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LOW-TEMPERATURE TOLERANCE AND COLD HARDENING OF CACTI[1]

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Abstract. Reduced uptake by the chlorenchyma cells of cacti of a stain (neutral red) was used as an indicator of low-temperature damage resulting from cooling stems in the laboratory. Necrosis set in a few degrees below the temperature at which the fraction of cells accumulating stain was reduced by 50%. *Coryphantha vivipara, Opuntia polyacantha,* and *Pediocactus simpsonii,* which range to over 3000 m altitude in southern Wyoming, were quite cold tolerant (50% inhibition of staining occurred from −17° to −20°C), while *O. bigelovii* and *O. ramosissima,* which are restricted to much warmer habitats, were not very cold tolerant (50% inhibition from −4° to −7°).

Relationships among tissue cold sensitivity, morphological features which protect the stems from low temperatures, and the occurrence of species in progressively colder regions were investigated. Differences in tissue cold sensitivity accounted for the ≈600 m higher elevational limit of *Coryphantha vivipara* var. *rosea* compared to the morphologically similar var. *deserti* in southern Nevada. In contrast, morphological differences alone could adequately explain the relative northern limits of the columnar cacti *Carnegiea gigantea* vs. *Stenocereus gummosus* and the barrel cacti *Ferocactus acanthodes* vs. *F. wislizenii* in the southwestern United States, as previously indicated using a computer model. Differences in both morphology and tissue cold sensitivity apparently influenced the relative northern ranges of *Lophocereus schottii* with respect to the other columnar cacti and *F. covillei* with respect to the other barrel cacti, as well as the relative elevational range of *Denmoza rhodacantha* with respect to *Trichocereus candicans* in northcentral Argentina.

Cold hardening in response to decreasing day/night air temperatures was observed for 10 species. A decrease from 50°/40° to 10°/0° lowered by 4° the temperature at which the fraction of the chlorenchyma cells taking up stain was reduced 50% for both *D. rhodacantha* and *T. candicans,* with a half-time for the shift of ≈3 d. The tolerance of subzero temperatures and the ability to cold harden allow cacti to range into regions with considerable wintertime freezing.

Key words: cacti; cold harden; distribution; freezing; morphology; supercooling; temperature; tolerance.

INTRODUCTION

Although some cacti occur in southern Canada or at high elevations where snow is common (Hitchcock et al. 1961, Earle 1963, Backeberg 1966), cacti generally are not native to regions with appreciable freezing (Levitt 1980). Cacti have high cellular water content, resulting in fairly high tissue osmotic potentials (Walter and Stadelmann 1974). For example, osmotic potentials range from −0.4 to −1.0 MPa for *Carnegiea gigantea* (Soule and Lowe 1970), which would lead to a freezing point depression of only 0.3° to 0.8°C. However, stems of *C. gigantea* can supercool (cool below the equilibrium freezing point) to −3° to −12° (Steenbergh and Lowe 1976), which could circumvent any limitation on freezing protection caused by high osmotic potentials. Another possibility for their general absence in cold regions is that cacti might not be able to cold harden. Thus, exposure to decreasing environmental temperatures may not lead to greater low temperature tolerance, as it commonly does for perennials from northern temperate regions (Parker 1963, Weiser 1970, Larcher et al. 1973, Levitt 1980).

Recently, a computer model has been developed that predicts the surface temperatures of cacti (Lewis and Nobel 1977, Nobel 1978), and such predictions have been used to help interpret the influence of morphological features on range boundaries. For instance, under the same environmental conditions, the simulated minimum surface temperatures were highest for *Carnegiea gigantea,* 1.8° lower for *Stenocereus thurberi,* and 3.8° lower for *Lophocereus schottii,* which is the same relative order as the northernmost limits of these three columnar cacti in the Sonoran desert (34°56′N, 32°38′N, and 31°55′N, respectively; Nobel 1980*a*). Based on a similar analysis incorporating stem height, diameter, spine properties, apical pubescence, and other morphological features of the four *Ferocactus* species (barrel cacti) occurring in the southwestern United States, *F. acanthodes* was predicted to range the furthest north, then *F. wislizenii,* then *F. covillei,* and finally *F. viridescens,* in agreement with field observations (Nobel 1980*b*). This approach presumes that the lowest wintertime temperatures are the major factor influencing the northern ranges of cacti in the United States, for which there is considerable evidence (e.g., Shreve 1914, Turnage and Hinckley 1938, Parker 1963), and that the tissue sensitivity to subzero temperatures within the set of cacti compared is the same, for which there is no evidence. For this reason,

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TABLE 1. Summary of chlorenchyma temperatures for 50% inhibition of staining. Data are presented as mean ± standard deviation for measurements on six stems in each case. Plants were maintained at day/night air temperatures of 10°/0° for 4–6 wk before measurements. Nomenclature is according to Backeberg (1966) for Argentina and Chile, Beatley (1976) for Nevada, Hitchcock et al. (1961) for Wyoming, and Shreve and Wiggins (1964) for the Sonoran Desert except Gibson and Horak (1978) for *Stenocereus*.

Species	Site (latitude, longitude; elevation)		Temperature for 50% inhibition of staining (°C)
Carnegiea gigantea	Central Arizona	(33°46′N, 112°41′W; 500 m)	−8.6 ± 0.4
Coryphantha vivipara	Southeastern Wyoming	(41°14′N, 105°53′W; 2240 m)	−20.3 ± 0.9
C. vivipara var. *deserti*	Southern Nevada	(36°40′N, 116°1′W; 1110 m)	−18.6 ± 0.7
C. vivipara var. *rosea*	Southern Nevada	(37°9′N, 116°11′W; 1970 m)	−22.1 ± 1.1
Denmoza rhodacantha	Northcentral Argentina	(32°26′S, 69°1′W; 2260 m)	−10.4 ± 0.8
Eriosyce ceratistes	Central Chile	(32°54′S, 70°15′W; 1940 m)	−10.1 ± 0.8
Ferocactus acanthodes	Southern California	(33°38′N, 116°24′W; 840 m)	−8.4 ± 0.9
F. covillei	Southern Arizona	(31°59′N, 111°39′W; 1160 m)	−7.2 ± 0.4
F. viridescens	Coastal southern California	(33°13′N, 117°22′W; 40 m)	−6.1 ± 0.7
F. wislizenii	Southern Arizona	(32°21′N, 111°2′W; 850 m)	−8.4 ± 0.8
Lophocereus schottii var. *schottii*	Southern Arizona	(31°55′N, 112°57′W; 410 m)	−7.2 ± 0.6
Opuntia bigelovii	Southern California	(33°38′N, 116°24′W; 850 m)	−7.3 ± 1.3
O. polyacantha	Southeastern Wyoming	(41°18′N, 105°50′W; 2230 m)	−17.1 ± 0.7
O. ramosissima	Southern California	(33°39′N, 116°23′W; 220 m)	−4.4 ± 0.6
Pediocactus simpsonii	Southeastern Wyoming	(41°38′N, 105°34′W; 2250 m)	−18.3 ± 0.7
Stenocereus thurberi var. *thurberi*	Northern Sonora, Mexico	(30°40′N, 112°6′W; 350 m)	−9.0 ± 1.2
Trichocereus candicans	Northcentral Argentina	(32°32′S, 69°0′W; 1860 m)	−7.4 ± 0.7
T. chilensis	Central Chile	(32°55′S, 70°16′W; 1760 m)	−7.8 ± 0.9

the tissue sensitivity to subzero temperatures was investigated for these seven species. Also, the potential for cold hardening was examined. Based on a recent study of low-temperature responses with *Coryphantha vivipara* (Nobel 1981), the accumulation of a stain (neutral red) by the chlorenchyma cells was used as a measure of membrane integrity and hence cell viability. Loss of ability to accumulate stain induced by subzero temperatures was followed by tissue necrosis, indicating that a substantial decrease in staining was a useful assay for low-temperature damage in cacti.

MATERIALS AND METHODS

Species names and sites where obtained are summarized in Table 1. Unless indicated otherwise, plants were transplanted into desert soil ("loamy sand") and maintained for at least 4 wk in environmental chambers with 12-h days at 10° ± 1°C air temperature and 350 μmole·m^{-2}·s^{-1} photosynthetically active radiation from 400 to 700 nm (determined with a Lambda Instruments LI-190S quantum sensor). Nighttime air temperature was 0° ± 1°. Tissue surface temperatures rose to 17° ± 2° during the daytime and fell to 0° ± 1° at night. Air and stem surface temperatures represent the average for three copper-constantan thermocouples 150 μm in diameter (agreement was generally ±0.3°). Stem temperatures were determined as close to the surface as possible and also 1 mm beneath the surface near the center of the chlorenchyma, where the temperature averaged 0.2° higher during cooling phases than at the surface. Unless stated otherwise, stem temperatures refer to the chlorenchyma, since the staining properties also refer to the chlorenchyma. Plants were watered weekly with 1/10 Hoagland's solution number 1 (Hoagland and Arnon 1950) so that the soil water potential (determined with Wescor PT 51-05 soil thermocouple psychrometers) near the roots was generally −0.2 ± 0.1 MPa.

To test the temperature dependence of the ability of chlorenchyma cells to accumulate a stain, air temperatures were lowered at ≈2°/h in a Revco ULT-385A deep freeze. Pieces of stem were removed at various temperatures, warmed at 10°/h (approximately the warming rate observed in the field at sunrise) to 10°, and then stain accumulation was examined for at least 200 chlorenchyma cells from ≈1 mm below the surface; sections 100 μm thick were examined at 400× using a Zeiss phase-contrast research microscope. The stain was 50 μmol/L neutral red (3-amino-7-dimethylamino-2-methylphenazine [HCl]) in 1 mol/L mannitol. The osmoticum caused some plasmolysis, which facilitated the determination that the stain was inside the cells. The fraction of cells that took up the stain was examined immediately after sectioning and at various times up to 24 h (stems meanwhile were maintained at 0° in the dark). The percentage of cells accumulating stain remained constant for *Carnegiea gigantea* but increased for a few hours for *Coryphantha vivipara* and for ≈18 h for *Lophocereus schottii* and *Stenocereus thurberi*. The maximum percentage observed was used for each species.

A computer model was employed to predict the surface temperatures of cacti to within 0.1° based on their morphology (Lewis and Nobel 1977, Nobel 1978). Morphological parameters included mean stem height, stem diameter, spine length, spine diameter, stem shading by the spines, and apical pubescence. The microclimatic data consisted of hourly measurements

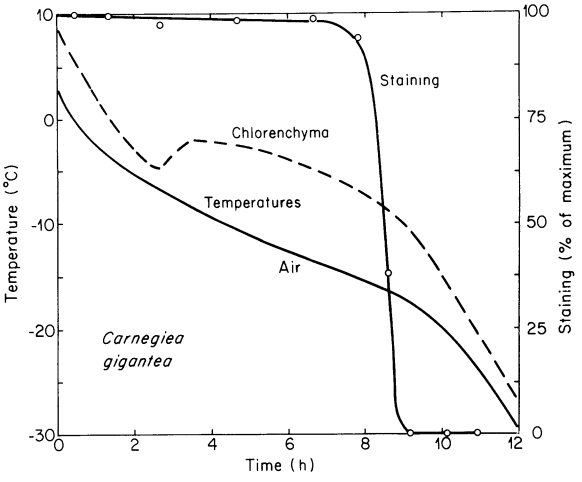

FIG. 1. Cooling curve, showing how the tissue temperature of *Carnegiea gigantea* decreased as the air temperature was lowered. Staining refers to the percentage of chlorenchyma cells taking up neutral red for the same stem.

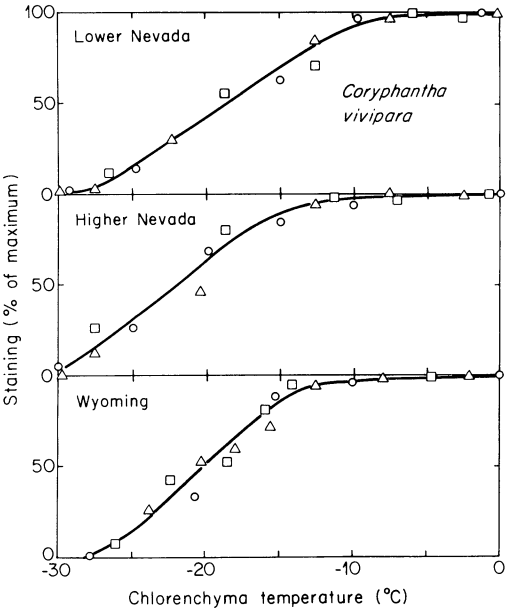

FIG. 2. Temperature dependence of the staining for *Coryphantha vivipara*. Data were obtained for the lower elevation (1110 m) var. *deserti* (Lower Nevada) and the higher elevation (1970 m) var. *rosea* (Higher Nevada) from Nevada and a high-elevation (2240 m) type from Wyoming (Wyoming). Different symbols indicate chlorenchyma temperatures of different individual plants.

of direct and diffuse shortwave irradiation, IR irradiation, wind speed, air temperature, relative humidity, and soil temperatures made over a 24-h period on a winter day (16 January 1976). The heat convection coefficient was based on that previously validated for *Ferocactus acanthodes* and columnar cacti (Lewis and Nobel 1977, Nobel 1978).

To study cold hardening, plants averaging 50 cm in height were maintained at day/night air temperatures of 10°/0° for at least 6 wk and then transferred to 50°/40°. At weekly intervals sections of a stem were removed for treatments at subzero temperatures, and the day/night air temperatures for the remaining stem were reduced by 10°.

RESULTS

When the air temperature was continuously decreased for *Carnegiea gigantea,* the chlorenchyma temperature decreased to −5°C and then rose to about −3° (Fig. 1). After the rise, the temperature decreased gradually to ≈−10° and then decreased more rapidly. The percentage of the chlorenchyma cells taking up a stain was fairly constant until the stem temperature reached −6°, and then it abruptly decreased, becoming halved near −9° and zero by −10° (Fig. 1). Visual observation of six stems cooled to −5° (and then returned to the environmental chamber and observed for a 1-mo period) indicated that they all were alive, whereas six out of six stems cooled to −10° became necrotic within 1 mo.

In comparison to *Carnegiea gigantea,* the decrease in ability to accumulate stain as the stem temperature was lowered was not as abrupt for *Coryphantha vivipara* and the temperatures where the staining decreased by 50% were considerably lower (Fig. 2). The three kinds of *Coryphantha vivipara* had somewhat different temperature sensitivities; 50% inhibition of staining occurred at −19° for the lower elevation var. *deserti* from Nevada, at −22° for the higher elevation var. *rosea* from Nevada, and at −20° for the one from Wyoming (Fig. 2). In all cases where the subzero temperatures caused <10% of the chlorenchyma cells to accumulate stain, the stems became necrotic within 1 mo. The morphological parameters of the two Nevada varieties are quite similar, e.g., mean heights for 20 stems of 5.1 cm and 4.6 cm, mean diameters of 6.8 cm and 6.6 cm, and mean shading of the stem by spines of 76% and 73% for var. *deserti* and var. *rosea,* respectively, and no apical pubescence for either. Hence, the surface temperatures predicted for each by the computer model for the same environmental conditions were within ± 0.5° of each other.

Table 1 summarizes the chlorenchyma temperatures leading to 50% inhibition of staining for all 16 species studied here. The range for 50% inhibition was from −22° to −4°. For *Coryphantha vivipara, Opuntia polyacantha,* and *Pediocactus simpsonii* from a cold site in Wyoming the temperatures for 50% inhibition averaged −18°, while the comparable temperatures averaged −6° for *O. bigelovii* and *O. ramosissima* from a warm site in southern California (Table 1).

The cold temperature tolerance and the possibility for cold hardening were investigated for those species whose range limits had previously been investigated using the computer model (Nobel 1980*a, b*). For three

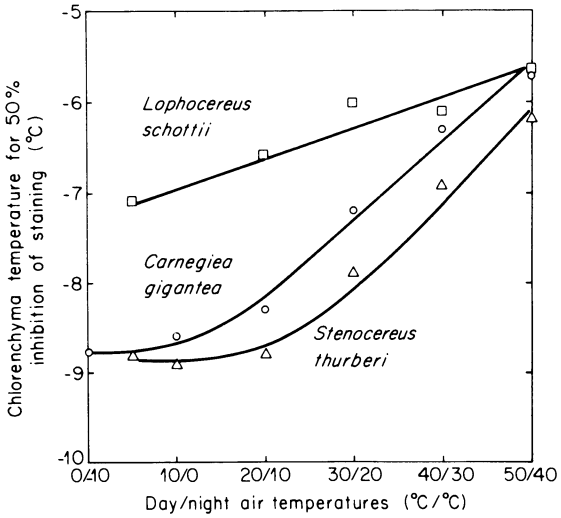

FIG. 3. Cold hardening in response to decreasing ambient air temperature for three species of columnar cacti from the Sonoran Desert, showing the chlorenchyma temperature where the ability of its cells to take up stain is halved. Plants were maintained at day/night air temperatures of 50°/40° for 1 wk, sections were removed and tested for stain accumulation at sub-zero temperatures as in Fig. 1, and then the remaining stem was placed at 10° cooler temperatures for another week until, by continuation of this sequence, the day/night air temperatures were lowered to 0°/−10°. No stems survived day/night air temperatures 5° below the lowest data point indicated.

species of columnar cacti from the Sonoran Desert, reducing the day/night air temperatures from 50°/40° to 0°/−10° decreased by 2° to 3° the temperature where the ability to accumulate stain was halved (Fig. 3). *Carnegiea gigantea* and *Stenocereus thurberi* tolerated the same minimum temperature (about −9°), while *Lophocereus schottii* was slightly more sensitive

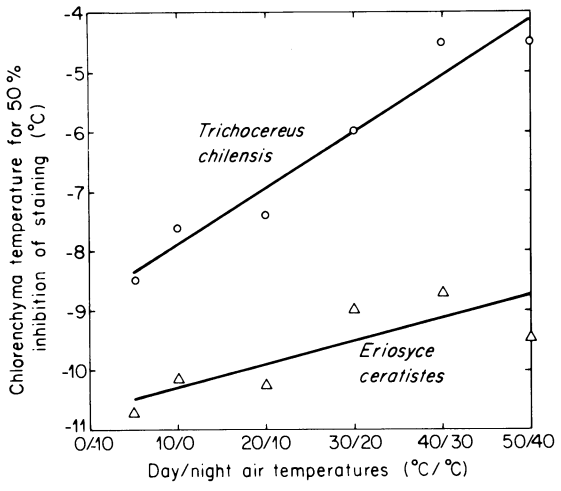

FIG. 4. Cold hardening for *Eriosyce ceratistes* and *Trichocereus chilensis* from Chile. Data were obtained for decreasing temperatures as in Fig. 3.

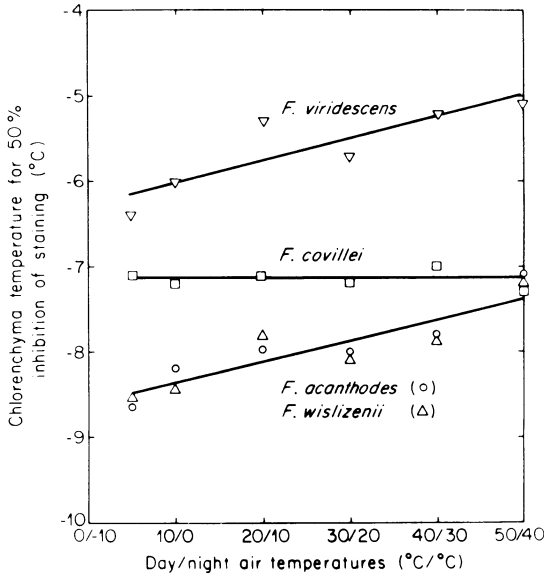

FIG. 5. Cold hardening for the four species of *Ferocactus* that occur in the southwestern United States.

to low temperatures. For the two species studied in central Chile, *Eriosyce ceratistes* always tolerated lower temperatures, but *Trichocereus chilensis* showed a greater degree of cold hardening (Fig. 4). All four species of *Ferocactus* from southwestern United States showed a cold hardening of 1° except *F. covillei*, which showed no cold hardening at all; *F. viridescens* was the most sensitive to low temperatures, and *F. acanthodes* and *F. wislizenii* were the least sensitive (Fig. 5).

The time course of cold hardening was examined for two species from northcentral Argentina, *Trichocereus candicans*, which occurred up to 1860 m ele-

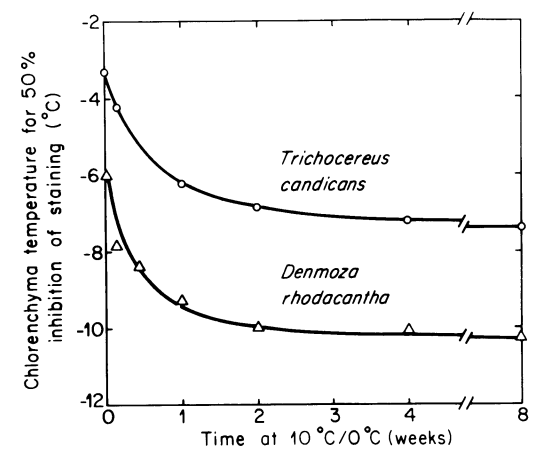

FIG. 6. Time course for the change in chlorenchyma temperature for 50% inhibition of staining after maintaining two species from northcentral Argentina at day/night air temperatures of 50°/40° for 4 wk and then switching to 10°/0°.

vation in the region studied, and *Denmoza rhodacantha*, which occurred up to 2530 m. After being maintained at day/night air temperatures of 50°/40°, a change to 10°/0° in one step caused a 4° lowering of the temperature where staining was 50% inhibited for both *T. candicans* and *D. rhodacantha* (Fig. 6). The half-time for the decrease was about 3 d. Morphologically these two species differ considerably; e.g., for 20 stems measured in the field, the heights averaged 17 cm and 69 cm, the diameters 12 cm and 25 cm, the apical pubescence depth 0.5 mm and 7.6 mm, and the apical spine shading 6% and 81% for *T. candicans* and *D. rhodacantha*, respectively. Using these morphological parameters in the computer model and environmental data for a winter day (Lewis and Nobel 1977), the minimum surface temperatures under the same microclimatic conditions were predicted to be 6.5° for *T. candicans* and 9.4° for *D. rhodacantha*.

Discussion

Cacti can survive subzero temperatures, the nonlethal range varying widely among species. For instance, Uphof (1916) in a study on five species of *Opuntias* noted that death occurred from −6°C for *Opuntia ficus-indica* to −18° for *O. ellisiana*, visual damage being evident about 2° above the killing temperature. In the present study, *O. bigelovii* and *O. ramosissima*, both of which are limited to elevations below 1200 m in a warm desert region of southern California, showed a 50% decrease in the percentage of chlorenchyma cells accumulating stain at −7° and −4°, respectively (Table 1). On the other hand, three species that can range up to 3000 m in southeastern Wyoming, *O. polyacantha*, *Pediocactus simpsonii*, and *Coryphantha vivipara*, had analogous temperatures of −17°, −18° and −20°, respectively. The range of these latter species to more northerly latitudes and higher elevations is undoubtedly related to their greater low-temperature tolerance. Previous studies indicated a lethal temperature of −24° for *O. polyacantha* (Rajashekar et al. 1979), which is fairly consistent with the present results, since necrosis generally set in a few degrees below the cold treatment that reduced staining of the chlorenchyma by 50%.

Species whose relative ranges have been predicted based on morphological parameters using a computer model (Lewis and Nobel 1977, Nobel 1978) were reexamined here for their tissue sensitivity to subzero temperatures. Since *Carnegiea gigantea* and *Stenocereus thurberi* had similar cold tolerances when maintained at low day/night air temperatures (Fig. 3), morphological differences may indeed be responsible for *C. gigantea* extending further northward in the Sonoran Desert than does *S. thurberi* (Nobel 1980*a*). Both morphology leading to less protection against cold (essentially no apical spines or pubescence) and greater cold sensitivity apparently restrict *Lophocereus schottii* to more southerly latitudes. Similarly, morphology apparently accounts for *Ferocactus acanthodes* ranging to colder regions than does *F. wislizenii*, mainly because spines on the former species shade nearly twice as much of the apical stem surface, which results in greater protection from cold nighttime skies (Nobel 1980*b*). The restriction of *F. covillei* to more southerly parts of Arizona apparently reflects its even lower spine coverage (three-fold less than *F. wislizenii* and six-fold less than *F. acanthodes* in the crucial apical region) as well as somewhat greater sensitivity to low temperatures. *F. viridescens* is apparently limited to even warmer regions in coastal southern California and Baja California as a consequence of both its morphology and tissue cold sensitivity.

Based on the elevational limits and morphology of *Trichocereus chilensis* and *Eriosyce ceratistes* in central Chile, *E. ceratistes* was predicted to have about the same low-temperature sensitivity as *T. chilensis* (Nobel 1980*b*), contrary to the present findings (Fig. 4). However, the rate and amount of cold hardening of *T. chilensis* is greater, so it eventually may withstand the same low temperatures as does *E. ceratistes*. The previous computer prediction depends on the particular microclimatic data employed (Lewis and Nobel 1977), where changes in a single parameter such as wind speed can have different effects on the simulated temperatures of different species, especially if they differ considerably morphologically, as these two species do (Nobel 1980*b*).

The two varieties of *Coryphantha vivipara* in southern Nevada purportedly have different elevational limits. Specifically, var. *deserti* is supposed to occur locally from 1300 to 1500 m (the present sample came from 1110 m) and var. *rosea* from 1900 to 2100 m (Beatley 1976). Since a lapse rate of about −0.6° in air temperature per 100 m increase in elevation might be expected (Smith and Geller 1979, Nobel 1980*b*), a 3.6° lower tissue tolerance for var. *rosea* would be expected if the upper elevational limit was due to low-temperature limitations in both cases (the effect of snow cover could modify this estimate). The temperature where staining was reduced 50% was 3.5° lower for var. *rosea* than var. *deserti* (Table 1; means significantly different, $P < .001$), which is consistent with but not proof of the hypothesis that low-temperature sensitivity determined the different upper elevational limits of the two varieties (morphological similarity led to surface temperatures predicted by the computer model to be within ±0.5° of each other for the two varieties). *Denmoza rhodacantha* ranged about 700 m higher than *Trichocereus candicans* at the field sites in northcentral Argentina. Using the 0.6° per 100 m lapse rate, a site 700 m higher would be ≈4.2° colder. Computer simulations incorporating the morphological differences indicate that *D. rhodacantha* would be 2.9° warmer than *T. candicans* under the same environmental conditions. Staining was 50% inhibited for *D. rhodacantha* at ≈3.0° lower tempera-

tures than for *T. candicans* (Fig. 6). Thus, both a morphology favoring higher surface temperatures and less tissue sensitivity to low temperatures may be about equally responsible for *D. rhodacantha* ranging to higher elevations than does *T. candicans*.

Carnegiea gigantea exhibited supercooling to $\approx -5°$, similar to previous results (Steenbergh and Lowe 1976), where such responses were predicted to protect juveniles from freezing damage. The exothermic reaction following such supercooling most likely represents the latent heat released as the extracellular water freezes (Weiser 1970, Burke et al. 1976, Levitt 1980). For *Coryphantha vivipara*, the exothermic reaction represents the freezing of $\approx 10\%$ of the stem water (Nobel 1981). This extracellular ice formation, which has previously been directly observed for cacti (Uphof 1916), is most likely not lethal, since the ice presumably does not cross the plasmalemma and enter the protoplasm. Moreover, no change in the ability of the chlorenchyma to accumulate stain was observed here during the supercooling, the exotherm, or for a few hours thereafter (Fig. 1). Thus, the supercooling may have little direct effect on the low-temperature tolerance of the chlorenchyma cells.

Of particular interest is the cold hardening observed, where the temperature for 50% inhibition of staining decreased as the environmental air temperatures were gradually lowered. For a lowering of the day/night air temperatures from 50°/40° to 10°/0°, the cold hardening averaged 2.3° for the 11 species of cacti examined (Figs. 3–6). It was greatest for *Denmoza rhodacantha*, *Trichocereus candicans*, and *T. chilensis*, amounting to 4.0°–4.2° in each case. Such changes could have significant effects on range boundaries, since minimum air temperatures at constant elevation can change $\approx 1°$ per degree latitude (Nobel 1980*a*, 1980*b*), and the lapse rate can be $-0.6°$ per 100 m of elevation. The half-time for the cold hardening was ≈ 3 d for both *D. rhodacantha* and *T. candicans*, suggesting that cacti can respond to fairly rapid changes in environmental temperature. Increased cold hardiness, which occurs for many plants in response to cooler temperatures in the fall and early winter (Mazur 1969, Larcher et al. 1973, Levitt 1980), should increase the survival of cacti during the winter. This response plus the ability to tolerate temperatures as low as $-20°$ allows cacti to occur where there is considerable wintertime freezing.

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