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HEIGHT DISTRIBUTIONS OF TWO SPECIES OF CACTI IN RELATION TO RAINFALL, SEEDLING ESTABLISHMENT, AND GROWTH

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In three populations of *Ferocactus acanthodes* and two of *Carnegiea gigantea*, multiple discrete peaks in the height distribution were observed, suggesting that seedling establishment was intermittent. To identify periods of establishment, we determined the relationship between stem height and age for each site, based on observed growth rates in the field, gas-exchange data, and weather records. The average yearly growth for the globular *F. acanthodes* was relatively constant at about 9 mm yr^{-1}, but for the club-shaped *C. gigantea*, it increased with age from 2 mm yr^{-1} in the first year to 44 mm yr^{-1} at 13 yr. In years suitable for establishment, seedlings grow to sufficient size that stored water is not depleted by cuticular transpiration during the ensuing drought. The pattern of such suitable years over the last 3 decades correlated with the measured height distributions when the relation between stem height and age was considered. At a Sonoran Desert site, major peaks in the height distribution were centered at 0.05 m and 0.19 m, which corresponded to suitable conditions for establishment in 1976 and 1959, respectively. Rainfall records from various weather stations indicated that both species occurred where at least 10% of the years are suitable for seedling establishment.

Introduction

Height distributions of cacti can help identify periods of abundant seedling establishment (SHREVE 1910; HASTINGS 1961; BRUM 1973). Low occurrence of small saguaros (*Carnegiea gigantea*) apparently reflects reduced seedling establishment resulting from cattle grazing (SHREVE 1911; NIERING, WHITTAKER, and LOWE 1963) or years of reduced summer precipitation (BRUM 1973). Years of seedling establishment have been directly related to rainfall amount and pattern for the desert agave, *Agave deserti* (JORDAN and NOBEL 1979), and for a barrel cactus, *Ferocactus acanthodes* (JORDAN and NOBEL 1981). Owing to the slow growth of these Crassulacean acid metabolism plants, the seedlings are still quite small and store little water at the end of the first growing season following germination. This low capacity for storing moisture per unit surface area causes first-year seedlings to be more susceptible than adults to lethal desiccation during extended droughts. Precipitation records indicate that droughts of sufficient length to prevent establishment have occurred in 16 of 17 yr for *A. deserti* and 10 of 18 yr for *F. acanthodes* in the northwestern Sonoran Desert (JORDAN and NOBEL 1979, 1981).

Durations of moist and drought periods, apparently critical in determining seedling establishment, are often not strictly related to the timing and amount of precipitation characteristic for a large region. Mountain ranges may force air masses to rise, increasing the frequency of local precipitation over that in adjacent areas (SHREVE 1922; TURNAGE and MALLORY 1941). The length of time when the soil is moist depends not only on rainfall but also on local runoff and shading, which can change the period when soil moisture is available (DANIN 1972; NOBEL 1978). Indeed, the effect of shading and runoff within a canyon was significant for seedling establishment of *F. acanthodes* (JORDAN and NOBEL 1981), extending the season when moisture was available so that newly germinated seedlings could achieve a greater size before the ensuing drought began. Soil moisture near the surface is particularly important for desert succulents, since their roots often extend to mean depths of only about 0.1 m (NOBEL 1976, 1977).

In the present study, height distributions of populations were measured for *F. acanthodes* and *C. gigantea* to help understand possible effects of episodic seedling establishment. Shifts in height distributions were noted for populations that had previously been measured. Also, the occurrence of these species at a number of sites varying in location and proximity to mountains was checked, and the results were compared with the frequency of years suitable for seedling establishment, predicted from rainfall records for each site.

Material and methods

Stem heights were measured for populations of *Ferocactus acanthodes* (Lem.) Britton and Rose (Cactaceae) at three locations in California over a north-south distance of 200 km (fig. 1): (1) Agave Hill (elevation 850 m, 33°38′N, 116°24′W) within the University of California Philip L. Boyd Deep Canyon Desert Research Center; (2) Deep Canyon (300 m, 33°39′N, 116°23′W), also within the Deep Canyon Desert Research Center; and (3) New York Mountains (1,400 m, 35°18′N, 115°19′W). Agave Hill and Deep Canyon are in the northwestern

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Sonoran Desert; New York Mountains are in the Mojave Desert. Height distributions were measured for *Carnegiea gigantea* (Engelm.) Britton and Rose near Wikieup, Arizona (845 m, 34°36′N, 113°28′W; see NOBEL 1980; fig. 1), and near Parker Dam, California (300 m, 34°19′N, 114°11′W), site of the densest stand of *C. gigantea* in California (PARISH 1905; BAXTER 1932; BRUM 1973).

Significant differences ($\alpha = 0.01$) among height distributions were identified with a χ^2 test (SIEGEL 1956). The summed deviations between the fraction in each of the height classes and the fraction in each of the height classes for the summation of the distributions were tested. Rainfall records from 14 United States Weather Bureau stations (fig. 1), including those closest to the above five sites, were analyzed to help interpret the height distributions and geographic distributions of the two species. Growth of *F. acanthodes* was monitored at Deep Canyon. Height measurements were from the lowest visible mark at which spines had originated to the highest point of the stem.

Results

HEIGHT DISTRIBUTIONS

Height distributions of *Ferocactus acanthodes* (fig. 2) at Agave Hill and New York Mountains indicated that tall individuals were less numerous in these populations. The greatest numbers were within height classes 0.04–0.08 m tall at Agave Hill and 0.22–0.24 m for the New York Mountains. Both distributions showed multiple major peaks, which were centered at 0.05, 0.19, and 0.33 m for Agave Hill and 0.11 and 0.23 m for the New York Mountains. The peaks indicate that establishment has not been equally probable in each year.

Height distributions for populations of *Carnegiea gigantea* (fig. 3) at Parker Dam and Wikieup were different from those for *F. acanthodes*. For both distributions of *C. gigantea*, peaks occurred at height classes of relatively large plants near 5 m tall. For Parker Dam, small individuals were almost absent; the smallest individual found was 0.36 m tall. By contrast, the Wikieup population included a relatively large group of small individuals, the smallest one detected being 0.03 m tall. Differences in numbers of small individuals suggest markedly different establishment success in recent years.

To characterize changes in height distributions over time, a population of *F. acanthodes* at Deep Canyon was measured 2.5 yr after a previous measurement (JORDAN and NOBEL 1981). The relative numbers in classes for the taller plants were similar in these separate measurements, but the most promi-

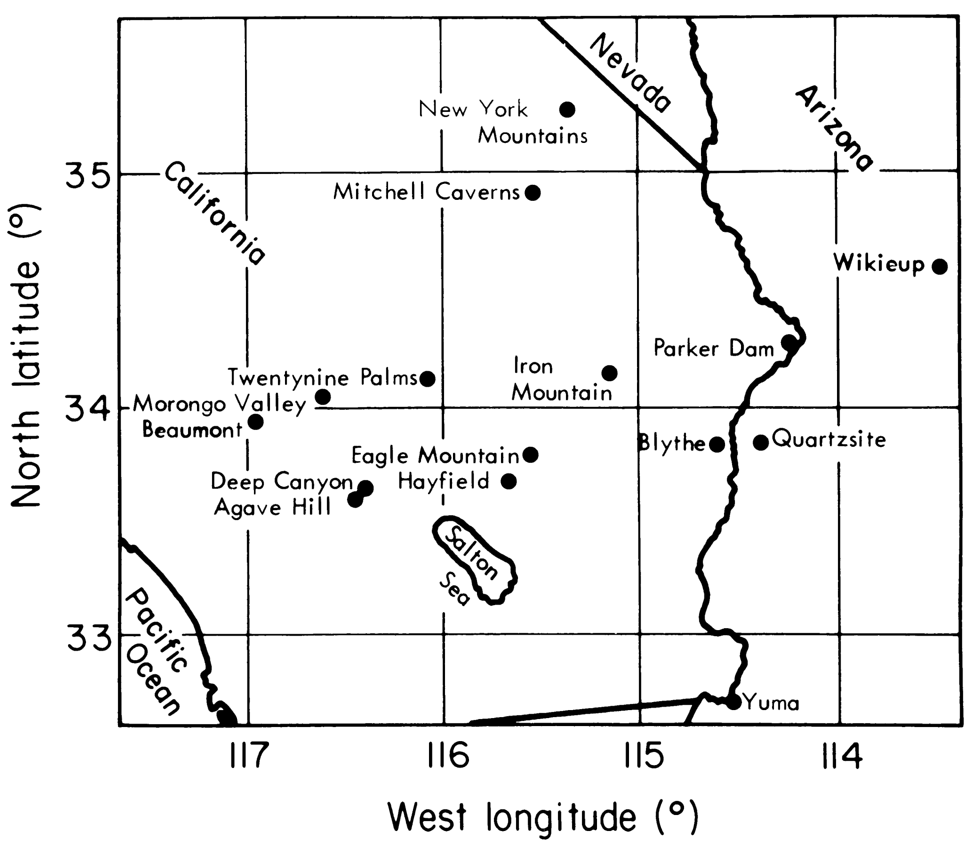

FIG. 1.—Study sites of *Ferocactus acanthodes* and *Carnegiea gigantea* in southern California and western Arizona. Map indicates the study sites for which height distributions and precipitation data were analyzed.

nent peak for small individuals was broader and shifted toward larger individuals. The center of this peak occurred at 27 mm in May 1979 and 39 mm in November 1981. For six individual plants (average height, 30 mm in May 1979) monitored over the same period, the increase in height was 10 ± 6 mm.

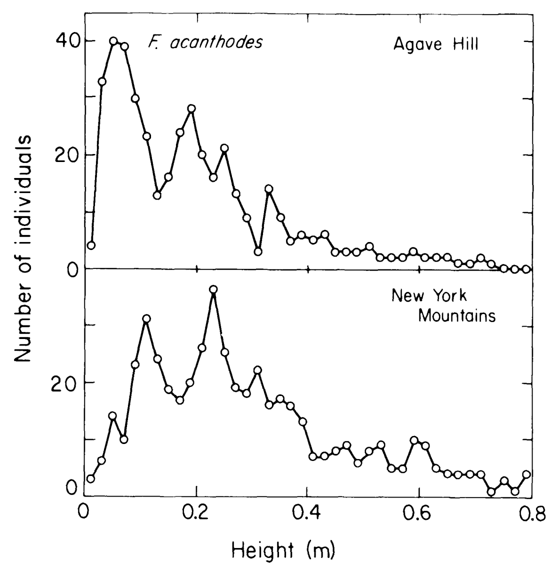

FIG. 2.—Height distributions of *Ferocactus acanthodes* at two sites displayed using 0.02-m-height classes. Data were obtained at Agave Hill in June 1980 and at New York Mountains in December 1980 (6% of the plants were taller than 0.8 m). The difference in shape of the two distributions is significant ($P < .0001$).

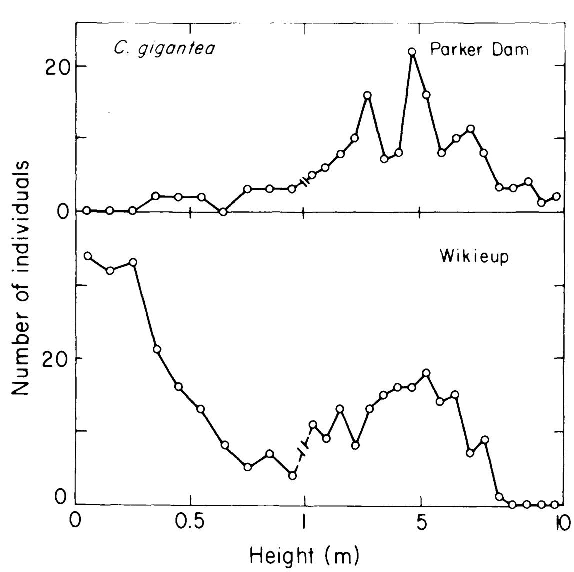

FIG. 3.—Height distributions of *Carnegiea gigantea* at Parker Dam, California, and Wikieup, Arizona. Distribution for classes below 1 m are displayed using 0.1-m-height classes. For classes above 1 m, 0.5-m-height intervals, are used and the horizontal scale is compressed eightfold. Data were obtained June 1980 and April 1982. For plants < 1 m tall, the difference in shape of the two distributions is significant ($P < .001$), but it is not for plants > 1 m tall ($P = .24$).

This growth is consistent with the shift in height distribution, and the large variation is consistent with the broadening of the peak over 2.5 yr. A similar shift in distribution for a population of *C. gigantea* was also detected. In a study preceding this one by 8 yr (BRUM 1973), the most prominent peak for Parker Dam was for plants 4.3 to 4.9 m tall. When the same height classes were used 8 yr later, the presumably same peak occurred in the next taller class, 4.9 to 5.5 m.

ESTIMATED SEEDLING GROWTH

The growth of seedlings of *F. acanthodes* and *C. gigantea* was predicted for each of the study sites to help determine the age of plants of particular heights. Age estimates for *F. acanthodes* up to 0.27 m tall were based on field growth measurements over the last 3 yr, adjusted with gas-exchange data (JORDAN and NOBEL 1981) to conditions in previous years deduced from weather records; CO_2 uptake rates were converted to rates of fresh weight and height increase, assuming that all CO_2 was converted to carbohydrate, that stem dry weight was 9.7% of the fresh weight, and that stem density was 999 kg m^{-3} (NOBEL 1977). Estimated growth for *C. gigantea* was derived from previous height measurements (HASTINGS and ALCORN 1961; STEENBERGH and LOWE 1977), which were adjusted for differences in rainfall and temperature between sites using the temperature response of CO_2 uptake (NOBEL and HARTSOCK 1981).

The annual growth in height of *C. gigantea* after initial expansion to 3 mm within 15 days of germination increased with age from 2 mm in year 1 to 44 mm in year 13 (fig. 4). Annual growth for *F. acanthodes* varied from a loss of 2 mm to a gain of 24 mm, averaging 9 mm (fig. 4). The growth rate of *F. acanthodes* in a particular year depended primarily on rainfall patterns and little on plant age (*F. acanthodes* was globular throughout this phase, while *C. gigantea* was initially globular but then became club shaped). Plants 0.25 m tall were 29 (*F. acanthodes*) and 12 yr old (*C. gigantea*) (fig. 4). Such estimates are used in the next section to identify the year of germination for individuals in various height classes.

ESTABLISHMENT IN RELATION TO RAINFALL

Since drought is a major factor limiting seedling establishment of succulents, drought periods were identified by using rainfall records for Agave Hill and New York Mountains (fig. 5) as well as for Wikieup and Parker Dam (fig. 6). Cactus germination typically occurs in the fall (STEENBERGH and LOWE 1969, 1977; JORDAN and NOBEL 1981), and seedling growth is largely determined by the number of days the soil is wet during the winter and spring. The number of days in years when soil moisture was adequate for growth varied from 0 during 2 consecutive years at Parker to 226 in a single year at New

York Mountains. The length of drought that a seedling of *F. acanthodes* can survive was assumed to equal the time necessary for depletion of tissue water to a lethal extent (840 kg H_2O lost per m^3 of fully hydrated volume [JORDAN and NOBEL 1981]) by means of cuticular transpiration (water vapor conductance of 4.0×10^{-3} mm s^{-1}) under average early summer conditions for the particular sites. Values for cuticular conductance and desiccation tolerance for *C. gigantea* were assumed to be similar to those for *F. acanthodes*. The actual length of drought in the summer following the initial seedling growth was estimated from rainfall records and previous measurements of soil moisture (NOBEL 1977, 1978; JORDAN and NOBEL 1981). Those years in which the length of drought that could be tolerated exceeded the length of drought that actually occurred were considered to be suitable for establishment. Of the past 30 yr, the number of suitable years varied from 1 for *C. gigantea* at Parker Dam (fig. 6) to 21 for *F. acanthodes* at New York Mountains (fig. 5).

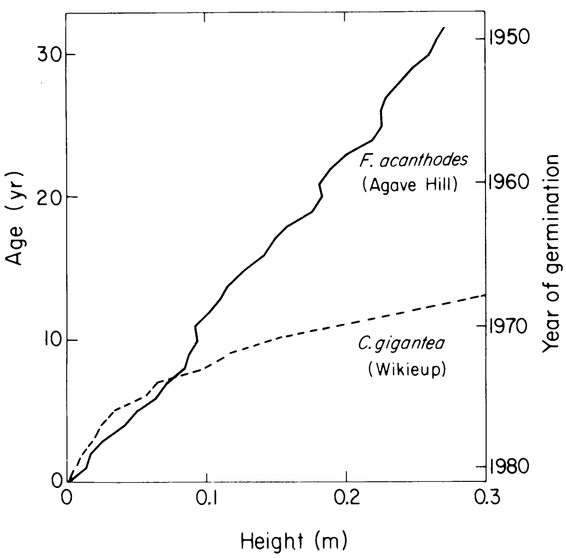

FIG. 4.—Estimated age and year of germination for *Ferocactus acanthodes* at Agave Hill and *Carnegiea gigantea* at Wikieup as a function of height in 1981. Height is for a fully hydrated individual.

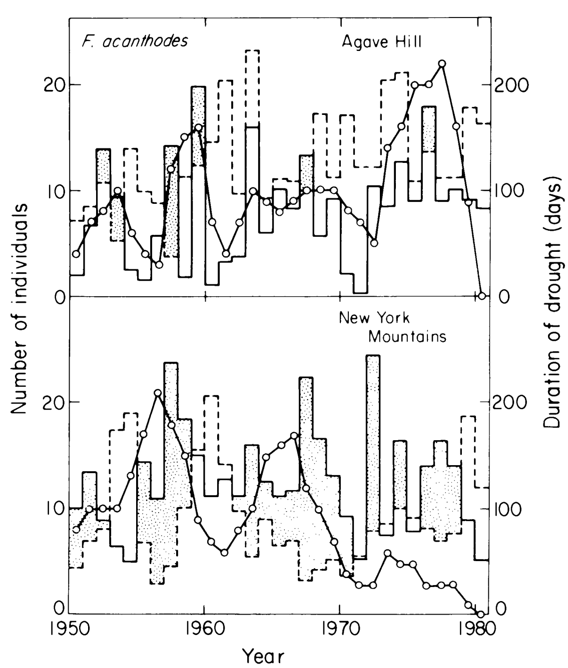

FIG. 5.—Comparison of number of individuals estimated to have germinated in specific years (○) with the years predicted to be suitable for establishment of *Ferocactus acanthodes* (stippled area). Individual age classes are based on estimated annual growth increments. Solid lines indicate the length of tolerable drought for seedlings germinating at the start of a fall moist season in the designated year, and dashed lines indicate the length of actual drought.

Height distributions were reconsidered, using classes corresponding to 1-yr age increments for the individual sites, as estimated from figure 4. For example, individuals of *F. acanthodes* germinating at Agave Hill in 1958 (fig. 4) were considered to be between 0.20 and 0.22 m tall. The age classes were plotted using 1-yr growth intervals (figs. 5, 6). Correspondence between peaks in these distributions and the patterns of years suitable for establishment was generally quite good. In particular, extended periods of suitable years (e.g., 1955 through 1958 and 1962 through 1971 for New York Mountains) corresponded to major peaks, and extended periods of unsuitable years (e.g., 1954 through 1963 and 1971 through 1975 for Wikieup) corresponded to troughs in the distributions. For Parker Dam, the lack of small *C. gigantea* is explained by the lack of suitable rainfall patterns in recent years. In 1976, abundant establishment appears to have occurred (fig. 5), which led to peaks in the Agave Hill height distribution for *F. acanthodes* located at 0.04 to 0.08 m (fig. 2) and in the Wikieup distribution for *C. gigantea* at 0.03 to 0.06 m (fig. 3).

ESTABLISHMENT IN RELATION TO GEOGRAPHIC LOCATION

To relate seedling establishment to geographic distribution, suitable years for establishment of *F. acanthodes*, based on the relative length of wet and dry seasons, were identified for eight additional sites in California for which precipitation data were available for 22–30 yr. For sites which conveniently fell into a north-south band (fig. 1), suitable years for establishment varied from 3% to 67% (fig. 7). In an east-west band, adequate years for establishment ranged from 6% to 94% (fig. 7). For Agave Hill and Deep Canyon, 17% and 43% of 30 yr were suitable, respectively.

The actual geographic and elevational distribution of *F. acanthodes* was examined at the above sites and in surrounding areas. The lowest and highest elevations within bands 20 km wide running north-south and east-west are plotted along with the elevational

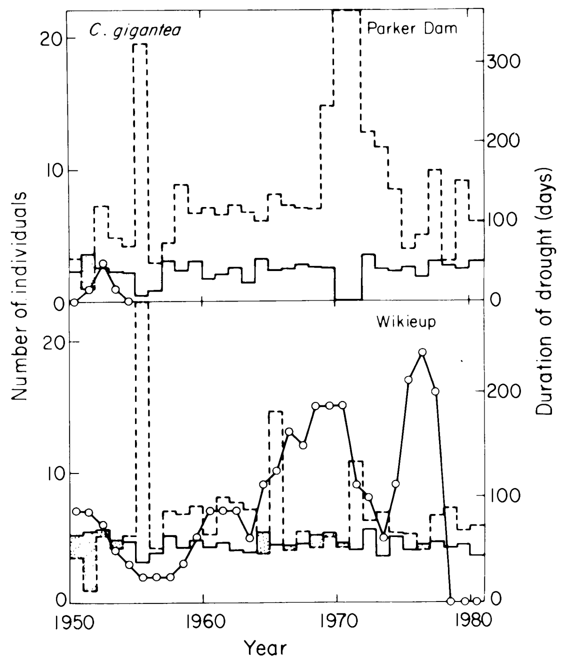

FIG. 6.—Numbers of individuals in particular age classes and predicted years of establishment for *Carnegiea gigantea*. Format is the same as for fig. 5.

range (hatched region in fig. 7). *F. acanthodes* occurs at sites where at least 10% of the last 22–30 yr were suitable for establishment (fig. 7). Sites having more than 10% of years suitable for establishment occurred near major mountain ranges. Also, *F. acanthodes* extends to lower elevations in the southern and eastern parts of the region studied and on southern and eastern slopes of mountain ranges.

Suitable years for seedling establishment of *C. gigantea* were similarly identified for four sites (fig. 1) along the Colorado River at the western margin of the geographic distribution for this species. From north to south, these sites are: Parker Dam, California; Quartzsite, Arizona; Blythe, California; and Yuma, Arizona. The suitable years for sites in the above order (rainfall records ranged from 44 to 110 yr) were 13%, 23%, 6%, and 3%, respectively. *Carnegiea gigantea* occurs at Parker Dam and Quartzsite but not at Blythe or Yuma, indicating that this species also can maintain populations where ca. 10% of the years are suitable for establishment.

Discussion

The length of a dry season relative to the previous wet season apparently determines yearly establish-

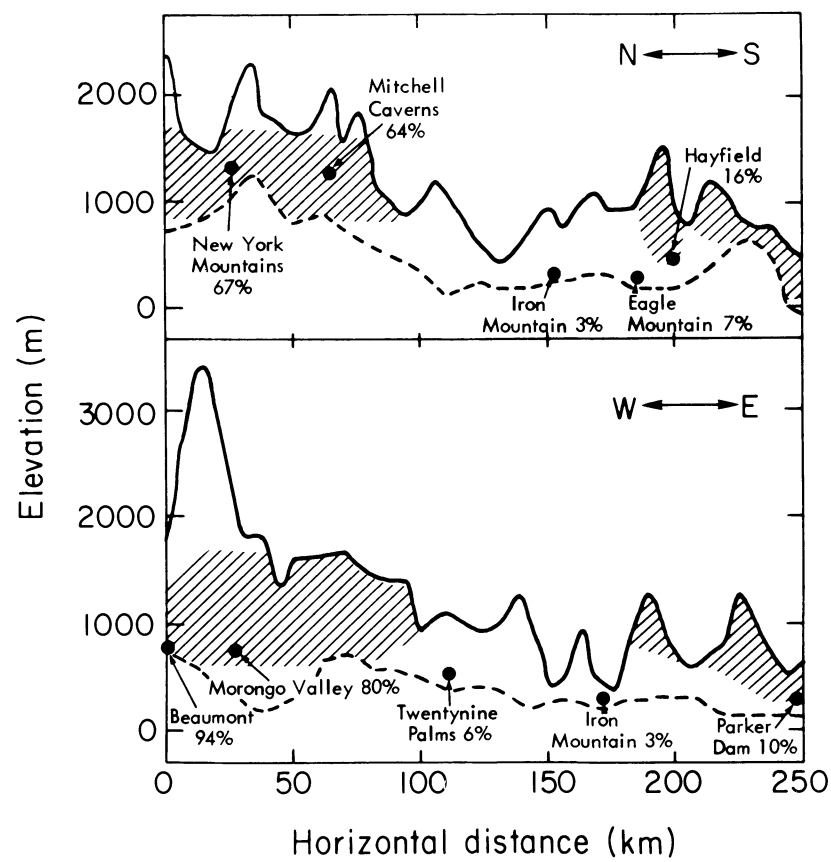

FIG. 7.—Elevational distribution of *Ferocactus acanthodes* in southern California. Elevational profiles indicate highest (———) and lowest (----) elevations within bands 20 km wide running north-south and east-west, elevations of the study sites (fig. 1), and the elevational range of *F. acanthodes* (hatched area). Percentages accompanying site designations are for the number of suitable years for seedling establishment in the last 30 yr.

ment success of cactus seedlings, and the pattern of suitable years determines the overall height distribution of a population (figs. 2, 3). Wet seasons have been quite variable in length at the sites studied, ranging from zero, when no precipitation sufficient for germination occurred, up to about three times the 30-yr mean. Such variability in rainfall led to 9 consecutive suitable years at the New York Mountains and 29 consecutive unsuitable years at Parker Dam. When plotted using height classes corresponding to 1-yr growth increments, height distributions for *Ferocactus acanthodes* and *Carnegiea gigantea* closely reflected the pattern of suitable years for the past 3 decades (figs. 5, 6). Peak stem numbers of *F. acanthodes* at New York Mountains occurred for plants 0.11 m and 0.23 m tall. These peaks corresponded to groups of favorable years centered around 1966 and 1956/1957.

A group of small *F. acanthodes* at Deep Canyon shifted to taller height classes over 2.5 yr, as did a broad peak in the distribution of *C. gigantea* at Parker Dam over 8 yr. The rate of shift in the peak for the *F. acanthodes* at Deep Canyon agreed with the estimate for growth rate (averaging 9 mm yr^{-1}) based on CO_2 uptake at nearby Agave Hill. This growth pattern differs from that for *C. gigantea*, which grew 2 mm yr^{-1} when newly germinated and about 44 mm yr^{-1} when 0.26 m tall (fig. 4) (STEENBERGH and LOWE 1977). The relative constancy of the estimated growth rate for *F. acanthodes* is a result of the globular form that is retained up to a diameter of 0.25 to 0.30 m. In agreement with this, growth in 1975/1976 predicted for a plant 0.05 m tall in the present study was similar to that actually measured in the same year for a 0.33-m-tall plant (NOBEL 1977). Large amounts of photosynthate for *F. acanthodes* are apparently allocated to lateral growth, whereas for *C. gigantea* taller than 0.07 m, relatively more photosynthate appears to contribute to vertical growth. This leads to a club-shaped plant, the growth rate of which can increase with increasing stem area for light interception and CO_2 uptake. Based on data for *C. gigantea* (STEENBERGH and LOWE 1977), plants about 5 m tall would grow about 0.35 m over the last 8 yr at Parker Dam, which is consistent with the shift in height distribution observed over this period (BRUM 1973, compared with fig. 3).

Ferocactus acanthodes tended to occur near major mountain ranges and at lower elevations on south and east slopes. This pattern may support the suggestion that summer storms are critical for seedling establishment of *F. acanthodes* (JORDAN and NOBEL 1981). Such storms tend to originate from the southeast in this region and could therefore lead to greater precipitation on sides of mountain ranges facing in this direction. Increases in the amount of rainfall with elevation and proximity to mountains have been demonstrated in southwestern North America (SHREVE 1922; MALLORY 1936; WHITTAKER and NIERING 1965; HANAWALT and WHITTAKER 1976). Also, a greater fraction of the yearly total rainfall occurs in the summer at higher elevations in the Santa Catalina Mountains of Arizona (TURNAGE and MALLORY 1941). The large number of years adequate for seedling establishment at the Mojave Desert sites is probably a consequence of proximity of these sites to major mountain ranges and their location at relatively high altitudes. In addition, mountain ranges arising from lower elevation plains were apparently more arid than mountains of similar maximum heights but greater elevation at the base in Arizona (SHREVE 1922). In accord with this, small mountain ranges arising from low elevation areas (center portions of fig. 7) do not support populations of *F. acanthodes*. Evidence of past geographic distributions (HENRICKSON and PRIGGE 1975; RAVEN and AXELROD 1978) indicates the influence of mountain ranges in preserving populations of certain species, perhaps including *F. acanthodes*, in the Mojave Desert as the overall region has become more arid.

Considering both species in this study, weather records indicated that establishment might have occurred in 3%–94% of all the years examined, but *F. acanthodes* and *C. gigantea* actually occurred only where at least 10% of these years were suitable for seedling establishment. This may indicate a minimum estimate of the frequency of suitable years necessary to maintain populations of these cacti. Maintenance of populations of both species at Parker Dam is probably marginal, since *F. acanthodes* apparently could have become established in only 10% of those years considered and *C. gigantea* in 13% (no years in the last 29). A lack of flowering of *C. gigantea* at Parker Dam has been noted (BRUM 1973), indicating that seed production may also be sensitive to low rainfall. Although establishment appears to have been possible a number of times (eight times in 84 yr) during the life of individuals already present, the combined effects of low seed supply and adult mortality may result in a long-term decline in these populations at Parker Dam.

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LITERATURE CITED

BAXTER, E. M. 1932. California cacti *Carnegiea gigantea*—giant cactus. Cactus Succulent J. **3**:134–135.

BRUM, G. D. 1973. Ecology of the saguaro (*Carnegiea gigantea*): phenology and establishment in marginal populations. Madroño **22**:195–204.

DANIN, A. 1972. Mediterranean elements in rocks of the Negev and Sinai deserts. Notes Roy. Bot. Garden, Edinburgh **31**:437–440.

HANAWALT, R. B., and R. H. WHITTAKER. 1976. Altitudinally coordinated patterns of soils and vegetation in the San Jacinto Mountains, California. Soil Sci. **121**:114–124.

HASTINGS, J. R. 1961. Precipitation and saguaro growth. Univ. Arizona Arid Lands Colloquia **1959–1960**:30–38.

HASTINGS, J. R., and S. M. ALCORN. 1961. Physical determinations of growth and age in the giant cactus. J. Arizona Acad. Sci. **2**:32–39.

HENRICKSON, J., and B. PRIGGE. 1975. White fir in the mountains of eastern Mojave Desert of California. Madroño **23**:164–168.

JORDAN, P. W., and P. S. NOBEL. 1979. Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the northwestern Sonoran Desert. Amer. J. Bot. **66**:1079–1084.

———. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. Ecology **62**:901–906.

MALLORY, T. D. 1936. Rainfall records for the Sonoran Desert Ecology **17**:110–121.

NIERING, W. A., R. H. WHITTAKER, and C. H. LOWE. 1963. The saguaro: a population in relation to environment. Science **142**:15–23.

NOBEL, P. S. 1976. Water relations and photosynthesis of a desert CAM plant, *Agave deserti*. Plant Physiol. **58**:576–582.

———. 1977. Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. Oecologia **27**:117–133.

———. 1978. Microhabitat, water relations, and photosynthesis of a desert fern, *Notholaena parryi*. Oecologia **31**:293–309.

———. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. BOT. GAZ. **141**:188–191.

NOBEL, P. S., and T. L. HARTSOCK. 1981. Shifts in the optimal temperature for nocturnal CO_2 uptake caused by changes in growth temperature for cacti and agaves. Physiol. Plantarum **53**:523–527.

PARISH, S. B. 1905. *Cereus giganteus* in California. Bull. Southern California Acad. Sci. **4**:122.

RAVEN, P. H., and D. I. AXELROD. 1978. Origin and relationships of the California flora. University of California Press, Berkeley.

SHREVE, F. 1910. The rate of establishment of the giant cactus. Plant World **13**:235–240.

———. 1911. The influence of low temperature on the distribution of the giant cactus. Plant World **14**:136–146.

———. 1922. Conditions indirectly affecting vertical distribution on desert mountains. Ecology **3**:269–274.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

STEENBERGH, W. F., and C. H. LOWE. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. Ecology **50**:826–834.

———. 1977. Ecology of the Saguaro. II. Reproduction, germination, establishment, growth, and survival of the young plant. Nat. Park Service Sci. Monogr. Ser. 8. Government Printing Office, Washington, D.C.

TURNAGE, W. V., and T. D. MALLORY. 1941. An analysis of rainfall in the Sonoran Desert and adjacent territory. Carnegie Inst. Washington Pub. **529**:1–45.

WHITTAKER, R. H., and W. A. NIERING. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology **46**:429–452.