High-Temperature Responses of North American Cacti

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HIGH-TEMPERATURE RESPONSES OF
NORTH AMERICAN CACTI[1]

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Abstract. High-temperature tolerances of 14 species of North American cacti were investigated. A reduction in the proportion of chlorenchyma cells taking up a vital stain (neutral red) and reduced nocturnal acid accumulation were used as indicators of high-temperature damage. All species tolerated relatively high tissue temperatures, the mean maximum tolerance being 64°C, with an absolute maximum of 69° for two species of *Ferocactus*. Such tissue tolerances to high temperature may be unsurpassed in vascular plants.

Morphological features can affect tissue temperatures. Specifically, thin-stemmed species such as the cylindropuntias attain lower maximum temperatures under identical microclimatic conditions than do more massive species; they also tend to be less tolerant of high-temperature stress. Stem diameter changes of three species of columnar ceroid cacti along a Sonoran Desert latitudinal transect were previously attributed to adaptation to progressively colder temperatures northward. Such changes can also be interpreted as a morphological adaptation to high temperatures, particularly in the southern Sonoran Desert. Interspecific differences in high-temperature tolerance may account for distributional differences among other species; e.g., the coastal-sage-inhabiting *Ferocactus viridescens* was less tolerant of high temperature than were the three *Ferocactus* species that inhabit warmer desert regions.

Acclimation of high-temperature tolerances in response to increasing day/night air temperatures was observed in all 14 species, especially at higher growth temperatures. From 40° day/30° night to 50°/40°, the tolerable tissue temperatures increased an average of 6°. Half-times for the acclimation shifts were 1–3 d. Although cacti attain extremely high tissue temperatures in desert habitats, tolerance of high temperatures and pronounced acclimation potential allow them to occur in some of the hottest habitats in North America.

Key words: acclimation; cactus; CAM; desert; hardening; heat; Sonoran; stress; tolerance.

INTRODUCTION

Cacti in desert habitats attain some of the highest tissue temperatures experienced by vascular plants. Due to their massiveness, stems of cacti can exhibit considerable divergence from air temperature during the daytime. For instance, stems can be from 10° to 22°C above air temperature, resulting in tissue temperatures of up to 65° (MacDougal and Working 1921, Huber 1932, Gates et al. 1968, Smith 1978). Such temperatures are at the upper thermal tolerance limit so far recorded in vascular plants (Larcher 1980).

Although numerous observations have been made of the extremely high tissue temperatures exhibited by cacti, relatively little is known about their absolute thermal tolerances or their acclimation to increasing environmental temperature. These aspects were recently studied for *Opuntia bigelovii*, a cylindropuntia that is widely distributed in the southwestern United States and northern Mexico. When maintained at day/night air temperatures of 30°/20°, 50% of the stems survived at 52° and essentially none at 59° (Didden-Zopfy and Nobel 1982). Maximum tissue temperatures observed in the field for this species are ≈49° (Gibbs and Patten 1970, Smith 1978). This species, therefore,

appears to approach stressful tissue temperatures under summer conditions. However, acclimation of the high-temperature tolerance was found to be important in *O. bigelovii*, apparently allowing its survival during extremely hot periods (Didden-Zopfy and Nobel 1982).

Cacti have a relatively high heat capacity and a small surface-to-volume ratio, resulting in inefficient heat dissipation by convection (Gates and Benedict 1963). Morphological features such as size, stem orientation, spine coverage, and ribbing may ameliorate tissue temperature extremes by affecting energy exchange with the environment (Hadley 1972, Nobel 1978). Species of contrasting morphology would thus be expected to exhibit different tissue temperatures under identical microclimatic conditions.

Northern and upper elevational limits to the distribution of some cacti are affected by morphology and tissue tolerances to low temperature (Nobel 1980a, b). Distributional limits may also be affected by morphology and high-temperature tolerance. The primary objectives of this study were to determine tolerance to high temperature and the potential for acclimation to it, and to see what morphological characteristics different species of cacti possess that might alleviate excessive tissue temperatures. High-temperature effects on both tissue viability and nocturnal acid accumulation, the latter being an indication of CO_2 uptake by these crassulacean acid metabolism (CAM) plants, were

TABLE 1. Species studied and collection sites. Nomenclature follows Shreve and Wiggins (1964), except Beatley (1976) for *Coryphantha vivipara,* Munz (1974) for *Ferocactus viridescens,* and Gibson and Horak (1978) for *Stenocereus thurberi.*

Species	Site
Ceroid cacti	
Carnegiea gigantea	near Phoenix, Arizona (33°46′N, 112°41′W, 500 m)
Lophocereus schottii var. *schottii*	northern Sonora, Mexico (31°45′N, 112°57′W, 410 m)
Stenocereus thurberi	northern Sonora, Mexico (30°40′N, 112°6′W, 350 m)
Barrel cacti	
Ferocactus acanthodes var. *lecontei*	southern Nevada (35°34′N, 115°25′W, 860 m)
Ferocactus covillei	near Tucson, Arizona (31°59′N, 111°39′W, 1160 m)
Ferocactus viridescens	coastal southern California (33°13′N, 117°22′W, 40 m)
Ferocactus wislizenii var. *wislizenii*	near Tucson, Arizona (32°21′N, 111°2′W, 850 m)
Cylindropuntias	
Opuntia acanthocarpa subsp. *acanthocarpa*	Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California (33°39′N, 116°22′W, 220 m)
Opuntia bigelovii	Deep Canyon Desert Research Center (33°38′N, 116°24′W, 850 m)
Opuntia ramosissima	Deep Canyon Desert Research Center (33°39′N, 116°22′W, 220 m)
Platyopuntias	
Opuntia basilaris var. *basilaris*	Deep Canyon Desert Research Center (33°39′N, 116°22′W, 220 m)
Opuntia chlorotica	near Pinyon, California (33°37′N, 116°25′W, 1210 m)
Short cacti (under 15 cm)	
Coryphantha vivipara var. *deserti*	Mercury, Nevada (36°40′N, 116°1′W, 1110 m)
Mammillaria dioica	Deep Canyon Desert Research Center (33°39′N, 116°22′W, 220 m)

therefore systematically investigated in 14 morphologically and geographically diverse species of North American desert cacti. The relative tendency for acclimation of high-temperature tolerance in response to increasing ambient temperature was also determined for seven species. The observed tissue sensitivities to high temperature, the degree of acclimation, and the actual maximum temperatures each species experiences in its natural habitat will aid in the determination of the role of high temperature in the distribution of these cacti.

MATERIALS AND METHODS

Plant material

Fourteen species of North American cacti distributed partly or entirely in the Sonoran Desert (Shreve and Wiggins 1964) were utilized in this study (Table 1). Field-collected, mature plants were rooted in desert soil and maintained under greenhouse conditions. The plants were then transferred to environmental chambers with a 14-h day at 30° C daytime and 20° nighttime air temperature (approximating the average daily maximum/minimum air temperature from May through October for the northern Sonoran Desert). Stem tissue temperatures at 1 mm below the surface (near the center of the chlorenchyma) ranged from 2° to 4° above air temperature during the day to 1° below air temperature at night (determined with copper-constantan thermocouples 250 μm in diameter; stem surface tem-

peratures were generally within ± 0.2° of the measured tissue temperatures). Photosynthetically active radiation (400 to 700 nm, measured with a Lambda Instruments LI-190S quantum sensor) averaged 500 μmol· m^{-2}·s^{-1} on the stem apex (horizontal) and 300 μmol· m^{-2}·s^{-1} at midheight on the sides (vertical). Relative humidity in the chambers (measured with a WeatherMeasure H311 hygrothermograph) was 40 ± 10% during the day and 60 ± 10% at night. Windspeed at midheight on the stems (determined with a Lambrecht 641N hot-wire anemometer) averaged 0.3 m/s. Plants were watered weekly with 1/10 strength Hoagland number 1 solution plus micronutrients (Hoagland and Arnon 1950) so that the soil water potential near the roots averaged −0.2 ± 0.1 MPa (determined with Wescor PT 51-05 soil thermocouple psychrometers).

High-temperature treatment

The response of chlorenchyma tissue to high temperature was measured for each species by immersing stem pieces (sealed in plastic bags) in water baths maintained at various temperatures from 30° to 70° (±0.2°). After treatment for 1 h, the pieces were cooled to 5° (surface cooling rate of ≈ 1°/min) and then assayed 24 h later, when stain uptake was maximal. Three or four fresh sections of chlorenchyma tissue 1–2 cell layers thick (70 μm) were taken from at least three different areas of each sample. Staining was done with 0.3 mol/ m^3 (0.1% by mass) neutral red (3-amino-7-dimethyl-amino-2-methylphenazine [HCl]) in 7 mol/m^3

KH_2PO_4/Na_3PO_4 at pH 7.4 (Stadelmann and Kinzel 1972). For each test, 500 cells from the four cell layers just beneath the hypodermis were examined at a magnification of 150× using a Zeiss phase-contrast research microscope. Neutral red is accumulated in the vacuoles of cells with intact tonoplasts, and so it can be used as a measure of membrane integrity and cell viability (Kreeb 1977, Onwueme 1979). Since the primary effect of lethal temperatures on plant cells is often the disintegration of cellular membranes (Daniell et al. 1969), utilization of stain uptake is a suitable method for examining high-temperature tolerance.

Acclimation of high-temperature tolerance was investigated by maintaining 5–6 plants of each species under day/night air temperatures beginning at 12°/2°. After 10 d, the high-temperature tolerance of the chlorenchyma was tested, and then the day/night temperatures were raised by 10° (or as indicated) up to 60°/50°. The effect of high temperature on nocturnal acid accumulation was examined by exposing stem pieces to a series of high temperatures for 1 h at the beginning of the dark period, and then allowing them to remain under chamber conditions for the rest of the dark period. Acid levels were determined immediately after the temperature treatment and at the end of the dark period, utilizing three 0.66-cm² stem samples (from each of three different plants) that were ground with sand, boiled in 80 cm³ of distilled water for 5 min, and then titrated to an endpoint of pH 6.4 with 5 mol/m³ NaOH (Hartsock and Nobel 1976). The tolerance temperature was defined as the treatment temperature leading to 50% inhibition in the number of cells showing stain uptake or to 50% inhibition of nocturnal acid accumulation (Didden-Zopfy and Nobel 1982). Statistical comparisons among sample means were made by least significant difference tests.

Field observations

Maximum tissue temperatures were measured in situ on *Ferocactus acanthodes, Opuntia acanthocarpa,* and *O. basilaris* at the Philip L. Boyd Deep Canyon Desert Research Center of the University of California at 33°38′N, 116°24′W, 290 m elevation. For each species, two thermocouples were placed 1 mm beneath the epidermis to obtain the temperature of chlorenchyma tissue in specific locations on each of two plants.

Changes in stem diameter with latitude were examined, and the effects of the observed morphological changes on maximum stem temperatures were simulated. Measurements were made from Tucson, Arizona, through Sonora, Mexico, to northern Sinaloa, Mexico, for three ceroid cacti (*Carnegiea gigantea, Lophocereus schottii,* and *Stenocereus thurberi*) and two barrel cacti (*Ferocactus covillei* and *F. wislizenii*). All measurements were made on stems >0.3 m tall for the barrel cacti and >1 m tall for the ceroid cacti (diameters are reported only for the thicker, immature stems of *Lophocereus,* since they have higher temperatures

than the thinner, mature stems; see Nobel 1980a). The latitudinal transect has relatively constant summer precipitation, but the July temperatures increase southward (reaching a maximum near Hermosillo, Sonora) and then decrease further southward (Hastings and Humphrey 1969). Simulations of the effect of stem diameter on maximum stem temperatures were made with a thermal model previously validated for *Ferocactus acanthodes* (Lewis and Nobel 1977) and the three ceroid cacti (Nobel 1978, Nobel 1980a). The heat convection coefficients were scaled using the inverse square root of diameter (Nobel 1974). The measured stem diameters along the latitudinal transect were incorporated into the model for each species, utilizing climatic data obtained in the northern Sonoran Desert on 21 July 1976 (Lewis and Nobel 1977).

RESULTS

Seasonal variation in field high-temperature tolerance

Previous laboratory observations indicating high-temperature acclimation of *Opuntia bigelovii* (Didden-Zopfy and Nobel 1982) were reinvestigated under field conditions. The same methods were used to measure stain uptake in the field and the laboratory. High-temperature tolerance, measured by the temperature at which the number of chlorenchyma cells taking up stain decreased by 50%, was 55°C in July and 51° in November (Fig. 1). In other observations, the temperature for 50% inhibition of stain uptake was also 55° on 25 August 1981, and 51° on 8 January 1982. Thus, high-temperature acclimation apparently occurred during the hot summer months. The stems attained
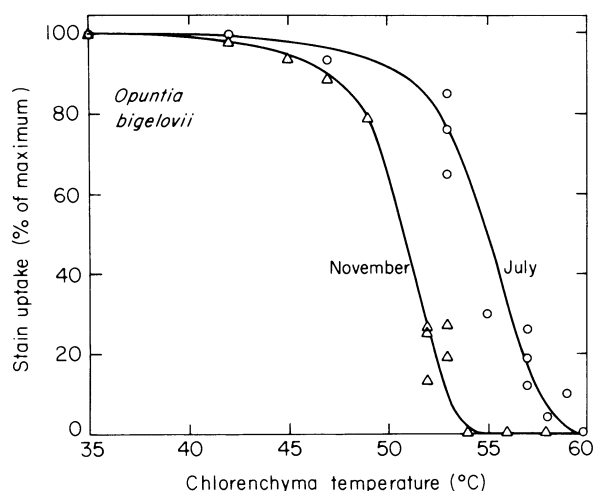

FIG. 1. Temperature dependence of the number of chlorenchyma cells taking up neutral red stain in terminal stems of *Opuntia bigelovii* at different seasons. Five hundred cells from ≈10 stem sections were examined in the field (Table 1) on 23–24 July (O) and 7–8 November (△) 1981 for each data point.
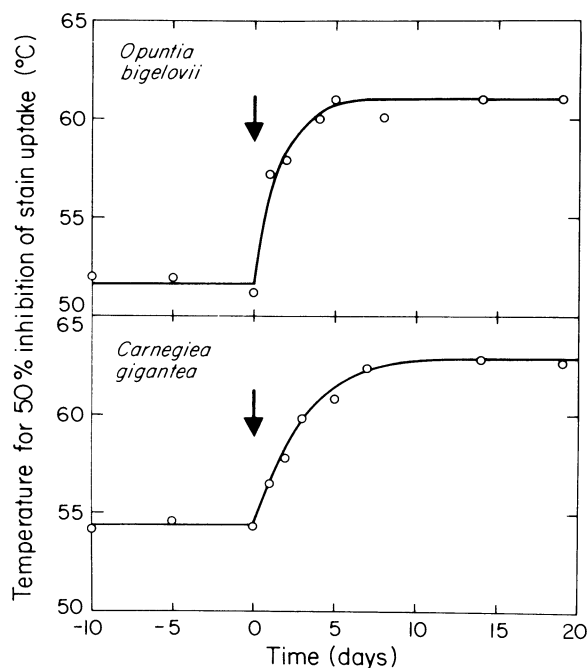
FIG. 2. The time course of high-temperature acclimation of *O. bigelovii* and *Carnegiea gigantea*. The temperature leading to a 50% inhibition of stain uptake was determined after transferring plants from 30°/20° to 50°/40° day/night air temperatures on day 0, as indicated by the arrows. Each data point represents the temperature at which a 50% reduction in the number of cells taking up stain occurred relative to control samples treated at 30°, as determined graphically from temperature-tolerance curves such as those in Fig. 1.

maximum tissue temperatures of 43° in July and 32° in November, and the mean daily maximum/minimum air temperatures for the week prior to measurements were 35°/27° in July and 21°/13° in November. Laboratory plants maintained under comparable conditions of day/night air temperatures of 40°/30° (tissue maximum of 43°) and 25°/15° had similar high-temperature tolerances of 56° and 51°, respectively (Didden-Zopfy and Nobel 1982), in good agreement with the field results.

Kinetics of high-temperature acclimation

The time course for high-temperature acclimation was measured in the laboratory by maintaining plants for 10 d at 30°/20° prior to changing to 50°/40° (Fig. 2). Acclimation of *O. bigelovii* to the temperature change was 50% complete after one day/night cycle and 90% complete after four cycles. For *Carnegiea gigantea*, acclimation was 50% complete after three day/night cycles and 90% complete after six cycles (Fig. 2). Plants were therefore allowed to equilibrate for 10 d at each day/night regime in subsequent acclimation studies.

Acclimation of ceroid cacti

Three species of ceroid cacti (*Carnegiea gigantea*, *Lophocereus schottii*, and *Stenocereus thurberi*) were

examined for changes in high-temperature tolerance under stepwise increasing day/night air temperatures (Fig. 3). All three species survived from 12°/2° to 50°/40°, but a further increase of the environmental temperatures to 55°/45° led to wilting, chlorosis, and eventual death. At 12°/2° and 50°/40°, maximal stain uptake was similar to that for the other growth temperatures, but nocturnal acid accumulation was markedly reduced.

The three species exhibited similar absolute tolerances and acclimation responses to the stepwise increased growth temperatures (Fig. 3). From 12°/2° to 30°/20°, stain uptake acclimated an average of 1.8° per 10° increase in growth temperatures, and nocturnal acid accumulation acclimated an average of 4.1° per 10° increase. At higher temperatures, acclimation was greater for stain uptake but fairly similar for nocturnal acid accumulation. For example, from day/night temperatures of 30°/20° to 50°/40°, stain uptake acclimated 4.4° per 10° increase in growth temperatures and nocturnal acid accumulation acclimated 5.0° per 10° increase (Fig. 3). At the highest growth temperatures, 50°/40°, the high-temperature tolerances averaged 64° for stain uptake and 57° for nocturnal acid accumulation.
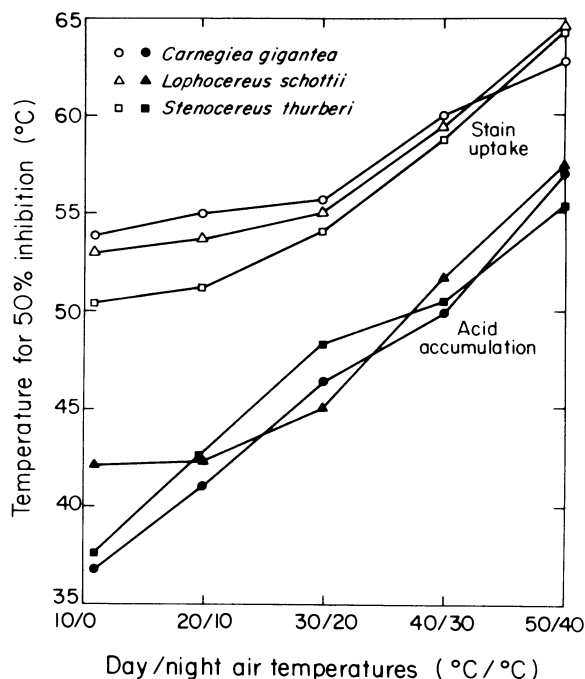
FIG. 3. High-temperature acclimation for three species of ceroid cacti. The tissue temperatures resulting in a 50% reduction in the number of cells taking up stain (open symbols) and acid accumulation (closed symbols) were determined graphically (see Fig. 1) after 10 d at each growth temperature, and then the day/night air temperatures were raised by 10° (or as indicated). The plotted means from four or five temperature tolerance curves had standard deviations <1° in all cases.
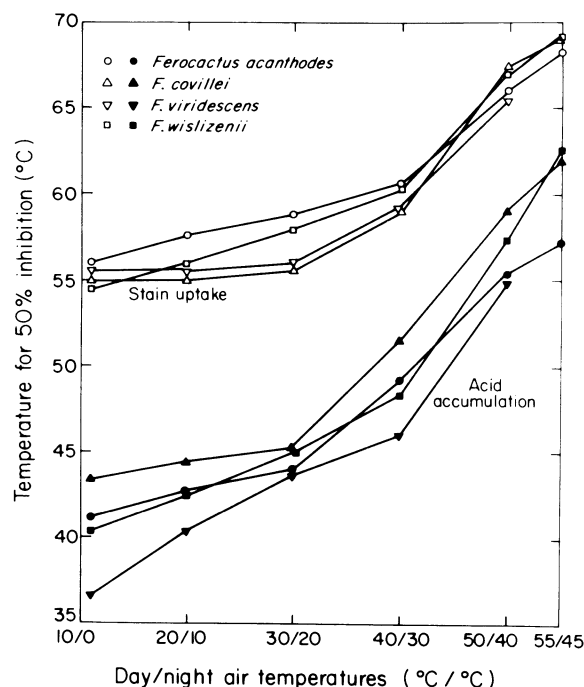
FIG. 4. High-temperature acclimation for four species of *Ferocactus*. Data were obtained as for Fig. 3.

Acclimation of barrel cacti

The general trends observed in high-temperature ac-
climation for the ceroid cacti were also found for four
Ferocactus species (Fig. 4). From 12°/2° to 30°/20°,
stain uptake and nocturnal acid accumulation accli-
mated an average of 1.0° and 2.2°, respectively, per 10°
increase in day/night temperatures. Acclimation was
greater from 30°/20° to 50°/40°, being 4.7° for stain
uptake and 6.1° for nocturnal acid accumulation per
10° increase in temperatures. In contrast to the ceroid
species, all four *Ferocactus* species except the coastal
one, *F. viridescens*, survived 1 wk at 55°/45° (60°/50°
led to desiccation of the stems and tissue death of these
three remaining species within 3 d). At the highest
growth temperatures indicated (Fig. 4), maximum tem-
perature tolerances for the *Ferocactus* species averaged
68° for stain uptake and 59° for nocturnal acid accu-
mulation, considerably higher than for the ceroid cacti.
The highest tolerances were obtained for *F. covillei* and
F. wislizenii, 69° for stain uptake and 62° for nocturnal
acid accumulation.

High-temperature tolerance of other cacti

Six other species of cacti, representing the cylindro-
puntias (*O. acanthocarpa* and *O. ramosissima*), the
platyopuntias (*O. basilaris* and *O. chlorotica*), and short
cacti (*Coryphantha vivipara* and *Mammillaria dioica*),
were examined for high-temperature tolerance at the
higher growth temperatures, 40°/30° and 50°/40° (Table

TABLE 2. Summary of temperatures for 50% decrease in
number of cells staining, for selected species of cacti. Data
are presented as mean ± SD for six temperature response
curves in each case. Plants were maintained at day/night
air temperatures of 40°/30° and 50°/40°C for 10 d before
measurements.

Species	Maintenance temperature	
	40°/30°	50°/40°
	Temperature for 50% inhibition of staining (°C)	
Cylindropuntias		
Opuntia acanthocarpa	53.9 ± 1.2	60.0 ± 1.9
O. ramosissima	54.6 ± 0.8	62.5 ± 0.9
Platyopuntias		
O. basilaris	57.3 ± 0.8	62.6 ± 0.7
O. chlorotica	56.7 ± 1.6	63.9 ± 1.1
Short cacti		
Coryphantha vivipara	58.7 ± 1.1	64.1 ± 1.5
Mammillaria dioica	59.5 ± 0.9	64.4 ± 1.3

2). The short cacti, which can have their whole stems
exposed to the very high temperatures near the ground,
had the highest heat tolerances, while the cylindro-
puntias had the lowest ($P < .05$). High-temperature
acclimation was similar for the three groups (Table 2).

Variation in high-temperature tolerance within individual stems

The possible differences in high-temperature toler-
ance in different parts of a plant were investigated in
three morphologically dissimilar species. For *Ferocac-
tus acanthodes* and *Opuntia basilaris*, a comparison of
east-facing and west-facing sides showed higher tem-
peratures and greater high-temperature tolerance of
chlorenchyma tissue on the west side of the plants (Ta-
ble 3; means for 50% inhibition were significantly dif-
ferent, $P < .05$ in all cases). For *O. acanthocarpa*, which
maintains green stems at or near the ground surface,
the maximum basal temperature was 2.0° higher than
at midheight and the high-temperature tolerance was
1.3° higher (Table 3; $P < .05$). Thus, in each species
examined, an increase in high-temperature tolerance
was observed in conjunction with increases in actual
maximum tissue temperatures.

Diameter influences on maximal temperatures

Stem diameter was examined along a north-south
transect in the Sonoran Desert for the three ceroid cacti
and two *Ferocactus* species, *F. covillei* and *F. wislizenii*.
For the three ceroid cacti, it decreased southward to
≈28°N (Table 4; $P < .05$), as has been previously ob-
served (Niering et al. 1963, Felger and Lowe 1967,
Nobel 1980a), and then increased ($P < .05$; the min-
imum mean stem diameters were at 28°48′N for *Car-
negiea*, 27°59′N for *Stenocereus*, and 27°38′N for *Lo-
phocereus*). In contrast, differences in mean stem
diameter with latitude did not occur for the two *Fer-
ocactus* species (Table 4).

TABLE 3. Variation in maximum tissue temperature and heat tolerance within the same stem for three species of cacti. Data were obtained at the Philip L. Boyd Deep Canyon Research Center on 8–9 July 1982 and are presented as mean ± SD ($n = 6$).

Species	Location on stem	Maximum chlorenchyma temperature (°C)	Temperature for 50% reduction in no. cells staining (°C)
Ferocactus acanthodes	east-facing, midheight	44.6 ± 0.4	58.2 ± 0.8
	west-facing, midheight	51.2 ± 1.0	60.2 ± 0.6
Opuntia basilaris	east-facing, midheight	48.6 ± 0.7	55.2 ± 1.0
	west-facing, midheight	50.6 ± 1.1	57.0 ± 1.3
Opuntia acanthocarpa	west-facing, midheight	43.1 ± 0.8	50.5 ± 0.7
	west-facing, base	45.1 ± 0.4	51.8 ± 0.9

Utilizing previously validated simulation models (Nobel 1978, 1980a), the effects of observed diameter differences on maximum (west-facing) stem temperatures were determined. Since variation in other morphological variables along the latitudinal gradient had relatively little effect on surface temperature, previously determined values were used in the simulations (Nobel 1978, 1980a), with only the diameter varied. Typical summer climatic data for the northern Sonoran Desert (maximum air temperature of 37°, maximum solar irradiance of 1020 W/m² were employed (see Lewis and Nobel 1977). Observed decreases in stem

TABLE 4. Diameter variations of three ceroid and two barrel cacti along a latitudinal transect in the Sonoran Desert. Data are from mature plants and are presented as mean ± SD (n = number of measurements). The maximum simulated midheight temperature, calculated utilizing climatic data typical of the northern Sonoran Desert in summer (Lewis and Nobel 1977), is given for each mean diameter.

Species	Location, elevation	Midheight diameter (cm) $\bar{x}$ ± SD	n	Maximum simulated midheight surface temperature (°C)
Carnegiea gigantea	32°10'N, 110°43'W, 970 m	46.0 ± 5.5	(20)	55.3
	30°40'N, 110°56'W, 840 m	39.1 ± 5.1	(15)	53.3
	28°48'N, 110°34'W, 490 m	32.4 ± 7.5	(14)	52.5
	27°59'N, 110°57'W, 160 m	34.8 ± 5.2	(14)	52.8
	27°9'N, 109°18'W, 450 m	38.1 ± 6.1	(14)	53.2
Lophocereus schottii	31°47'N, 113°2'W,* 430 m	14.3 ± 0.6	(18)	51.0
	30°42'N, 111°56'W,* 430 m	14.0 ± 0.8	(18)	50.9
	28°52'N, 110°45'W,* 310 m	11.8 ± 0.6	(18)	49.8
	27°59'N, 111°1'W, 10 m	9.7 ± 0.5	(18)	48.2
	27°38'N, 109°54'W,* 80 m	7.3 ± 0.7	(18)	45.4
	26°54'N, 109°25'W, 120 m	7.9 ± 1.0	(20)	46.2
Stenocereus thurberi	32°14'N, 112°48'W,* 540 m	15.1 ± 0.7	(18)	50.3
	31°29'N, 112°34'W,* 460 m	14.9 ± 0.6	(18)	50.3
	30°40'N, 110°56'W, 840 m	12.9 ± 0.8	(15)	49.9
	29°42'N, 111°2'W,* 560 m	12.4 ± 0.9	(18)	49.6
	28°48'N, 110°34'W, 490 m	10.9 ± 0.9	(15)	48.7
	27°59'N, 110°57'W, 110 m	10.5 ± 1.6	(20)	48.5
	27°7'N, 109°11'W, 250 m	11.6 ± 1.6	(30)	49.2
	26°54'N, 109°25'W, 120 m	12.3 ± 1.4	(24)	49.6
	25°59'N, 108°59'W, 120 m	12.4 ± 1.7	(23)	49.6
	25°19'N, 107°58'W, 150 m	12.6 ± 1.8	(15)	49.7
Ferocactus covillei	32°11'N, 112°10'W, 850 m	34.8 ± 4.8	(22)	49.7
	31°59'N, 111°39'W, 1220 m	36.4 ± 6.1	(15)	49.8
	30°36'N, 111°5'W, 760 m	37.4 ± 6.2	(13)	49.9
	28°49'N, 110°58'W, 260 m	35.5 ± 6.0	(15)	49.7
	27°59'N, 110°57'W, 90 m	36.2 ± 6.3	(15)	49.8
F. wislizenii	32°59'N, 111°22'W, 520 m	31.6 ± 7.0	(35)	49.4
	32°10'N, 112°46'W, 530 m	31.1 ± 5.3	(20)	49.4
	27°46'N, 109°53'W, 140 m	33.0 ± 6.6	(21)	49.5
	26°27'N, 109°4'W, 130 m	32.9 ± 6.2	(22)	49.5
	25°19'N, 107°58'W, 150 m	33.2 ± 4.7	(16)	49.6

* Diameter data for these sites from Nobel (1980a).

diameter of 30% for *Carnegiea,* 49% for *Lophocereus,* and 30% for *Stenocereus* resulted in simulated decreases in maximum stem temperatures of 2.8°, 5.6°, and 1.8°, respectively (Table 4). The increases in stem diameter and simulated maximum surface temperature in the southern part of each species' range were less than the northern increases, and resulted in increases in maximum simulated surface temperature of 0.7°, 0.8°, and 1.2° in *Carnegiea, Lophocereus,* and *Stenocereus,* respectively.

DISCUSSION

The high-temperature tolerance of most vascular plants is correlated with the maximum temperatures of their natural habitats (Alexandrov 1964, Larcher 1980), suggesting that cacti should be able to survive very high tissue temperatures. Indeed, the cacti studied here exhibited some of the highest temperature tolerances ever reported for vascular plants. At the 50°/ 40°C growth temperatures, the upper tolerance temperature (as measured by the temperature at which a 50% reduction in stain uptake, i.e., cell viability, occurs) averaged 61° for the cylindropuntias (Table 2; Didden-Zopfy and Nobel 1982); 63° for the platyopuntias (Table 2); 64° for the ceroid cacti (Fig. 3) and the short cacti (Table 2); and 66° for the barrel cacti (Fig. 4). Of the four barrel cacti, the species from the cooler, coastal habitat, *Ferocactus viridescens,* could not tolerate as high a temperature as the three desert-inhabiting species, 65° vs. 69°.

Most plants exhibit high-temperature acclimation, in which the tolerance of specific processes to high-temperature extremes increases with increasing environmental temperatures (Levitt 1980). This may reflect increased stabilization (or protection) of certain membrane-bound proteins (Alexandrov et al. 1970), or perhaps changes in membrane permeability due to changes in lipid composition (Pike and Berry 1980). For certain species, more negative osmotic potentials of the chlorenchyma are correlated with greater high-temperature tolerance (Levitt 1980), but this was not the case for *Opuntia bigelovii* (Nobel 1983). The previous laboratory observation of a pronounced high-temperature acclimation for *O. bigelovii* (Didden-Zopfy and Nobel 1982) was found to be widespread among cacti, occurring in all 13 of the other species examined in the laboratory (Figs. 3 and 4, Table 2), as well as for *O. bigelovii* in the field (Fig. 1). Also, plant parts exposed to higher tissue temperatures, such as tissues on the west-facing side or near the ground, tolerated higher temperatures (Table 3). The increase in high-temperature tolerance tended to be greater at the higher growth temperatures. From 40°/30° to 50°/40°, it increased 4.4° for the ceroid cacti, 5.2° for the short cacti, 6.3° for the platyopuntias, 6.7° for the barrel cacti, and 7.0° for the cylindropuntias, or an average of 5.9°. As well as ensuring survival during the hot summer months, this

high acclimation potential may be especially important in establishment of young plants.

Inhibition of photosynthesis due to high-temperature stress occurs at sublethal temperatures (Alexandrov 1964, Levitt 1980). This results in part from the greater susceptibility of the thylakoid membranes to high temperature compared to the cellular membranes (Schreiber and Berry 1972, Krause and Santarius 1975), and can lead to complete inhibition of photosynthesis 3° to 12° below the lethal temperature (Bauer et al. 1975, Berry and Björkman 1980). Cacti generally exhibit an optimal temperature for nocturnal CO_2 uptake near 10° to 20° (Nobel and Hartsock 1981), but the light-dependent photosynthetic reactions and dark respiration of cacti may function efficiently at relatively high temperatures (Szarek and Ting 1974, Gerwick et al. 1978). Furthermore, pronounced seasonal acclimation in the optimum temperature for CO_2 uptake has been observed in numerous species of cacti (Nisbet and Patten 1974, Nobel and Hartsock 1981), potentially resulting in net carbon gain in the warmest months of the year (Gulmon and Bloom 1979). As previously observed in *Opuntia bigelovii* (Didden-Zopfy and Nobel 1982), cacti also exhibit pronounced acclimation of nocturnal acid accumulation in response to high-temperature stress, confirmed here for ceroid and barrel cacti (Figs. 3 and 4). With increasing growth temperatures, the increase in the temperature at which a 50% inhibition in nocturnal acid accumulation occurred was similar to the increases in high-temperature tolerance as indicated by stain uptake. The upper tolerances of nocturnal acid accumulation averaged 57° for both the ceroid and the barrel cacti (at 50°/40° growth temperatures), which were ≈8° below the upper tolerances for cellular stain uptake in the two groups. For two of the desert-inhabiting *Ferocactus* species (*F. covillei* and *F. wislizenii*), the high-temperature tolerance of nocturnal acid accumulation reached 62° at 55°/ 45° growth temperatures, just exceeding the upper temperature limit of net photosynthesis in vascular plants of 55° to 61° (Bauer et al. 1975).

Plants could show adaptation to high-temperature stress morphologically. One such example could be a reduction in diameter. The thickness of the air boundary layer, and thus the resultant effectiveness of convective heat dissipation, depends on the square root of diameter for both cylinders (Nobel 1974) and spheres (Nobel 1975), and so diameter has an important influence on stem temperature. In this study the diameter of all three ceroid cacti decreased southward in the Sonoran Desert to ≈28°N. The simulations indicated that the decreases in stem diameter lowered the predicted maximum stem temperatures at midheight by 2° to 6° (Table 4). This latitudinal diameter change has previously been described as an adaptation to low temperatures at the northern limits of certain ceroid cacti (Niering et al. 1963, Felger and Lowe 1967), with the diameter changes actually allowing the extension of

specific ranges northward (Nobel 1980a). Present observations of slightly increased stem diameters below ≈28°N strongly suggest that adaptation to high temperature also plays an important role in the observed diameter changes. The warmest mean July air temperatures, and presumably maximum annual air temperatures, in the Sonoran Desert occur near Hermosillo (29°N; Hastings and Humphrey 1969). Further south, the Sonoran Desert gradually gives way to thorn forest, a less open habitat with reduced July air temperatures (Shreve and Wiggins 1964). In this region slightly increased stem diameters were observed in each ceroid species, particularly in *Stenocereus*. Thus, the observed minimum in stem diameters near the hottest part of the Sonoran Desert may aid in survival. A maximum air temperature of 37° was used in the simulations of stem temperature. However, air temperatures of up to 48° are not uncommon in the Sonoran Desert, which would result in maximum tissue temperatures of >60°, thus approaching tolerance limits. Under very hot conditions, the predicted reduction of maximum stem temperature by 2° to 6° may be quite important in preventing heat damage of the tissue, just as increases in the minimum apical temperatures of cacti by <1° on very cold days can prevent freezing damage in several species of cacti (Nobel 1980a, b).

Cacti are able to survive the high-temperature stress of desert environments because of both metabolic and morphological properties. Cacti with smaller diameters, such as the cylindropuntias, tend to attain lower maximum tissue temperatures than the larger ceroid and barrel cacti under identical microclimatic conditions. In addition to being massive, barrel cacti are relatively short and can be markedly influenced by ground temperatures, which can be quite high. Consistent with this, the barrel cacti exhibited the highest temperature tolerance for both nocturnal acid accumulation and cellular integrity, and the cylindropuntias the lowest. The degree of high-temperature tolerance of at least certain morphologically dissimilar species of cacti thus matches the maximum tissue temperatures experienced in the field. However, nearly all cacti are relatively massive compared to typical leaves, and also they lack appreciable daytime transpirational cooling because of their CAM metabolism. Thus, cacti exhibit very high tissue temperatures during times of high air temperature and high solar insolation. Morphological adaptations, although important in some cacti and essential in most desert plants, are largely ineffective in alleviating such high tissue temperatures. To counteract this, cacti exhibit very high heat tolerance levels, particularly the more massive and/or short ones, which may be unsurpassed among the vascular plants (see Larcher 1980, Kappen 1981). Furthermore, the potential for high-temperature acclimation of cacti in response to increasing growth temperatures is extremely great, especially at the higher growth temperatures, where it was 4° to 7° per 10° increase in growth

temperature. Their high-temperature tolerance and substantial acclimation potential allow cacti to occur in some of the hottest habitats in North America, and thus they apparently are not greatly limited in their geographical distributions by high-temperature stress.

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