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The Saguaro: A Population in Relation to Environment

Reproduction and survival are more affected by man's intrusion than by environmental extremes.

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The saguaro (*Cereus giganteus, Carnegiea gigantea*) a giant cactus, is a conspicuous and important plant of the Sonoran Desert in southern Arizona and northern Mexico (Sonora). Since the turn of the century it has been known to be failing to reproduce in certain environments (*1*). This failure has stimulated considerable research on various aspects of its biology (*2*). Decline in reproduction dates from the rapid growth of the cattle industry in the 1880's, an influence which has left a lasting imprint on parts of the Southwest. The aim of this article is to combine the knowledge of saguaro biology with the authors' population data from the Santa Catalina Mountains and adjacent ranges in a discussion of saguaro as a natural population in relation to environment and disturbance. The influence of climate, soils, overgrazing, and heavy rodent populations is considered in relation to saguaro survival (*3*).

Biology and Distribution

The saguaro (*Cereus giganteus, Carnegiea gigantea*) is often more than 9 meters tall, with a trunk more than 40 centimeters in diameter in larger individuals. A member of an essentially subtropical group (the subfamily Cerinae), it occurs mainly in the Sonoran Desert, where it grows primarily at elevations below 1400 meters (4500 ft). It flowers in May and June and produces large numbers of seeds; the larger plants produce as many as 200 fruits of 2000 seeds each (*4, 5*). Any of various circumstances may prevent the seeds and seedlings from developing: because of environmental conditions they may not germinate; rodents may eat them; the roots of young plants may be washed out; and the plants may be killed by freezing temperatures (*4, 6, 7*). A very small fraction of the seedlings survive and maintain the population. Most of the seedlings that survive are in sheltered places, underneath paloverde (*Cercidium microphyllum*) and other plants, within shrubs and grass cushions, and on rocky slopes between rocks and in mats of *Selaginella*. Groups of several saguaros of different ages may often be seen beneath, and rising through, a single paloverde tree or other "nurse plant." Growth in the early years is slow; it probably takes a plant about 10 years to reach a height of 2 centimeters and 20 to 50 years to reach 1 meter (*4*). Later growth is at a rate of about 5 to 10 centimeters per year, varying with age and summer precipitation (*1, 8*). The age-height relation makes it possible to estimate the ages of saguaros of different heights in a population.

Saguaros reach ages of probably 150 to 200 years (*9*). The mortality for mature individuals in an undisturbed stand is estimated as 0.7 percent per year (*10*, p. 344). Death may result from washing out of roots, from windthrow, from freezing, and from bacterial necrosis. The bacterium *Erwinia carnegieana* is transmitted by a moth and its larva (*7, 11*). Although saguaros become infected from time to time, their ability to wall off larval tunnels, woodpecker holes, and other wounds with corky tissue (*12*) generally prevents spread of the infection. Death of the saguaro by freezing or other cause is accompanied by rapid multiplication of the bacteria and by tissue disintegration. While it is clear that bacteria multiply in dying tissue and moribund individuals, it has not been established to what extent bacteria are capable of becoming pathogenic in large, otherwise healthy individuals.

Study Areas

The primary study area of our investigation is a transect along the Mt. Lemmon Highway in the Santa Catalina Mountains from an elevation of 1400 meters (4500 ft) to the base of the mountains at 900 meters (2900 ft), and down the valley slope or bajada to Tucson, 750 meters (2500 ft). North of the city, samples were taken also on the upper part of the bajada along Campbell Avenue. Other study areas are Tumamoc Hill, in the Tucson Mountains, and the two parts of Saguaro National Monument — the original monument in and below the Rincon Mountains east of Tucson and the new Tucson Mountain District west of Tucson, on the west slope of the Tucson Mountains.

The rocky slopes of the Catalinas and Rincons are composed primarily

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of granitic gneiss; the Tucson Mountains are primarily volcanic. On the rocky slopes, soil development is limited, occurring primarily in shallow pockets on the granite and, on Tumamoc Hill, within the interstices and beneath volcanic boulders. A deeper soil characterizes the basin or valley deposits of the bajadas, although the texture is variable. Soils of the bajadas below the Rincon Mountains and along the Mt. Lemmon Highway are primarily sandy gravels; those along Campbell Avenue are rocky, coarser soils. Those of the Tucson Mountains include both these textural types.

An ideal of physiological ecology is the establishment, by experiment, of the level of a critical factor which limits a population along an environmental gradient. The context in which populations occur in the field makes simple application of the factor-boundary concept impossible for several reasons. (i) Most natural populations along continuous environmental gradients show, instead of sharp boundaries, curves of population abundance that are apparently binomial in form (*13*). The population has its maximum density in an optimum environment and declines gradually and continuously away from this, with decreasing numbers of individuals as a result of decreases in the probabilities of reproduction and survival. (ii) The width of the environmental gradient occupied by the population is a function not merely of the physiological tolerance of an average individual but also of the range of genetic diversity in the population (*14*). The occurrence of different biotypes permits the population to survive at opposite extremes of its environment. (iii) The environmental gradient affecting the level of population is a "complex-gradient" of many environmental variables which change in parallel (*14*). More than one of these variables may affect the probability of survival of different biotypes; different factors differently affect different stages of the life history; and some factors may be effective mainly through averages affecting normal population processes, others through extreme fluctuations that result in catastrophe for a population. (iv) Effects of other organisms may be essential factors in the environmental gradient (*15*). Along a given gradient the population may decline in one direction primarily because the physical environment is increasingly unfavorable, whereas it may decline in the other direction primarily because of increasing competition of other species which flourish more than the species in question as the environment becomes more favorable. Consequently, in the presence of other organisms, the population center or optimum in the field may depart widely from the physiological optimum where the plant in question might grow best if there were no competition.

Elevation and Temperature

The first three histograms of Fig. 1 show the relation of the saguaro population to elevation on rocky south-facing slopes of the Santa Catalina Mountains. The population declines with increase in elevation, from maximum levels on the hottest, lower slopes of the mountains to low levels above 1200 meters (4000 ft); only a few individuals occur up to 1400 meters. South-facing slopes below 1200 meters support the spinose-suffrutescent phase of the Sonoran desert scrub (major plants are *Cercidium microphyllum*, *Fouquieria splendens*, *Prosopis juliflora*, *Encelia farinosa*, *Janusia gracilis*, *Jatropha cardiophylla*, *Calliandra eriophylla*, and *Opuntia* spp.); southern slopes above 1200 meters support desert grasslands. Along this gradient, increase in elevation implies decreases in mean and extreme temperatures, increase in precipitation and decrease in evaporation (*16*), and change in plant competition with increasing grass cover.

It was suggested by Shreve (*17*) that distribution of saguaro is limited to the north, or with elevation, by the latitude or altitude at which infrequent winter freezing temperatures persist for more than 24 hours. Recent experimental work by Lowe (*6*), with analysis of weather-station records for areas inside and outside the distributional boundary for saguaro, strongly supports Shreve's thesis. Sensitivity to temperature is also manifested in the saguaro, as in some of its relatives (*18*), by an increase in diameter and a decrease in the number of flutings of the stem from the southern toward the northern part of its range, where a low surface-mass ratio is advantageous, increasing the plant's capacity to retain heat—a botanical Bergmann trend.

From 11 to 13 January 1962, the effects on saguaros of one of the winter freezes which, from time to time, kill or damage the plants in the northern part of their range were studied by Lowe in the Santa Catalina Mountains. He observed tissue temperatures, air temperatures, and saguaro mortality. Freezing temperatures continued after the first night through the next day and into the second night. During the first night some of the smaller saguaros were frozen; retention of heat by the massive stems of larger individuals delayed the fall of temperature in these plants, but many froze during the second night. In the morning the thawed tissues lost turgor; during the weeks that followed, the dead tissues decomposed through bacterial necrosis. Saguaro stands on the lower slopes of the Catalinas became scenes of devastation (Fig. 2). The most severe damage was to the larger saguaros some meters above ground level and on the southeast sides of the trunks, where freeze effects were aggravated by wind and rapid thawing of tissues struck by the morning sun.

Such environmental catastrophe may produce population pulsation—slow expansions terminated by abrupt contractions. The freeze of 1962, however, reduced the density rather than the spatial extent of the saguaro population. The average mortality of saguaros more than 3½ meters tall in the samples increased with elevation, from 10 percent at 900 to 1050 meters, through 22 percent at 1050 to 1200 meters, to 30 percent above 1200 meters (Fig. 1, *a–c*, solid bars). Even where mortality was highest (up to 70 percent on an exposed upper slope, Fig. 1, *g*; Fig. 2), some larger saguaros, perhaps of more resistant genotypes, survived. For smaller saguaros, sheltered under other plants and between rocks that re-radiated heat during the night, the percentages of survival were higher. Some of the densest populations of small saguaros (5 to 30 cm tall), with mortality of less than 20 percent, were found in stands where mortality of the larger saguaros exceeded 50 percent (Fig. 1, *g*). Even so definite an environmental limitation as the occurrence of freezing temperatures for more than 24 hours acts (in this case, through differences in the percentages of mortality in different biotypes and age groups) to produce the gradual decline in population density with increasing elevation.

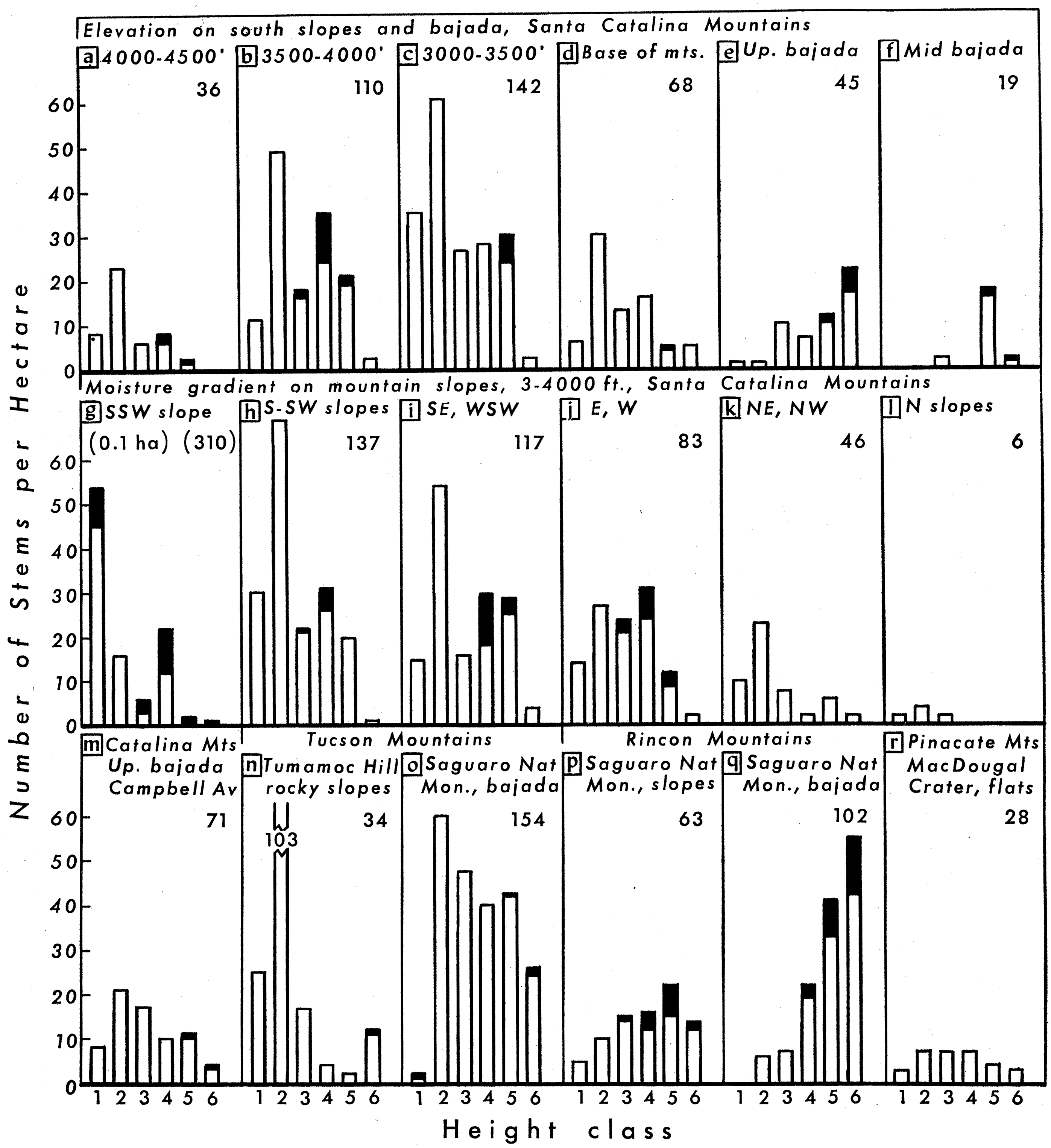

Fig. 1. Population histograms for saguaro in the area of Tucson, Arizona. The heights of bars indicate numbers of individuals per hectare (2.5 acres), as determined on the basis of ten 0.1-hectare samples in which the saguaros were counted, their heights and diameters were recorded, and the associated vegetation was analyzed (sample *g* is for a single 0.1-hectare area). "Height classes" are as follows: (1) up to 1 foot (0.3 m); (2) 2 to 6 feet (0.6 to 1.8 m); (3) 7 to 12 feet (2.1 to 3.6 m); (4) 13 to 18 feet (3.9 to 5.5 m); (5) 19 to 24 feet (5.7 to 7.3 m); (6) over 24 feet. Shaded portions of bars represent recently dead individuals, mostly killed in the freeze of January 1962. The number at upper right in each graph is the number of living individuals more than 0.3 meter tall per hectare. Age-height relationships for the bajada at Saguaro National Monument (where growth is probably faster than it is in most of the populations illustrated) are as follows: 0.3 meter, 13 years; 1.8 meters, 30 years; 3.6 meters, 48 years; 5.5 meters, 74 years; 7.3 meters, 102 years (*8*). Sample *r* is for a stand in the Pinacate Mountains, Sonora. [Data courtesy of R. M. Turner and J. R. Hastings]

Moisture Gradient

In the mountains, an environmental gradient that leads from open southwest-facing slopes through east- and west- to north-facing slopes (and from these to sheltered lower slopes and canyon bottoms) is a topographic moisture gradient. Maximum exposure to the afternoon sun renders the southwestern slopes the dry-hot extreme of this gradient. Along the gradient toward northern slopes, evaporation decreases, available moisture increases, exposure to sunlight decreases, and temperatures decrease (*16, 19*). Figure 1, *g* to *l*, shows the response of the saguaro population to the gradient from southwestern to northern slopes.

Maximum populations occur in the most arid environments in the mountains, the open southern and southwestern slopes at lowest elevations. Although the saguaro population is limited at the western edge of its geographic distribution by increasing aridity (*17, 20*), the driest conditions in the Tucson area are within the range of conditions at which the maximum population may occur. From the southern through the eastern and western slopes, all bearing the spinose-suffrutescent desert described, the population declines until the "more favorable" moisture conditions of northern slopes are reached, where the spinose-suffrutescent desert grades into a somewhat different Sonoran desert scrub with larger shrubs (*Simmondsia chinensis*, *Coursetia microphylla*, *Aloysia wrightii*, and so on). Although there are few saguaros on northern slopes, larger numbers are found in some shrub and mesquite communities in draws and canyons where, presumably, there is more moisture than there is on open northern slopes. Consequently, it seems possible that a decrease in exposure to light, as well as a decrease in temperature, limits the occurrence of plants such as these, with a photosynthetic surface that is small relative to their mass, on steep northern slopes. The fact that many of the largest saguaros occur in canyons and draws suggests that the environmental optimum for maximum population density on dry slopes, and the physiological optimum for best growth of individuals in moister conditions, are widely separated.

Slope and Bajada

The saguaro population decreases abruptly from the mountain slopes down to the valley plains or bajada in the transect area (Fig. 1, *c–f*). As compared to densities on the slopes, the densities of larger individuals are about half as high on the upper edge

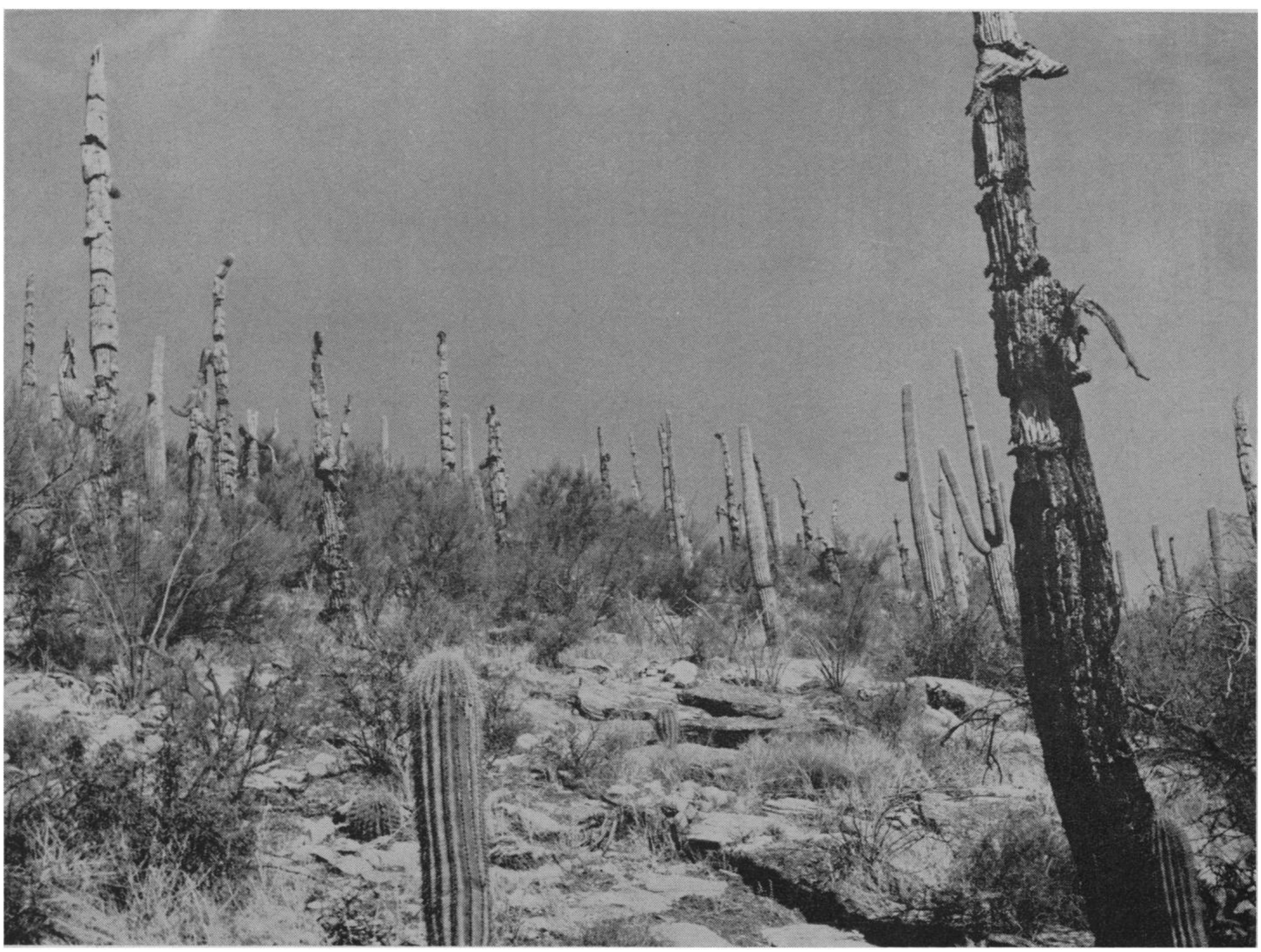

Fig. 2. A saguaro stand in January 1963, on an upper southern slope of the Santa Catalina Mountains (925 m), showing severe damage caused by the freeze of January 1962 and by bacterial necrosis that followed. Paloverde and ocotillo (*Fouquieria splendens*) comprise the larger associated vegetation. Note the excellent ground cover, the result of 25 years of protection against grazing. Data for the stand are given in Fig. 1, *g*.

of the bajada, on rock platform or pediment with spinose-suffrutescent desert (Fig. 1, *d*) and on coarse upper-bajada soils with paloverde-bursage (*Cercidium microphyllum-Franseria deltoidea*) desert (Fig. 1, *m*). From the upper edge of the bajada the population declines gradually down the valley slope through middle bajada (Fig. 1, *d–f*) to the lower-bajada creosote-bush (*Larrea divaricata*) desert near Tucson, in which the saguaros are few and widely scattered. The primary environmental change down the bajada is a change in soil characteristics (*21*), including a gradual shift from coarse soils in which saguaro reproduces effectively to the finer soils of the creosote-bush desert. Because of the thermal inversion of the valley (*22*), winter temperatures become lower and less favorable to the survival of saguaros as one goes down the bajada.

Some of the very finest stands, in which thousands of serried saguaros may be viewed across miles of desert plains (Fig. 3), occur on upper bajadas, especially those that support less xerophytic desert communities and those that are transitional between desert and desert grassland. Such stands may have both high population densities and high proportions of large individuals (Fig. 1, *o* and *q*), but in most of these stands there are few young plants to replace older ones that die. Parallel occurrences of numerous young individuals on rocky slopes and poor reproduction on the bajadas may be seen for the three study areas represented in Fig. 1.

Effects of Grazing

As we mentioned earlier, age-height relationships suggest that, in many stands, saguaro reproduction has declined since the 1880's (*1*). At that time, great numbers of cattle were brought into Arizona in a favorite get-rich-quick scheme (*23*, *24*); by 1890 there were about 114,000 cattle in Pima County alone (*25*). With reduced productivity or destruction of valley grasslands by grazing and erosion, the herds spread widely into more arid areas, into remote valleys, and up mountain slopes. As a result of overgrazing and of drought from 1891 to 1893, great numbers of cattle died (*24–26*), and the cattle populations declined thereafter to more reasonable levels.

During this period, disturbance of plant cover, both in the centers of valleys and on slopes that drained into the valleys, produced increased runoff from storms, floods of new intensity, the gouging of deep new channels or arroyos in valleys, and destruction of valley forests and meadows by erosion and the lowering of water tables—processes that have been effectively described for the Tucson area by various authors (*10, 24, 26–28*). Failure of the saguaro to reproduce may thus be a detail in the broader picture of the

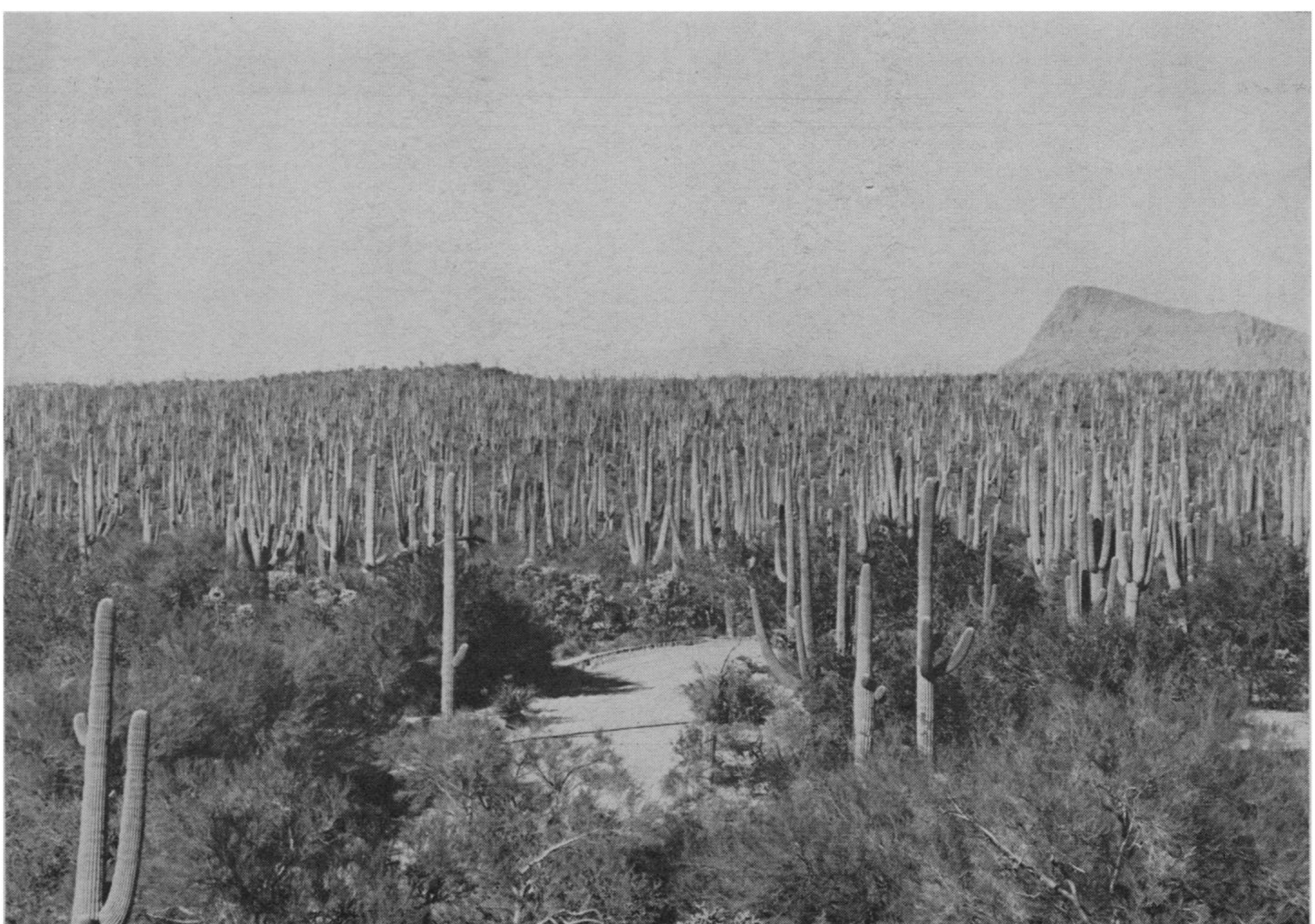

Fig. 3. A mature stand of saguaro on bajada in the Tucson Mountains section of Saguaro National Monument, in 1962. Paloverde is the conspicuous associate; cane cholla may be seen in the foreground. Data for the stand are given in Fig. 1, *o*. [Hiram L. Parent]

consequences of man's use of the Southwest—of the cutting of arroyos and channels and of changes in the character of desert grasslands that resulted from grazing and efforts to protect these lands against fire (*29*).

The data on saguaro reproduction suggest a pattern. The rock and shrub cover of steep mountain slopes offer young saguaros protection against cattle. Saguaro is reproducing on all such mountain slopes observed in our study, including slopes on which there was moderate grazing, but intensive grazing can prevent the reproduction of saguaro even on rocky slopes, as observed by Shreve (*1*) for Tumamoc Hill and for lower slopes of the Santa Catalina Mountains. The paloverde-bursage desert has never contained much grass and has been lightly grazed (*30*); in most such stands saguaro is reproducing (Fig. 1, *m*). Plant communities of the lower bajada and those transitional to desert-grassland have contained grass; they have been grazed, and in them saguaro has, in general, been reproducing poorly since the 1880's.

Damage by Rodents

Rodents and rabbits have much to do with the difference in density of saguaro on the slopes and on the bajada, and with the effects of grazing. Some rodents eat young saguaros with apparent relish, presumably more for water than for food. In one test at Saguaro National Monument, all but 14 of 800 young saguaros planted in the desert were dead in 6 months; after 2 years these 14 and all but 30 of 800 plants in cages were dead. All but about 100 of the 1570 dead saguaros were killed by rodents; the wire cages merely delayed death until the rodents had tunneled under the wire (*7*). Consumption by rodents is probably the principal hazard to young saguaros, and this (together with microclimatic effects) explains why most young saguaros that survive under natural conditions are those that are hidden by shrubs, grasses, and rocks, where they are less apt to be discovered and eaten by rodents.

Rodent populations differ both quantitatively and qualitatively under the very different soil conditions of rocky slopes and bajada (Table 1). It has been observed in both field and laboratory that the ground squirrels and wood rats which predominate on the bajada eat young saguaros; species which predominate on rocky slopes do so less frequently (*Peromyscus eremicus*) or not at all (*Perognathus intermedius*).

The rodent populations may thus tend to keep saguaro populations at

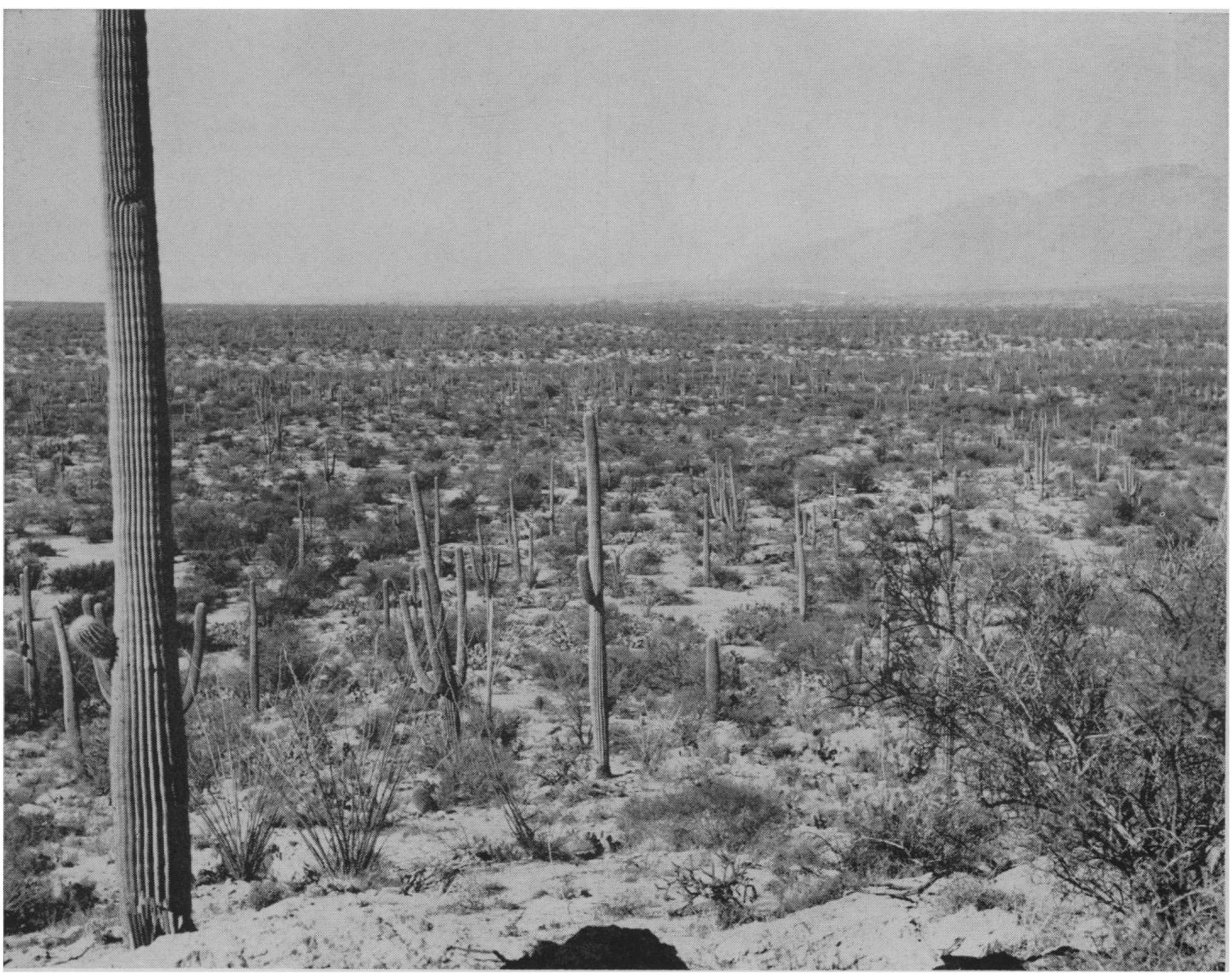

Fig. 4. A disturbed stand of saguaro (grazed until 1958) on upper bajada and lower slopes of the Rincon Mountains section of Saguaro National Monument in January 1963. Paloverde, ocotillo, and prickly pear are the conspicuous associated vegetation. The Santa Catalina Mountains appear in the background.

lower levels on the bajada than on rocky slopes. Grazing intensifies the difference. Vulnerable grasses and low shrubs on the bajada are easily destroyed by grazing, while other species, including cholla (*Opuntia fulgida*), prickly pear (*Opuntia phaeacantha*, *O. engelmannii*, and so on), burroweed (*Haplopappus tenuisectus*), and snakeweed (*Gutierrezia* spp.) increase. An abundance of these and other species characteristically indicates that the desert and desert grassland has been disturbed through grazing. As grass cover decreases and cacti increase, the density of wood rats increases. The wood rats, which use dead cholla and segments of dead prickly pear to build their nests and live prickly pear as a principal food (*31*), feed also on saguaro and other species and may become numerous enough to affect the survival of plant populations and the composition of the plant community. With grazing, the population of jackrabbits also increases, and these affect the plant community by browsing paloverde and other saguaro "nurse plants," as well as cacti (*32*). In such an overgrazed community the young saguaro faces a combination of adversities—the reduction or extinction of protecting grass and shrubs, an increase in the population of rodents that eat the unprotected plants, and trampling and consumption by cattle.

The role of rodents in the effects of overgrazing may be further aggravated by an increase in the rodent population that results from programs of coyote control. The lack of saguaro less than 30 centimeters tall on the bajada in the Tucson Mountains section of Saguaro National Monument (Fig. 1, *o*) is believed to be a consequence of grazing prior to 1938 and of a program of coyote control in the 1930's. A high rodent population developed in the sandy soils and has kept saguaro reproduction at low levels from the 1930's to the present. The Rincon Mountains section of the National Monument has been severely affected by a combination of overgrazing and predator control. The area has been grazed since the grazing heyday of the 1880's; grazing continued in the lower elevations of the Monument from the time of its establishment to 1958, and the upper slopes are still being grazed (*33*). There is some reproduction of saguaro on the rocky slopes (Fig. 1, *p*), but the growth on many of these slopes differs from that on slopes in the Catalina Mountains study area. The effects of continuous heavy grazing of the Rincon slopes are reflected in a pronounced reduction of saguaro reproduction and in cover of smaller perennial plants (Table 2), suggesting the condition of overgrazed lower slopes of the Catalinas, as shown in early photographs (*10*, plates 64, 65), and indicated by soil erosion.

The vegetation at low elevations in the Rincon Mountains section of Saguaro National Monument represents an advanced stage of the degradation process in a vulnerable community (Fig. 4). On the lower flats and adjacent parts of the study area (Fig. 1, *q*) there is no reproduction of saguaro, while older saguaros are dying at a rate (about 2 percent per year) which implies that the last individuals will disappear from this part of the Monument between 1990 and 2000 (*34*). Undergrowth of the stand is strongly dominated by prickly pear (308 clumps per hectare), cholla, and burroweed (1048 plants per hectare); there are almost no grasses, and the herb and semi-shrub cover, except for burroweed (Table 2), is the lowest that we found in our studies of vegetation in the area. Wood-rat nests are numerous (25 dens per hectare in the study area). Holes where tissues have been eaten by rodents are conspicuous in some older saguaros, especially where branches of paloverde nurse trees give wood rats access to the upper parts of saguaro stems. In some saguaros the rats have eaten circular staircases through the tissues surrounding the central column (Fig. 5). Soil erosion is evident, and though in the past dead, mature paloverdes were rarely seen (*35*), there are numerous such dead trees in this community. Intensive browsing on young paloverde by rabbits is reducing the rate of replacement of these nurse plants. Here the saguaro is a dying population in a stricken community. When the deterioration

Table 1. Relative densities (individuals per 100 traps, per night of trapping) and species biomasses (live weights in grams per 100 traps, per night of trapping) of rodents and lagomorphs, for disturbed desert on bajada at Saguaro National Monument below the Rincon Mountains, and for rocky slopes of southern to western exposure protected from grazing, at altitudes of 975 to 1035 meters in the Santa Catalina Mountains. The data are based on 535 trap-night units (number of traps times nights of trapping) for the same period (from 16 to 19 May 1963) at both stations.

Species	Density		Biomass	
	Bajada	Rocky slope	Bajada	Rocky slope
Ground squirrel (*Citellus harrisi* and *C. tereticaudus*)	10.8	0.6	879	56
Wood rat (*Neotoma albigula*)	4.3*	2.4	460*	406
Cactus mouse (*Peromyscus eremicus*)	0.4	7.1	14	144
Grasshopper mouse (*Onychomys torridus*)	0.2		4	
Kangaroo rat (*Dipodomys merriami*)	4.7		183	
Pocket mouse (*Perognathus* spp.)	8.4	15.9	147	208
Cottontail (*Sylvilagus auduboni*)	0.2		137	
Totals	29.0	26.0	1824	814

* Data for *Neotoma* on bajada were obtained from 24 to 27 April 1963.

Table 2. Coverage (in percentages) in protected and overgrazed desert in the Santa Catalina Mountains (protected from grazing for about 25 years) and in the Rincon Mountains region of Saguaro National Monument (grazed).

Site	Catalina Mountains, protected		Rincon Mountains, grazed	
	South slopes (915–1220 m) (spinose-suffrutescent)	Upper bajada (825–850 m) (paloverde bursage)	South slopes (945–1000 m) (spinose-suffrutescent)	Upper bajada (885 m) (disturbed desert)
Paloverde and mesquite	9.8	12.6	4.3	9.9
Spinose shrubs	5.8	1.8	2.7	3.9
Cacti	2.5	2.7	2.7	7.2*
Suffrutescent (except for burroweed)	9.4	22.6	4.0	0.92
Grass	2.5	0.4	0.9	.02
Other perennial herbs	0.13	.003	.22	
Burroweed				1.4
Selaginella	4.4		.2	

* The value for bajada in the transect area was determined separately.

that results from grazing has proceeded to this point, the original community has been replaced by a new one, in which the wood rat and ground squirrels are a dominant influence, in which the saguaro cannot recover, and in which any change, even though grazing should be wholly eliminated, is likely to be very slow by the time-scale of human purpose.

Grazing and Climate

Heavy grazing, drought, and the cutting of arroyos occurred simultaneously in much of the Southwest. A number of authors have discussed the possibility that drought was an important secondary, or even primary, cause of arroyo cutting (*10*, *28*, *36*). Both grazing and drought may produce arroyo cutting through reducing plant cover, and both climate and grazing must affect the probability of survival of saguaro seedlings. So pervasive was the influence of grazing, even on mountain slopes and in remoter areas, that it is difficult to find control areas where the effects of grazing and of drought may be separated.

Much evidence, in addition to that discussed, bears on the failure of saguaro to reproduce. (i) The reproduction of saguaro was reduced, on both bajadas and rocky slopes, during the period of most intense grazing. Since then, the rate of reproduction has increased both on rocky slopes and on some bajadas protected from grazing [for example, Tumamoc Hill, fenced in 1907 (Fig. 1, *n*), and Campbell Avenue (Fig. 1, *m*), protected for 25 years]. (ii) In those locations, reproduction, which had declined sharply under the earlier grazing-plus-drought conditions, was adequate during the post-1942 drought, which was considered more severe (*37*). (iii) During peak periods of grazing, reproduction of saguaro continued in some very inaccessible situations. Many young saguaros may be seen in photographs of very steep slopes in Sabino Canyon (for example, in Arizona Pioneers' Historical Society Museum photographs Nos. 7-4092 and 7-4069), taken about 1900. No sharp decrease in reproduction accompanied drought in MacDougal Crater (Fig. 1, *r*), where steep rock walls exclude cattle, even though the crater floor is of level, sandy soils of the type which elsewhere are most vulnerable to grazing damage and favorable to the development of high rodent populations, and despite the apparent effects of the post-1942 drought in killing paloverde and creosote bush in the same community (*10*, p. 357). (iv) The heaviest reproduction of saguaro at present in the Tucson area is on some of the driest slopes, and populations are reproducing well in more arid climates west of Tucson, for example in the Pinacate Mountains (Fig. 1, *r*) (*10*). (v) The same decrease in the reproduction of saguaro during peak periods of grazing is reflected in the histograms for different slopes in Fig. 1 (the 2.1- to 3.6-m class in histograms *a–d* and *g–j*, when allowance is made for slower growth than at Saguaro National Monument; the 3.9- to 5.5-m class in the less arid slope of histogram *k*) and for different bajadas. Thus, the availability of more moisture did not compensate in some of these situations for climatic drought; in all situations the populations were affected by grazing. Our data are consistent with the view that the failure of saguaro to reproduce depends on two factors in combination—the amount of grazing and the relative vulnerability of the community to harmful effects of grazing, as determined by the soil.

It should not be assumed that all arroyo cutting is a consequence of grazing, but for the Santa Cruz Valley one may make several observations. (i) The time sequence strongly sug-

Fig. 5. A group of saguaros which became established under a paloverde nurse tree, showing severe damage from rodents. There is a wood-rat den within the clump of cacti, and an internal spiral rodent runway may be seen in the second stem from the right. The group is on upper bajada of the Rincon Mountains section of Saguaro National Monument.

gests that, here, arroyo cutting was a consequence of grazing; the valley and the slopes were heavily grazed for years before the drought of 1891–93 intensified the effects of grazing on plant cover and runoff and thus initiated channel cutting. (ii) The numbers of cattle and the intensity of grazing seem clearly to have been sufficient to produce increased runoff, floods, and channel cutting. It is doubtful that the drought of 1891–93 was of such extraordinary intensity, by comparison with previous droughts, as to have caused the channel cutting. (iii) Photographs taken at the turn of the century show these mountain slopes denuded of grass cover, through grazing (*10*, especially pp. 212–222). In Arizona, such slopes have recovered their grass cover where they were not overgrazed, despite the post-1942 drought, but in Sonora similar denudation may be seen at present in comparable overgrazed desert grasslands and oak woodlands. Known changes in vegetation that occurred between 1880 and 1910, which both increased runoff and made the valley floor vulnerable to cutting, may be regarded as direct consequences of grazing. Primary responsibility for arroyo cutting may lie with man himself (*26*, *38*), and it is likely that in the Santa Cruz Valley the drought did little more than (to reverse Bryan's metaphor) pull the trigger of a gun loaded by years of overgrazing.

As for the future of the saguaro, it is evident that this is a highly successful species, well adapted to growth in a dry and unstable climate, maintaining itself well where it is not disturbed by man and grazing animals. The saguaro is in no danger of disappearing on ungrazed slopes of desert mountains or in undisturbed paloverde-bursage desert on bajadas. In many other bajada communities the saguaro is likely to disappear if there is no protection from grazing, or if the effects of grazing are already too far advanced for the saguaro population to recover even if it is now protected. The population on the rocky slopes of Saguaro National Monument in the Rincon Mountains may be expected to recover from the effects of grazing when the cattle are removed; the bajada stand that extends westward from these mountains is in such a state of deterioration that it can probably be salvaged only through extraordinary effort. It may now be of value principally as a demonstration of the ruinous effects of long-continued grazing on a once-splendid saguaro forest of the upper bajada—a forest which the Monument was created to preserve.

Summary

The saguaro is a major plant of the Sonoran Desert, occurring in a number of types of desert and extending into some desert grassland. The center of maximum population density in the Tucson area is on the driest slopes of mountains, at low elevations; the finest stands of large individuals occur on some of the upper parts of valley plains or bajadas. Toward higher elevations in the mountains the population is limited by low winter temperatures, which periodically kill large proportions of the population by freezing. Down the bajada slopes the population is limited by the occurrence of finer soils and by other factors. The population is reproducing well on rocky slopes and in some bajada communities but is failing to reproduce on the finer soils of bajadas affected by grazing. The kill by freezing is a temporary catastrophe, for many younger individuals survive the freeze. Grazing subjects the population to a gradual disaster, with slow decline to disappearance resulting from failure of the saguaro to reproduce. When the effects of grazing are far advanced and rodent populations are high, as in parts of Saguaro National Monument, these effects are largely irreversible.

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