. For *T. terscheckii*, the largest difference between equatorial and polar samples was the percentage of samples with epicuticular wax buildup. For equatorial surfaces, 37% of all samples showed buildup, while only 15% of all south surfaces had buildup. This difference was also reflected in the higher stomatal density for polar surfaces.

Surfaces of *E. chilensis* exhibited mostly sheeting and buildup with virtually no differences due to surface direction. The same situation was evident for *E. scotsbergii* (Table 1). Virtually all surfaces of these two Chilean cacti exhibited sheeting and buildup, with no samples having flaking. The reasons for the high degree of sheeting and buildup are unknown.

Table 1. Microscopic analyses of surface characteristics of several species of columnar cacti from Argentina and Chile

Species/Location	Direction	Number of cacti exhibiting characterstics of epicuticular waxes				
		Flaking	Pitting	Sheeting	Buildup	Mean density of visible stomata (number per mm^2)
Trichocereus pasacana						
Humahuaca	E	0	8b*	0b	27a	0b
	P	0	18a	8a	9b	51.0a
Trichocereus terscheckii						
Andalgala	E	0	9	13b	12a	1.52
	P	0	8	21a	5b	2.35
Echinopsis chilensis						
Til Til	E	0	0	2	4	0.57
	P	0	0	3	3	0.60
Curacavi	E	0	0	0	13	0.55
	P	0	0	0	13	0.40
Echinopsis scotsbergii						
Parc Nacional Fray Jorge	E	0	0	3	18	0.62
Population #2	P	0	1	2	18	0.47
	E					

*For equatorial (E)–polar (P) comparisons of a species, values with different letters are significantly different ($P < 0.05$) by Chi-square analysis.

DISCUSSION

Data from 400 individuals (100 each from four species) of long-lived columnar cacti support the hypothesis that long-lived columnar cacti of Argentina and Chile have surficial injuries similar to those of *Carnegiea gigantea* (saguaros) from the Sonoran Desert of North America. The four species observed in Argentina and Chile had surficial injuries similar to those found on *C. gigantea*. All species exhibited scaling and barking on both rib crests and rib troughs in the same spatial pattern, e.g. more injuries on rib crests with less on rib troughs.

The second hypothesis, that cacti of the Southern Hemisphere will exhibit surficial injuries predominantly on equatorial (northern) surfaces, was also supported by the data. For all four species at least twice as much barking occurred on equatorial surfaces compared with polar surfaces, except population #1 of *Echinopsis scotsbergii*. The greatest difference between these two directions occurred for *E. chilensis* at Til Til where crest barking was four times greater on equatorial than on polar surfaces.

The two cactus species from Argentina showed rather similar degrees of rib crest barking, loss of spines, and trough barking. In contrast, the two species from Chile showed more diversity. *Echinopsis chilensis* exhibited many more surficial injuries than E. scotsbergii. The *E. chilensis* population at Til Til exhibited 60% ridge barking on northern surfaces. In contrast, population #2 of *E. scotsbergii* had only 30% ridge barking.

Microscope analyses of EH samples taken for this study show a wide variety of conditions. *Trichocereus pasacana* and *T. terscheckii* exhibited the greatest differences between equatorial and polar surfaces. Indeed, *T. pasacana* had the strongest contrast in which no stomata were observed on surfaces of trough samples taken from the north side. For *T. terscheckii* injury, as measured by the percentage of samples exhibiting buildup, was more than twice on equatorial samples than on polar samples.

Echinopsis chilensis and *E. scotsbergii* showed no significant north and south differences with regard to epicuticular wax buildup. This occurred because of the high degree of wax buildup on most of the samples observed. However, visible surface injury was relatively low on polar surfaces of these two species (as low as 10–15% barking for *E. chilensis* and 10–23% barking for *E. scotsbergii*). Compared with results of the two species from Argentina and *C. gigantea* in North America, the microscopic injuries to the two species of *Echinopsis* were excessive for the amount of visible surficial injury.

Gibson and Nobel[4] discuss the process of bark formation in cacti. They showed cell divisions of epidermal cells of *Ferocactus robustus* that gave rise to a cork cambium. They also described periderm formation on *C. gigantea*. Their illustrations show what is referred to here as scaling and barking. Our observations to date of the epidermis/hypodermis of *C. gigantea* do not show a distinct cork cambium, and if the scaling and barking materials are removed with a scalpel, stomata are present (personal observations), so it seems that the scaling and bark of this species are only a matter of a buildup of epicuticular waxes. However, further studies may be necessary to resolve this point.

Similar differences in surficial injuries between equatorial and polar surfaces occurred with several other species of columnar cacti in these two countries. Much more injury was present on equatorial than on polar surfaces of *Echinopsis coquimbanus* [= *Trichocereus coquimbanus* near Coquimbo (30°S, 71°30′W), *E. litoralis* [*Trichocereus litoralis*] near Con-Con, *Eulychnia acida* near Los Vilos (31°50′S, 71°30′W), *Eulychnia breviflora* near La Serena (29°55′S, 71°20′W) in Chile. In Argentina, these same differential surficial injuries occurred on *Cereus forbesii* near Catamarca (28°40′S, 66°W), *Trichocereus tarijensis* [= *Trichocereus poco* = *E. poco* = *E. tarijensis*] near El Aquilar (23°15′S, 65°45′W) south of Tres Cruces, and *Oreocereus celsianus* near Abra Pampa (22°40′S, 65°45′W). In this manner, more surficial injuries occurred to equatorial than polar surfaces for 11 species of long-lived columnar cacti in Chile and Argentina.

The directional effects documented herein are not specific to cacti in Argentina and Chile but are present on *C. gigantea* throughout Arizona and northern Mexico.[1] Moreover, surficial injuries have been shown to occur to three other species of long-lived columnar cacti of the Sonoran Desert (Evans and Fehling, personal communication). These species, *Pachycereus pringlei*, *Stenocereus thurberi* and *Lophocereus schottii*, exhibit sheeting and buildup of epicuticular waxes, and barking on ridges, but do not have a significant amount of barking on troughs. Barking of crests occurs on three species throughout the Sonoran Desert. This lack of a geographically localized response of cacti suggests that the causative agent of epidermal browning is not specific to any one location but is occurring at many locations.

Although there is a lack of geographic localization to the injuries to long-lived columnar cacti discussed above, there are some differences in the extent of surficial injuries. For example, surficial injuries are much greater on *E. chilensis* at Til Til than at Curacavi. Moreover, *E. scottsbergii* exhibited much lower amounts of surficial injuries compared with E. chilensis. Another difference in response is with loss of spines; the two Argentine species, *T. terscheckii* and *T. pasacana*, lost nearly 20% of spines on crest areas with barking, but the two Chilean species; *E. chilensis* and *E. scottsbergii*, showed little loss of spines with barked crests. The reasons for these differences are unknown, but such differences in responses may be used as a tool to understand the causative agent of these injuries.

Surficial injuries are strongly correlated with azimuth. Germane to this conclusion are calculated PAR measurements derived from the model of Geller and Nobel.[3] Calculated annual PAR on the surface of a vertical cylinder at 30°S latitude, a latitude similar to several sites of this study predicts that about four times as much total annual accumulated irradiance on equatorial surfaces compared with polar surfaces. These results are interesting, since injury to equatorial facing crests and troughs are as much as four times greater than that on polar surfaces.

In summary, the hypothesis that increased sunlight exposure could be the causative agent, or at least contribute to superficial injuries, is consistent with all of the present circumstances that relate to epidermal browning of *C. gigantea* in North America.[1,2] These circumstances are: (1) total fluences on equatorial exposures is four times that of polar exposures at a latitude of 30°S and injuries to rib ridges and troughs on equatorial exposures on cacti are up to four times greater than on polar facing surfaces; (2) crest areas which receive less shading than trough areas show symptoms of visible injury before trough areas; and (3) visible injuries are not localized but are occurring on a large number of cactus species under a wide range of habitats in South America.

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