Morphology, Nurse Plants, and Minimum Apical Temperatures for Young Carnegiea gigantea

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MORPHOLOGY, NURSE PLANTS, AND MINIMUM APICAL TEMPERATURES FOR YOUNG CARNEGIEA GIGANTEA

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The northern limit of *Carnegiea gigantea* (Engelm.) Britton and Rose apparently depends on minimum apical temperatures. Diameters, apical spine coverage, and effects of nurse plants on incoming long-wave (infrared [IR]) radiation, all of which affect apical temperatures, were therefore determined for stems of *C. gigantea* up to 4 m tall at four sites along a north-south transect in Arizona. A simulation model indicated that the increase in diameter accompanying stem growth raised the minimum apical temperature more than 3 C. Thus, plants with the shortest stems would be expected to be the most vulnerable to freezing damage; indeed, freezing damage on stems <0.5 m tall without nurse plants was fairly common at the colder sites. Nurse plants obstructed a greater portion of the sky for *C. gigantea* at the colder sites; e.g., the effective environmental temperature for IR radiation at such locations was raised more than 10 C for stems under 1 m tall. If the northern limit of *C. gigantea* reflects wintertime survival of juveniles, nurse plants could extend the range by offering some protection against freezing.

Introduction

The giant cactus or saguaro (*Carnegiea gigantea*) extends the farthest northward of any member of the ceroid subtribe, a distinct group of the Cactaceae containing the tall columnar cacti. Its northern range and elevational limit may be determined by minimum tissue temperatures. Shreve (1911) suggested that *C. gigantea* was restricted to those regions where freezing of the tissue did not persist for 24 h, thus emphasizing the importance of infrequent cold periods for the populations. Niering, Whittaker, and Lowe (1963) indicated that *C. gigantea* increased in diameter from the southern to the northern part of its range. Computer simulations show that the increase in diameter from 33 cm at 30°25′ N to 44 cm at 34°50′ N for mature plants would increase the minimum surface temperature near the apical meristem by 2 C, which could help extend the range northward (Nobel 1980). A severe freeze in 1962 killed 30% of the *C. gigantea* taller than 3.5 m above 1,200 m but only 10% near 1,000 m (Niering et al. 1963), demonstrating the effect of temperature on the elevational distribution. Very little is known about the surface temperatures experienced by seedlings and juveniles.

Here the interplay among morphology, microclimate, and minimum apical temperatures was investigated for juvenile and young adult plants of *C. gigantea*. The stem apex was chosen because calculations using an energy budget model indicate that minimum surface temperatures generally occur there, due to the net loss of infrared (IR) radiation to cold nighttime skies (Lewis and Nobel 1977). This is supported by observations that freezing damage on columnar cacti often occurs at the stem apex (Turnage and Hinckley 1938; Benson 1974; Nobel 1980). Also, the apical meristem is involved in stem growth, and thus the apex is a very critical region.

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To evaluate the effects of morphological or microclimatic changes during development, a computer model was employed that predicted the apical surface temperature of *C. gigantea* within about 1 C of that measured hourly over a 24-h period (Nobel 1978). Using the validated model, the effect of diameter, spine shading, and the presence of nurse plants on the minimum apical temperature could be examined quantitatively for plants up to 4 m tall. Emphasis was placed on nurse plants, which so far have not been quantitatively examined for their effects on minimum apical temperatures.

Material and methods

Carnegiea gigantea (Engelm.) Britton and Rose (Cactaceae) was investigated at four sites in Arizona where all age classes were represented, from seedlings to large dead skeletons. Terminology follows Steenbergh and Lowe (1976), who defined juvenile as the postseedling stage (about 1 yr, 5 mm tall) up to the initial flower-bearing height (about 32 yr, 2 m tall). Freezing damage was identified by apical patches of necrotic tissue as described by Steenbergh and Lowe (1976).

The thermal model predicted the temperature at various locations on the stem surface to 0.1 C, using an iterative procedure that was terminated when the temperature was within 0.05 C of the previous iteration (Nobel 1980). The environmental data consisted of hourly microclimatic measurements (direct and diffuse shortwave radiation, long-wave radiation, wind speed, air temperature, relative humidity, and soil temperatures) made over a 24-h period at the Kofa Game Range near Quartzite, Arizona, where the model was field validated for *C. gigantea* (Nobel 1978). To incorporate effects of nurse plants, the incoming long-wave radiation previously used in the model for an exposed plant was replaced by that determined for plants in the present study. This long-wave flux was equated with σT_{env}^4, where σ is the Stefan-Boltzmann constant and T_{env} is the effective environmental temperature for IR radiation. T_{env} was measured with an Eppley PIR pyrgeometer placed horizontally (facing upward) at the stem apex and checked with a Barnes Engineering PRT-10 IR field thermometer.

The apical region was defined as the central 2% of the hemispherical top (LEWIS and NOBEL 1977). Apical spine shading was estimated by comparing the apical region of each stem with a graded series of apical spine drawings of precisely known shading. The heat-convection coefficient was based on that used previously in the model (LEWIS and NOBEL 1977; NOBEL 1978) but scaled for stems of various sizes by making it proportional to the inverse square root of diameter (NOBEL 1974).

Results

The effects of nurse plants on T_{env} and the occurrence of freezing damage for exposed and protected juveniles under 0.5-m stem height were examined at four Sonoran desert sites in Arizona (table 1). Extrapolations from the closest U.S. Weather Bureau stations for 1931 through 1960 gave 0.1 C as the mean monthly minimum January temperature for the Wikieup site, 2.5 C for White Tanks County Park, 1.2 C for Saguaro National Monument, and 3.4 C for the Organ Pipe Cactus National Monument site (U.S. WEATHER BUREAU 1955, 1964). More freezing damage on *Carnegiea gigantea* was observed at the colder sites (Wikieup, Saguaro National Monument) than at the two warmer sites. Also, nurse plants for *C. gigantea*, mainly *Cercidium microphyllum* (Torr.) Rose and Johnston, were more common at the colder sites, often leading to increases greater than 10 C in T_{env} (table 1). The nurse-plant influence decreased as the stems became taller.

Stem diameter increased and apical spine shading decreased with stem height. At Wikieup, where the lowest air temperatures would be expected because of its latitude and elevation, the mean diameter increased from 11 cm for the 0.0–0.5-m height class to 42 cm for the 3.5–4.0-m class; the mean apical spine shading decreased from 84% to 15% for these two height classes (fig. 1). A similar decrease in apical spine shading with increasing height was observed for *Pachycereus pringlei* (S. Wats.) Britton and Rose in Sonora, Mexico, at 30°26′ N, 112°27′ W, 290 m; it went from 63% ± 8% on eight stems 0.5–1.2 m tall to 6% ± 4% on 11 stems 4.0–5.0 m tall. Another parameter that can greatly influence apical temperatures is the apical pubescence (NOBEL 1978, 1980), but its depth did not change significantly with stem height or between sites, averaging 8.5 ± 1.1 mm for *C. gigantea*.

The surface temperatures of the stem were predicted hourly over a 24-h period with the computer model, using microclimatic and morphological parameters previously determined for *C. gigantea* (NOBEL 1978). The model was modified to include the effect of nurse plants on the incoming IR irradiation, the diameters, and the apical spine shading measured at Wikieup for height classes at 0.5-m intervals (table 1, fig. 1). The minimum apical temperature under field conditions increased from 9.0 C for the

TABLE 1

EFFECTS OF NURSE PLANTS AND FREEZING DAMAGE FOR CARNEGIEA GIGANTEA

	INCREASE IN T_{env} (C)			
HEIGHT CLASS (m)	Wikieup (34°36′ N, 113°28′ W, 845 m)	White Tanks County Park (33°31′ N, 112°32′ W, 390 m)	Saguaro National Monument (west) (32°16′ N, 111°13′ W, 735 m)	Organ Pipe Cactus National Monument (31°54′ N, 112°52′ W, 405 m)
0.0–0.5	16±7 (19)	3±3 (10)	11±8 (15)	7±4 (13)
0.5–1.0	11±6 (28)	1±1 (24)	6±4 (19)	3±3 (21)
1.0–1.5	9±5 (12)	0±1 (12)	5±5 (12)	4±4 (13)
1.5–2.0	6±5 (11)	1±1 (13)	1±1 (11)	1±2 (11)
2.0–2.5	3±4 (11)	0±0 (12)	0±0 (10)	0±0 (9)
2.5–3.0	0±0 (10)	0±0 (11)	0±0 (11)	0±0 (11)
3.0–3.5	0±0 (10)	0±0 (9)	0±0 (8)	0±0 (12)
Freezing damage:				
Exposed	4 out of 7	0 out of 11	3 out of 13	0 out of 15
Protected	2 out of 21	0 out of 3	0 out of 12	0 out of 5

NOTE.—Effective environmental temperatures for IR radiation (T_{env}) were determined for the vertically upward hemisphere above stems of various heights on April 4–7, 1979; T_{env} above the stems minus T_{env} at exposed locations (where it averaged 34 C below air temperature) are presented as mean ± SD followed by the number of measurements in parentheses. Freezing damage was noted on June 1–3, 1979, for stems up to 0.5 m tall that were exposed (less than 2 C increase in T_{env} at stem apex caused by nurse plants) or protected (greater than 10 C increase in T_{env} due to nurse plants). Figures in parentheses under locations are latitude, longitude, and elevation, respectively.

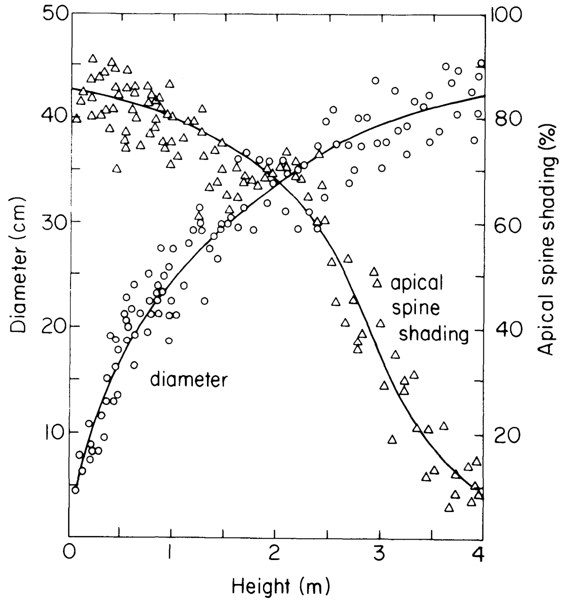

FIG. 1.—Diameter at midheight and apical spine shading for *Carnegiea gigantea* of various heights. Data were obtained on April 6, 1979, near Wikieup, Arizona (see table 1).

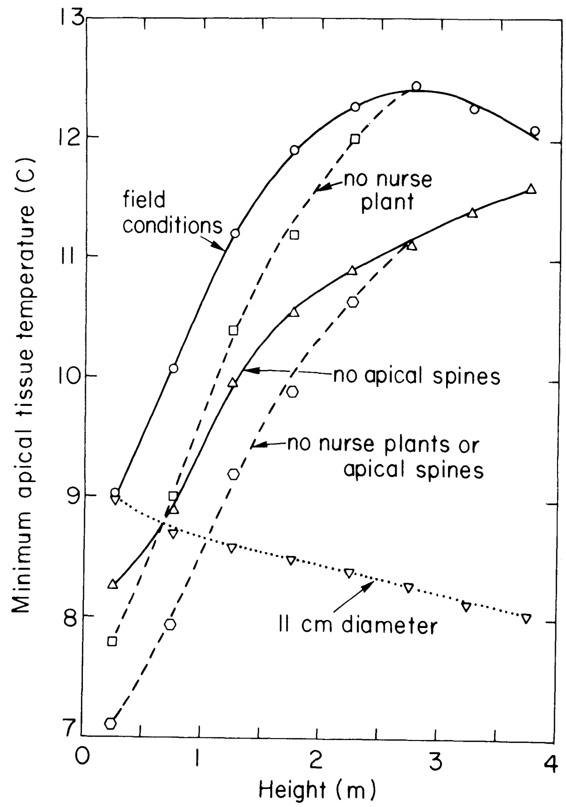

FIG. 2.—Simulated minimum apical surface temperatures for *Carnegiea gigantea* in various height classes. Conditions were as described for April 20, 1977 (NOBEL 1978), except using the height, diameter, apical spine shading, and T_{env} measured at Wikieup ("field conditions"). The absence of nurse plants was simulated by using T_{env} for exposed locations, and the absence of apical spines was simulated by setting the spine shading equal to zero at the apex.

shortest height class to 12.4 C as the stem height was increased to 3 m, and then it decreased for taller plants (fig. 2). The decrease was caused by the decreasing apical spine shading with height (fig. 1), since the minimum apical temperature monotonically increased with height in the simulated absence of apical spines (fig. 2).

The presence of nurse plants increased the minimum apical surface temperature more than 1 C for the smallest height class and continued to have a substantial effect on stems up to about 2 m tall. No effect occurred on plants above 2.5 m, since T_{env} was not affected by nurse plants for the taller stems (table 1). When the diameter was kept constant in the simulations at the 11-cm value for the lowest height class (0.0–0.5 m), the minimum apical temperature progressively decreased with increasing height (fig. 2), reflecting the decreasing apical spine coverage and loss of nurse-plant protection as the stem becomes taller.

Discussion

Nurse plants increase the survival of seedlings and juveniles of *Carnegiea gigantea*. They can protect the young plants from high temperatures (SHREVE 1931; TURNER et al. 1966; DESPAIN 1974), reduce water loss (TURNER et al. 1966), and help avoid consumption by rodents or lagomorphs (NIERING et al. 1963; STEENBERGH and LOWE 1969). The present results demonstrate that nurse plants lessen net IR loss to the sky for *C. gigantea* juveniles and, therefore, may protect the meristem from freezing damage. Similar conclusions were reached by STEENBERGH and LOWE (1976), who found that freezing survival of transplanted 36-mo-old (1.1 cm tall) and 42-mo-old (2.0 cm tall) *C. gigantea* increased from 58% in the open to 70% under *Cercidium microphyllum*. STEENBERGH and LOWE (1977) also pointed out the importance of nurse plants for winter survival at the northern extensions of the range of *C. gigantea*.

The increase in T_{env} by nurse plants was greater at the colder field sites (table 1), where exposed juvenile plants had much more freezing damage than at the warmer sites. Factors other than nurse plants can also influence the net IR exchange. Rocky habitats have proved effective for seedling establishment of *C. gigantea* (STEENBERGH and LOWE 1969) and may cause part of the exposure to the cold nighttime sky to be replaced by an IR source at a higher T_{env}. Freezing damage to seedlings of *C. gigantea* at 32°10′ N, 110°43′ W, 970 m in 1965 and 1966 was greatly reduced in rocky microhabitats compared with adjacent flat regions (STEENBERGH and LOWE 1969). As the distance from rocks increased, winter survival of young *C. gigantea* increasingly depended on nurse plants (STEENBERGH and LOWE 1977).

The present results indicate that the seedling and juvenile stages of *C. gigantea* have lower apical temperatures than adult plants 2–4 m tall under the same environmental conditions. At Wikieup, apical spine shading had nearly as much influence on the minimum apical temperatures as did nurse plants. Stem diameter had even more effect on thermal relations. Its increase with development greatly increased the minimum apical temperature (fig. 2). The diameter increase more than offset the thermal effects of the decline in apical spine shading (fig. 1) or loss of nurse-plant protection (table 1) as the stems grew taller.

Because of their lower temperature, shorter plants should be more vulnerable to freezing damage. Two catastrophic freezes at Saguaro National Monument (1962 and 1971) killed 15% of natural populations of *C. gigantea* under 0.5 m tall and only 2% that were 0.5 to 3.8 m tall (STEENBERGH and LOWE 1976). KINRAIDE (1978) suggested that the northern range boundary of the cactus *Opuntia imbricata* (Haw.) DC. in Colorado reflected the temperature sensitivity of seed germination or seedling establishment, since transplanted adult *O. imbricata* could survive north of the natural boundary. Likewise, the northern limit of *C. gigantea* may be set by a low temperature vulnerability of an early stage. On the other hand, a very infrequent cold spell (once every 50 yr or so) may affect the whole population and thus limit the northern range of these plants, which can live up to about 200 yr (SHREVE 1910; HASTINGS and ALCORN 1961). In either case, the thermal protection of the apical meristem by nurse plants and spines can give *C. gigantea* juveniles a greater chance to survive low temperatures, which could extend the northern limit of this cactus.

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