

ORIENTATION AND SLOPE PREFERENCE IN BARREL CACTUS (*FEROCACTUS ACANTHODES*) AT ITS NORTHERN DISTRIBUTION LIMIT

James Ehleringer¹ and Donna House¹

ABSTRACT.— Microsite distribution and diurnal tissue temperature fluctuations were measured in *Ferocactus acanthodes* (barrel cactus) at its northern distribution limit in the Beaver Dam Mountains of southwestern Utah. At this location, barrel cacti were limited to south-facing slopes. Orientation (azimuth and angle) of both the cactus stem and of the apical region at the top of the cactus were nonrandom, strongly facing south. The potential adaptive significance of this orientation in minimizing apical meristematic tissue damage under low wintertime conditions and minimizing high temperature damage under summertime conditions is discussed.

Barrel cactus (*Ferocactus acanthodes* (Lemaire) Britt. and Rose) is a globular-columnar cactus common to the warm desert regions of southwestern North America (Shreve and Wiggins 1964, Benson 1982). It is commonly found on rocky, well-drained slopes. Overall, the distribution of this species is from north-eastern Baja California in the south to the lower slopes of the Beaver Dam Mountains, Utah, in the north. Little is known about the factors limiting the distribution of this species, although Nobel (1980a) has suggested that *F. viridescens*, a small globular species, is limited to warmer sites than *F. acanthodes* because of its smaller size and greater heat loss characteristics.

Low wintertime temperatures can be an important factor limiting the distributions of many cacti (Shreve 1911, 1914; Turnage and Hinckley 1938). Osmotic water potentials of Sonoran Desert cacti range from -0.4 to -1.8 MPa (Walter and Stadelmann 1974), which will lower the freezing point less than 1 C. Minimum temperatures on the slopes of the Beaver Dam Mountains are often below freezing, and 24-hour periods of subfreezing temperatures are rare, but known to occur (U.S. Weather Bureau Records). Thus, freezing tissue temperatures would appear to be possible at the northern distribution limit of the barrel cactus.

The purpose of this study was to investigate factors influencing the distribution of *F. acanthodes* at its northern distribution

limit. To do this, we measured the relationships between plant density and micro-distribution as related to wintertime solar radiation heating and the diurnal tissue temperature fluctuations in the winter and summer seasons.

METHODS AND MATERIALS

The study site was on the southwestern slopes of the Beaver Dam Mountains in an area within 1 km of Castle Cliffs (lat. 37°04' N, lat. 113°52' W). The mean elevation of the sites sampled was approximately 1250 m. *Ferocactus acanthodes* (Lemaire) Britt. & Rose was studied in situ on the rocky slopes where they occur in the transition zone between the Great Basin and Mohave Desert vegetation types. This transition community was dominated by *Larrea divaricata*, *Coleogyne ramosissima*, *Krameria parviflora*, *Prunus fasciculata*, *Opuntia acanthocarpa*, and *Yucca brevifolia*.

Cactus tissue temperatures were measured at a depth of 2–3 mm below the epidermal surface using 24-gage copper-constantan thermocouples. Air temperature at 50 cm was measured with a 24-gage copper-constantan thermocouple shielded to reduce radiation errors. All temperature data were sampled at one-minute intervals using a portable micrologger (model CR21, Campbell Scientific, Logan, Utah) and averaged over a 60-minute period.

¹Department of Biology, University of Utah, Salt Lake City, Utah 84112.

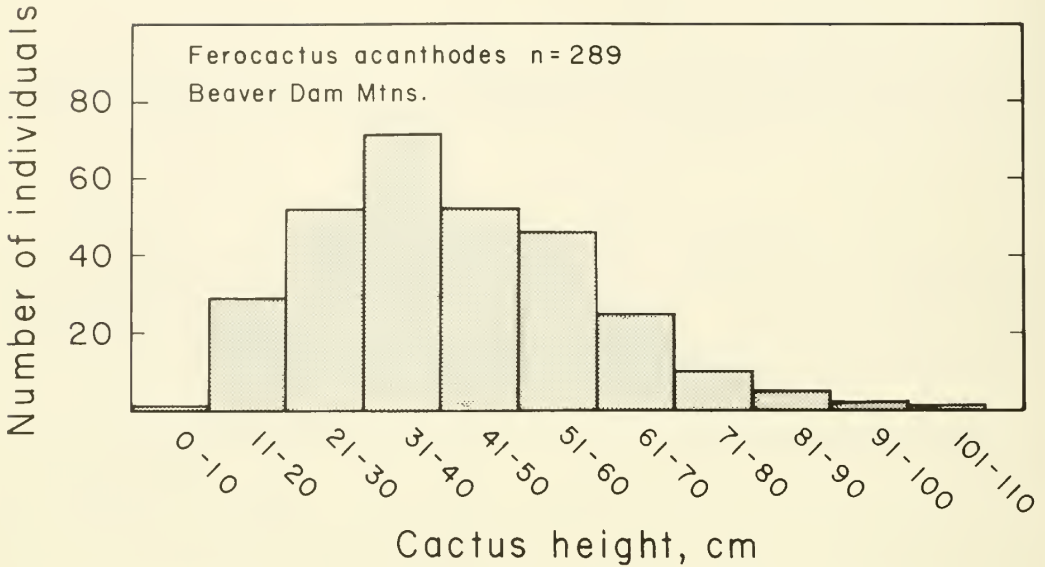


Fig. 1. Frequency histogram for height of *Ferocactus acanthodes* individuals in the Castle Cliffs population in the Beaver Dam Mountains, Utah.

Orientation of the barrel cactus and of the slopes were determined by measuring the azimuth and the inclination. Azimuth was measured with a compass to the nearest 5 degrees and corrected for magnetic deviation from true north. In expressing azimuth data, zero is due south, east is -90° , and west is $+90^\circ$. Inclination was measured with an inclinometer to the nearest 5 degrees, with a horizontal surface being 0° . Mean azimuths and angular dispersion were calculated trigonometrically as described by Zar (1974). Angular dispersion is used as a measure of the variance about the mean angle. Angular dispersions range from a maximum dispersion of 0 to a minimum dispersion of 1, with maximum dispersion being refined by a perfectly uniform distribution of angles around the circle (and an undefined mean angle) (Zar 1974).

In measuring the orientation of the cactus, two separate sets of measurements were collected. First, the tilt or orientation of the cactus body was measured. Second, the orientation of the apical region at the top of the cactus, which is planar, was also measured.

Calculations of the amount of direct solar radiation incident on a slope were made using equations available in Campbell (1977) and List (1966).

Barrel cactus densities were measured on slopes with different orientations. All slopes within the area were sampled, but data are presented for only those slopes having barrel cacti. For these data, the slope area sampled was determined by the size of the slope that had a uniform orientation and varied in area from 100 m^2 to 2800 m^2 .

RESULTS

Barrel cactus height at this site, which is the northern distribution limit for the species was not uniform (Fig. 1). Plant height varied from 10 cm to 107 cm, with the mode being 31–40 cm. There was no difference between the height distributions of barrel cactus with neighboring plants and those without neighboring plants, and therefore the two distributions were lumped. The height distribution was skewed to the left, and only 15% of the plants were taller than 60 cm. For the most part, the smaller plants were globular. The larger the cactus was, the more columnar was its shape. Diameter was only correlated with height for the smaller individuals. In larger cactus, the diameter was essentially constant. As a consequence, 88% of the plants had diameters 20–39 cm.

Orientation of the cactus was determined by measuring the angles and azimuths of the

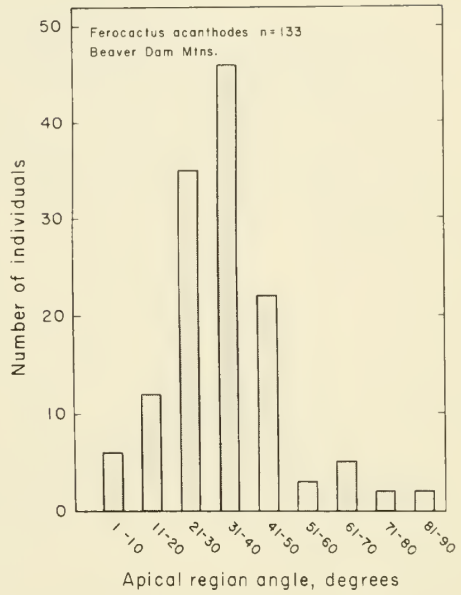
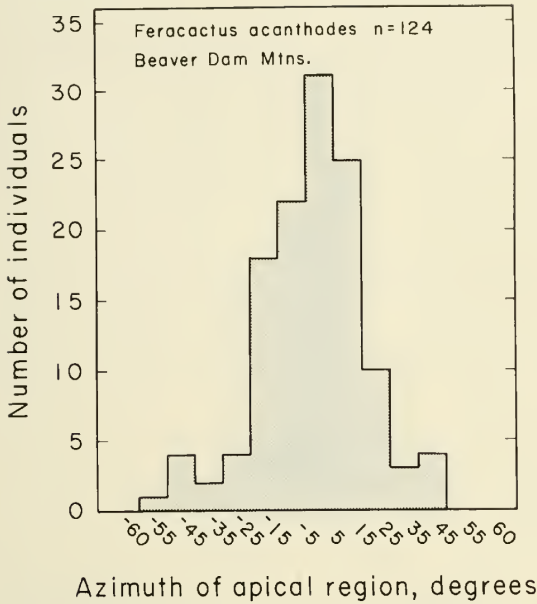


Fig. 2. Frequency histogram for azimuth direction of the apical meristematic region of *Ferocactus acanthodes* in the Castle Cliffs population in the Beaver Dam Mountains, Utah. South is 0°, east is -90°, and west is +90°.

Fig. 3. Frequency histogram for inclination of the apical meristematic region of *Ferocactus acanthodes* in the Castle Cliffs population in the Beaver Dam Mountains, Utah.

apical region and of the entire body. There was a strong tendency for the apical region of the cactus to face south mean azimuth of 5.7° and a dispersion of 0.88 (Fig. 2). In fact, 77% of the apical regions were facing within 15° of due south. There was also a strong tendency for the body of the cactus to tilt from the vertical. The mean azimuth direction of the tilt was 4.8° with a dispersion of 0.82 (n = 124), which again was in effect facing south. The mean angle of the apical region plant was 33.8° ± 1.3° (Fig. 3). There were 35% of the angles in the 31°-40° range and 76% 21°-50°. Body angles of the entire cactus showed essentially the same variation as the angles of the apical region plane and averaged 47.5° ± 2.3°.

As a consequence of their large mass and nonrandom orientations, cactus tissue temperatures were above air temperatures for much of the time, and the diurnal variation in tissue temperatures was orientation specific. Figure 4 shows the diurnal course of air and tissue temperatures in the winter and summer seasons. Although cactus tissue temperatures were correlated with air temperatures, there was a time lag for this response and the response was very much dependent

on a consideration of azimuth orientation. Tissue temperatures on the east side of the cactus warmed quickly after sunrise, peaking before noon and slowly declining throughout the remainder of the day. Tissue temperatures on the west side of the cactus exhibited an almost opposite response, with temperatures peaking in the late afternoon (data not presented). Tissue temperatures on the apical region and the south-facing cactus tissues tracked air temperature changes during the summer, but greatly exceeded air temperatures during the winter, when the solar elevation angle was lower.

An interesting feature of the temperature data was that in the winter apical region and south-facing tissue temperatures were much warmer during the day than those of the east-west facing tissues. The opposite pattern was observed in the summer. This pattern is explained by the changes in the declination of the sun between the two seasons. In the winter, when the sun was low in the sky, the apical region and south-facing tissue received more direct solar radiation and therefore heated more during the day. In the summer months, when the sun was higher overhead, it was the east-west-facing tissue that received greater intensities of solar radiation.

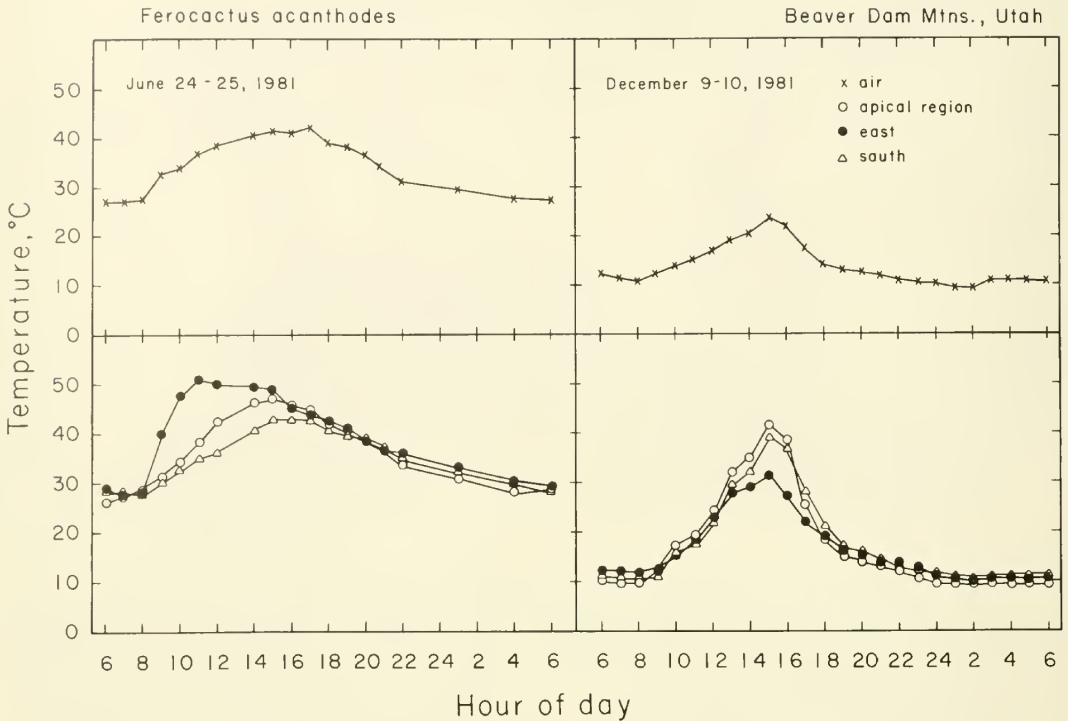


Fig. 4. Diurnal fluctuations in air and *Ferocactus acanthodes* tissue temperatures at Castle Cliffs 24-25 June and 9-10 December 1981.

Also consistent with both the summer and winter data sets was the observation that the apical region was cooler at night than other parts of the cactus and was usually cooler than air temperature. The significance of this observation will be discussed in the next section.

The micro-distributions of the barrel cactus were not uniform on all slopes. The cacti were found effectively only on slopes that faced south (Fig. 5). The density of barrel cactus ranged as high as 0.385 individuals m^{-2} on due-south-facing slopes, but quickly decreased to zero when slope azimuth deviated 60 degrees in either direction from south. On all slopes where the cactus density was greater than 0.06 individuals m^{-2} , the slope angles were inclined, ranging 20°-25°. In contrast, the slope angles at sites where the density was less than 0.06 were mostly less than 20°.

One aspect of the apparent restriction of barrel cactus to south-facing slopes was that the amount of solar radiation incident on these slopes during the winter was much higher than would occur on either a horizontal surface or on tilted slopes with different

orientations. On a clear day at the winter solstice (December 21), the total daily amount of direct solar radiation incident on a horizontal slope would be approximately 8 MJ m^{-2} . From our observations, the barrel cactus did not occur on slopes with less than 11.5 MJ $m^{-2} day^{-1}$ total solar radiation, and high densities of cacti did not occur until the total solar radiation exceeded 13 MJ $m^{-2} day^{-1}$ (Fig. 6).

It seems likely that the size distributions of barrel cactus on slopes with contrasting orientations should be different. Unfortunately, the limited population sizes on non-south-facing slopes were so small that statistical analyses of frequency-size distributions could not be made.

DISCUSSION

The distribution of the barrel cactus (*Ferocactus acanthodes*) may be limited by two factors at its northern distribution limit: the ability of seedlings to become established (drought) and the ability of both seedlings and mature plants to avoid temperature extremes. These temperature extremes could

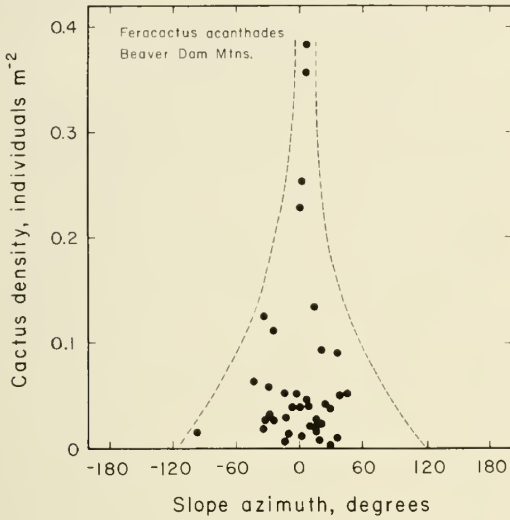


Fig. 5. Density of *Ferocactus acanthodes* as a function of the azimuth of the slope on which they occurred for the Castle Cliffs population in the Beaver Dam Mountains, Utah.

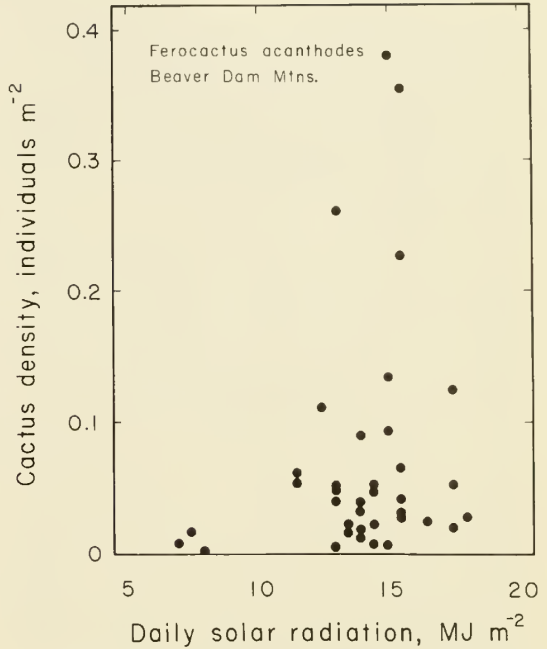


Fig. 6. Density of *Ferocactus acanthodes* as a function of the total daily amount of solar radiation incident on the slope surface for a clear day on the winter solstice for the population at Castle Cliffs in the Beaver Dam Mountains, Utah.

include low minimum tissue temperatures, which may cause freezing damage, as well as high tissue temperatures resulting in high rates of water loss and tissue desiccation.

Minimum tolerable tissue temperatures and the length of time an individual is exposed to subzero temperatures have been proposed by several authors as primary factors limiting the distributions of a number of desert cacti in southwestern North America (Shreve 1911, 1914, Turange and Hinckley 1938, Niering et al. 1963, Kincaide 1978). During low air temperature conditions, microsite distribution may play an important role in survival. South-facing slopes will receive greater heating by solar radiation during the cold winter months than any other slope orientation. As such, plants on south-facing slopes should be exposed to higher air temperatures and should additionally warm more because of the higher incident solar radiation heat loads. In this study, we observed that *F. acanthodes* were restricted to south-facing slopes and that the highest densities were on slopes with angles 20°–24°. The highest densities were found on those slopes that received greater heating during the winter months.

Ferocactus acanthodes also occurs throughout much of the Mohave and Sonoran deserts. Yeaton and Cody (1979) showed that

the density of plants varied with microsite in those deserts as well. In particular, they found that in the warmest year-round site (Sonoran Desert) *F. acanthodes* were most common on south-facing slopes, but did occur in lesser amounts on east-west and north-facing slopes. At the cooler Mohave Desert sites, *F. acanthodes* occurred on east-west and south-facing slopes, but not on north-facing slopes. Thus, we see from these three sites a trend: as winter temperatures decrease, the barrel cactus decrease in density from the slopes that receive less winter solar heating.

Perhaps the most cold temperature-sensitive region of the barrel cactus is the apical region at the top of the cactus. Freezing temperature damage in this region will result in mortality, since stems are solitary. Nobel (1980a, 1980b, 1981) has shown that the minimum nighttime tissue temperature of the apical regions of columnar cacti species are up to several degrees cooler than the sides, because of the greater net long-wave radiation loss to the sky. The extent of nighttime cooling of the apical region will be a function of the surface area to volume ratio, so

that the barrel cactus cools more slowly than the cylindrically stemmed *Opuntia* cactus. Our data corroborate these previous observations as nighttime tissue temperatures in the apical region were approximately 2 C cooler than the cactus sides, both in the winter and in the summer.

Since the apical region faced south, winter tissue temperatures should rise quickly during the day. The amount of solar radiation absorbed is accentuated by steep tissue angles, such as were observed in this study. As a consequence of this orientation, midday apical region tissue temperatures in the winter were as much as 19 C above air temperatures. Under subzero air temperatures, which may occasionally occur during the winter, the orientation of the apical region should result in tissue temperatures being above zero during the daytime hours. This would limit the time that the apical region was exposed to potentially low, lethal temperatures to the nighttime only.

Air temperature and relative humidities during the hot summer months will determine the evaporative demand imposed on the cactus. Jordan and Nobel (1981) showed that seedling establishment in *F. acanthodes* was restricted to wetter, cooler than average years, since in most years seedlings died of desiccation during the long summer drought. The globular shape observed in younger plants decreases the surface to volume ratio, thereby reducing the relative surface area exposed for transpiration. This also reduces the surface area for photosynthesis.

During the summer months, however, very little positive net photosynthesis occurs in these plants (Nobel 1977). The barrel cactus possesses CAM photosynthesis and during drought periods open their stomates at night for only a short time. Under prolonged drought these plants "idle" and do not open their stomates at all. Under these low photosynthesis conditions, Ehleringer et al. (1980) hypothesized that it may be advantageous for a cactus to orient such that the photosynthetic surfaces (sides of the cactus) received minimal amounts of solar radiation. This is what was observed in *F. acanthodes* where the body (stem) of the cactus was tilted at approximately 47° in a southerly direction. Such an orientation will minimize solar

radiation incident on the sides of the cactus during the peaks of the drought period in the study area (September–October).

Cactus height distributions can help identify the periods of seedling establishment in a population (Shreve 1910, Brum 1973, Jordan and Nobel 1981, 1982). At our study site in the Beaver Dam Mountains, there was a single peak in height distribution at the 31–40 cm interval. Additionally, there was only a single individual observed to be less than 11 cm tall (it was 10 cm). Jordan and Nobel (1982) determined that the average yearly growth rate was a constant 9 mm yr⁻¹ for *F. acanthodes*. Using this estimate, we calculate that no new barrel cactus plants have become established in the Beaver Dam population since approximately 1969 and that a major period of establishment was 1937–1947. Precipitation records for the region bear out that these were abnormally wet periods.

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