

LOW TEMPERATURE RESPONSES OF CACTI: A REVIEW

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SUMMARY

Differences in distributional limits of various species of cacti caused by susceptibility to low wintertime temperatures can often be explained by the influence of differences in stem morphology on shoot temperatures. However, the tolerances of tissues to subzero temperatures, which vary considerably among cacti, must also be taken into account. During a low-temperature episode, supercooling of cactus stems below the tissue freezing point is followed by a temperature rise that represents the heat released during the formation of extracellular ice crystals. Future research will help elucidate whether the accompanying intracellular dehydration is responsible for the tissue death. Breeding and biotechnology programs to prevent freezing damage and thus to increase the cultivation of cactus species important for fruit, vegetable, and fodder production can then be undertaken in an informed manner.

Contents: Summary; Early Observations; Morphology and Models; Low Temperature Tolerance; Mechanisms of Damage; Future Research; Literature Cited.

EARLY OBSERVATIONS

In the 1920s, Shreve called attention to the importance of low air temperatures in establishing the northern limits of Carnegiea gigantea, Lemaireocereus thurberi, and Lophocereus schottii in the Sonoran Desert of North America (Shreve, 1911, 1914). He observed that C. gigantea can withstand 19 h of subzero temperatures and suggested that it is restricted to regions where freezing episodes are shorter than 24 h, a hypothesis that has received some support (Niering, Whittaker, and Lowe, 1963). On the other hand, Echinocereus polyacanthus and Opuntia versicolor can withstand 66 h of continuous freezing and O. missouriensis (= O. polyacantha) can withstand 375 h (Shreve, 1911, 1914). Uphof (1916) noted that opuntias had a wide range of low temperature sensitivities, death occurring at -8°C for O. ficus-indica, -10°C for O. fuscicaulis, -17°C for O. castille (= O. megacantha), and -18°C for O. ellisiana (= O. lindheimeri).

In 1916, Uphof microscopically observed the freezing process for prickly-pear cacti. In particular, he noted that ice crystals form extracellularly in cacti upon gradual freezing, both in the intercellular air spaces as well as between the cell wall and the plasmalemma. However, most observations on the low-temperature responses of cacti

have probably not been published, such as those made by botanical garden personnel or by hobbyists, who are often concerned with the extensive damage that can occur to their collections by a single low-temperature episode. Despite the validity of such observations, death of cacti may not be immediate, as certain Carnegiea gigantea exposed to a severe freeze in January 1937 in Arizona did not die until 3 years later (Turnage and Hinckley, 1938; Gill, 1942; Steenbergh and Lowe, 1976), and some exposed in 1971 did not die until 9 years later (Steenbergh and Lowe, 1983).

MORPHOLOGY AND MODELS

Beginning in the late 1970s, a computer model was developed that can predict the surface temperatures of cacti based on their morphology and the prevailing environmental conditions (Lewis and Nobel, 1977; Nobel, 1978). The cactus stem is modeled as a set of subvolumes and the temperature is predicted for each subvolume using an energy budget analysis that takes into consideration absorption of shortwave (solar) radiation, absorption and emission of longwave radiation, convective heat exchange based on wind-induced air movement, evaporative cooling accompanying transpiration, and heat conduction within the stem and to the ground (Nobel, 1988a,b). Predicted surface temperatures are generally within 1°C of those measured hourly for the barrel cactus Ferocactus acanthodes (Lewis and Nobel, 1977), the small globular cactus Mammillaria dioica, and the columnar cactus Carnegiea gigantea (Nobel, 1978). The average surface temperature is substantially influenced by the air temperature, as a simulated 5.0°C change in air temperature causes the predicted surface temperature to change by 4.0°C to 4.4°C. Greater daily extremes in surface temperature occur at lower wind speeds that reduce convective heat exchange. The simulations also show the asymmetrical heating of the stem caused by direct solar irradiation (Nobel, 1978).

Using such a model, the influence of morphological features such as stem diameter and stem absorptance on tissue temperature can be quantitatively evaluated. Particular attention has been focused on the spine shading and the pubescence that covers the apical meristem responsible for stem growth (Nobel, 1978). For instance, the thick apical pubescence at the apex of C. gigantea leads to a simulated 2.4°C higher nocturnal temperature compared with a plant without pubescence, which affects the distribution of this species (Nobel, 1980a). Nurse plants, which affect the longwave exchange by partially replacing the potentially cold nighttime sky with a radiator (the branches and the leaves of the nurse plant) at air temperature, can increase the nocturnal stem temperatures and thereby extend the range of C. gigantea to colder regions (Nobel, 1980b).

The computer model helps explain the northernmost limits of columnar cacti in the Sonoran Desert; under the same environmental conditions the minimum apical temperatures are 7.7°C, 5.9°C, and 3.9°C for C. gigantea, Lemaireocereus thurberi, and Lophocereus schottii, respectively, the same order as their northernmost limits (34°56'N,

32°38'N, and 31°55'N; Nobel, 1980a). Likewise among barrel cacti, *E. acanthodes* has the highest predicted minimum apical temperature and hence is predicted to range the furthest north, followed by *Ferocactus wislizenii*, then *F. covillei*, and finally *E. viridescens*, in agreement with field observations (Nobel, 1980c). Using the computer model to analyze morphological differences in stem diameter and apical properties, the upper elevational limits of *Eriosyce ceratistes* and *Trichocereus chilensis* for slopes of the same angle and exposure can be predicted to within ± 20 m, corresponding to only $\pm 0.1^\circ\text{C}$, over a wide range in latitudes extending over 500 km from 20°S to 35°S in the Andes Mountains of Chile (Nobel, 1980c). A computer model that allows for ectotypic differences in stem morphology has apparently not been used for other species, nor has a sharp elevational cutoff been predicted for other species, although treelines and other elevational changes in species distribution are commonly observed.

LOW TEMPERATURE TOLERANCES

The computer model allows for a quantitative interpretation of the influence of morphology on shoot temperatures. However, the tissue sensitivities to low temperature must also be considered when predicting plant distribution. From an ecological point of view, plant survival is an ultimate criterion, but plant death may not occur until a few years after a low-temperature episode, as already indicated. For experimental purposes a more rapid technique for assessing cell viability is needed, such as the uptake of the vital stain neutral red [3-amino-7-dimethylamino-2-methylphenazine (HCl)]; Gurr, 1965; Onwueme, 1979. Specifically, when cellular uptake of neutral red is reduced to zero by a 1 h treatment at some subzero temperature (1 hour is chosen for the treatments, as extreme temperatures can be experienced for such periods by cacti in the field), such cells and the tissues in which they occur eventually die (Nobel, 1988a). Indeed, the lack of stain uptake indicates that the plasmalemma and/or the tonoplast are no longer functioning. Moreover, studies with neutral red show that cacti exhibit low-temperature hardening, or acclimation, as the minimal temperature that can just be tolerated decreases as the ambient temperatures decrease over days or weeks (Nobel, 1988).

Studies based on plant death indicate that *Opuntia polyacantha* can tolerate -24°C (Rajeshekar, Gusta, and Burke, 1979) and that *O. erinacea*, *O. humifusa*, *O. phaeacantha*, *O. spinosior*, and *O. stricta* can tolerate -17°C or -18°C but not -20°C (Nardina and Mukhammedov, 1973). The first cactus species whose low-temperature tolerance was examined using neutral red is *Coryphantha vivipara*, which is distributed from northern Mexico (30°N) to southern Canada (50°N; Nobel, 1981). Low temperature acclimation occurs in this species, as lowering the ambient air temperature from 30°C to -10°C in 10°C steps at weekly intervals causes the subzero temperature that eliminates stain uptake to decrease from -15°C to -22°C . Since the study with *C. vivipara*, the low-temperature tolerance and the low-temperature acclimation have been determined for 22 other species of cacti (Table 1).

Based on the elimination of uptake of neutral red by chlorenchyma cells, the lowest temperature tolerated by cacti for a subzero treatment of 1 h at an ambient day/night air temperature of 10°C/0°C ranges from -8°C to -26°C with an average of -13°C. The low-temperature acclimation per 10°C decrease in ambient day/night air temperatures ranges from 0.0°C to 3.7°C with an average of 1.0°C (Table 1). The half-time for the low-temperature acclimation for two species of cacti from north-central Argentina, Denmoza rhodacantha and Trichocereus candicans, is about 3 days (Nobel 1982). Low-temperature acclimation is important for tolerating subzero temperatures in the field, as species with the greatest low temperature tolerance when fully acclimated (-25°C and lower), such as C. vivipara and O. humifusa, show substantial low-temperature acclimation. Indeed, the substantial low-temperature acclimation of O. humifusa may be responsible for its wide distribution over 30 states in eastern and central United States plus the province of Ontario in Canada (Benson, 1982; Nobel and Loik, 1990). Other cacti that can tolerate very low temperatures include Oroya peruviana and Tephrocactus floccosus, which occur at 4700 m elevation in Peru (Keeley and Keeley, 1989), and O. fragilis, which can occur up to 58°N in western Canada, where winter temperatures can be below -40°C (Benson, 1982; Wieprecht, 1983).

MECHANISMS OF DAMAGE

Cacti as a group generally have cellular osmotic pressures of 0.5 to 1.2 MPa in the stems (Soule and Lowe, 1980; Nobel, 1988a). Because the freezing point depression is only 0.4°C to 1.0°C for such osmotic pressures, cacti cannot avoid freezing by equilibrium responses corresponding to such low osmotic pressures. However, cacti can supercool (Fig. 1), meaning that the stem temperature can decrease below the temperature that at equilibrium leads to freezing but with the stem water remaining in the liquid phase (no ice formation). For plants in general, supercooling is favored by small cell size, low amounts of intercellular air spaces, the absence of ice nucleators (or the presence of antinucleators), and relatively low tissue water content (Levitt, 1980). Also, the accumulation of certain solutes acting as cryoprotectants can favor a greater degree of supercooling.

Supercooling to -3°C to -12°C has been proposed to protect young plants of C. gigantea from freezing damage on cold slopes (Steenbergh and Lowe, 1976). Coryphantha vivipara cools to about -6°C, followed by an exothermic reaction (Fig. 1), as the tissue is heated by the release of the heat of fusion of water (Nobel, 1981). Based on the heat of fusion (the heat required to melt unit mass of ice) and the specific heat of water, the extent of the temperature rise corresponds to the freezing of about 10% of the stem water, presumably in an extracellular region. In particular, the ice crystals may be in the intercellular air spaces and, in any case, are outside the protoplast (because of lack of contrast and melting during specimen preparation, such crystals are difficult to observe with a light microscope). The ice crystals grow in size as water is distilled from within the protoplast and crystallizes onto them, thereby concentrating the cellular solutes left behind and raising the cellular osmotic pressure. Such dehydration results in the increasingly shrunken appearance noted for the protoplasts of C. vivipara at different stages along a cooling curve, such as Figure 1 (Nobel, 1981), and is known as "frost

plasmolysis." Evidently, the growing ice crystals do not enter the cell and are not the cause of cellular death. Rather, the intracellular dehydration leads to the death of the tissue, so freezing damage is thus analogous to a water stress injury (Fig. 1).

For *C. vivipara*, death of unacclimated plants occurs near -15°C , which corresponds to an osmotic pressure of 18 MPa. This is about 16 times greater than the osmotic pressure of the hydrated stem, which, if the osmotic pressure varies inversely with the water content, represents a loss of 94% of the cellular water at death. Other experiments indicate that a drought-induced dehydration of 91% of the stem water causes death of *C. vivipara* (Nobel, 1981). Likewise, loss of 96% of water by drought causes death for seedlings of *Ferocactus acanthodes*, compared with a predicted loss of 93% of intracellular water accompanying the growth of extracellular ice crystals that would cause death by frost plasmolysis for this species (Jordan and Nobel, 1981).

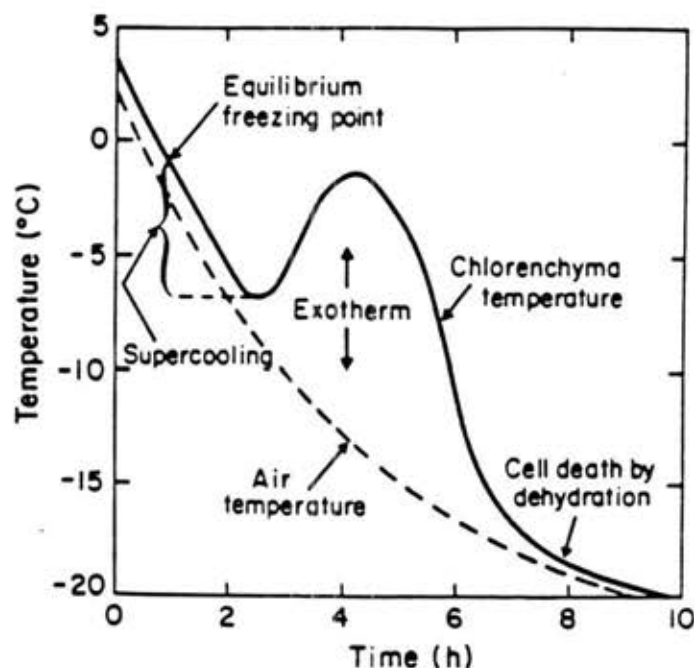


Figure 1. Generalized representation of the influence of gradual cooling of cactus stems on the chlorenchyma temperature. The stem supercools below the equilibrium freezing point, then an exothermic reaction occurs as ice crystals form extracellularly, followed by continued cooling accompanied by water distilling out of the cells and being incorporated into the growing crystals, eventually leading to the concentrating of cellular contents and death by cellular dehydration.

Table 1. Low-temperature tolerance and low-temperature acclimation of cacti. The low-temperature tolerance is the subzero temperature (determined graphically) at which the uptake of the vital stain is just eliminated following a 1 h treatment. The low-temperature acclimation indicates the lowering of such a temperature as the day/night air temperatures are lowered from 20°C/10°C to 10°C/0°C over a 1-week period. Data are adapted from Nobel (1982, 1984a, 1990) and Nobel and Loik (1990).

Species	Temperature just leading to elimination of stain uptake by chlorenchyma cells for plants maintained at 10°C/0°C	Low-temperature acclimation per 10°C decrease in day/night air temperatures
	(°C)	(°C)
<i>Carnegiea gigantea</i>	-13	0.5
<i>Coryphantha vivipara</i>	-24	1.7
var. <i>deserti</i>	-23	-
var. <i>rosea</i>	-26	-
<i>Denmoza rhodacantha</i>	-14	1.0
<i>Eriosyce ceratistes</i>	-14	0.8
<i>Ferocactus acanthodes</i>	-13	0.3
<i>F. covillei</i>	-11	0.0
<i>F. viridescens</i>	-10	0.3
<i>F. wislizenii</i>	-12	0.3
<i>Lophocereus schottii</i>	-11	0.5
<i>Opuntia bigelovii</i>	-11	0.8
<i>O. ficus-indica</i> (five accessions)	-9 to -12	0.2 to 1.4
<i>O. fuscicaulis</i>	-10	1.7
<i>O. humifusa</i> (two populations)	-13 to -15	3.6 to 3.8
<i>O. hyptiacantha</i>	-9	0.2
<i>O. megacantha</i>	-9	1.1
<i>O. polyacantha</i>	-21	-
<i>O. ramosissima</i>	-8	-
<i>O. rastrera</i>	-12	2.6
<i>O. streptacantha</i> (five accessions)	-8 to -14	0.6 to 2.7
<i>Pediocactus simpsonii</i>	-22	-
<i>Stenocereus thurberi</i>	-13	0.3
<i>Trichocereus candicans</i>	-11	1.0
<i>T. chilensis</i>	-12	0.9

FUTURE RESEARCH

One of the intriguing aspects of the freezing of cacti is supercooling. While in the supercooled state, certain platyopuntias still maintain net CO₂ uptake. For instance, *Q. humifusa* can have net CO₂ uptake at a chlorenchyma temperature of -4°C (Nobel and Loik, 1990), as does *Q. streptacantha* at -3°C (Nobel, 1990). As the low-temperature tolerance increases, the exotherms following supercooling of *Q. humifusa* represent the freezing of decreasing amounts of tissue water. Specifically, 3.7% of the stem water freezes during the exotherm for plants maintained at 25°C/15°C, 2.5% at 15°C/5°C, and 1.0% at 5°C/-5°C (Nobel and Loik, 1990). Higher temperatures for ice nucleation and different kinetics for the freezing also occur as the ambient temperatures are lowered. The interpretation of these phenomena with respect to the acclimation process awaits future research, as does a full understanding of the supercooling of cacti, including the mechanism of the nucleation of ice crystals.

Because cacti are apparently less susceptible to a particular freezing episode when they are dehydrated, many hobbyists and botanical garden personnel withhold water from cacti when winters with subzero temperatures approach. Also, under natural conditions the osmotic pressures of *Q. erinacea* and *Q. humifusa* increase during the autumn (Koch and Kennedy, 1980; Littlejohn and Williams, 1983), which may reflect a decreased soil and root hydraulic conductivity at the lower temperatures, leading to less water uptake by the plants. *Ferocactus acanthodes* tolerates 2°C lower subzero temperatures when dehydration increases the chlorenchyma osmotic pressure from 0.5 MPa to 1.3 MPa (Nobel, 1984b). Less water is available for freezing under the dehydrated condition, which could postpone the growth of the extracellular ice crystals that may eventually become large enough to disrupt the plasmalemmas. Alternatively, a lower water content may result in slower water movement out of the cells during freeze dehydration, resulting in less irreversible damage (Nobel and Loik, 1990). In any case, the exact mechanism by which dehydration prevents freezing damage is unclear. A related matter is the increase as winter approaches in soluble sugars and other solutes that might act as cellular cryoprotectants. The length of the photoperiod also changes as winter approaches, but the low-temperature tolerance of *C. vivipara* does not change as the photoperiod is varied from 3 h to 21 h (Nobel, 1983), and that of *F. acanthodes* is unchanged by photoperiods ranging from 4 h to 20 h (Nobel, 1984b). The effect on freezing tolerance of changes in light quality, which accompany changes in photoperiod under natural conditions, apparently have not been studied for cacti.

Besides the physiological as well as ecological interest in understanding the mechanism of freezing damage in cacti, considerable economic benefits could result from increasing the low-temperature tolerance of certain platyopuntias and other cacti cultivated for their fruit or their stems (used as a vegetable for humans and as forage or fodder for cattle and other animals; Hernandez Xolocotzi, 1970; Russell and Felker, 1987a). Indeed, platyopuntias such as *Q. ficus-indica* can have an annual aboveground biomass productivity exceeding that of conventional crops such as maize, rice, sorghum,

soybean, and wheat; moreover, because cacti utilize Crassulacean acid metabolism with its high water-use efficiency, such productivity can be achieved at a much lower water cost than that of conventional crops (Nobel, 1988a). However, cultivation of platyopuntias is often limited by low wintertime temperatures, such as is the case in Texas (Russell and Felker, 1987b). Breeding of cacti for low-temperature tolerance will be important in the future, as considerable genetic diversity with respect to low-temperature damage is evident, both among species and among accessions of a particular species (Russell and Felker, 1987b; Nobel, 1990). Also, tissue-culture and biotechnological approaches could be advantageously applied to cacti that have current or potential agronomic importance. Indeed, reducing low-temperature damage is crucial for expanding the cultivation of Q. ficus-indica and other economically important species in the United States, an expansion that is favored by the rising atmospheric CO₂ levels and the possibility of its accompanying global warming (Nobel and Garcia de Cortazar, 1990). Progress in understanding the mechanism of low-temperature damage of cacti at a cellular level coupled with subsequent breeding and biotechnological programs should lead to a substantial enhancement of the agricultural utility of these crops.

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