Ecology of the Saguaro: II

ECOLOGY OF THE SAGUARO: II

Reproduction, Germination, Establishment, Growth, and Survival of the Young Plant

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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources." The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.

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Frontispiece: Ripe fruits of the saguaro giant cactus. These are the "red flowers" of the saguaro originally described by Dr. C. C. Parry reporting on an expedition down the Gila River in 1852. The flowers—white, not red—appear on the tips of stem and branches in late spring and early summer; the fruits ripen in June and early July.

We dedicate this work to the memory of Dr. Homer L. Shantz whose foresight and active concern for the preservation of its exceptional natural qualities were a vital contribution to the establishment of Saguaro National Monument.

Nowhere in the world is there so fine a stand of the giant sahuara (*Carnegia gigantia*) as in the area included in the University Cactus Forest. Here the plants rise so close together that at times it is difficult to see through them for any great distance. Unique as is the area because of the close stand of sahuara, it is none the less remarkable for the fine stand of cholla, viznaga, ocotilla, palo verde, and hackberry, as well as hundreds of other interesting plants. Those who know every portion of the great Southwest maintain that the area surpasses them all.

To allow this area to pass to private ownership and to allow these great plants to be destroyed or shipped and sold, would not only be a calamity to Arizona but to the nation and to science as well. Unfortunately the area had already been homesteaded, but the vegetation still remains in its virgin state. Many people have been interested and have contributed to the preservation of this area. Now it stands as outlined in the statement. No finer natural area can be found—but an area that must be protected or it will soon be destroyed. It ranks with the great Redwoods, not in age and not in mass of vegetation, but certainly in unique character and surpasses it in variety of form.—

Homer L. Shantz, 1932.

Preface

As a direct result of the criteria used in the selection of natural features and phenomena for designation as National Parks and National Monuments, the National Park Service has inadvertently acquired unique problems with respect to maintaining the living natural resources assigned to its custody. This is especially true with regard to those National Park Service areas that were selected because of the unique qualities of specific plant populations.

The very qualities that made these plant populations attractive, unique, or superlative examples of their kind, were the unrecognized expression of exceptional conditions, i.e., atypical environments within the overall species range in space or time. Thus the National Park Service has been entrusted with the care of plant populations that are the resulting relicts of past climatic conditions, such as redwoods and sequoias, or that are situated near the critical geographic limits of the species distribution such as saguaros.

Instability is a primary characteristic of such populations responding—often in a dramatic manner—to a constantly changing climatic environment. Such is the prevailing condition of the saguaro populations at Saguaro National Monument and elsewhere along the margins of its distribution in Arizona and northern Sonora. It is within this context that we have examined and report here on the question of the factors concerning the germination, establishment, growth, and survival of the saguaro to the age of first reproduction. It is within this same context that we offer recommendations for the management of these populations.

This volume is Part II of reports on our continuing investigations on a particularly sensitive and responsive plant population in the Sonoran Desert. Part I (Steenbergh and Lowe 1976) concerns the role of freezing weather on saguaro populations along the eastern and northern margins of saguaro distribution in Arizona and northern Sonora. In Part II, this report, we offer results and conclusions on our experiments and observations on the reproduction, germination, establishment, growth, and survival of the young saguaro to the age of first reproduction.

In Appendix I we offer management recommendations based on our investigations. These will be of interest to the National Park Service not only in relation to the management and interpretive programs at Saguaro National Monument but also at the three other National Park Service areas in Arizona where responsive populations of the saguaros and other warm desert plant species also occur—Casa Grande National Monument, Tonto National Monument, and Organ Pipe Cactus National Monument. In Appendix II we provide for the benefit of others with an interest in the ecology and history of the saguaro, a revised version of the earlier bibliography by Steenbergh (1974).

Scientific and vernacular names generally follow Kearney and Peebles (1969) for plants, except for cacti for which we follow the classification used by Benson (1969). Nomenclature for birds is from Monson and Phillips (1964); mammals from Hall and Kelson (1959), see also Cockrum (1960, 1964).

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WARREN F. STEENBERGH
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1
Introduction

Observe constantly that all things take place by change, and accustom thyself to consider that the nature of the Universe loves nothing so much as to change the things which are, and to make new things like them.—Marcus Aurelius Antoninus, "Meditations," 36.

Ours is a constantly changing environment and we most easily relate to and understand those responses that are immediate and that occur over a short span of time. As the time span of those changes increases it becomes increasingly difficult for us to relate to them, more so to understand them. We have particular difficulty understanding and accepting the observed effects of causal events that long pre-date our association with such results.

So it is with the saguaro, that we regard as a "problem" the dramatic fluctuations in some populations that we have witnessed during our brief temporal contact with the continuing process of evolution. With a maximum life span nearly twice our own, living saguaros have survived climatic events that long pre-date our recollection or knowledge. The species has survived through continuing environmental changes and has evolved during millions of years in environments that we have not experienced, and can but vaguely comprehend. However, examination of the question of what has happened, what is happening, and what will happen to the saguaro—at Saguaro National Monument and elsewhere throughout the range of its distribution in the Sonoran Desert—requires that perspective (Fig. 1). It is within the framework and perspective of

Figure 1 is a map located at the back of the book.

the evolutionary process that we explore the ecology of the saguaro.[1]

The National Park Service long has been concerned with the nature and cause of dramatic fluctuations that have altered grossly the structure of saguaro populations in certain portions of Saguaro National Monument (Fig. 2).[2] In the Cactus Forest area of the original Saguaro

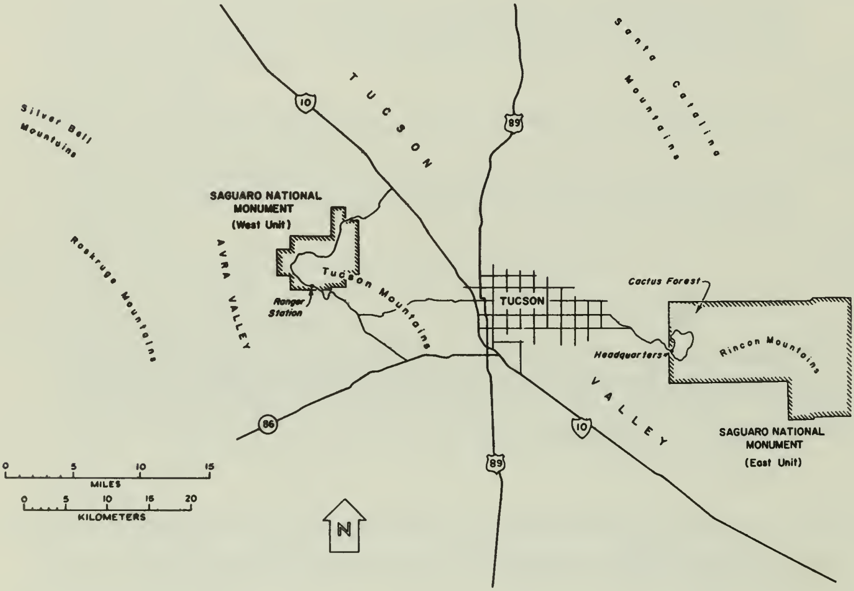

Fig. 2. Vicinity map of Tucson and Saguaro National Monument.

[1] Investigations on the saguaro giant cactus (*Cereus giganteus* Engelm., *Carnegiea gigantea* [Engelm.] Britt. and Rose) reported here and elsewhere were independently initiated in 1951 by co-author C. H. Lowe. Subsequently, the work was continued with the support of the National Park Service (and others) in recognition of the need for basic knowledge of the biology of the species to provide information essential for ecologically sound management of the natural resources of Saguaro National Monument and other National Park System areas in southern Arizona. Vernacular and scientific names now most commonly used are saguaro and sahuaro, and *Cereus giganteus* or *Carnegiea gigantea*.

[2] Saguaro National Monument is comprised of two separate units situated on opposite sides of the Tucson basin. The original, Rincon Mountain Section (east unit), is located approximately 15 miles (24.2 km) east of the Tucson city center. The more recently established Tucson Mountain Section (west unit) is located about 15 miles (24.2 km) northwest of Tucson. Shelton (1972) provided a general description and account of the natural and human history of the Saguaro National Monument.

National Monument, the once spectacularly dense concentration of giant old saguaros has dwindled in a few decades to an unimpressive population of sparsely scattered and dying old individuals (Fig. 3).

More important to the present and future condition of this population, however, is the relative sparsity of younger plants. That condition—the lack of sufficient younger saguaros to replace dead and dying older saguaros— insures absolutely that the number of large saguaros in this population will continue to decline.

The problem long pre-dates the establishment of the original Saguaro National Monument in 1933. The predominance of older saguaros and the lack of young individuals in photographs taken more than 40 years ago clearly reveal a population already many years in trouble (Fig. 3A). To a greater or lesser degree, other saguaro populations within Saguaro National Monument and elsewhere have undergone similar recent fluctuations (Figs. 4-6).

In recognition of the needs of the National Park Service, our continuing investigations on the ecology of the saguaro are designed to provide definitive knowledge of the problem and to develop information essential for interpretive and resource management programs. Those portions of our investigations we report here concern the second aspect of the problem—the establishment, growth, and survival of the young saguaro. Our experimental designs and the hypotheses that they test are directed specifically toward obtaining information on the operation of natural selection through climatic and other physical and biotic factors that are critically limiting on saguaro populations.

More amazing perhaps than any aspect of its biology is man's emotional involvement with the saguaro—the saguaro is a "hero" among plants. He has endowed it with human attributes and bestowed upon it affection and concern for its "problems." Moreover, he has embraced myths, half-truths, and even eulogies generated by reporters and feature writers concerned more with the production of sensational and emotionally appealing "doomsday" stories than with the effective communication of accurate information. Cast in the role of a "dying hero," the saguaro has been accorded affection and credited with traits of character that have seriously beclouded general understanding of the true nature of its biology.

The truth in its great complexity lacks such direct emotional appeal. In place of such appeal, the truth offers a far more satisfying and significant understanding of a fascinating scheme for survival—the continuing process of evolution through millennia of natural selection in a rigorous and ever-changing environment. It is for those who find satisfaction in such understanding that we offer the results of these investigations.

While the concerns of the National Park Service are necessarily provincial, the answers to the question of the fate of saguaros in

Fig. 3A. Dr. Homer L. Shantz and the Cactus Forest as it appeared in 1930, immediately prior to establishment of the original Saguaro National Monument. The superlative quality of this stand—the abundance of large, old saguaros—together with the near absence of smaller, young saguaros clearly indicates a population already in trouble. Homer L. Shantz photograph collection, University of Arizona Herbarium. Photographed 22 Feb. 1930.

Fig. 3B. Dramatic changes are evident in this view of the site shown in Fig. 3A, photographed 38 years later. In less than 4 decades, the forest of giant saguaros has been reduced to a few sparsely scattered individuals. No less significant is the death of all of the chain-fruit cholla *(Opuntia fulgida)* present in the 1930 photograph. Photographed 19 Feb. 1968.

Fig. 4A. Overview of the Cactus Forest, Saguaro National Monument (east). The Cactus Forest is situated in a gently sloping north-draining basin between the north-facing slopes of the Rincon Mountains (behind) and the south-facing slopes of the Santa Catalina Mountains on the horizon. Photographed 21 Feb. 1969.

Fig. 4B. Within the Cactus Forest, the die-off of saguaros continues in response to recurring catastrophic freezes. The abnormally slender stems and contorted form of moribound saguaros in the background, and the oozing black rot of the saguaro in the foreground are typical stages in the delayed collapse of freeze-damaged saguaros. As many as 9 years can elapse between lethal injury and the final collapse of a freeze-damaged saguaro. Photographed 28 May 1969.

Fig. 5A. At Saguaro National Monument (west), a dense and vigorous saguaro population occupies the rocky footslopes and upper bajadas of the Tucson Mountains. Rock outcrops and the southwestern slope exposure mitigate extremes of winter cold. Photographed 28 April 1974.

Fig. 5B. January 1971 freeze-killed saguaros on the lower bajada at Saguaro National Monument (west). Here, in the Cactus Forest of Saguaro National Monument (east) and in other topographically similar situations, cold air drainage contributes to the severity of recurring catastrophic freezes. Photographed 21 Nov. 1971.

Fig. 6A. A young saguaro population on the eastern footslopes of the Tucson Mountains. A total of 48 juvenile and unbranched young adult saguaros is visible within the photograph. There are no living individuals of the parent generation on this southwest-facing slope. Photographed 2 April 1970.

Fig. 6B. An old saguaro population on the lower bajada at Saguaro National Monument (west). Compare with the nearby young population shown in Fig. 6A. Fluctuation in density and age-structure is characteristic of saguaro populations in the cold-limiting parts of the range of this subtropical species. Photographed 16 April 1971.

Saguaro National Monument transcend political boundaries to include the species population and the environmental factors that control the limits of its distribution. Thus we have examined and report here not simply upon our specific observations and experiments conducted within Saguaro National Monument and at the University of Arizona, but also upon our investigations and those of others made elsewhere throughout the range of the saguaro.

The question of what has happened, what is happening, and what will happen to saguaros at Saguaro National Monument is a long-standing one of primary concern to the National Park Service. Further, the answers to that question directly relate to the condition and management of saguaro populations at Tonto National Monument and Organ Pipe Cactus National Monument (Fig. 1).

The applicability of these findings likewise is not limited by political boundaries; neither is the operation of factors that control the fate of the saguaro in the northern portions of its distribution in Arizona and northern Sonora limited in its controlling effects only to the saguaro. To a greater or lesser degree, the same factors are involved in controlling the northern limits of distribution and population dynamics of a large number of the tropically derived Sonoran Desert species in Arizona and Sonora. Particularly, many similar relationships occur in similarly evolved species of giant columnar cacti that reach the northern limits of their distributions either in Sonora or in adjacent southern Arizona: organpipe, senita, cardon, and hecho[3] (Figs. 7-9).

The Species

Distribution

The saguaro giant cactus is a drought-adapted, cold-intolerant, warm-desert species that occurs throughout the length and breadth of most of the Sonoran Desert (Figs. 1, 3-12; Shreve 1951; Shreve and Wiggins 1964; Benson 1969; Hastings et al. 1972). Within that distribution, it grows primarily on the coarse soils of south-facing rocky slopes and adjoining bajadas[4] and occurs sparsely or not at all on north-facing slopes

[3] Organpipe or pitahaya (*Cereus thurberi*, *Lemaireocereus thurberi*); senita or old-man cactus (*Cereus schotti*, *Lophocereus schotti*); cardon (*Cereus pringlei*, *Pachycereus pringlei*); hecho (*Cereus pecten-aboriginum*, *Pachycereus pecten-aboriginum*). See Benson (1940, 1950, 1969) and review by Felger (1970); Shreve and Wiggins (1964).

[4] A bajada is the broad, gently sloping alluvial plain extending from the base of the mountains to the valley floor.

or in the poorly aerated fine alluvial soils on the floor of the broad valleys that separate the characteristically discontinuous mountain ranges of the Basin-Range Province (Fig. 11).

At the southern limits of its distribution in southern Sonora, small disjunct populations occur on the basalt outcrops of hills (Fig. 12B). Disjunct populations also occur on rocky, south-facing slopes along the eastern and northern limits of its distribution in Sonora and Arizona (Fig. 12A). The Gulf of California marks the western limits of its distribution in Sonora (Fig. 9A). In southwestern Arizona and at the westernmost limits of its distribution in southeastern California within a few miles of the Colorado River near Blythe, sparse populations are directly associated with areas of concentrated runoff (Fig. 9A). The metropolis of the species population near the Arizona-Sonora border coincides more or less with the center of its geographic distribution (Fig. 11B).

Adaptive evolution and co-evolved species

The saguaro is one of a large group of tropically derived species of columnar cacti. Recent revision of the genus by Benson (1969) has been received with mixed reaction (see Felger 1970). The saguaro occurs only in the Sonoran Desert where it overlaps the distribution of four other closely related and ecologically similar species of columnar cacti: *Cereus pecten-aboriginum*, *C. pringlei*, *C. schotti*, and *C. thurberi* (Figs. 7-9). In South America, an evolutionary homolog of the saguaro,*Trichocereus terscheki*, occurs in the Monte of Argentina in a climate analogous to that of the Sonoran Desert.

Reported investigations on these co-evolved, warm-adapted species are few but significant in the relationship of those findings to a more complete understanding of the biology of the saguaro. Solbrig (1972) has reported on continuing investigations on the evolutionary significance of floristic disjunctions, between the Monte in Argentina and the Sonoran Desert in Mexico and the United States, that include columnar cacti. Felger and Lowe (1967) have described adaptive clinal variations in physical characteristics of the stems of the senita cactus (*Cereus schotti*).

McDonough (1963) has reported on phytosociological relationships of the organpipe cactus (*Cereus thurberi*) and compared germination responses (1964) with those of the saguaro.

Details on the physiological adaptations of the saguaro are little known. Soule and Lowe (1970) offer the only report on physiological adaptations of the saguaro to the environmental gradients within the geographic range of its distribution. They examined the relationship of

Fig. 7A. The cold-intolerant senita cactus (*Cereus schotti*) reaches the absolute northern limits of its distribution in Organ Pipe Cactus National Monument in southwestern Arizona. Truncated and prostrate stems are the result of freeze-caused injuries. Photographed 7 May 1971.

Fig. 7B. The organpipe cactus (*Cereus thurberi*), only slightly more cold-tolerant than the senita cactus (*Cereus schotti*), occurs north of the United States–Mexico border almost entirely within and a few miles north of Organ Pipe Cactus National Monument. Nearly every large individual in this northernmost part of its range bears a series of scars from recurring freezes. Photographed 12 July 1974.

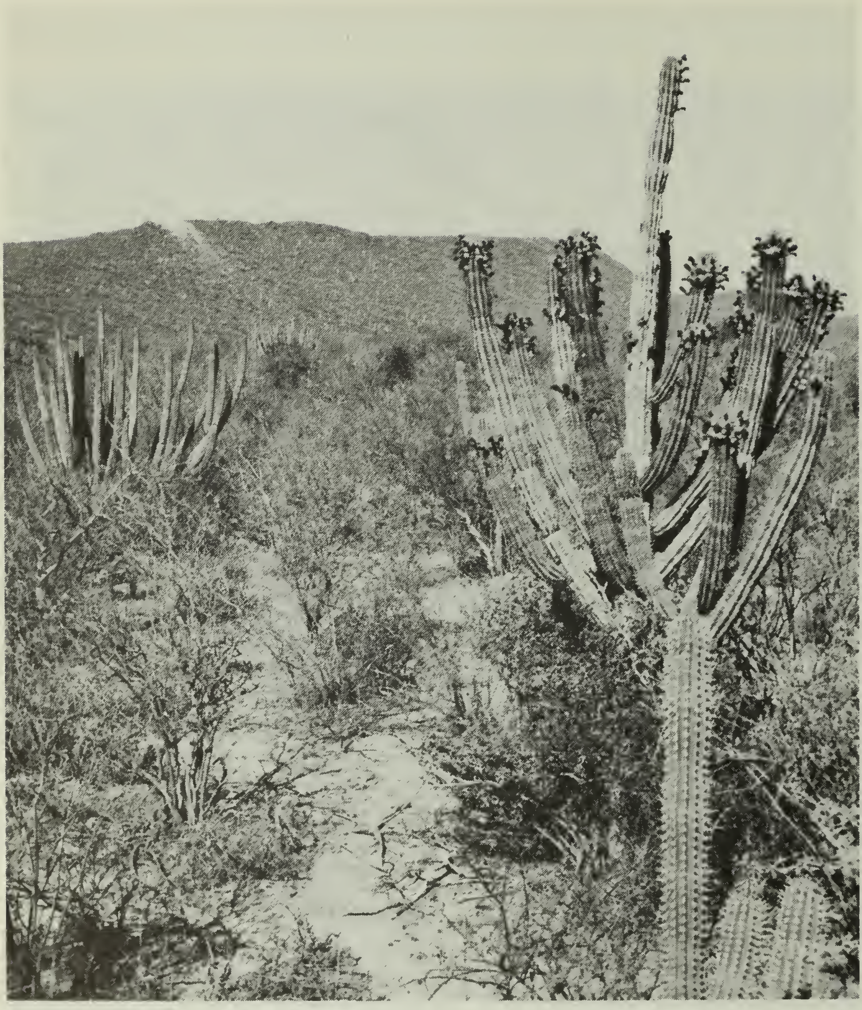

Fig. 8A. The southernmost saguaros grow on the slopes of Cerro Masiaca, 48 km (30 miles) south of Navojoa, Sonora, Mexico. On the slopes, it occurs with the closely related organpipe cactus (*Cereus thurberi,* left foreground) and hecho (*Cereus pecten-aboriginum*, right foreground). Photographed 7 Jan. 1972.

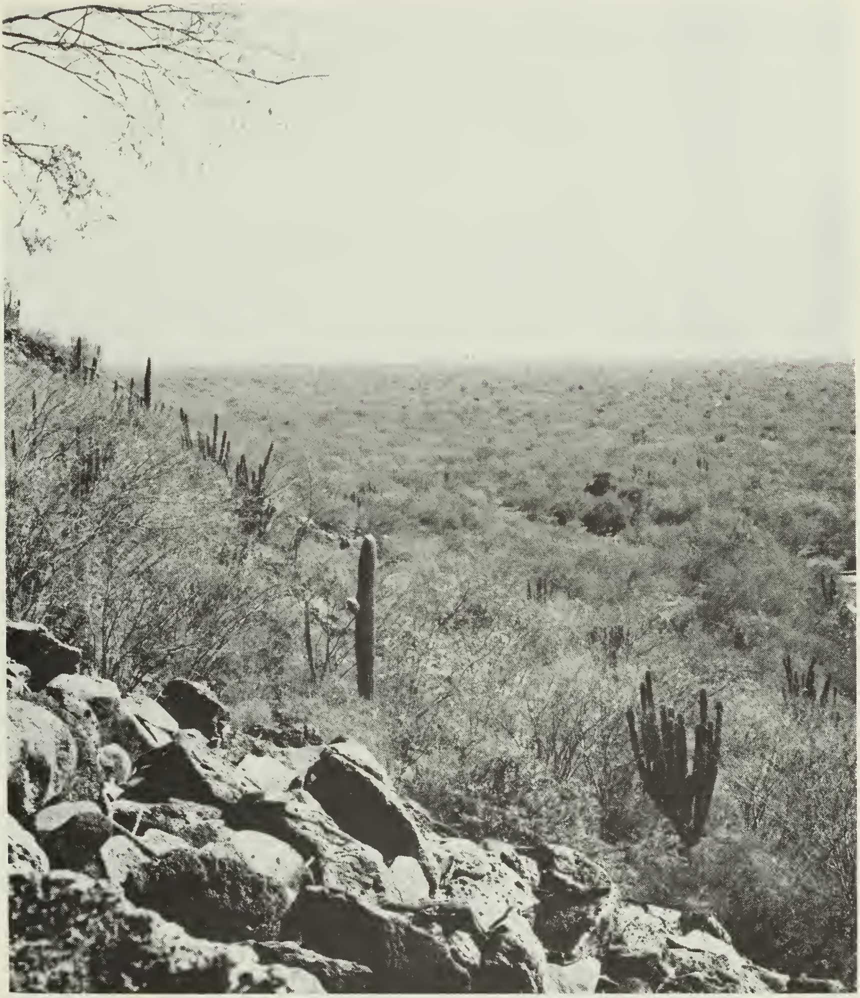

Fig. 8B. Cerro Masiaca and the southernmost saguaro population. The saguaros occur among basalt boulders and only on the south-facing slope of the hill—they do not occur on the adjoining plain. Subtropical deciduous thorn-forest, as seen in Fig. 8A, blankets the plains of southern Sonora and continues into northern Sinaloa on the distant horizon. Photographed 27 Dec. 1973.

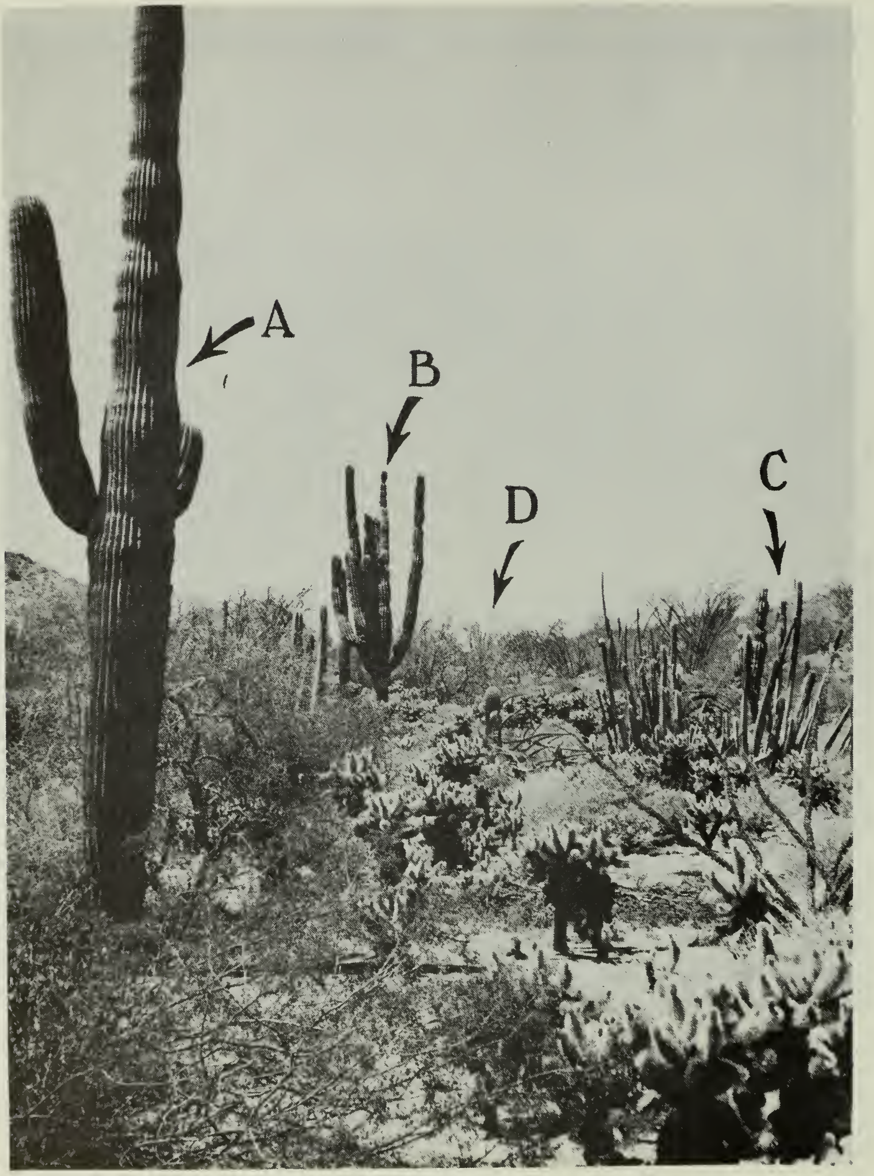

Fig. 9A. The saguaro (left foreground and right background, arrow A) occurs with cardon (*Cereus pringlei*, arrow B), senita (*Cereus schotti*, arrow C), and organpipe (*Cereus thurberi*, arrow D) cacti in the vicinity of Puerto Libertad, and elsewhere along the Sonora coast of the Gulf of California. Teddybear cholla (*Opuntia bigelovi*) and octillo *(Fouquieria splendens)* are conspicuous in right foreground. Most of the associated plant species–but not the saguaro–also occur in Baja California, on the west side of the gulf. Photographed 19 April 1974.

Fig. 9B. Sparsely scattered saguaros grow with "desert riparian species," desert ironwood *(Olneya tesota)* and foothill paloverde *(Cercidium microphyllum)*, at the western base of the Mohawk Mountains in Yuma County, southwestern Arizona. Along the *moisture-limited* westernmost boundaries of its distribution in the United States, the saguaro is associated with moisture-concentrating drainage channels. The nonriparian desert species conspicuous in the foreground are creosotebush (*Larrea divaricata*) and white bursage (*Ambrosia dumosa*). Photographed 13 April 1968.

Fig. 10A. At the *cold-limited* northern, eastern, and upper elevational extremes of its distribution in Arizona and northern Sonora, the saguaro grows on south-facing slopes in close association with boulders and rock outcrops.

The northernmost saguaros (shown) occur at an elevation of approximately 1524 m (5000 ft) in Cottonwood Canyon approximately 3.2 km (2 miles) northwest of Hualpai Peak, Mojave County, Arizona. All of the 11 adult saguaros at this site grow against the base of the vertical south-facing cliff; 10 saguaros are visible in the photograph. Associated plant species on the rocky slope include *Canotia holacantha* (crucifixion thorn), *Eriogonum fasciculatum* (shrubby buckwheat), *Larrea divaricata* (creosotebush), *Fouquieria splendens* (ocotillo), *Opuntia acanthocarpa* (buckhorn cholla), *Opuntia basilaris* (beavertail cactus), *Yucca baccata* (banana yucca), *Aplopappus laricifolius* (turpentinebush), and *Gutierrezia sarothrae* (snakeweed). Photographed 4 May 1975.

Fig. 10B. Vertical distribution of saguaros on Tanque Verde Ridge (Rincon Mountains), Saguaro National Monument (east). On this northwest exposure, the uppermost saguaros grow at an elevation of approximately 1350 m (4400 ft). On the southern slopes of these mountains, a few individuals grow in a rocky south-facing canyon at approximately 1524 m (5000 ft) elevation.

The saguaro species boundary line runs *through* the monument–the saguaro population at Saguaro National Monument (east) is a marginal one in every sense of the word. Photographed 14 Nov. 1969.

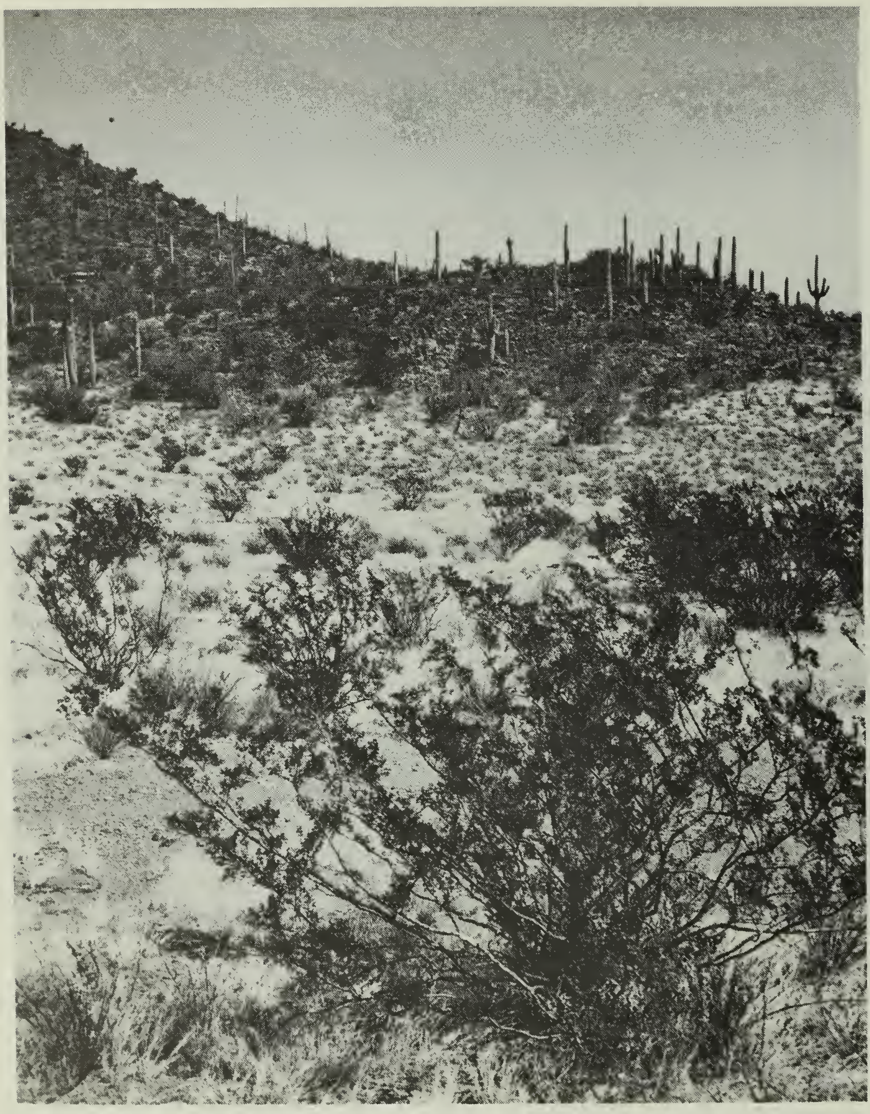

Fig. 11A. Saguaros growing on a south-facing rocky slope 72 km (45 miles) west of Tucson, Arizona. Throughout the vast range of its distribution in the Sonoran Desert, the saguaro grows primarily on the coarse soils of south-facing rocky slopes and adjoining bajadas. It occurs sparsely or not at all on north-facing slopes or in the poorly aerated, fine alluvial soils on the floor of the broad valleys that separate the characteristically discontinuous mountain ranges of the Basin and Range Province. Photographed 11 Feb. 1972.

Fig. 11B. Saguaro population west of Quijotoa (elev. 794 m; 2600 ft) in south-central Pima County, Arizona. This population, growing nearer the geographic center of the species' distribution, exhibits a relatively well-balanced distribution of age-size classes. The relatively more stable age distribution of the population indicates less severe winter freeze-kill than at Tucson and Saguaro National Monument. The community is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951), in which foothill paloverde *(Cercidium microphyllum)*, triangle bursage *(Ambrosia deltoidea)*, ocotillo *(Fouquieria splendens)*, jojoba *(Simmondsia chinensis)*, and several chollas and prickly pears (*Opuntia* sp.) are conspicuous dominants. Photographed 11 Feb. 1972.

Fig. 12A. A small, isolated population of saguaros growing on a south-facing rocky slope near Ruby, Santa Cruz County, Arizona. Note oak-studded grassland on adjacent north-facing slope. Other small disjunct populations growing in topographically similar situations occur elsewhere along the northern and eastern boundaries of the species' distribution in Arizona and northern Sonora. Photographed 24 Mar. 1968.

Fig. 12B. In southern Sonora, at Cerro Masiaca (and Cerro Prieto, 48 km = 30 miles northward) small disjunct saguaro populations, at the southern limit of the saguaro's range, are limited to the basalt boulder-covered, south-facing slopes clothed with subtropical thornscrub vegetation. Young saguaros are found growing in the boulder patches. Photographed 27 Dec. 1974.

differences in the osmotic potential of saguaro tissues to soil characteristics and climatic gradients over the range of the species in Sonora and Arizona.

Further studies on the adaptive mechanisms of the saguaro and other species of columnar cacti will certainly contribute to our knowledge of the ecology of each of these species, and to fuller understanding of the basic ecology of desert ecosystems.

Hypotheses on Saguaro Population Change

Some saguaro populations fluctuate markedly in density and age-structure (Figs. 3-6). This is especially true *and even characteristically so* in the cold-limiting parts of the range of this subtropical species (see Harper 1967; Steenbergh and Lowe 1976). Regarding such fluctuations, as seen for example at Saguaro National Monument, we comment briefly here on: (1)overgrazing; (2) climatic change; (3) "disease"; and (4) environmental limiting factors.

The first three hypotheses, more or less distinct and with relatively long histories, have originated in the Tucson area. In various combinations these basically differing hypotheses attempt to explain these fluctuations of saguaro populations in various localities. We briefly discuss here some of their more important limitations as they relate to the interpretation of the experimental results and observations of others, and to our own investigations since 1951 on the role of freezing weather and other limiting factors in the regulation of saguaro populations.

The grazing-plus-rodents hypothesis

Wilder and Wilder (1939:160) were the first to suggest the possibility that the sparsity of young saguaros in some nonrocky habitats might be related to ". . . the effects of erosion and cattle grazing. . . ." Mielke (1944:4), reporting on investigations at Saguaro National Monument (east), noted the sparsity of young saguaros and, concerning conditions necessary for establishment, states "This cannot take place in the presence of over-grazing or of the large rodent population, particularly of ground squirrels, now on the Monument."

In regard to saguaro populations including those at Saguaro National Monument, the question was further examined and discussed by Niering et al. (1963) and Niering and Whittaker (1965). They concluded that in some habitats grazing-caused alteration of the plant community results in increased density of rodent populations that destroy young saguaros, that this leads to slow decline and disappearance of saguaro populations in these habitats resulting from failure of the saguaro to reproduce, and that rodent populations may tend to keep saguaro populations at lower levels on the bajada than on rocky slopes. Further, they concluded that when, in some habitats, the effects of grazing are far advanced and rodent populations are high, these effects are largely irreversible.

A report on the influence of rodents and lagomorphs on the survival of transplanted saguaro seedlings at Saguaro National Monument (east) by Turner et al. (1969) concluded that ". . . there is no conclusive evidence that lagging reproduction of the saguaro forest at the monument is a result of increased feeding by small mammals on cacti."

Burgess (1964) examined saguaro populations at Tonto National Monument, Arizona, and discussed grazing in relation to observed bimodal age-class structure of the saguaro population at that location. He hypothesized that historic grazing may be responsible for the relative sparsity (10%) of saguaros 30-75 years old, and that the much larger proportion of younger plants (33%) may be correlated with protection from grazing during the previous 24 years.

Obviously, overgrazing produces changes in the natural environment that are seriously detrimental to the establishment and survival of young saguaros. However, the hypothesis may overestimate the ultimate impact of rodents, and fails to accord sufficient importance to the *controlling* effect of recurring catastrophic freezes in these marginal habitats.

The climate change hypothesis

Climatic change (together with grazing) has been proposed as a possible cause of the lack of young saguaros in the "valley portions" of Saguaro National Monument. Turner et al. (1966:102) suggested that failure of saguaro "population recovery" in these habitats may be dependently related to a decline in shrubs and trees; that "General forces, such as grazing or climatic change, which cause the loss of perennials, first affect the nurse plants, and then the influence of these forces is relayed to the saguaro populations."

The question of historic changes in saguaro populations and associated vegetation in Saguaro National Monument has been explored by Hastings and Turner (1965). Photographs they provide support earlier observations that the saguaro population in the flat habitat of the Cactus Forest area and the adjacent rolling hill habitat of the east monument was not maintaining itself. Further, they observed that ". . . in the rocky foothills and along the lower slopes of the Tangue Verde Mountains . . . the saguaro seems to be re-populating and the plant communities appear to be stable." The report also provides documentation of fluctuations in the status of associated perennial plant species populations and offers the observation that ". . . the giant cactus is dying out, but so, in many parts of Saguaro National Monument, is much of the rest of the community associated with it" (Hastings and Turner 1965:197).

Important as these observations are, they are not explained in relation to those authors' interpretations of climatic change. The observed die-off of large saguaros is attributed to "bacterial necrosis," and they offer that ". . . the disease has probably always been a major cause of death" (Hastings and Turner 1965:195).

The possibility that the sparseness of young saguaros in these populations is related to the reported climatic trends could be assumed. However, Hastings and Turner (1965) drew no specific conclusions concerning the relationship of the reported climatic changes to the observed sparsity of young saguaros in these unstable populations, or to observed changes in the associated plant community.

From their analysis of weather records back to 1898, Hastings and Turner (1965:287) concluded: "With fluctuations, winter rainfall has dropped markedly and winter temperatures have risen; summer rainfall has remained about the same, or has decreased slightly; . . ." Such trends would doubtless affect saguaro populations in California, western Arizona, and northwestern Sonora where lack of moisture controls the western limits of the species distribution. However, as we will further show in this report, the observed changes in the saguaro populations along the eastern and northern boundaries of its distribution—where the species is limited neither by lack of moisture nor high temperature—cannot be explained either by a decrease in mean winter or summer precipitation or by a rise in mean winter temperatures.

The "bacterial necrosis disease" hypothesis

Catastrophic freeze-caused lethal injury to saguaros is followed by the dramatic breakdown of damaged tissues—often not evident till long after the critical freeze. The bacterial necrosis of such damaged tissues—the so-called "bacterial necrosis disease"—is the long-recognized, natural, and ecologically important process of natural decomposition. The once presumed fatal disease is a *result,* not a cause, of saguaro death.

"Bacterial necrosis disease" has been called a "major cause of saguaro death" (Hastings and Turner 1965:195). The attrition of saguaros in the Cactus Forest area of Saguaro National Monument (east) attributed primarily to "bacterial necrosis disease" together with failure to "maintain an adequate rate of natural repopulation" has led to the prediction that this plant population will cease to exist by the end of this century (Alcorn and May 1962).

In his original description of the species, Engelmann (1852) remarked on the ". . . decomposition of the fleshy parts" of the saguaro. Numerous others during the following 120 years observed and reported on various causes of saguaro death and described the subsequent process of decomposition and the many diverse organisms associated with that ecologically important process.[5]

Shreve (1910:238) noted that saguaro deaths ". . . are due in at least 90% of the cases to mechanical factors . . ." and are ". . . followed by the work of bacteria and fungi." Shreve (1911) subsequently established that freezing is an important cause of saguaro deaths (see also Thornber 1916). Apparently unaware of this important early work, Lightle et al. (1942) identified a rot-associated bacterium (*Erwinia carnegieana*) and unfortunately termed the long-known necrosis of the saguaro a "disease."

A comprehensive survey on the condition of saguaro populations at Saguaro National Monument (east), in the Tucson Mountains, and at Organ Pipe Cactus National Monument was begun in 1941 by the USDA Bureau of Plant Industry. At the same time the bureau initiated a massive experimental "sanitation program" involving "surgery" or the removal of all rotting saguaros from a 0.5 mile^2 area (1.29 km^2) of the Cactus Forest portion of the Saguaro National Monument (east).

The unpublished reports of those investigations (Gill and Lightle 1942, 1946; Mielke 1944; Gill 1951) contain a large amount of valuable information relevant to the understanding of the population ecology of the saguaro in Arizona.

Particularly relevant to the question on the factors limiting the establishment and survival of young saguaros is the following important observation by Mielke (1944:3) that "Many seedling saguaros, grown in the greenhouse, have been inoculated with the bacterium, but none of them have ever developed any symptoms of the disease. Rot pockets developed in some older plants inoculated by members of the Plant Pathology Department of the University of Arizona, but the pockets calloused out and the plants did not die."

Conclusions relating bacterial necrosis to vigor and age were offered by Gill and Lightle (1946:4): "Mortality is directly correlated with size, the larger plants being subject to higher death rates . . . the mortality rate rises sharply in plants over 18 feet high.", and by Mielke (1944:1):

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[5] The list of references includes Hooker 1892; Hubbard 1899; MacDougal 1908b; Shreve 1910, 1911, 1920, 1929, 1931a, 1945, 1951; Brown et al. 1942; Lightle et al. 1942; Gill and Lightle 1942, 1946; Brown and Boyle 1944; Mielke 1944; Boyle 1949; Gill 1951; Howes 1954; May and Palmer 1959; Alcorn 1961a, 1961b, 1966; Santana 1961; Alcorn and May 1962; Graf 1965; Takacs 1967; Schuyler 1968.

". . . only the older saguaros and those apparently lacking in vigor are killed as a result of attack by the rot." Gill (1951:4) concluded that the rot was "linked with overmaturity."

Massive freeze-caused death of saguaros in 1962 followed by bacterial necrosis was reported by Niering et al. (1963) and Lowe (1964, 1966). Steenbergh (1970) reported on rejection of bacterial rot by saguaros and on bacterial necrosis following lightning kill (1972). Bacterial necrosis of saguaros following catastrophic freeze-kill of saguaros in January 1971 is described by Steenbergh and Lowe (1976).

The relationship between freezing and the collapse and decomposition of vegetable tissue has long been recognized. M. A. de Candolle accurately described the relationship in 1838 (1852; see Chap. VI).

More than a century—125 years—was to pass, however, before de Candolle's important discovery was recognized as the obvious explanation for the reported "epidemics of bacterial necrosis disease of the saguaro."

Limiting Factors

The saguaro giant cactus at Saguaro National Monument is not some rare exception to the fact that *environmental limiting factors* modify all terrestrial plant species from population to population wherever located within the ultimate limits of the species distribution, at which boundary such factors finally become 100% limiting. Moreover, Saguaro National Monument is not only just near the saguaro's distribution limits, the saguaro species boundary line runs *through* the monument (Figs. 1, 10A). The monument (east) population is a marginal one in every sense of the term.

Temperature, precipitation, topography, soil, and predators are examples of powerful ecological factor groups that operate as density-dependent or density-independent limiting factors. Wiggins (1937) noted the population disaster of the subtropical organpipe cactus at the northern extremity of its range in southwestern Arizona during the serious winter freeze of 1937. In a concise rephrasing of Taylor's (1934) observations on the importance of extremes on the geographical limits of the distribution of species, Wiggins (1937) emphasized that ". . .it is the greatest extreme of a year of unfavorable conditions or the greatest extreme of a series of unfavorable years that finally limits the distribution of species. . . ." This is especially true for cold-limited subtropical species as they occur, for example, at their northern latitude and elevational extremities in the southern parts of California, Arizona, New Mexico, and Texas.

Thus the extremes, not the means, are in final control. Short of becoming limiting, the extremes alter the population age-structure and growth according to the intensity and periodicity of the factor. For pertinent discussions on the ecological problem in general and southwestern communities in particular, see Thornber (1911, 1916), Shreve (1911, 1915), Good (1931), MacGinitie (1933), Taylor (1934), Mason (1936, 1947), Wiggins (1937), Turnage and Hinckley (1938), Cain (1944), Went (1957), Lowe (1959, 1964), Daubenmire (1964), Harper (1967), and Odum (1971).

Among the many physical and biotic factors that are controlling, climate is the most clearly overriding. In the light of such effective modifiers of population systems through natural selection such as climate, topography, soils, predators, et al., there is no mystery to the geographical and ecological distribution of the saguaro, nor is there mystery to the wide geographic variation in structure, function, density, and fluctuation of saguaro populations within the huge southwestern range of the species (Fig. 1).

We devoted the first of these volumes on the ecology of the saguaro to the role of freezing weather—the most periodically damaging as well as finally limiting density-independent climatic factor affecting the saguaro at Saguaro National Monument and elsewhere at the edge of its range in Arizona. Throughout the present volume, limiting factors appear continuously as we discuss drought, freezing, soil-type, slope exposure, animals, et al., in relation to experiments and observations on germination, establishment, growth, and survivorship in natural populations of saguaros.

Ecological Perspective

We have previously reported on various aspects of the ecology of the saguaro since these continuing investigations were initiated in 1951. The subjects of previous reports include critical factors during the first years of life (Steenbergh and Lowe 1969), bacterial decomposition (Steenbergh 1970), osmotic characteristics of tissue fluids (Soule and Lowe 1970), lightning-caused destruction (Steenbergh 1972), and the role of freezing weather (Lowe 1959, 1964, 1966; Steenbergh and Lowe 1976).

In this report we include results and conclusions on additional experiments and observations on saguaro reproduction and germination, establishment, survival, and growth to the age of first reproduction together with related results and conclusions from our earlier reports. In the concluding section of this report we offer a brief review and a discussion of natural and human historical factors that bear on the question of the past, present, and future of the saguaro at Saguaro National Monument and elsewhere in the northern portions of its distribution in Mexico and the United States.

The results and the conclusions presented here offer a basis for management policy and decisions affecting the saguaro populations in question. In addition, this report provides information that can serve as a basis for an interpretive program that offers an understanding of basic ecological concepts that underlie the interactions of all living things with each other and with the environment in which they live—and die.

Management recommendations based on our investigations, offered in Appendix I, are of particular interest to the National Park Service not only as they relate specifically to saguaro populations at Saguaro National Monument but also to populations in the three other national monuments in Arizona where the saguaro also occurs: Casa Grande National Monument; Tonto National Monument; and Organ Pipe Cactus National Monument. To a greater or lesser degree, saguaro populations in the latter national monuments are and have been responding to natural and man-caused environmental factors. To a large extent, these same recommendations are applicable to the management of Organ Pipe Cactus National Monument populations of the closely related and similarly responsive organpipe and senita cacti.

The saguaro is the long-lived integrator of the natural environment and the historic uses and abuses of its habitat within Saguaro National Monument and elsewhere throughout most of the Sonoran Desert. Thus the saguaro provides a long and useful on-site record of the historic environment that spans nearly the entire range of the climatic extremes of temperature and moisture of the Sonoran Desert. Knowledge of the ecology of this responsive species, therefore, offers valuable insights to the understanding of the adaptive evolution and the interrelationships of other associated desert species and to their relationships to each other and to the environment, past and present. It is within that perspective that we have examined and report here our findings and conclusions, and it is within that framework that we offer management recommendations on the saguaro giant cactus.

2
Reproductive Growth

> *Dr. Parry was informed that the flowers were produced in May and June, from the summit of stem and branches; they are said to be white, with a red centre, and three inches in diameter. The fruit matures in August, and is set with small spines: it is obovate, one and a half inches in diameter, red, pulpy, of sweet taste.*—George Engelmann, "Notes on the *Cereus giganteus* of south eastern California, and some other Californian Cactaceae," 1852:337.

Phenology

The saguaro blooms and produces a crop of succulent fruits during the driest period of the year—the hot, often rainless months of late spring and early summer. In the absence of other moisture, fruit development is insured by the reservoir of moisture stored within the succulent stem. Thus, each year, the saguaro produces a large crop of seeds that mature just prior to the start of germinating summer rains.

The chronology of saguaro flower and fruit production has been described by Engelmann (1854) and subsequently by other observers including Toumey (1897), MacDougal and Spalding (1910), Shreve (1929), and Thackery and Leding (1929). In addition, numerous references concerning historical observations on the timing of saguaro fruit harvest by aboriginal peoples are noted by Castetter and Bell (1937). Johnson (1924) reported on the effects of solar radiation and internal stem temperatures on the development of blooms.

The timing of saguaro flower and fruit production appears to be controlled primarily by the arrival of warm spring temperatures coupled to increasing day length (Johnson 1924). This is reflected in the difference in the date of the appearance of the first buds, blooms, and the beginning, peak, and decline of fruit maturation in different portions of the plant's geographic range in Arizona and Sonora.

The initiation and development of buds, flowers, and fruits occurs on progressively later dates from south to north, and from lowest to highest elevations. Moreover, in the Tucson area there is a lag of 1-2 weeks between the first appearance of buds and open flowers at the Saguaro National Monument west of Tucson and their development at the original higher elevated monument 30 miles (48.3 km) eastward. The difference in flowering time (also dates for budding and fruiting) between these saguaro populations is due to relative differences in temperature that result from differences in elevation, topographic association, cold air drainage, and slope exposure (Table 1).

Flowering date and the time for saguaro fruit maturation are highly variable from year to year depending upon the temperatures occurring during the late winter and spring of the particular year and the genetically controlled variability within the population.

In the vicinity of Tucson, the first flower buds ordinarily appear on most individuals sometime during the last 15 days of April. The blooming peak ordinarily occurs during the last week of May or the first week of June. A few individuals bear their first ripe fruits at that time. Thereafter, the number of ripe fruits increases rapidly, reaching a peak that occurs from the last week of June into the second week of July according to year. The remaining fruits ripen and the number remaining on the plants falls abruptly during the following 10 days in any year (Fig. 13A).

A few individual saguaros produce blooms and mature fruits in late summer, fall, and even during winter months. On one plant, ripening fruits were observed on 6 January 1969. Other genetically divergent individuals have been observed to bloom in December, and in September and October. Generally, such blooming produces only a few fruits (or none), and these are usually consumed by birds as fast as they ripen. It is unlikely that any germination results from such off-season fruit production, and none has been observed, inasmuch as germination is associated with the summer warm-season monsoon.

Early or late arrival of warm spring temperatures (March into May) can produce substantial year-to-year variation in the timing of bud, flower, and fruit development. Similarly, because of warmer temperatures there, the peak of fruit maturation regularly occurs approximately 5-7 days earlier in habitats of the western (Tucson Mountain) section of the monument (elevations upward from 616 m [2021 ft]) than in the comparatively cooler habitats of the eastern (Rincon Mountain) section of the monument (elevations upward from 823 m [2700 ft]; Fig. 13, Table 1). A similar lag of a week to 10 days in any given year occurs from the edge of the Gulf of California (e.g., in the vicinity of Bahia Kino) inland to the mountains in the vicinity of Hermosillo, Sonora, a distance of 80 km (50 miles) and difference of 700 m (2297 ft) elevation.

TABLE 1. Locality, elevation, topographic association, and slope exposure of four habitats in the Tucson region sampled to obtain saguaro flowering phenology. See text.

Locality	Elevation		Topographic association	Slope exposure
	m	ft		
Saguaro Natl. Mon. (east) (Cactus Forest flats)	870	2850	Adjacent to north slope of a conifer-clad mountain (elev. 2641 m; 8666 ft)	north
Tucson Mountains (east bajada)	701	2300	Adjacent to east slope of a desert mountain range (elev. 1429 m; 4687 ft)	east
Saguaro Natl. Mon. (west) (west bajada)	716	2350	Adjacent to west slope of a desert mountain range (elev. 1429 m; 4687 ft)	west
Silverbell Mountains (east bajada)	665	2180	Adjacent to east slope of a desert mountain range (elev. 1277 m; 4190 ft)	east

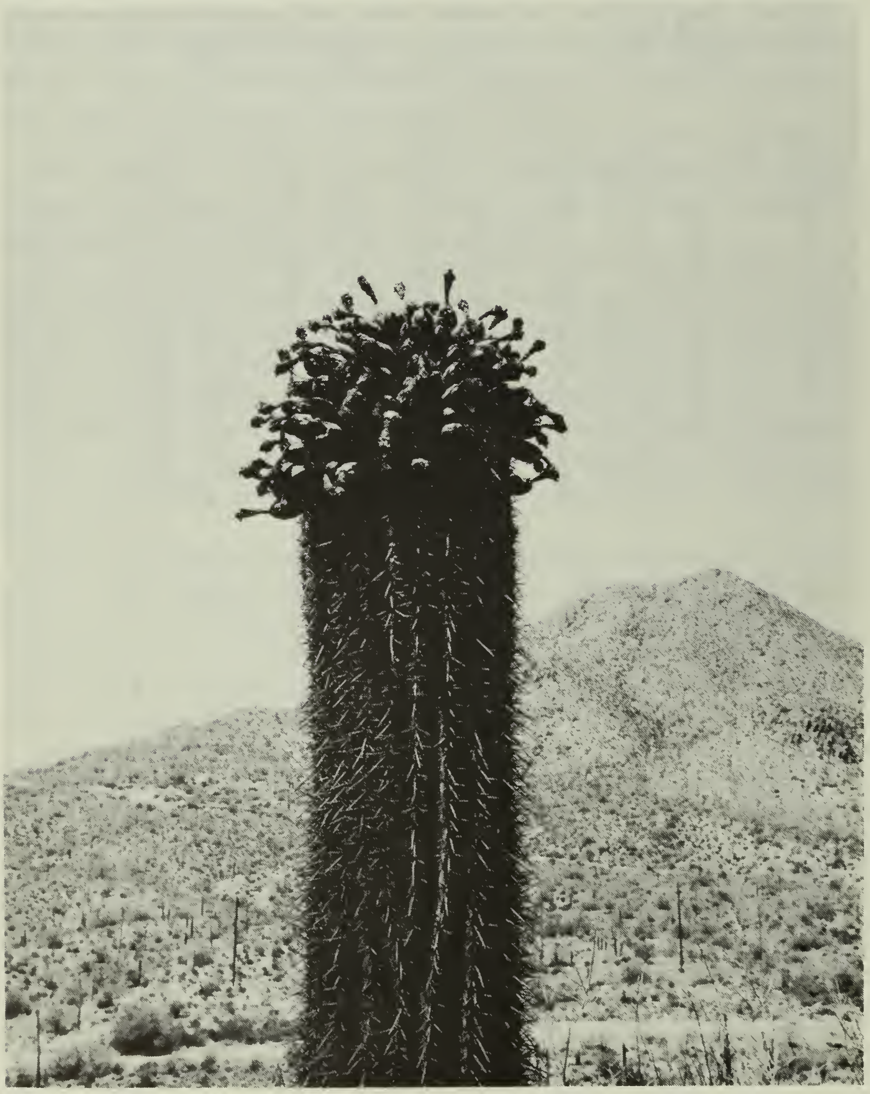

Fig. 13A. Approximately 100 ripening fruits on a 4.5-m (14.8-ft) saguaro in mid-June.

Fruits develop during the driest period of the year–the hot and usually rainless months of late spring and early summer. The peak of fruit ripening in the Tucson vicinity occurs from the last week of June into the second week of July, depending upon the early or late arrival of warm spring temperatures in March-April. Photographed 17 June 1974.

Fig. 13B. Reproductive growth of a "dead" saguaro completely severed from its roots by lightning in early September 1969. The undamaged upper portion of the stem produced buds (arrow) and flowers during the spring of 1970, and again in 1971.

Energy for reproductive growth derived from succulent stem tissues allows flower and fruit production to proceed independently of year-to-year variation in rainfall. Thus, an annual crop of saguaro seeds is guaranteed even following a year or more of extreme drought. Photographed 13 May 1971.

At Sacaton, Arizona, Thackery and Leding (1929) observed that the period for development and ripening of saguaro fruits averaged 30 days for flowers that appeared in June. At Tucson, McGregor et al. (1962) found that the average time for fruit development from flowering to maturity was 37 days (range 31-45 days). They also observed that fruits from late-blooming flowers matured at a faster rate (the low end of the range) than those which opened at an earlier date.

During years when flowering is delayed by cold spring temperatures, we have observed that there occurs a similar speed-up in fruit development. During occasional years when low temperatures delay spring blooming by as much as a full month, the subsequent delay in fruit development may be only 7-10 days due to process "catch-up" toward the end of the reproductive season. Such a 1-2 week delay in seed drop coupled with an earlier-than-usual arrival of good summer rains have occasionally produced a bumper crop of saguaro seedlings.

The flowers of the saguaro open during the early nighttime hours and remain open until afternoon of the following day (see Peebles and Parker 1941). We have found that saguaro flowers and those of other large columnar species stay open longer on cool days and on days earlier (cooler) in the spring flowering season.

Natural pollination, which is accomplished by animals, occurs primarily during nighttime and early morning hours. Cross-pollination, essential for fertilization and fruit development, is effected by a variety of flying animals (insects, birds, and bats) that feed upon the pollen and copious nectar of the open flowers (MacDougal 1905; Alcorn et al. 1959, 1961; McGregor et al. 1959, 1962).

Freeze and Drought Limitations

Reproductive growth occurs during the driest period of the year, and is supported by energy derived from succulent stem tissues (Lloyd 1907; Fig. 13B). Extreme drought conditions during winter and spring appear to have little or no diminishing effect upon reproductive growth (Thackery and Leding 1929). Thus, regardless of year-to-year variations in rainfall, the saguaro produces an annual crop of seeds.

Winter freeze-caused injuries can effect a drastic reduction in the current year's fruit production. Subsequent to severe freezes in January 1962 and in 1971, most reproductive saguaros in the Tucson area exhibited abnormal fruiting patterns and diminished production of fruits. Normally productive areas of stem and arm tips, often showing no evident signs of injury, failed to produce fruits (Fig. 14A; Table 2).

We estimate that in the Tucson area in southeastern Arizona, January freeze-caused injury reduced the 1971 seed crop to less than 20% of that for the previous year (Fig. 14A). To a lesser degree the 1971 injuries also reduced fruit production in 1972, when permanent injuries were evidenced by barren and sometimes scarred areas on arm and stem tips (Table 3).

TABLE 2. Effect of freezing on fruit production of two unbranched saguaros at Saguaro National Monument (east), mature fruits present on 25 June.

Critical subfreezing temperatures, occurring 3-10 January 1971, produced no obvious damage to stem tissues of these plants. However, fruit production the following summer was less than 25% of that for the previous year. Other plants, some with visible damage to apical stem tissues, exhibited a similar reduction in fruit production (see Fig. 14A).

Plant no.	1970 Stem height (cm)	Matured fruits		% Decrease
		1970	1971	
69B	441	201	46	77.1
69D	461	141	28	80.1
Total	902	342	74	–
Mean	451	171	37	78.4

TABLE 3. Number of fruits maturing on each of four unbranched saguaros at Saguaro National Monument (east). Summer production in 1971 was reduced by 78% after January freeze 6 months earlier (see Table 2). The stem freeze-effect on fruiting also persisted into 1972 and 1973.

Saguaro	1969	1970	1971	1973
69A	73	–	6	11
69B	100	169	46	55
69C	76	–	68	91
69D	40	112	28	97

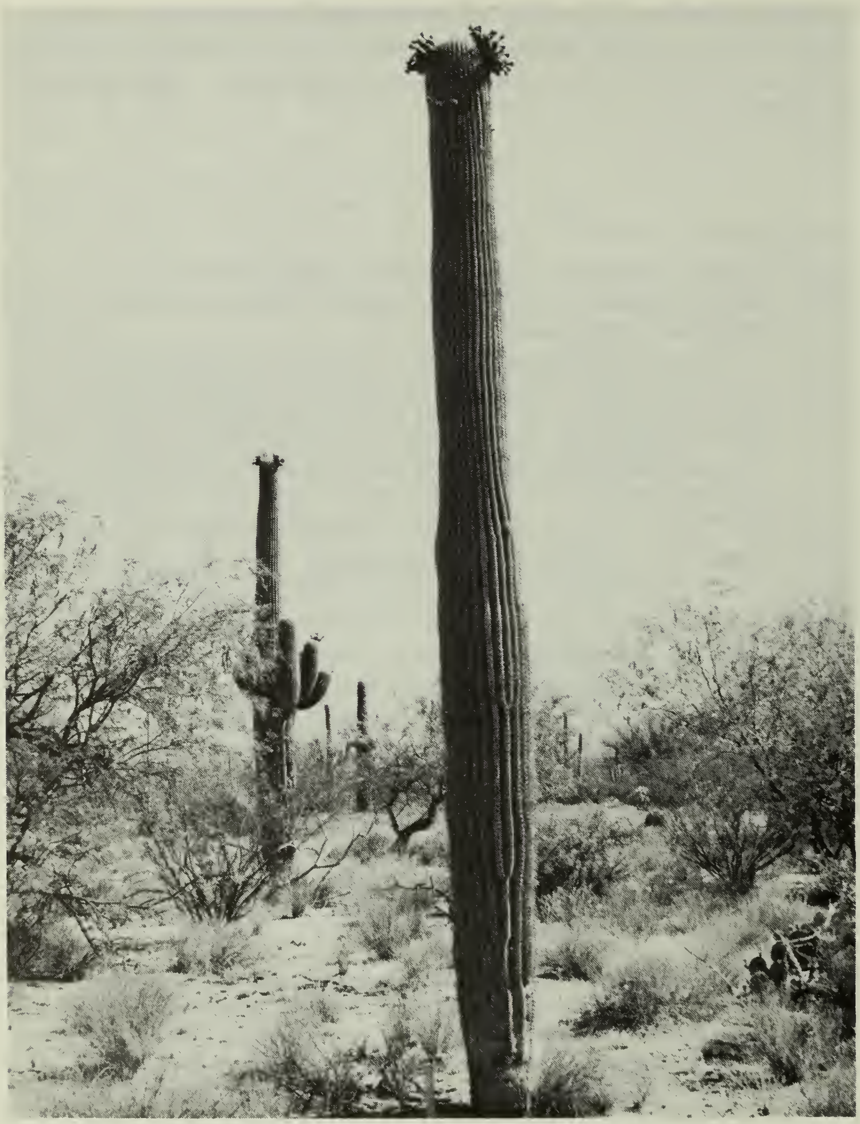

Fig. 14A. The effect of freeze-caused injury on saguaro fruit development at Saguaro National Monument (east). Compare with the normal plant shown in Fig. 13A.

The normally productive barren area of the crown separating the two clusters of fruit on this 4.5-m (14.8-ft) plant is a result of freeze-caused injury received the previous January. In 1970, a year without critical freezing conditions, 201 fruits were present on this plant on 25 June. On the same date in 1971, 46 fruits were present (Table 2). Most other adult saguaros in the Tucson area were similarly affected.

Along the *cold-limited northeastern boundary* of its range, saguaro seed production is significantly reduced during years when catastrophic freezes occur. Photographed 25 June 1971.

Fig. 14B. Reproductive growth of a senescent saguaro (arrow). The slender plant on the right (ht 12 m; 39.4 ft) bears two buds, ten flowers, and two well-developed fruits. Compare with the healthy saguaro at far left.

A common sight in Saguaro National Monument, the shriveled upper stem and arms that indicate a senescent condition are the delayed result of lethal freeze-caused injury–the plant is dead. Water uptake capability has been destroyed by freeze-caused internal damage to the lower stem. Long pre-existence of that condition (more than one year) is evidenced by the severely withered condition of the upper stem and arms which after the injury have continued to provide energy for reproductive growth. The ability to continue seed production for one or more years after the occurrence of a lethal freeze provides an added survival potential for populations along the *cold-limited northern and eastern margins* of the species range. Photographed 6 June 1973.

In some saguaro stands such as the Cactus Forest of the east monument, a long-term decline in reproductive growth accompanies the general loss of vigor produced by recurring catastrophic freezes (Steenbergh and Lowe 1976). Such stands are characterized by the apparent senescence of a larger proportion of the older plants. Their normal water-uptake capability damaged or destroyed by freeze-caused injuries to the root crown and stem base, these plants exhibit abnormally slender upper stems and arms (Fig. 14B). Such plants continue to bloom and set fruits each year in declining numbers, until the moribund plants collapse (see MacDougal 1908b; MacDougal and Spalding 1910; Pool 1916). This may occur up to 9 years or more after lethal freeze-caused injury. Some saguaros badly frozen in January 1962 began to fail immediately but did not completely disintegrate until 1968-70.

Completely doomed plants continue to flower long after their death has been insured by complete severing of the stem (Fig. 13B) or stem systems (Fig. 14B). Reproductive growth, occurring, in fact, after the "death" of the plant, involves an adaptive strategy that significantly enhances chances for survival of the population.

Reproductive Potential

Reproductive growth of a healthy saguaro begins when the plant is approximately 2.2 m (7.2 ft) tall (Table 4; Figs. 15A, 16). The first blooming may result in the production of only one or two fruits. The number of fruits increases rapidly, however, in succeeding years, and production commonly exceeds 100 fruits per year by the time the plant has attained a height of 4.5 m (14.8 ft) (Table 3; Fig. 13). At that time, the first arm buds develop on vigorous individuals. As early as the third spring thereafter, when they have attained a length and diameter of about 15 cm (5.8 inches), the spherical arms begin to produce fruits (Fig. 15B).

The number of fruits borne on the arms increases rapidly in succeeding years. The function of arms on the saguaro is to increase the number of fruits, and hence, the number of seeds produced by the plant.

Mature fruits weigh about 50 g (1.8 oz) each and contain approximately 2250 seeds (Table 5; Fig. 17). Under natural field conditions at Saguaro National Monument, the authors have obtained up to 60% germination success from broadcast seeds. Under controlled conditions, seed viability closely approaches 100%. Heit (1970) obtained 98% germination of wild Arizona seeds in the laboratory (14 days) with alternating daily temperatures (20-30°C; 68-86°F) and exposure to light (8 hr per day) with seeds in closed dishes and a uniform moisture supply. McDonough (1964) obtained similarly high germination percentages of

TABLE 4. Reproductive status of young saguaros at Saguaro National Monument (west), based on presence or absence of reproductive structures (buds, flowers, or fruits) for all plants 1–4 m (3.3–13.1 ft) ht in transects in flat habitat (20 × 700 m; 66 × 2297 ft) and rocky habitat (20 × 350 m; 66 × 1148 ft) 10 June 1968.

The mean density of saguaros 1–4 m ht was approximately four times greater in the rocky habitat (78.6 stems/ha; 31.4 stems/acre) than in the flat habitat (18.6 stems/ha; 7.4 stems/acre). Data graphed in Fig. 16.

	Reproductive structures						
Height Class (m)	Flats		Rocks		Total		
	Present	Absent	Present	Absent	Present	Absent	%
1.00–1.49	0	3	0	13	0	16	0.0
1.50–1.99	2	6	3	15	5	21	15.4
2.00–2.49	1	1	4	4	5	5	50.0
2.50–2.99	5	0	4	0	9	0	100.0
3.00–3.49	2	0	7	0	9	0	100.0
3.50–3.99	6	0	5	0	11	0	100.0
Total	16	10	23	32	39	42	

90-100% with fresh seeds and noted the lower values reported by Alcorn and Kurtz (1959).

According to Shreve (1931b), the saguaro begins reproductive growth at age 50-75 years—a conservative estimate, see Tables 4 and 28—and lives 150-175 years. Based on an estimated average production of 200 fruits per year, a healthy saguaro produces a total of 40 million viable seeds during its 100-year reproductive life span. Saguaro populations at Saguaro National Monument and elsewhere in the Tucson area are characterized by high densities of reproductive saguaros (Gill and Lightle 1942; Alcorn and May 1962; Niering et al. 1963). In bajada stands at Saguaro National Monument, Niering et al. (1963) reported densities of reproductive size saguaros (plants greater than 2 m ht; 6.6 ft) of 101 stems/ha (2.5 acres) in the east monument, and 154 stems/ha in the west monument.

Fig. 15A. Reproductive growth of a saguaro begins when the plant is approximately 2.2 m (7.2 ft) tall (see Fig. 16). The first blooming commonly results in the production of only one or two fruits. The production of fruits increases rapidly in succeeding years and commonly exceeds 100 fruits per year by the time the plant has attained a height of 4-5 m (13.1-16.4 ft). Photographed 17 July 1973.

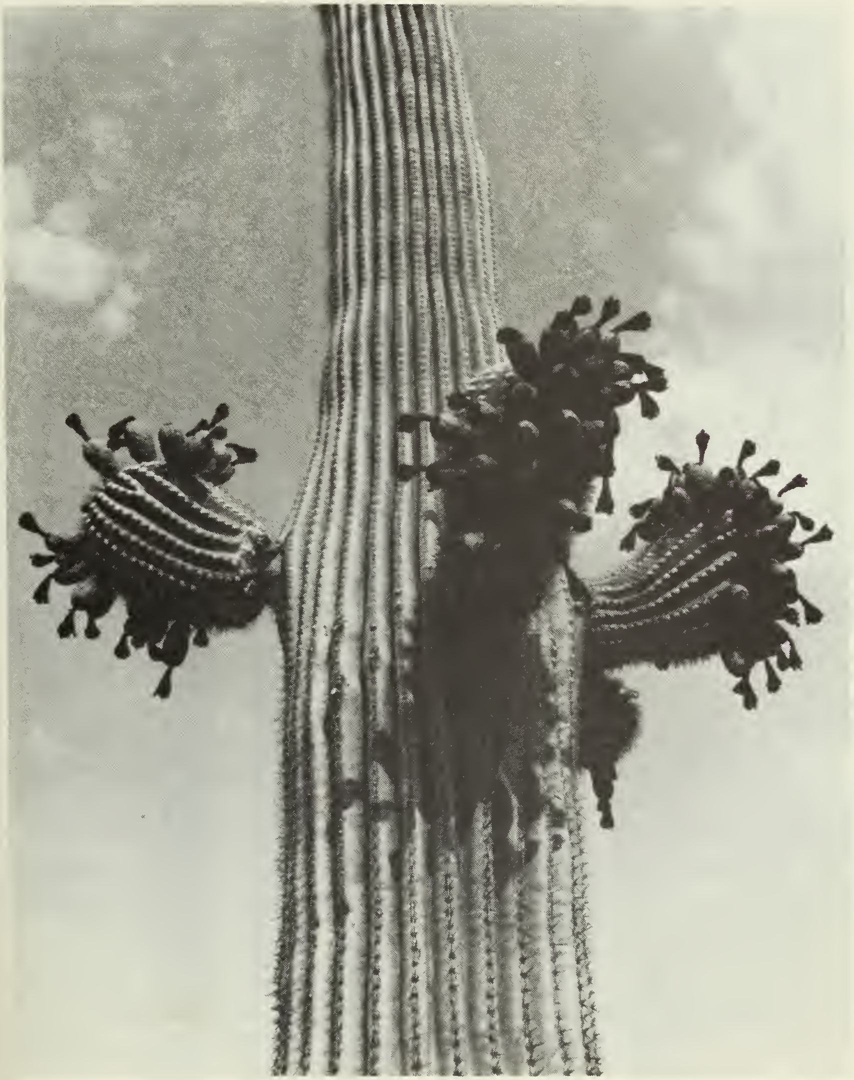

Fig. 15B. Five small arms produced 113 of the total annual crop of 182 fruits on this 5-m (16.4-ft) saguaro. During the fourth spring after their first appearance, three visible 30-cm (12-inch) arms bear a total of 103 ripening fruits. Two third-year arms behind (16 and 18 cm; 0.5 and 0.6 ft) produced an additional four and six fruits, respectively.

Arm buds emerge during the summer growth period, when the plants have attained a stem height of 4-5 m (13.1-16.4 ft) or more. Reproductive growth on arms has been observed the third spring thereafter when the arms have attained a diameter of about 15 cm (5.8 inches).

The function of arms on the saguaro is to increase the number of fruits, and hence the number of seeds, produced by the plant. Photographed 25 June 1974.

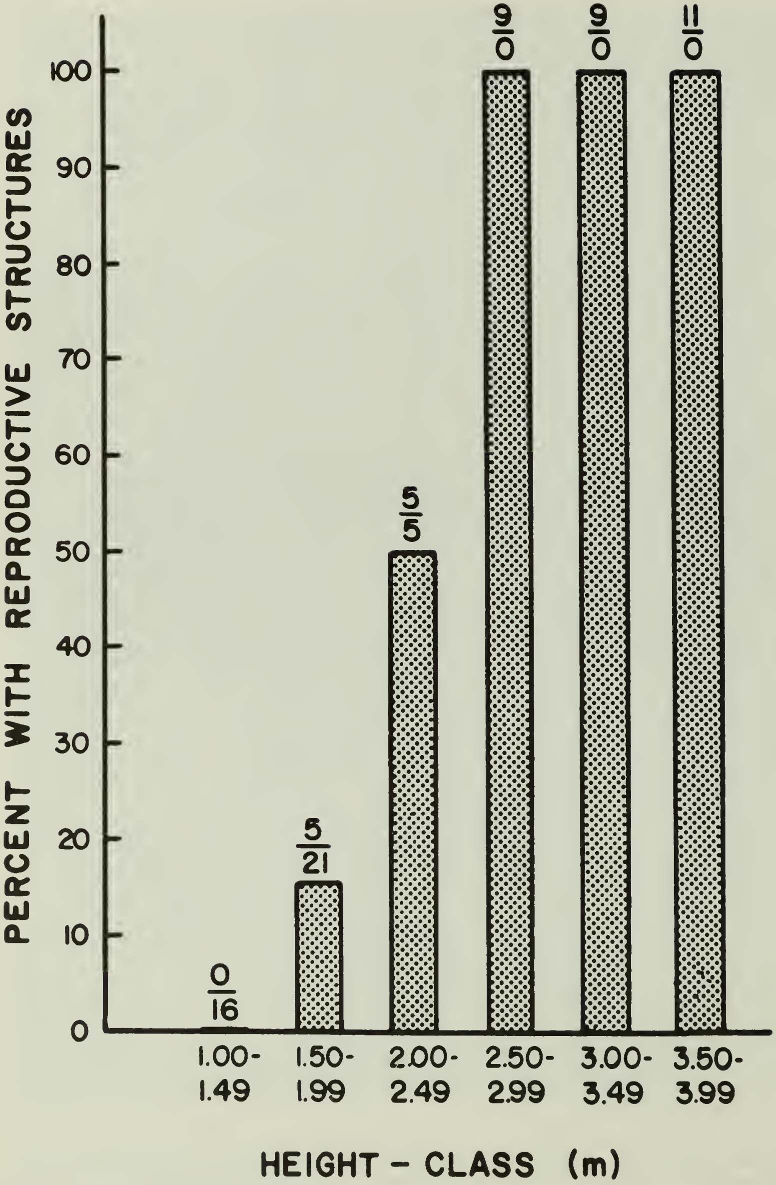

Fig. 16. Heights and percentage of saguaros with reproductive structures (buds, flowers, or fruits) at Saguaro National Monument (west); N = 81. The sample includes all plants 1-4 m (3.3-13.1 ft) tall in transects in flat habitat (20 X 700 m; 66 X 2297 ft, N = 26) and rocky habitat (20 X 350 m; 66 X 1148 ft, N = 55). The numbers above each bar are the reproductive (upper number) and nonreproductive plants (lower number) in each height class.

In this population the approximate mean height at the age of first flowering is 2.25 m (7.4 ft). Data in Table 4.

TABLE 5. Size, weight, and seed content of ripe saguaro fruits (N = 18) collected 21 June 1968, Saguaro National Monument (west). The mean seed weight is 1.3 mg (0.02 grain).

Measurement	Mean (± SE)	Range	95% Confidence limits
Whole fruits			
Length (mm)	70.28 ± 1.99	57–83	63.97–76.59
Max. Dia. (mm)	38.39 ± 0.52	34–43	37.30–39.48
Volume (cc)	52.22 ± 1.95	36–64	48.09–53.31
Weight (g)	52.55 ± 1.91	37.09–63.99	48.51–56.59
Seeds per fruit (air -dry)			
Weight (g)	3.01 ± 0.15	1.79–3.89	2.69–3.33
Number[a]	2263.00 ± 108	1488–3124	2035–2490

[a] Based on 100% count of seeds from 2 fruits and 200 seed samples from the remaining 16 fruits.

Assuming an average annual productivity of 200 fruits per plant (Thackery and Leding 1929), the annual reproductive potential of the east monument stand is 40.4 million seeds/ha (2.5 acres) and for the west monument, 61.6 million seeds/ha (2.5 acres). It is evident that the heretofore reported sparsity of young saguaros in these stands cannot be attributed to a lack of viable seeds.

Fig. 17A. Ripe saguaro fruit; seed mass drying in open receptacle with dried flower still attached. The receptacle splits open upon ripening, exposing the sugary, bright red matrix containing the small black seeds (see Fig. 17B). Photographed 15 July 1974.

Fig. 17B. Seeds from a single saguaro fruit. A common dressmaker's pin (lower left) provides scale. Each seed is about 1.5 mm (0.06 inch) long and weighs approximately 1.3 mg (0.02 grain). An average size saguaro fruit during an average year contains 2000-2500 seeds. Photographed 15 July 1974.

Summary and Conclusions

We estimate that a healthy saguaro produces on the order of 40 million viable seeds during an average reproductive life span of 100 years. For a population to maintain itself or to grow, one of those seeds must, within that period, germinate and survive approximately 30 years or more, to the age when it becomes a reproductive member of the population.

The peak of saguaro fruit ripening and seedfall occurs in late June or early July prior to the arrival of germinating summer rains. Variations in the date of that peak as well as the size of the current year's seed crop are related to year-to-year variations in climatic factors.

Early or late occurrence of peak seedfall, regulated respectively by early or late arrival of warm spring temperatures, importantly affects probabilities for seed survival. Early seedfall lengthens the period of seed exposure to decimating factors. Late seedfall shortens that exposure and accordingly affects the number of germinable seeds remaining on the ground at the time of germinating summer rains.

Drought does not have a significant diminishing effect upon the size of the annual seed crop, fruit production being dependent upon energy and moisture reserves stored within succulent stem tissues. Moreover, prostrate saguaro stems completely severed from their roots are capable of producing buds and flowers for at least 2 years.

Recurring winter freezes that frequent Arizona and northern Sonora effect a significant reduction in reproductive growth. Damage to incipient buds caused by such freezes directly reduces the number of fruits produced the following spring. Freeze-damage may affect flower production on the same plant for one or more years after the event, although to a lesser degree.

Freezing permanently diminishes the reproductive base of the population by selectively removing the largest and potentially most productive members from the population. The most severely damaged individuals collapse within the year. Others, moribund or dead, appear to senesce, often over a period of several years, each year producing diminishing numbers of fruits by utilizing stored energy reserves from the succulent stem until terminated by the ultimate collapse of the stricken plant.

Reproductive potential in spectacular stands of large saguaros in the Tucson area—including those at Saguaro National Monument—and elsewhere near the northern and eastern limits of the distribution of the plant in both northern Sonora and northern and eastern Arizona is more than adequate to maintain existing population levels. The density of large, reproductive individuals within stands along the edge of the species range far exceeds that in other portions of the plant's range where stands exhibit more normal distribution of age classes. The relative sparsity of young saguaros within the stands at Saguaro National Monument cannot reasonably be attributed to a lack of viable seeds. The causes of the wide departure from stable age distribution must instead be sought in the factors that control the survival of the seed, its germination, and survival of the plant to the age of reproduction.

3

The Fate of the Seed: Dispersal, Attrition, and Germination

> *Immediately, the enormous crop of fruit is set upon by birds, rodents, and coyotes, as well as by the Indians of the area. Almost every fruit that falls is soon divested of its pulp and seeds. Probably not more than one seed in 10,000 ever germinates.*—Forrest Shreve, "The saguaro, cactus camel of Arizona," 1945:696.

Seed Dispersal

Saguaro seeds reach the ground in many ways. Some fall to the soil surface while they are still in the flesh of ripe, open fruits and in dried receptacles.

Relatively heavy seedfalls occur during summer rainstorms. Rains soften and dislodge seeds from ripe fruits and dried receptacles remaining on the plant as well as from those that become lodged in the branches of associated trees and shrubs, and those already on the ground.

Summer rains aid importantly in transporting saguaro seeds to protected downslope sites affording both concealment from predators and favorable conditions for germination. After rains, seeds are found in the first few millimeters of the soil, in sand and gravel, under rock and in litter (usually mud-spattered), and nearly all are invisible to the naked eye. Natural germination occurs in such protected physical situations (Steenbergh and Lowe 1969).

Animals play a primary role in dispersal and the transport of seeds to sites suitable for germination and seedling establishment. Most fruits drop to the ground, resulting in a high concentration of seeds at the base of the parent plant and providing an attractive supply of food for mammals, birds, and insects (Figs. 18A and 18B). The congregation of herbivorous predators[1] not only results in low probabilities for seed sur-

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[1] For lack of more appropriate terms we use the words "predator" and "predation" as broadly defined to include consumption and destruction of seeds and/or plants by animals.

vival but also severely limits seed germination and seedling establishment. Moreover, intensive digging, especially by rodents, effectively reduces protective plant cover at the base of the parent saguaro and destroys young saguaros or exposes them to other hazards. Generally, the probability of seed survival, germination, and seedling survival increases with distance from adult plants.

In a matter of a few days, animal activity beneath the parent saguaro changes the situation from one resembling a *fruit basket* to the *seed shadow* associated with some tropical plant species as described by Janzen (1970) and Krebs (1972:520). This explains why young saguaros are seldom found beneath the seed-producing parent plant. Those few seedlings that begin their establishment there do not survive the continuing heavy animal traffic at such stations.

In addition to providing an important mechanism for seed dispersal, birds frequently deposit seeds in protected locations provided by trees and shrubs away from areas of intensive animal foraging at the base of fruiting plants. Such protected locations not only increase the probability of seed survival, they generally offer more suitable conditions for seed germination and seedling establishment.

Seed Consumption and Loss

A large part of the annual saguaro seed crop is consumed by mammals, birds, and insects (Marcou 1869; MacDougal 1908a; Shreve 1951). The percentage of the annual seed crop so consumed varies greatly from one community to another depending upon the relative abundance of particular species of consumers (Fig. 18A and 18B). Field observations in Saguaro National Monument indicate that the principal seed consumers are white-winged doves (*Zenaida asiatica*) and western mourning doves (*Zenaida macroura*) (see Neff 1940) which feed on freshly opened fruits still attached to the plant, harvester ants (*Pogonomyrmex* sp.), and round-tailed and Harris' antelope ground squirrels (*Spermophilus tereticaudus*, *Citellus harrisi*) which feed intensively upon fruits that drop to the ground (Figs. 19 and 20).

Ordered by the estimated relative quantity of seeds consumed, other bird-consumers are Gambel's quail (*Lophortyx gambeli*), curve-billed thrasher, (*Toxostoma curvirostre*), cactus wren (*Campylorhynchus brunneicapillus*), gila woodpecker (*Centurus uropygialis*), gilded flicker (*Colaptes chrysoides*), and brown towhee (*Pipilo fuscus*) (see Gilman 1915; Hensley 1954; Hungerford 1962). Secondary mammal-consumers include the kangaroo rat (*Dipodomys* sp.), pocket mouse (*Perognathus* sp.), white-throated woodrat (*Neotoma albigula*), cactus mouse (*Peromyscus eremicus*), long-nosed bat (*Leptonycteris nivalis;* Beatty

Fig. 18A. Typical accumulation of ripe fruits beneath mature saguaros in flat habitats at the west Monument. On 9 July, with six ripe fruits remaining on the plant, 179.5 g (6.3 oz)–approximately 131 thousand seeds–were recovered from detached seed masses and 52 fruit receptacles surrounding the base of this 3-branched, 9-m- (29.5-ft) tall saguaro.

Relatively low density populations of harvester ants (*Pogonomyrmex* sp.) and Harris' antelope ground squirrels (*Citellus harrisi harrisi*) are present, and round-tailed ground squirrels (*Spermophilus tereticaudus*) do not occur at this location. In the absence of heavy predation, a relatively large proportion of the annual seed crop *remains on the ground* until the occurrence of germinating rains (compare with Fig. 18B).

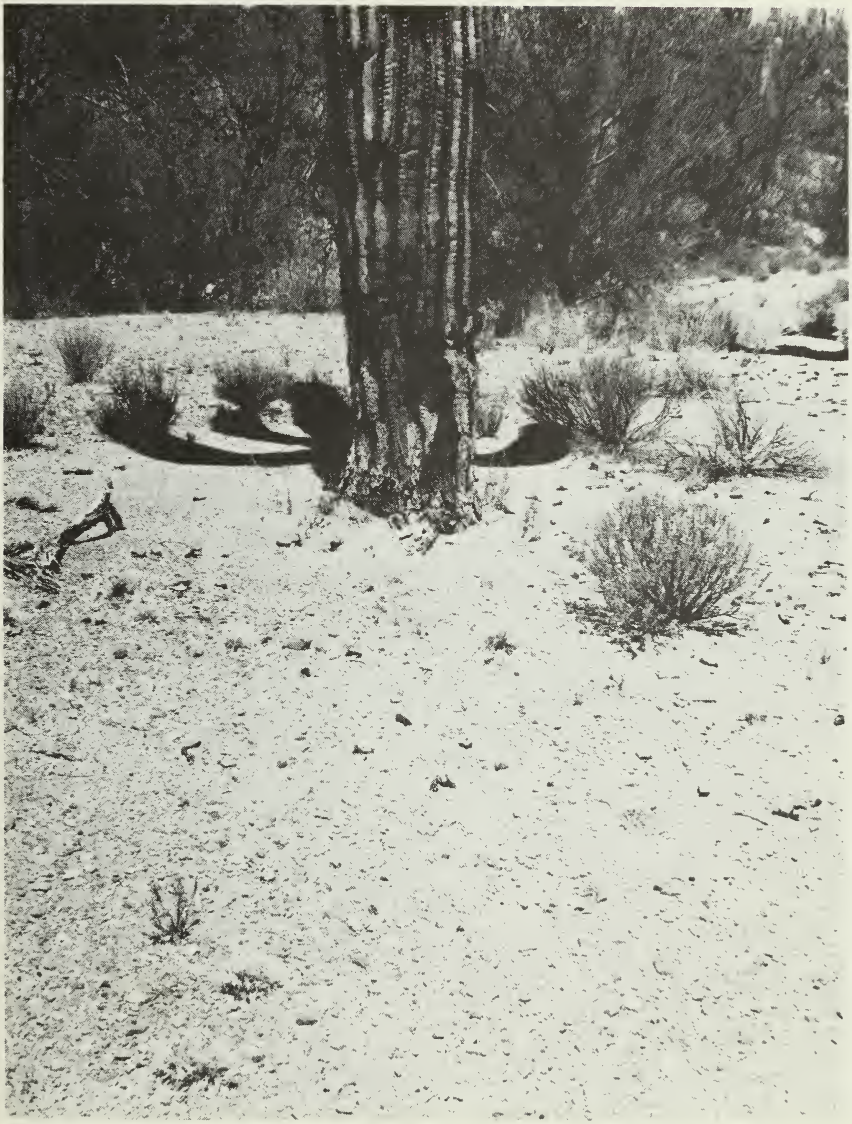

Fig. 18B. Typical absence of fruit at the base of mature saguaros in flat habitats at the east monument (compare with Fig. 18A). Detached seed masses are absent and no seeds are present in 45 receptacles remaining on the ground beneath this vigorous 5-branched, 11-m (36.1-ft) tall plant. One ripe fruit still remains on the plant.

Relatively dense populations of harvester ants (*Pogonomyrmex* sp.) and round-tailed ground squirrels (*Spermophilus tereticaudus*) consume most of the seeds within a few hours after the fruits drop to the ground. In this habitat, the area surrounding the base of an adult saguaro provides little or no protection–either for seeds or seedlings–from the intensive foraging of mammals, birds, and insects. Photographed 19 July 1971.

Fig. 19A. Twenty-one dried, empty receptacles of saguaro fruits (arrow) surround the entrance to the den of a round-tailed ground squirrel (*Spermophilus tereticaudus*) in the Cactus Forest at Saguaro National Monument (east). The succulent fresh fruits of the saguaro are an important source of moisture (as well as food) during the critically arid weeks immediately prior to the arrival of monsoon rains. Photographed 30 June 1969.

Fig. 19B. Galvanized hardware cloth exclosure was used in experiments to determine the effect of vertebrate animals on the survival of saguaro seeds and young plants at Saguaro National Monument. Net germination in plots so protected was approximately 1.3 times that in adjacent unprotected plots. The difference is attributed primarily to the effect of seed removal by birds and rodents. Photographed 21 Feb. 1969.

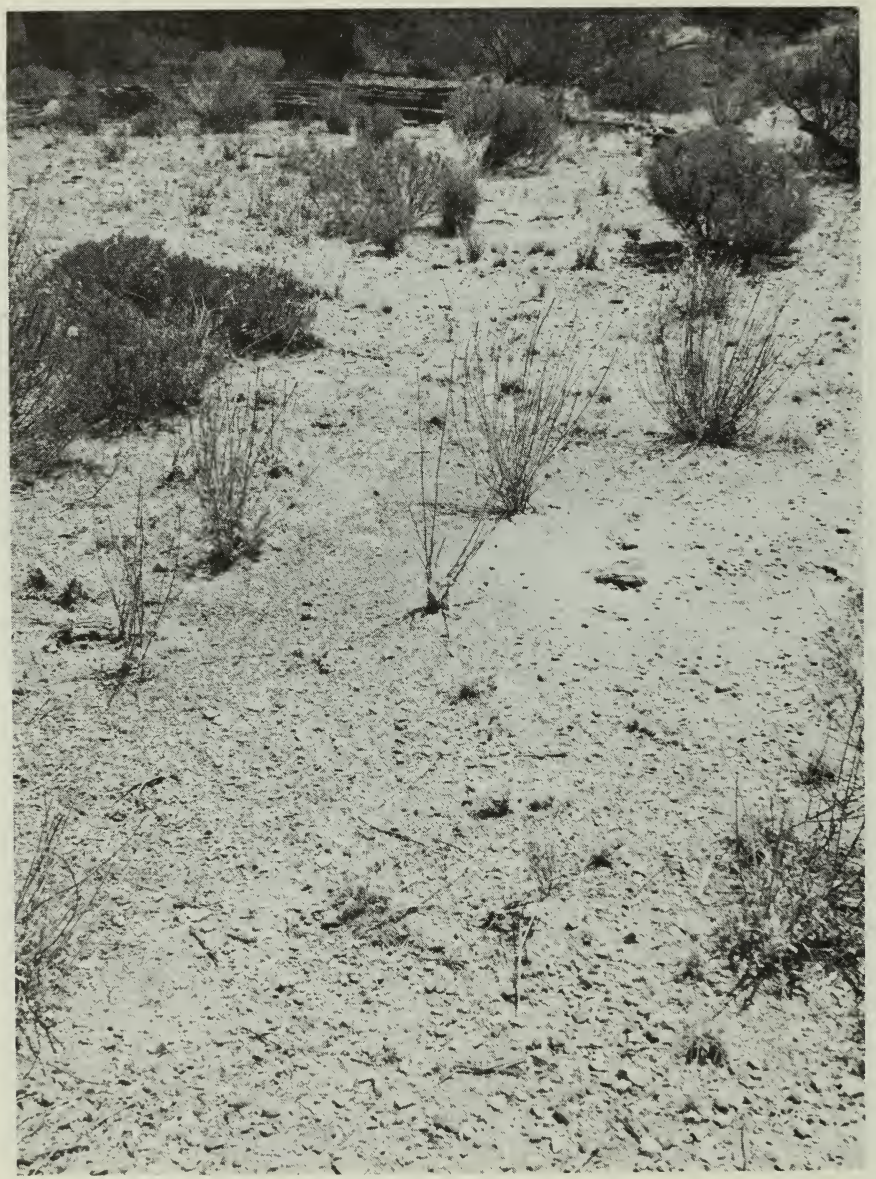

Fig. 20A. Harvester ant (*Pogonomyrmex barbatus*) nests are usually situated in exposed situations away from trees and large shrubs. Such nests are abundant in the Cactus Forest (shown) at Saguaro National Monument (east), but comparatively sparse in the west monument. Commonly foraging more than 20 m (66 ft) from the nest, harvester ants concentrate on the gathering of saguaro seeds throughout the period of fruit drop during late June and early July. Photographed 30 June 1969.

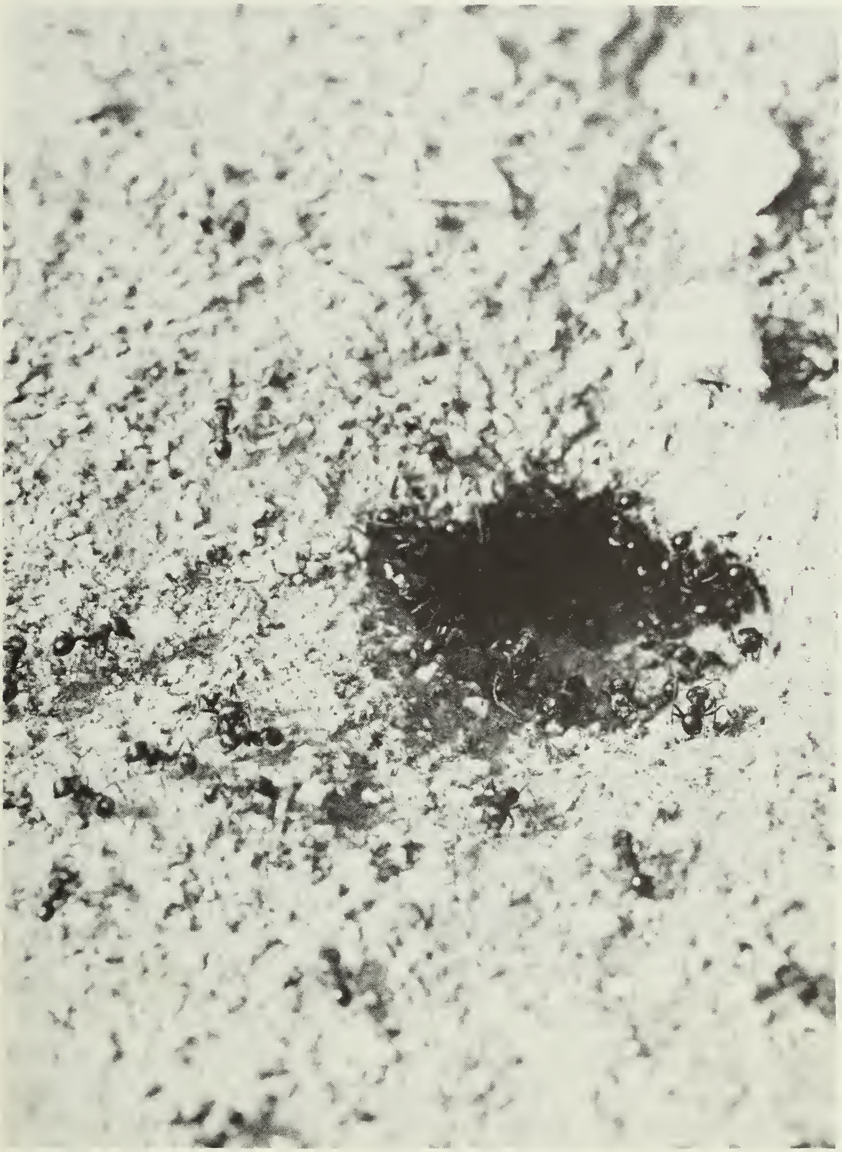

Fig. 20B. Harvester ants (*Pogonomyrmex barbatus*) efficiently remove large numbers of saguaro seeds that fall to the ground. In localities such as the Cactus Forest of Saguaro National Monument (east) where they are abundant, harvester ants play a primary role in limiting the number of viable seeds that survive on the ground until the occurrence of summer conditions suitable for germination. Photographed 25 June 1974.

1955), coyote (*Canis latrans*), and collared peccary (*Pecari tajacu;* Eddy 1959).

The proportion of the annual seed crop harvested by birds and mammals does not provide a direct measure of potential seed survival and natural germination. Rather, the impact of such consumption must be evaluated separately for each animal species based upon the diversity of its feeding habits and the efficiency of its digestive processes. Seeds consumed by obligatory seed-eaters such as white-winged and mourning doves, kangaroo rats, pocket mice, and cactus mice are destroyed during digestion. However, a portion of saguaro seeds consumed by other species (including round-tailed ground squirrels, Harris' antelope ground squirrels, woodrats, coyotes, and omnivorous birds), which benefit primarily from the succulent tissues of the matrix, pass undamaged through their digestive tracts (Table 6 and 7; also see Shreve 1951).

Coyote scats collected in July consisted of approximately 95% undigested saguaro seeds. Viability is essentially unaffected by passage through the coyote digestive tract (Table 6). Eddy (1959) reported collared peccary scats containing 85% undigested saguaro seeds. These mammal species together with the curve-billed thrasher, cactus wren, gila woodpecker, and gilded flicker are potentially important disseminators of saguaro seeds.

Generally, the number and proportion of whole viable seeds present in mammal droppings increase with the size of the species and/or the diversity of its feeding habits. As with mammals, birds that are primarily seed-consumers are relatively low dispersers (viable seeds are not found in feces in large numbers).

In some localities, insects play a primary role in limiting the number of viable seeds that remain on the ground until conditions suitable for germination occur. Harvester ants (*Pogonomyrmex barbatus*, Fig. 20) efficiently remove large numbers of seeds. Other observed seed gathering taxa include *Lasius* sp. and *Leptothorax* sp. (Steenbergh and Lowe 1969).

The results of experiments utilizing exclosures (Fig. 19B) to measure the effect of predation on germination success are given in Table 8. Low germination success (0-3.2%) in plots at three sites (see Table 8;SERS,SWRS,SWF) was associated with and is attributed to seed removal by harvester ants. Conversely, harvester ant activity was not observed in plots where comparatively high numbers of germinations were recorded. Low values for two of the east monument north-facing slope (Table 8:SERN site) plots are attributed to the localized occurrence of relatively unfavorable soil characteristics associated with deep gravel.

The difference in germination percentages in open and in exclosure

TABLE 6. Viable saguaro seed content of native mammal feces. Feces collected in the field were washed to obtain *Canis* and *Pecari* seed samples. Other seeds were washed from 24-hr accumulations of feces of rodents maintained on a saguaro fruit diet. Viability of whole seeds was tested in the laboratory at room temperature (22° ± 1°C) in closed petri dishes with uniform moisture supply.

Species	Feces Dry wt (g)	Whole seeds recovered			
		Wt		No.	% Germ.
		g	% of feces		
Canis latrans	–	–	–	(100)	97.0
Pecari tajacu	–	–	–	(100)	31.0
Spermophilus tereticaudus	2.15	0.064	3.0	53	64.2
Citellus harrisi	2.10	0.052	2.5	43	53.5
Neotoma albigula	1.65	0.007	0.4	6	50.0
Dipodomys merriami	1.09	0	–	0	–
Peromyscus eremicus	0.51	0	–	0	–
Perognathus baileyi	0.40	0	–	0	–
Controls (3)	–	–	–	300	82.3

TABLE 7. Viable seed content of native bird feces. Seeds were washed from 24-hr accumulations of feces of birds maintained on a diet of saguaro fruits consisting of air-dried seed masses reconstituted to original weight by addition of water. Viability of whole seeds was tested in closed petri dishes with uniform moisture supply.

Species	Feces Dry wt (g)	Whole seeds recovered			
		Wt		No.	% Germ.
		g	% of feces		
Campylorhynchus brunneicapillus	1.78	0.696	39.21	557	76.0[a]
Toxostoma curvirostre	2.60	2.460	16.43	1297	54.7[a]
Zenaida asiatica (No. 1)	2.32	0.004	0.2	3	100.0
Zenaida asiatica (No. 2)	3.41	0.002	0.1	2	100.0
Controls	–	–	–	300	73.7[a]

[a] Mean of three lots of 100 seeds each.

TABLE 8. The effect of predation on germination success in protected and exposed 0.25 m^2 (2.7 ft^2) plots. Plots were seeded (1000 seeds per plot) on 26 June 1968 and covered with 16 (0.16 cm; 0.06 inch) mesh window-screen (3 replications), 0.5-inch (1.3 cm) mesh hardware-cloth exclosures (Fig. 19B), or exposed (open) until the first rain (6 July) when all plots were covered by window-screen exclosures. Plus signs indicate observation of harvester ants (*Pogonomyrmex*) activity. Site locations are: SE = east **monument**, SW = west **monument**, F = flats, RN = rocky north-facing slope, and RS = rocky south-facing slope.

Study site	Ants obs.	No. of seeds germinated (7/31-8/3)					% Germ.	
		Exclosure plots				Open plots		
		Screen A	Screen B	Screen C	Mesh		Excl.	Open
SERS	+	101	266	0	1	28	9.4	2.8
SWRS	+	0	0	0	66	112	11.6	11.2
SERN		30	239	31	35	13	8.4	1.3
SWRN		244	480	335	354	374	35.3	37.4
SEF		166	284	114	117	42	17.0	4.2
SWF	+	28	32	17	7	16	2.1	1.6
Total			2003		980	585		
Mean			111.3		163.3	97.5	12.4	9.8

plots is a measure of the effect of seed removal by vertebrate consumers (Table 8). Net germination within exclosure plots was 1.27 times that in open plots. The difference is attributed primarily to the elimination of seed predation by birds and rodents.

No harvester ant activity was observed on north-facing slopes. In other areas where harvester ants were present (south-facing slopes and flat habitats), their impact was highly localized. In some of these plots all visible seeds were removed within a few days after seeding, while seeds in plots a few meters distant were essentially undisturbed. It appears that high densities of harvester ant colonies are commonly associated with stands of reproductive (adult) saguaros.

Germination success in exclosures did not provide an effective means of comparing the separate effects of seed removal by birds, mammals, and insects. Rather, the results suggest that in competition with harvester ants, the impact of larger, less efficient seed-gatherers on seed survival is relatively unimportant; the principal effect is exerted by the most efficient forager.

Thus the high attrition of seeds between seedfall and germination is due to seed removal by animals. In the Tucson area, approximately 4 in 1000 saguaro seeds that reach a site where natural germination can occur survive to become seedlings (Table 9). During the 1- to 5-week pre-germination period, native animal predators (birds, mammals, and insects) are the principal agents of saguaro seed attrition.

TABLE 9. Summary of natural germination in experimental plots from broadcast saguaro seeds, 1965-68. Experimental sites, all in representative saguaro habitats, were located at the east monument in 1965 and 1966, east and west monument in 1967 and, in addition, included one site on the south slopes of the Catalina Mountains in 1968. The number of germinations shown are the total number of seedlings that sprouted between 1 July and 10 August in experimentally seeded study plots. Results for 1965-67 are from 60 unprotected plots exposed to all natural environmental factors.

The mean annual germination rate in these plots was 0.353%. Greater germination success in 1968 reflects partial protection by exclosures used to limit animal predation activity (see Table 8).

Year	Sites (no.)	Plots (no.)	Seeds (1000)	Germinations	
				No.	%
1965	4	28	28	96	0.34
1966	4	13	36	87	0.24
1967	9	19	95	461	0.48
Subtotal	–	60	159	644	0.40
1968	8	40	40	7595	18.99

Generally, seeds remaining on the ground at summer's end are destroyed by other agents prior to the ripening of the next crop Seemingly whole seeds from the previous year's crop collected in June from the soil surface proved to be nonviable. Seed coats showed signs of entry by small insects, or the embryos were withered and brown. Seeds which remain over winter on the ground make no important contribution to the following summer's germinable seed supply.

At Saguaro National Monument, the consumption of seeds by birds, mammals, and insects is higher at the east monument (Rincon Mountains) than at the west monument (Tucson Mountains). An approximate measure of the relative seed attrition at these two locations is offered by July observations on seeds remaining on the ground beneath vigorous adult saguaros in equivalent stages of fruit maturation. In flat habitat at the west monument, 179.5 g (6.3 oz) of seeds (approximately 131,000 seeds) were recovered from fruits collected beneath a 9-m (29.5 ft) plant with three productive arms (Fig. 18A). In similar habitat at the east monument, no seeds were present in 45 receptacles surrounding an 11-m (36.1 ft) plant with five productive arms (Fig. 18B).

The difference in yearly seed loss between the east and west monument areas is attributed primarily to consumption by animals, the round-tailed ground squirrels—abundant at the east site and absent at the west site—and harvester ants present in much greater abundance at the east site.

Germination

> *Germination takes place only in the first week after the beginning of the summer rains, and the seedlings are hidden in the litter under bushes or among the small stones which cover the ground.*—Forrest Shreve, "The saguaro, cactus camel of Arizona," 1945:696.

The saguaro is a subtropical species and its seeds germinate only in the summertime. Germination occurs principally in July and August during the southwestern summer monsoon. Thus, successful germination and early establishment depend on a short period of coincident high levels of moisture and warmth during but a few weeks of the desert year. We are not surprised, therefore, to find that this highly successful desert species has acquired adaptive strategies that fit a set of germination requirements to an environment characterized by a persistently high evaporation which is only partially offset by scanty and often uncertain rainfall.

Seedfall is completed just prior to the normal arrival of summer rains. In exceptional years, the two events—seedfall and rainfall—actually overlap. The first summer rains contribute importantly to seed survival by dispersing seeds and by washing them into locations that offer concealment from predators. Little or no germination, however, results from these late June and early July rains. Rigid light and moisture requirements interact to inhibit germination and prevent losses that would result from germination at that time, for sporadic early monsoon rains seldom provide a sufficiently reliable supply of moisture to promote germination and support the initial establishment of seedlings.[2] The increasing frequency of rains during the second half of July offers progressively more favorable conditions for seed germination.

The highly variable spatial and temporal distribution of summer rainfall importantly affects the number of saguaro seed germinations occurring at a given location (see Shreve 1914; Humphrey 1933; Mallery 1936). Further, the number of germinations varies in accord with the characteristically large year-to-year variability of monsoon precipitation patterns. Our experimental and field observations, however, indicate that the most favorable conditions for saguaro seed germination do not necessarily occur during years with the highest total summer precipitation. Rather, natural germination is associated with temporal clustering of summer rainstorms that provide continuously high moisture levels at and near the soil surface during the 2- to 3-day germination period.

Most germination takes place during the period from mid-July through the first week of August. Then, with continuing availability of high surface moisture resulting from short-spaced rainstorms and supplemented by dewfall, germination proceeds to completion within a period of 2-3 days—initial establishment of the seedlings takes place at a time when temperatures and moisture are optimum for their growth.

The high temperature limitations on saguaro seed germination operate to restrict natural germination to shaded sites where periods of high moisture are sufficiently prolonged to permit germination (Table 10; Fig. 21). During wet periods such sites seldom reach temperatures high enough to inhibit germination (Alcorn and Kurtz 1959; McDonough 1964). Inhibition of germination by low temperatures effectively restricts germination to the warm-wet periods of June, July, August, and September in the overall distribution of the saguaro.

Genetically controlled variability in the time required for completion of the germination process further insures that the entire annual seed

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[2] While it is commonly said that "seedlings germinate," plant seedlings "sprout" and proceed to establish or die; only seeds can germinate.

TABLE 10. Percent soil moisture in shaded and unshaded saguaro-paloverde habitat at Saguaro National Monument (east), July 1967. Samples of the top 0.5 inch (1.27 cm) and top 1 inch (2.54 cm) of soil were collected at approximately 1300 hr beneath the crown of a mature foothill paloverde at 1 m (3.3 ft) from the trunk (shade), and from an unshaded (open) level site approximately 5 m (16.4 ft) outside the crown. Data graphed in Fig. 21.

	Soil moisture (%)			
Date July	Shade		Open	
	0.5 inch (1.27 cm)	1 inch (2.54 cm)	0.5 inch (1.27 cm)	1 inch (2.54 cm)
18	15.23	15.34	6.01	8.12
19	10.06	9.63	3.13	6.69
20	3.40	8.87	2.36	5.45
21[a]	1.85	6.33	1.39	4.47
22	11.45	9.96	7.80	7.54
23	5.15	8.10	2.43	4.50

[a] Estimated by regression (log % on time).

crop will not respond to conditions that are marginal for seedling establishment. Approximately 10% of seeds tested under ambient summer light and temperatures required 4 days or more of continuous exposure to free water for completion of germination. Thus, even under conditions that permit extensive germination, a substantial portion of the germinable seeds remain viable and available for subsequent germination.

The light requirement may seem to present an apparent survival disadvantage because it seemingly dictates that germination must occur at or near the soil surface where the predation pressures are greatest and requisite moisture conditions are least apt to prevail. However, in view of the characteristic development pattern of the monsoon rains, an important adaptive strategy can be recognized. In the presence of insufficient moisture to complete germination and initial establishment of the seedling, the light requirement acts to stop the germination process without loss of seed viability. Buried seeds retain their viability, and will germinate quickly when exposed by subsequent rains, animal digging, other natural forces, or experimental exposure.

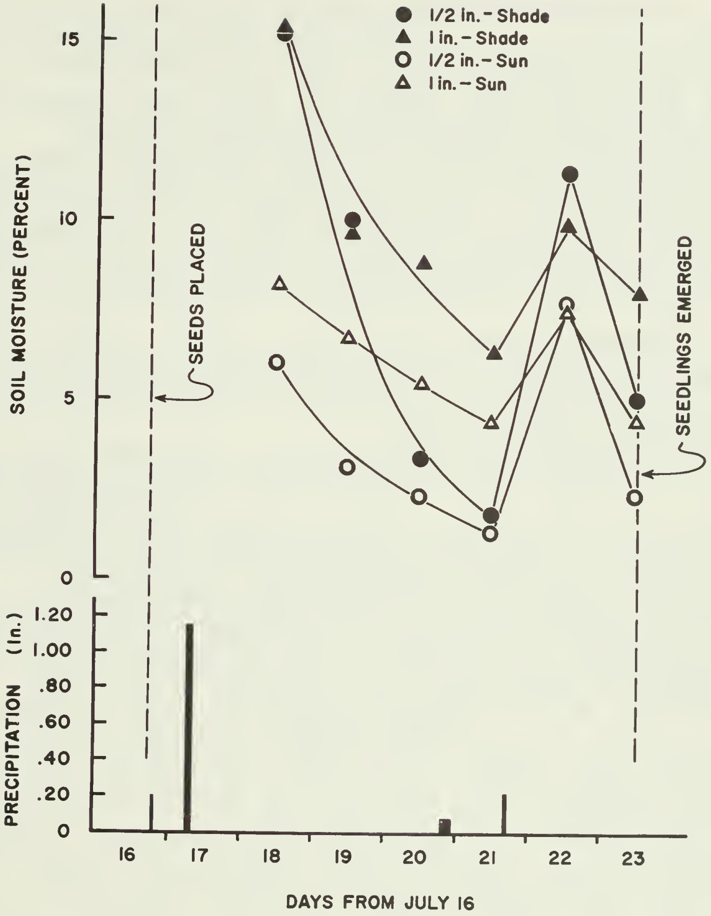

Fig. 21. Natural field germination of saguaro seeds (on 23 July 1967) and accompanying precipitation (inches [Original units of measurement; 1 inch = 25.4 mm]) and soil moisture at 0.5 inch (1.27 cm) and 1 inch (2.54 cm) depth.

Seeds were broadcast beneath the crown of a foothill paloverde (*Cercidium microphyllum*) on 16 July immediately prior to receiving 0.20 inch (5 mm) precipitation the same day. No germination occurred during the period of high soil moisture following a heavy rain the next morning, followed by clear skies (17 July, 1.5 inches; 38 mm). Germination took place after two periods of light precipitation (0.04 inch; 1 mm, 0.21 inch; 5 mm) and broken overcast skies on 21 and 22 July. The first seedlings emerged on 23 July, 3 days after the start of these rains. Amount (bar height) and period (bar width) of precipitation is shown.

Saguaro seed germination is dependent upon the continued availability of moisture at the soil surface as determined by temporal distribution of rainfall, cloud cover, and other factors that aid in continuously maintaining high relative humidity and surface moisture for a period of 2-3 days during the summer rainfall season. Generally, natural germination is associated with the occurrence of two or more rains within a 2- to 3-day period. Data in Table 10.

The light requirement insures germination sufficiently near the soil surface for the globular seedling to emerge and immediately receive adequate light for subsequent growth (Fig. 24A). Sensitivity to far-red light may also permit better utilization of energy from nocturnal reradiation thus hastening completion of the germination process.

Field observations indicate that in nature germination of shallowly buried seeds accounts for a substantial portion of the annual saguaro seedling crop. This observation appears to conflict with knowledge that germinating seeds must receive exposure to light after they have imbibed water, that little or no germination ($<1\%$) will occur in total darkness. Extensive laboratory tests using a variety of environmental, mechanical, and chemical treatments have revealed no mechanism by which germination might occur naturally in the absence of light (Alcorn and Kurtz 1959; McDonough 1964).

Based on successful use of acid treatments in promoting dark germination, McDonough (1964) suggested that passage through the digestive tracts of animals might promote germination in the absence of light. However, we have attained no success in the dark-germination of saguaro seeds recovered from the feces of native rodents or birds.

In fact, the natural germination of buried saguaro seeds requires no complex mechanism for explanation. In view of the brief exposure and low intensities of light required for germination as found by all investigators, the natural translucence and gravelly surface of the soils of the saguaro habitat will admit sufficient light in most instances to permit germination of seeds buried to a depth of 5-10 mm (0.2-0.4 inches), the approximate maximum depth from which the seedling can emerge. A further mechanism for satisfying the light requirement exists in the soil churning and washing action occurring during typical summer rainstorms. Such action permits burial of seeds after wetting and exposure to light.

Germination of saguaro seeds requires contact with free water and exposure to light (Alcorn and Kurtz 1959; Alcorn 1961a). Under ambient summer light and temperatures in a laboratory environment, initial germination of saguaro seeds maintained in continuous contact with free water occurs approximately 48 hr after initial wetting and 50% germination is reached in approximately 72 hr (Table 12; Fig. 23; also see Keswani and Upadhya 1969). However, within the natural environment of the saguaro such prolonged periods (3 days) of continuously available water are a rare, almost nonexistent occurrence during July and August when most natural germination takes place. Rather, natural germination commonly follows two or more shorter periods of water availability with interspersed drying conditions at the soil surface resulting from the occurrence of two or more distinct rainstorms within a 2- to 5-day period (Steenbergh and Lowe 1969).

In a humid atmosphere, saguaro seeds hygroscopically imbibe and retain moisture required for germination. Such pre-exposure to high relative humidity effectively speeds the germination process and reduces the required period of seed contact with free water. First germination of seeds so pre-conditioned can take place after 24 hr of wet contact and 50% germination can occur within 48 hr. In a near-saturated atmosphere, maximum hygroscopic imbibition (approximately 20% of the air-dry seed weight) is reached in approximately 20 hr (Table 11; Fig. 22).

In an experiment to determine the effect of such treatment on the required period of contact with free water, treated seeds reached 50% germination in 46.5 hr, 21.5 hr sooner than untreated (air-dry) seeds (68.0 hr) (Table 12; Fig. 23). Hygroscopic imbibition can reduce by approximately one day the required pre-germination period of seed contact with free water.

Germination under natural conditions, therefore, need not depend upon the rare occurrence of a continuously saturated soil surface over a prolonged period of time; but rather it can be sustained by a period of high relative humidity followed by a relatively brief period of saturation. Thus, hygroscopic imbibition allows rapid germination with intermittent high moisture levels commonly associated with the characteristic summer storm patterns of the Sonoran Desert.

Requisite environmental conditions for saguaro seed germination occur far beyond the bounds of the plant's natural distribution. Only at the western boundaries of its occurrence—in the lower Colorado River Valley—where summer rainfall is seldom adequate to promote germination, does the range of the species appear to be limited primarily by germination requirements. With that exception, therefore, the factors that limit its distribution and control populations along the margins of its range must act during the post-germination stage of the plant's development.

TABLE 11. Hygroscopic imbibition by saguaro seeds in the laboratory at high relative humidities (90-100%). Air-dry 2-g (0.07-oz) seed samples were placed in petri dishes suspended over saturated paper towels in closed chambers in full room shade (indirect light) and ambient July air temperatures (ca. 70-95°F; 21-35°C). Data are given as weight and as moisture uptake (percent air-dry weight). Dashed line represents break in curve at maximum moisture uptake (see Fig. 22). Sample I (in clear plastic chamber) was subjected to ambient light; sample II (in a light-proof metal chamber) received light only at the times of weighing.

Time (hr)	Weight (g)	Uptake (%)
	I - *AMBIENT LIGHT*	
0	2.00	0.0
1	2.10	5.0
2	2.16	8.0
4	2.23	11.5
6	2.26	13.0
17	2.35	17.5
19	2.36	18.0
21	2.32	16.0
23	2.30	15.0
25	2.29	14.5
	II - *TOTAL DARKNESS*	
0	2.00	0.0
12	2.36	17.8
15	2.37	18.5
21	2.41	20.5
23	2.41	20.5
25	2.40	20.0

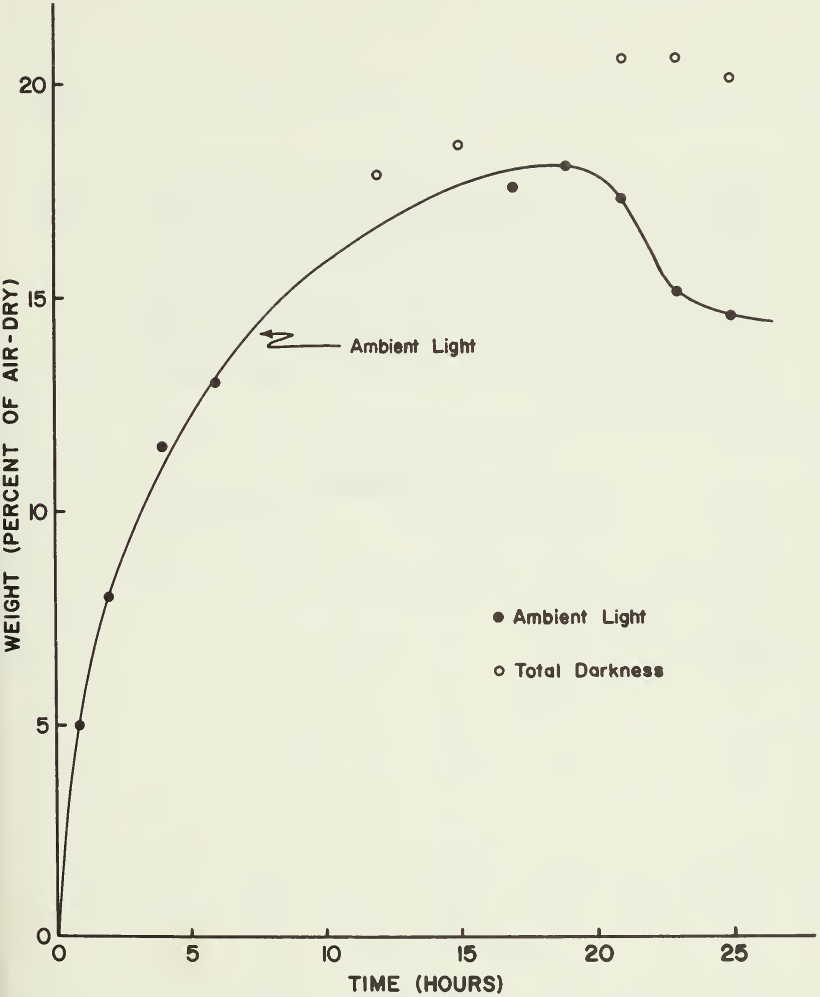

Fig. 22. Hygroscopic moisture uptake by saguaro seeds at high relative humidities (90-100%).

In a near-saturated atmosphere without condensation, saguaro seeds absorb atmospheric moisture up to approximately 20% of their air-dry weight. Maximum hygroscopic imbibition is reached in approximately 20 hr, i.e., ca. one day. Data in Table 11.

TABLE 12. Number and percent germination of humidified (pretreated) and of air-dry (untreated) saguaro seeds in the laboratory under ambient summer light and temperatures (full shade, ca. 65-95°F; 18.3-35.0°C). Pretreated seeds were held 5 days in open petri dishes in a near saturated atmosphere (see Table 11, Fig. 22) immediately prior to testing. Hours to germination of treated (2-100 seed lots) and untreated (3-100 seed lots) seeds is measured from time of initial contact with free water (15 August, 0800 hr). Data graphed in Fig. 23.

Hours Wet	Germination			
	Humidified (200 seeds)		Air dry (300 seeds)	
	No.	%	No.	%
24	7	3.5		
26	16	8.0		
28	27	13.5		
30	39	19.5		
42	95	47.5	11	3.7
48	116	58.0	22	7.3
54	148	74.0	88	29.3
72	167	83.5	169	56.3
120	184	92.0	254	84.0

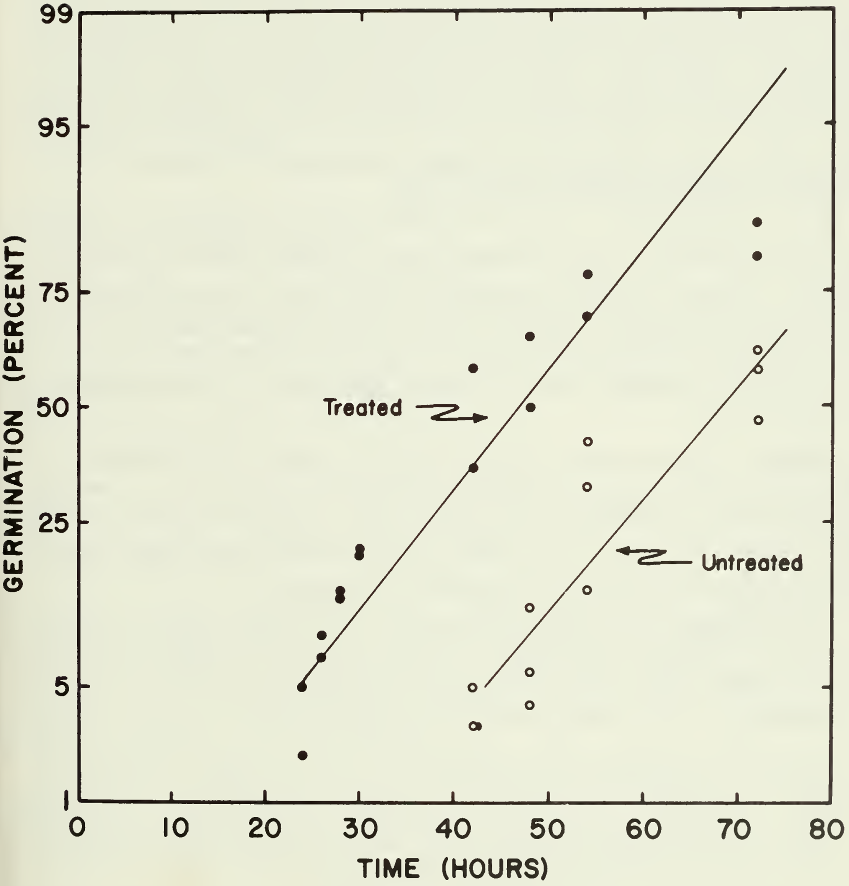

Fig. 23. Effect of pre-exposure to high relative humidity on the rate of saguaro seed germination after contact with free water. The time for seeds pre-exposed (pretreated) to a near-saturated atmosphere to reach 50% germination (46.5 hr) was approximately 21.5 hr less than the time (68.0 hr) for untreated (air-dry) seeds.

Hygroscopic imbibition can reduce by approximately one day the required period of seed contact with free water to germinate under natural conditions. Thus, in the desert environment where moisture is critically limiting, chances for germination are greatly increased by this adaptive mechanism that can reduce—by as much as a whole day—the required period of contact with a saturated soil surface.

Germination 50% points determined by regression analysis after probit transformation (Table 12).

Summary and Conclusions

Dispersal. Early summer rains in late June and early July effect a major contribution to the dispersal of saguaro seeds by dislodging seed masses still remaining on the plant, and by washing individual seeds into protected locations that provide concealment from predators and are favorable sites for subsequent germination and establishment. The early rains reduce the attrition of seeds and ordinarily set the stage for germination during subsequent summer rains.

Such seed dispersal to more favorable sites accomplished by gravity and rainfall runoff is mainly effective for downslope dispersal in sloping habitats. Animal consumers, principally birds, which pass undigested viable seeds through their digestive tracts, are the primary agents for seed dispersal upslope and in flat habitats. Obligatory seed-eaters that efficiently digest consumed seeds, however, make little or no contribution to seed dispersal.

Attrition. In the complete life cycle of the saguaro, the greatest mortality occurs during the pre-germination (seed) stage, the 1- to 5-week period between seedfall and the occurrence of germinating summer rains. During that period the major portion of the annual seed crop is consumed by animals—birds, mammals, and insects.

To some degree, the fruits of the saguaro are utilized either as food or a source of moisture by nearly every warm-blooded animal member of the community and by several species of insects. Initially heavy losses to feeding birds, especially doves, occur while fruits are still attached to the plant. The greatest losses, however, accrue after fruits drop to the ground where the diversity of consumer species ranges from ants to coyotes. The relative importance of consumer species varies according to their size and foraging efficiency, diversity of feeding habits, and relative abundance within the particular community.

Generally, obligatory seed-eaters—principally harvester ants, doves, and heteromyid rodents—exert the greatest impact as they are abundant and efficient consumers. However, in habitats where they are abundant (such as the Cactus Forest of the east monument), round-tailed ground squirrels consume the major portion of dropped fruits. The impact of specific saguaro fruit consumers varies greatly from one desert community to another. In flat habitats of the east monument, relatively dense populations of harvester ants and round-tailed ground squirrels quickly remove most of the seeds which reach the ground. However, in flat habitats of the west monument where neither species is abundant, a large proportion of the seed crop remains on the ground, undisturbed throughout the pre-germination period.

In some locations, seeds remain over winter on the ground. However, as a result of destruction by insects, microorganisms, or climatic action, few if any survive or contribute significantly to the following year's germinable seed supply.

Most of the fruits drop to the ground immediately beneath the parent plant. Intensive animal activity sponsored by this abundance of food not only results in heavy attrition of seeds from these sites but also severely limits the suitability of such sites for germination and seedling survival, especially in flat habitats.

In view of abundant germination observed during favorable years, it is unlikely that the lack of young saguaros evident in some habitats is attributable to attrition of seeds.

Germination. The principal germination of saguaro seeds takes place in July and August from seeds of the current year's crop. Optimum conditions for natural germination coincide with the first full development of monsoon storms. Then, during the period from mid-July to mid-August, germination is normally associated with the occurrence of two or more rainstorms within a 2- to 5-day period.

The availability of moisture is the critical determinant in the germination process; temperature and light requirements are readily satisfied within all natural habitats of the saguaro. In continuous contact with free water, germination takes place in 48-72 hr.

The germination process is facilitated by the capability of seeds to absorb moisture hygroscopically. We conclude that this is an important adaptive strategy. Pre-conditioning by hygroscopic imbibition can reduce the critical period of required contact with free water by as much as one day, importantly mitigating the need for a prolonged period of saturation at the soil surface.

The saguaro is dependent in its germination requirements on a physically modified microenvironment produced by trees, shrubs, rocks, or other shade-producing objects. These shaded microhabitats provide moderated daytime temperatures that are within the upper range required for germination and prolong periods of high moisture availability at the soil surface. Ultimately, the number of adequately shaded sites suitable for saguaro seed germination is limited by the physical structure of the community.

Experimental evidence indicates that fewer than 1 in 200 seeds that reach a site where germination can occur survive to the seedling stage. We estimate that the net natural survival to the initial stage of seedling establishment is less than 1 per 1000 seeds produced.

The summer climatic environment of the Tucson area is well within the range necessary for saguaro seed germination; this exceeds, in germination suitability, the drier, more westerly portions of the species' range. At Tucson, depending upon the overall intensity of monsoon development, the year-to-year suitability of conditions for natural germination ranges from poor to near optimum, but some natural germination occurs in all years.

It seems likely that the western limits of saguaro distribution in California, Arizona, and northern Sonora are controlled by insufficient moisture for germination. Elsewhere to the northeast and south, it is clear that summer climatic environments would permit natural germination far beyond the present limits of saguaro distribution. Those limits, therefore, must be determined by factors that operate during the post-germination stages of the plant's growth.

4
Establishment and Survival

> *The seeds which reach the ground quickly germinate in the baking soil, and the tiny capsules of acid water stored in the plump spineless hypocotyl constitute a most attractive morsel for the thirsty and hungry animals, and not one seedling in a million survives the first year in consequence.*—D. T. MacDougal, "Across Papagueria," 1908b:98.

Of the many thousands of saguaro seedlings that emerge each summer, all but a few are doomed to destruction within the year. Most of the succulent, weakly rooted seedlings are eaten or uprooted by foraging animals, or they die from drought or winter cold. The few surviving individuals are usually concealed beneath protecting shrubs, fallen limbs, or among rocks. There they may be further hidden by detritus.

The average life expectancy of a newly sprouted saguaro seedling is less than 6 weeks. Emerging within a few days after the end of the prolonged drought of the arid fore-summer when other sources of moisture are scarce, the succulent seedling is prey to an abundance of insects, rodents, and even to destruction by foraging birds.

The relatively few survivors proceed toward establishment, which is the process of stabilization that takes place from *germination* through *seedling* development into *juvenile* saguaro status (Figs. 24-26). The *juvenile* is a well-rooted and self-supporting young plant in which a certain continuance is assured. The *seedling* saguaro is the emerged young plant—after rupture of the seed coat at germination—that remains relatively vulnerable without benefit of the self-sustaining features that characterize later life as an established juvenile plant (Fig. 24A). For the saguaro establishment is ordinarily reached at an age of 12-14 months (Fig. 24B). Thus, the tenuous process of establishment is accomplished by a seedling saguaro during its first biological year of life, a period that may exceed a calendar year by 1 or 2 months.

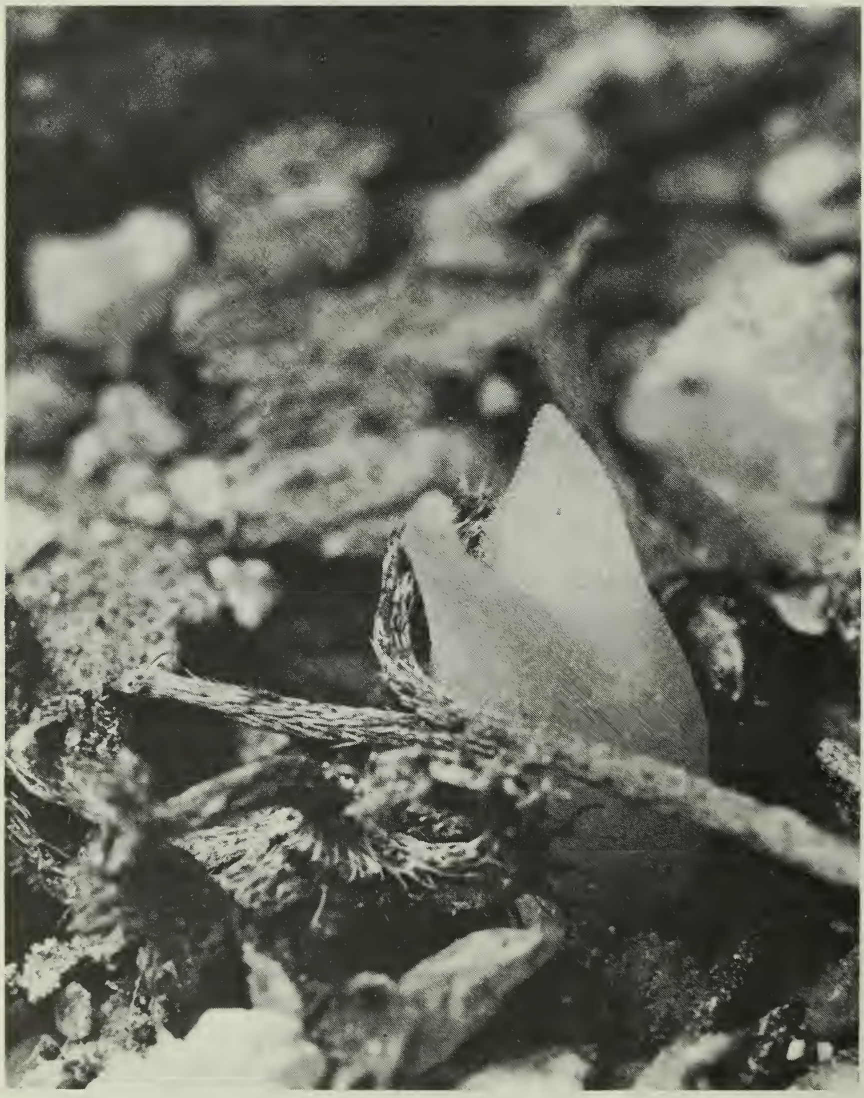

Fig. 24A. A newly sprouted saguaro seedling in the Cactus Forest at Saguaro National Monument (east). In this habitat the average life expectancy of such naturally growing seedlings of a few millimeters in size is less than 6 weeks. Most of the tiny succulent seedlings die from lack of moisture or are destroyed by a variety of insects, rodents, and foraging birds during the first summer and fall of life. Photographed by Harold T. Coss, 23 July 1970.

Fig. 24B. Yearling saguaro, Cactus Forest, Saguaro National Monument (east). Barely 5 mm (0.25 inch) tall, the established plant has survived the numerous hazards of the first year of life. With the resumption of growth during the second summer of life, the seedling enters the globose juvenile stage of development. Photographed by Harold T. Coss, 23 July 1970.

Fig. 25A. Juvenile saguaro, globose stage, height approximately 2.5 cm (1 inch), in rock outcrop. Rocks concentrate and prolong availability of soil moisture. Re-radiation during cold winter nights moderates the intensity and duration of low temperatures. Such environmental modification and concealment that is found in rocky habitats markedly enhance probabilities of both the seedling's establishment and its following survival during the vulnerable juvenile years. Photographed 13 Feb. 1970.

Fig. 25B. Juvenile saguaro, globose stage, height approximately 2.5 cm (1 inch), beneath the crown of a foothill paloverde tree (*Cercidium microphyllum*) in nonrocky habitat. Pebbles and detritus provide concealment and protection from destruction by animals. Shade from overhanging crown of trees and shrubs prolongs availability of soil moisture. Overhanging canopy reduces nocturnal heat loss and provides protection from freezing. As in rocky habitats (see Fig. 25A), the concealment and the modification of limiting factors favor both the establishment and the following survival of young saguaros. Photographed 14 Dec. 1969.

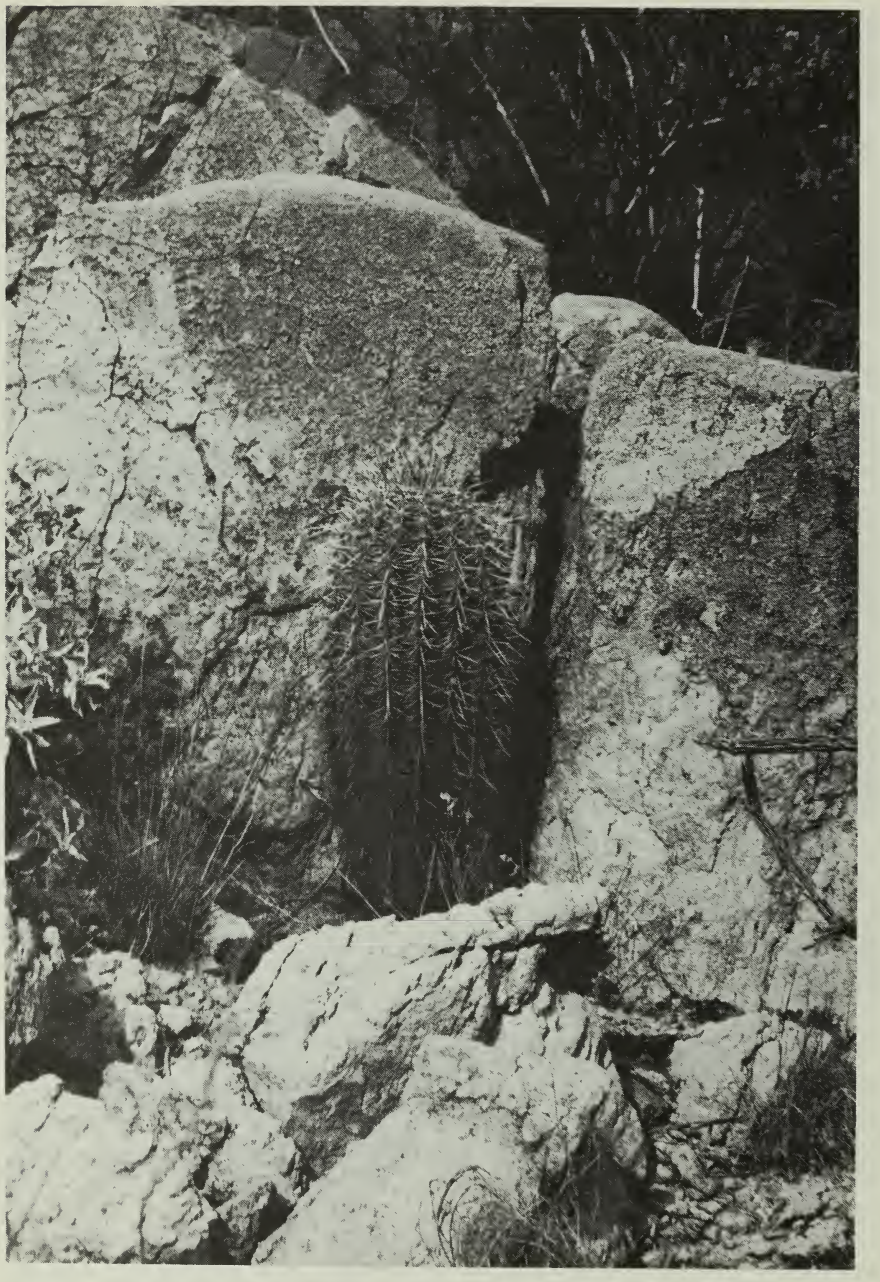

Fig. 26A. Juvenile saguaro, columnar stage, ht 50 cm (20 inches), in rocky habitat. Transition from globose to columnar "club" form occurs when the plant reaches a height of 5-10 cm (2-4 inches), Nocturnal re-radiation from the adjacent rock face aids winter survival throughout the life of the plant by protecting it from lethal subfreezing temperatures. Photographed 22 Jan. 1971.

Fig. 26B. Juvenile saguaro, columnar stage, ht 50 cm (20 inches), in a low shrub (triangle bursage [*Ambrosia deltoidea*]). The young saguaro has outgrown the protection of its "nurse-plant." The projecting cold-sensitive tip of the plant now radiates directly to the night sky and is fully exposed to extremes of winter cold. Freeze-caused damage to the apex—and often death—is a common occurrence in the Tucson vicinity and elsewhere in the colder portions of the saguaro's distribution. Photographed 17 June 1974.

Biotic Factors

Rodents and birds

Rodents are a major cause of first-year saguaro mortality. In the absence of other sources of food and/or moisture, most if not all of the species of rodents that occur commonly in the principal saguaro habitats at Saguaro National Monument and elsewhere in the Sonoran Desert will feed upon saguaro seedlings (Tables 13 and 14). In addition to direct destruction by consumption, a substantial number of young saguaros are uprooted or buried by intensive digging, especially by the Harris and round-tailed ground squirrels.

We have found, however, that only the white-throated woodrat can subsist entirely on a diet of live saguaro tissues (Fig. 27). This is because the species of *Neotoma* are able to metabolize and neutralize oxalates, compounds that are lethal to other rodents. The story is well told by Schmidt-Nielsen (1964).

TABLE 13. Consumption of saguaro seedlings by species of rodents occurring commonly in saguaro habitats at Saguaro National Monument.

All rodents, live-trapped during mid-summer 1971, were held indoors without food or water for 24 hr prior to feeding. Each animal was then provided with a single pot containing 15-day-old seedlings growing in native soil. In every instance, all seedlings offered were eaten within 24 hr. These results are similar and not significantly different from those of previous experiments. Experiments of similar design conducted in the field laboratory at Navojoa with rodents from southern Sonora (see Table 14) produced results similar to those obtained at Tucson, Arizona.

Species	Seedlings consumed		Digging activity (Soil disturbance)
	Hr	No.	
Spermophilus tereticaudus	17	56	overturned
Citellus harrisi	6	54	overturned
Neotoma albigula	5	65	slight
Dipodomys merriami	24	94	overturned
Perognathus baileyi	9	33	overturned
Perognathus penicillatus	24	24	overturned
Peromyscus eremicus	24	60	none

TABLE 14. Native rodents and lagomorphs occurring in saguaro habitats in the Mohave Desert, Sonoran Desert, and in thornscrub in southwestern Sonora, Mexico. Grasshopper mice (*Onychomys*), cotton rats (*Sigmodon*), and gophers (*Thomomys*) are not listed.

Species[a]	Subspecies in area of		
	Southwestern Sonora (Thornscrub)	Centwestern Arizona–Centwestern Sonora (Sonoran desertscrub)	Northwestern Arizona (Mohave desertscrub)
	Plant eaters		
Desert Cottontail *Sylvilagus auduboni*	*a. goldmani*	*a. arizonae*	*a. arizonae*
Antelope Jackrabbit *Lepus alleni*	*a. palitans*	*a. alleni*	*a. alleni*
Blacktail Jackrabbit *Lepus californicus*		*c. eremicus*	*c. eremicus*
White-throat Woodrat *Neotoma albigula*[b]	*a. melanura*	*a. albigula*	*a. albigula*
Sonoran Woodrat *Neotoma phenax*	*phenax*		
Desert Woodrat *Neotoma lepida*[b]		*l. devia*	*l. devia*
Cactus Mouse *Peromyscus eremicus*	*e. anthonyi*	*e. eremicus*	*e. eremicus*

TABLE 14.–(Continued)

Species[a]	Subspecies in area of		
	Southwestern Sonora (Thornscrub)	Centwestern Arizona–Centwestern Sonora (Sonoran desertscrub)	Northwestern Arizona (Mohave desertscrub)
	Plant eaters		
Riparian Mouse *Peromyscus merriami*	*m. goldmani*	*m. merriami*	*m. merriami*
Deer Mouse *Peromyscus maniculatus*		*m. sonoriensis*	*m. sonoriensis*
Canyon Mouse *Peromyscus crinitus*[b]		*c. pallidissimus*	*c. pallidissimus*
Fulvous Harvest Mouse *Reithrodontomys fulvescens*	*f. tenuis*	*f. fulvescens*	
Sonora Harvest Mouse *Reithrodontomys burti*	*burti*	*burti*	
Western Harvest Mouse *Reithrodontomys megalotis*		*m. megalotis*	*m. megalotis*
Rock Squirrel *Citellus variegatus*	*v. grammurus*	*v. grammurus*	*v. grammurus*
Roundtail Ground Squirrel *Citellus tereticaudus*	*t. neglectus*	*t. neglectus*	*t. neglectus*

TABLE 14.–(Continued)

Species[a]	Subspecies in area of		
	Southwestern Sonora (Thornscrub)	Centwestern Arizona–Centwestern Sonora (Sonoran desertscrub)	Northwestern Arizona (Mohave desertscrub)
	Plant eaters		
Sonora Antelope Squirrel *Citellus harrisi*[b]		*h. harrisi*	*h. harrisi*
Desert Cliff Chipmunk *Eutamias dorsalis*		*dorsalis* (Sonora)	
	Seed gatherers		
Merriam Kangaroo Rat *Dipodomys merriami*[b]	*m. merriami*	*m. merriami*	*m. merriami*
Desert Kangaroo Rat *Dipodomys deserti*[b]		*d. deserti*	
Bannertail Kangaroo Rat *Dipodomys spectabilis*		*s. perblandus*	
Ord Kangaroo Rat *Dipodomys ordi*		*o. ordi*	*o. chapmani*
Bajada Pocket Mouse *Perognathus baileyi*[b]	*b. baileyi*	*b. baileyi*	

⇩

TABLE 14.–(Continued)

Species[a]	Subspecies in area of		
	Southwestern Sonora (Thornscrub)	Centwestern Arizona–Centwestern Sonora (Sonoran desertscrub)	Northwestern Arizona (Mohave desertscrub)
Seed gatherers			
Thornscrub Pocket Mouse *Perognathus goldmani*	*g. goldmani*		
Sinaloa Pocket Mouse *Perognathus pernix*	*p. pernix*		
Desert Pocket Mouse *Perognathus penicillatus*[b]		*p. pricei*	*p. penicillatus*
Rock Pocket Mouse *Perognathus intermedius*[b]		*i. lithophilus*	*i. lithophilus*
Arizona Pocket Mouse *Perognathus amplus*[b]		*a. rotundus*	*a. pergracilis*
Little Pocket Mouse *Perognathus longimembris*[b]		*l. bombycinus*	

[a] Scientific names, vernacular, and ranges for mammals in saguaro habitats follow Hall and Kelson (1959) the most recent reference, and communication from Drs. E. Lendell Cockrum (UA) and James L. Patton (UCB).

[b] Other subspecies in area(s) in addition to tabulated. And other subspecies.

Seedlings of saguaros (and those of other cacti) that are not well hidden on the desert floor are vulnerable "canteens" that are approximately 90% water. In the desert, such cactus "feeding" rises sharply during the hot-dry months of May and June that precede the summer rains. Experimentally, however, we have found that under the hot-dry stress when ample free water and other fresh green plant material (grasses and forbs, both with and without seeds, and leaves) are available at the same time of year (and any other time), the same ground squirrels (*Citellus*) and desert mice (*Peromyscus*, *Onychomys*) refuse cactus of any species, age, or succulence. Because of oxalate poisoning, only one of these mammals (*Neotoma*) is able to incorporate the saguaro (and cacti in general) into its diet as a substantial food item. Desert rodents in general, and certain larger mammals as well (Fig. 27B), irregularly ingest limited amounts of cactus tissue primarily or wholly for its water content rather than for its caloric value. Packrats can and do have it both ways, saguaros included.

Destruction of recently emerged seedlings by cactus wrens has been observed. However, uprooted plants are not eaten. There is no doubt that the similar intensive foraging and digging activities of the curve-billed thrasher, gilded flicker, and gila woodpecker also result in destruction of young seedlings.

In nonrocky habitats, seedlings are rarely found near the base of adult saguaros, and almost never become established there. Such stations are subject to intense disturbance by foraging animals. Generally, the probability of seedling survival increases with distance from reproductive adult saguaros.

Insects

Young saguaros are subject to predation by a diversity of plant-eating insect species, none of which are known to feed exclusively on saguaros. The list of predators shown in Table 15 is by no means complete. Our own field observations and reports by others (Turner et al. 1966; Mann 1969) indicate that a complete listing of insect predators on young saguaros would include additional families, and many times the number of species identified. Although some insect-caused mortality of young saguaros takes place during every month of the year, the heaviest predation occurs during the humid summer months immediately following germination, and again with the arrival of warm weather in April and May.

During the first weeks following germination, the succulent seedlings are particularly vulnerable to destruction by the newly hatched larvae of lepidopterous insects. Immediately after hatching, the larva enters at the base or at the apex of the seedling to feed on the succulent inner tissues.

Fig. 27A. Juvenile saguaro at Saguaro National Monument (east) severely damaged by white-throated woodrat (*Neotoma albigula*) and subsequent freezing. Woodrat tunnels often extend like a winding staircase completely through the stem. Such damage occurs on both juvenile and adult saguaros and increases vulnerability to freezing and to wind-caused stem breakage. Photographed 15 Sept. 1968.

Fig. 27B. Juvenile saguaro on the Cabeza Prieta Game Range (west of Organ Pipe Cactus National Monument). In the more arid portions of the saguaro's range, and elsewhere during periods of severe drought, jackrabbits utilize the succulent stem tissues as a source of moisture. Similar consumption by desert bighorn sheep has been observed (Simmons 1969). Although such damage does not in itself usually kill the saguaro, such "girdling" increases the plant's vulnerability to destruction by wind and freezing. Photographed 3 Feb. 1971.

TABLE 15. Insect consumers of young saguaro cacti, collected in saguaro habitats at Saguaro National Monument (east). Insects were placed in closed containers with young saguaros. All species fed, consuming the entire succulent portions of the stems of one or more plants.

Species	Month collected	Stage
Lepidoptera		
Cactobrosis fernaldialis (Hulst)	June, July	larva
Feltia subterranea (Fabricus)	June	larva
Heliothis zea (Boddie)	April, May	larva
Orthodes alfkeni (Grote)	July, Dec., Feb.	larva
Peridroma margaritosa (Hawthorn)	June, July	larva
Spodoptera exigua (Hubner)	April	larva
Orthoptera		
Melanoplus sp.	July	nymph
Heleastus sp.	July	nymph
Gryllidae 2 spp.	July	adult
Coleoptera		
Aneflus protensus (Le Conte)	July	adult

Leaving the epidermis largely intact, the larva then moves on to an adjacent plant. The remaining withered epidermis presents the appearance of death resulting from lack of moisture. Some of the previously reported summer drought-kill based on observations of desiccated seedlings (Steenbergh and Lowe 1969) may be more correctly attributable to such destruction by insects. Subsequent observations indicate that insects are second only to rodents as a cause of seedling death during the first weeks following germination.

By the end of the first summer growth period, the relatively tough epidermal tissues protect the seedling from entry by small insect larvae and the well-developed spines protect the tender apex. However, the seedling remains vulnerable to destruction by larger insect predators: grasshoppers, crickets, beetles, and the larger larvae of certain moths.

Cutworms (noctuid moth larvae) appear to be the most common insect-consumers of saguaros that have survived beyond the first summer (Steenbergh and Lowe 1969; Table 15). Leaving only the roots and spines of demolished plants, cutworms frequently make a meal of several adjacent young plants (incidentally relieving competition for the survivors). Consumption of an entire 4-year-old plant (1.5 cm; 0.6 inch ht) within a 24-hr period was observed. The ability of the young saguaro to survive insect-caused damage increases with age and size—the saguaro outgrows the individual consumptive capacity of most predatory insects within the first 5 years of life.

Gerstaeckeria turbida (Lec.), a weevil reported by Turner et al. (1966) to be the principal insect responsible for the deaths of transplanted (cultured) young saguaros at Saguaro National Monument, was not observed during our investigations on causes of mortality in seedlings naturally germinated on-site in saguaro habitats.

A few species of large insects do occasionally invade larger juvenile saguaros. At Saguaro National Monument (east) the destruction of transplanted saguaros up to 30 cm (1 ft) tall by the larva of a large weevil [*Cactophagus validus* (LeConte)] has been observed. Our observations on *naturally established* saguaros, however, indicate that insect-caused deaths of such larger juvenile saguaros rarely occur in nature. Further, our observations strongly suggest that such destructive invasion of large juvenile saguaros by insects is limited to weak, moribund, or dead individuals damaged by freezing or other factors.

Experimental exclosures

Seed broadcasting and experimental exclosures were used on-site in both the east and west units of Saguaro National Monument (Tables 19-22; Figs. 19B, 29, 30). Details on the structure and placement of the wire exclosures are given in Steenbergh and Lowe (1976).

Comparison of 1968 seedling survival in open (unprotected) and exclosure (protected) plots clearly shows that vertebrate predators are a primary cause of saguaro seedling mortality during the first 5 pre-winter months of the first year of life (Tables 19-22; Figs. 29 and 30).

The life expectancy of seedlings protected by exclosures that effectively excluded all vertebrate animals (but not insects) was approximately 10 times that of seedlings subject to natural predation (Table 21).

TABLE 16. First-year survivorship of 231 saguaro seedlings naturally germinated July 1967 from seeds broadcast within seven 1-m^2 plots at Saguaro National Monument. Location-habitat symbols are: SE = east monument, SW = west monument, F = flats, H = rolling hills, RN = rocky north-facing slope, and RS = rocky south-facing slope. Data graphed in Fig. 28.

Obs. date	Elapsed days	Survival													
		East Monument										West Monument			
		SEF N = 73		SERS N = 23		SERN N = 17		SEHS N = 10		SEHN N = 49		SWRS N = 26		SWRN N = 33	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
1967															
Aug. 1	31			9	39.1	10	58.8	7	70.0	8	16.3				
Aug. 2	32											19	73.1	29	87.9
Aug. 3	33	10	13.7												
Aug. 8	38	10	13.7	8	34.8	10	58.8	7	70.0	8	16.3				
Aug. 9	39											17	65.4	23	69.7
Aug. 15	45	10	13.7	8	34.8	10	58.8	3	30.0	8	16.3				
Aug. 18	48											10	34.5	21	63.6
Aug. 21	51											8	30.8	20	60.6
Aug. 22	52	9	12.2	7	30.4	8	47.1	3	30.0	8	16.3				

⇩

TABLE 16. –(Continued)

Obs. date	Elapsed days	Survival													
		East Monument										West Monument			
		SEF N = 73		SERS N = 23		SERN N = 17		SEHS N = 10		SEHN N = 49		SWRS N = 26		SWRN N = 33	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
Sept. 7	68											5	19.2	13	39.4
Sept. 8	69	4	5.5	6	26.1	6	35.3	3	30.0	4	8.2				
Sept. 19	80											1	3.8	7	21.2
Sept. 20	81	2	2.7	6	26.1	6	35.3	2	20.0	2	4.1				
Oct. 3	94											1	3.8	1	3.0
Oct. 4	95	2	2.7	5	21.7	1	5.9	1	10.0	0	0.0				
Oct. 18	109	2	2.7	5	21.7	1	5.9	1	10.0			0	0.0	1	3.0
Nov. 1	123	2	2.7	5	21.7	0	0.0	1	10.0					0	0.0
Nov. 15	137	1	1.4	5	21.7			1	10.0						
Nov. 28	150			5	21.7			1	10.0						
Nov. 29	151	1	1.4					1	10.0						

⇩

TABLE 16. –(Continued)

Obs. date	Elapsed days	Survival													
		East Monument										West Monument			
		SEF N = 73		SERS N = 23		SERN N = 17		SEHS N = 10		SEHN N = 49		SWRS N = 26		SWRN N = 33	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
Dec. 13	165	1	1.4	5	21.7			1	10.0						
Dec. 19	171	1	1.4	5	21.7			1	10.0						
1968															
Jan. 4	187	1	1.4	3	13.0			1	10.0						
Jan. 10	193	1	1.4	3	13.0			0	0.0						
Jan. 24	207	1	1.4	3	13.0										
Feb. 7	221			3	13.0										
Feb. 8	222	1	1.4												
Feb. 21	235	1	1.4	3	13.0										
Mar. 6	249	0	0.0	3	13.0										
June 25	360			3	13.0										

TABLE 17. Regression equations for post-germination survival of saguaro seedlings germinated July 1967; probit conversion of percent survival of seedlings (Y) on time in days from 1 July (X) by least squares. Habitat symbols as in Table 16; data in Table 16 is graphed in Fig. 28.

Habitat	N	Equation	r
SEF	18	Probit $Y = -0.006\ X + 3.897$	–0.882
SEHS	15	Probit $Y = -0.010\ X + 5.225$	–0.828
SEHN	6	Probit $Y = -0.016\ X + 4.645$	–0.922
SERS	20	Probit $Y = -0.003\ X + 4.617$	–0.890
SERN	8	Probit $Y = -0.025\ X + 6.230$	–0.943
SWRS	7	Probit $Y = -0.040\ X + 6.762$	–0.968
SWRN	8	Probit $Y = -0.040\ X + 7.299$	–0.982

TABLE 18. Post-germination survival and establishment rates of saguaro seedlings (N = 231) naturally germinated July 1967 in representative habitats at Saguaro National Monument; predicted survival and establishment rates estimated by regression equations in Table 17. Habitat symbols as in Table 16.

"N" is the original number of seedlings under observation. Survivorship is shown as time in days to 0.001 survival (1 survivor per 1000 seedlings). Establishment rate is expressed as number of seedlings per 1000 surviving to the end of the first year of life (15 July 1968). Data in Table 16, graphed in Fig. 28.

Habitat	N	Survivorship To 0.001 (days)	Establishment 1st year (no.)
SEF	73	334.6	0.4
SEHS	10	3269.0	0.1
SEHN	49	175.2	<0.1
SERS	23	1207.6	68.2
SERN	17	171.1	<0.1
SWRS	26	120.2	<0.1
SWRN	33	134.3	<0.1

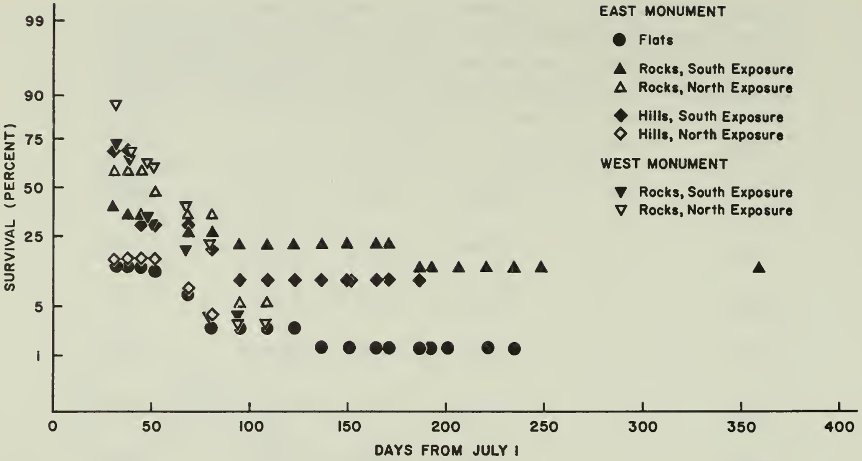

Fig. 28. Post-germination first-year survivorship of saguaro seedlings (N = 231) naturally germinated July 1967 in representative habitats at Saguaro National Monument; percent survival on time in days from 1 July. Data in Table 16, regression equations in Table 17.

Within exclosures, consumption by insects was the principal cause of seedling deaths. However, despite relatively mild winter minimum temperatures, there were four freeze-caused seedling deaths within the two north-slope plots.

The relatively high rate of survival within the east monument "flats" exclosure is especially noteworthy. In that habitat, the pre-winter July to November climatic environment is highly favorable for seedling survival. There, also, it appears that the foraging activities of birds and rodents are most detrimental to seedling survival.

Although seedling survival in rocky habitats was improved vastly by the use of exclosures, the relative suitability of north-facing and south-facing slopes for seedling survival was not altered by the exclusion of vertebrate animals. The differences in the relative suitability of these habitats for pre-winter (July to November) seedling survival must be attributed to other factors, namely, consumption by insects and, to a lesser extent at Saguaro National Monument (west), to differences in moisture availability.

TABLE 19. First-year survivorship in protected (exclosure) plots of 1018 saguaro seedlings naturally germinated July 1968 from seeds broadcast within five 0.25 m^2 (2.7 ft^2) plots. Seedlings were continuously protected from predation by vertebrate animals (mammals and birds) by 0.5-inch (1.3 cm) mesh exclosures. Habitat symbols as in Table 16. Data graphed in Figs. 29 and 30.

		Survival											
		East Monument						West Monument					
Obs. date	Elapsed days	SEF $N = 283$		SERS $N = 232$		SERN $N = 237$		SWF $N = 30$		SWRS $N = 151$		SWRN $N = 85$	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
July 31	30	283	100.0	232	100.0							85	100.0
Aug. 1	31					237	100.0	30	100.0	151	100.0		
Aug. 7	37	240	84.8									85	100.0
Aug. 8	38			221	95.3	227	95.8	30	100.0	145	96.0		
Aug. 14	44	225	79.5					30	100.0	142	94.0	85	100.0
Aug. 15	45			206	88.8	185	78.1						
Aug. 21	51	225	79.5					30	100.0	138	91.4	85	100.0
Aug. 22	52			155	68.8	161	67.9						
Sept. 4	65	220	77.7	130	56.0	20	8.4						
Sept. 5	66							30	100.0	129	85.4	85	100.0

TABLE 19.–(Continued)

		Survival											
		East Monument						West Monument					
Obs. date	Elapsed days	SEF *N* = 283		SERS *N* = 232		SERN *N* = 237		SWF *N* = 30		SWRS *N* = 151		SWRN *N* = 85	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
Sept. 18	79	164	58.0	84	36.2	7	3.0						
Sept. 19	80							28	93.3	123	81.5	84	98.8
Dec. 9	161	150	53.0	84	36.2	7	3.0						
Dec. 10	162							26	86.7	97	64.2	84	98.8
1969													
Jan. 6	189	150	53.0										
Jan. 8	191			80	34.5	7	3.0	26	86.7	97	64.2	81	95.3
Feb. 3	217	142	50.2	80	34.5	7	3.0	22	73.3	90	59.6	79	92.9
Mar. 3	245	138	48.8	80	34.5	7	3.0	22	73.3	90	59.6	76	89.4
April 1	274	138	48.8	80	34.5	7	3.0	22	73.3	90	59.6	75	88.2
May 6	309	138	48.8	75	32.3	6	2.5						

⇩

TABLE 19.–(Continued)

Obs. date	Elapsed days	Survival											
		East Monument						West Monument					
		SEF *N* = 283		SERS *N* = 232		SERN *N* = 237		SWF *N* = 30		SWRS *N* = 151		SWRN *N* = 85	
		Live	%	Live	%	Live	%	Live	%	Live	%	Live	%
May 7	310							22	73.3	89	58.9	75	88.2
June 2	336	137	48.4	74	31.9	6	2.5	21	70.0	89	58.9	72	84.7
July 1	365	137	48.4										
July 2	366							20	66.7	89	58.9	62	72.9
July 3	367			74	31.9	6	2.5						
July 31	395	137	48.4	74	31.9	5	2.1						
Aug. 1	396							18	60.0	79	52.3	57	67.1

TABLE 20. First-year survivorship in unprotected (open) plots of 250 saguaro seedlings naturally germinated July 1968 from seeds broadcast within five 0.25 m^2 (2.7 ft^2) plots; habitat symbols as in Table 16. Data graphed in Figs. 29 and 30.

Obs. date	Elapsed days	Survival									
		East Monument						West Monument			
		SEF *N* = 114		SERS *N* = 27		SERN *N* = 37		SWF *N* = 13		SWRN *N* = 59	
		Live	%	Live	%	Live	%	Live	%	Live	%
July 31	30	114	100.0							59	100.0
Aug. 1	31			27	100.0	37	100.0	13	100.0		
Aug. 7	37	94	82.5							58	98.3
Aug. 8	38			22	81.5	30	81.1	11	84.6		
Aug. 14	44	81	71.0					10	76.9	58	98.3
Aug. 15	45			9	33.3	23	62.2				
Aug. 21	51	25	21.9					10	76.9	43	72.9
Aug. 22	52			6	22.2	5	13.5				
Sept. 4	65	4	3.5	4	14.8	1	2.7				
Sept. 5	66							5	38.5	26	44.1
Sept. 18	79	0	0.0	1	3.7	0	0.0				
Sept. 19	80							0	0.0	1	1.7
Dec. 10	162			0	0.0					0	0.0

TABLE 21. Comparison of post-germination survival and establishment rates of saguaro seedlings (N = 1268) in paired protected (exclosure) and unprotected (open) 0.25 m^2 (2.7 ft^2) plots for seedlings naturally germinated July 1968. Exclosure plots were covered from the date of seedling emergence with 0.5-inch (1.3-cm) mesh hardware-cloth cages (30 cm; 11.8 in ht × 61 cm; 24.0 in dia.) to exclude birds and mammals (Fig. 19B).

Survival and establishment rates estimated using regression equations in Table 22. Habitat symbols as in Table 16. "N" is the original number of seedlings under observation. Survivorship is shown as time in days to 0.001 survival (1 survivor per 1000 seedlings). Establishment rate is expressed as number of seedlings surviving to the end of the first year of life (15 July 1969). Data in Tables 19 and 20, graphed in Figs. 29 and 30.

Habitat	Survivorship and Establishment					
	Open			Exclosure		
	N	To 0.001 (days)	1st year (no.)	N	To 0.001 (days)	1st year (no.)
SEF	114	76.5	<0.1	283	1442.0	498.6
SERS	27	100.2	<0.1	232	968.8	223.4
SERN	37	74.2	<0.1	237	462.9	60.6
SE-(all)	178	85.9	<0.1	752	806.9	122.1
SWF	13	129.0	<0.1	30	1316.4	629.0
SWRN	59	91.8	<0.1	85	1001.7	737.8
SWRS	–	82.1[a]	<0.1[a]	151	1128.4	463.1

[a] Estimated values based on analysis of 1967 data.

Abiotic Factors

Drought

Drought-caused mortality of saguaro seedlings is related importantly to the date of germination and subsequent conditions for growth. Seedlings which sprout during July and early August usually attain sufficient size and volume during the summer growth period to survive through the autumn and fore-summer drought periods. During occasional years with heavy September and/or October rains, survival is further aided by additional growth.

Few seedlings that result from late summer germination (late August and September), however, survive to the start of the second year of life.

TABLE 22. Regression equations for post-germination survival of saguaro seedlings germinated July 1968; probit conversion of percent survival of seedlings (Y) on time in days from 1 July (X) by least squares.

Habitat symbols as in Table 16. Data in Tables 19 and 20, graphed in Figs. 29 and 30.

Habitat	N	Equation	r
		UNPROTECTED PLOTS	
SEF	4	Probit $Y = -0.103\ X + 9.805$	-0.979
SERS	5	Probit $Y = -0.056\ X + 7.471$	-0.920
SERN	4	Probit $Y = -0.109\ X + 9.971$	-0.973
SE (all)	13	Probit $Y = -0.077\ X + 8.558$	-0.837
SWF	4	Probit $Y = -0.046\ X + 7.836$	-0.959
SWRN	5	Probit $Y = -0.100\ X + 11.059$	-0.977
		PROTECTED PLOTS	
SEF	14	Probit $Y = -0.003\ X + 5.788$	-0.846
SERS	14	Probit $Y = -0.004\ X + 5.736$	-0.724
SERN	14	Probit $Y = -0.007\ X + 5.108$	-0.701
SE (all)	42	Probit $Y = -0.004\ X + 5.541$	-0.442
SWF	10	Probit $Y = -0.004\ X + 6.675$	-0.941
SWRS	14	Probit $Y = -0.004\ X + 6.423$	-0.884
SWRN	10	Probit $Y = -0.006\ X + 7.870$	-0.962
SW (all)	34	Probit $Y = -0.005\ X + 6.924$	-0.668

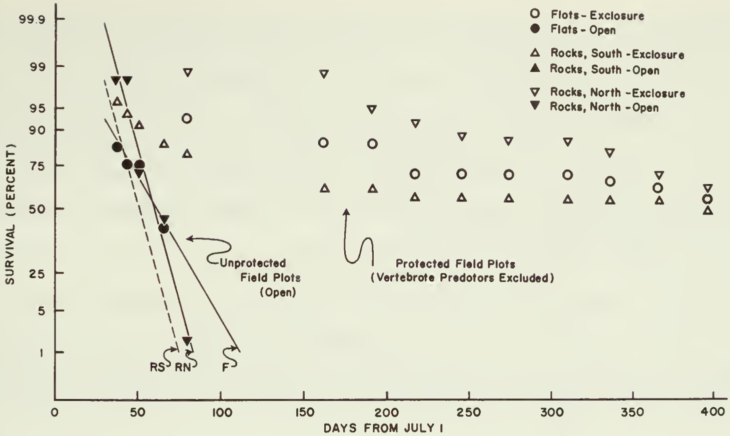

Fig. 29. First-year post-germination survivorship in open and protected field plots of saguaro seedlings (N = 338) germinated July 1968 at Saguaro National Monument (west).

As in the east monument, high rates of survival within exclosures indicate that mammals and birds are a primary cause of first-year seedling mortality in all habitats. Relative survivorship within exclosures on north-facing and south-facing slopes is reversed from that observed in the east monument (see Tables 21 and 22; Fig. 30).

In this arid environment the higher rate of survival on the north-facing slope is attributed to the more favorable moisture relationships that prevail in that habitat during critical drought periods.

Regression equations in Table 22, data in Tables 19 and 20.

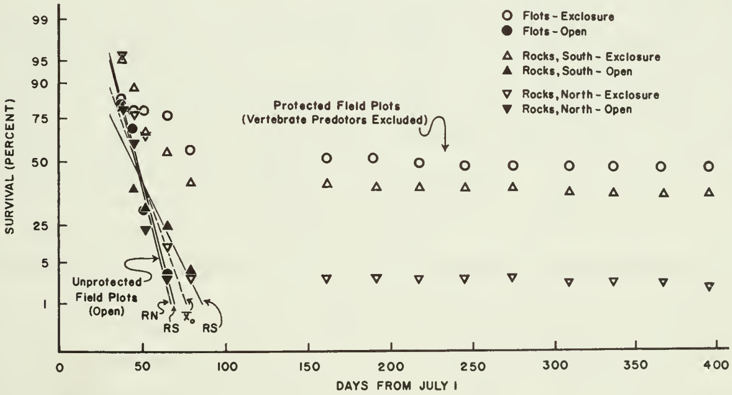

Fig. 30. First-year post-germination survivorship in open and protected plots of saguaro seedlings (N = 930) germinated July 1968 at Saguaro National Monument (east).

The results clearly indicate that vertebrate predators (mammals and birds) are a primary cause of saguaro seedling mortality during the first year of life. In the flat (nonrocky) habitat, the rate of survival in the exclosure plot indicates that the pre-winter climatic environment in that habitat is highly favorable for seedling survival, and suggests that destructive foraging activities of birds and rodents are most intense in that habitat. Regression equations in Table 22, data in Tables 19 and 20.

Such seedlings do not develop sufficient water-storage capacity in the brief remaining growth period to survive prolonged periods of drought. Poorly developed seedlings that survive the arid after-summer are usually eliminated by the more severe drought conditions of the following arid fore-summer (Steenbergh and Lowe 1969). Our observations on winter mortality of seedling and young juvenile saguaros, however, support the conclusion that low levels of hydration increase resistance to freezing (Soule and Lowe 1970).

Desiccation and moisture stress resulting from freeze-caused injury to seedlings and young juvenile saguaros are important causes of apparent drought-kill during the arid fore-summer (Steenbergh and Lowe 1976). Although the death of such plants finally results from critical moisture stress, their death must be attributed to freezing rather than to drought.

Freezing

The results of the 1967 and 1968 seed-broadcasting experiments offer a reasonable measure of seedling establishment in the principal desert habitats at Saguaro National Monument during years with relatively mild winters (Tables 16-22; Figs. 28-30). During the two winters of those experiments, the lowest recorded minimum temperatures at the University of Arizona weather station were 22°F (−5.6°C) and 30°F (−1.1°C), 1°F (0.6°C) and 9°F (5.0°C), respectively, above the 77-year mean (21.1°F; −6.1°C) for that station.

The ultimate suitability of these habitats for the establishment and survival of young saguaros is determined, however, not by any climatic average but, rather, by the extreme minimum temperatures of the most severe winter that they must endure. Catastrophic freezes, a common occurrence in this region, critically limit survival not only of seedlings but of survivors from previous years as well (Steenbergh and Lowe 1976). At those times, the highest probability for continued survival of the young plant becomes abruptly and decisively associated with specific topographic situations (*sensu* microhabitats) that effectively moderate the intensity and duration of critical winter minimum temperatures, i.e., south-facing slopes, rocky footslopes, and the upper portions of adjoining valleys (Fig. 31). These are winter-warm microenvironments. Moreover, saguaros at the highest elevation (approximately 1585 m; 5200 ft) are growing only against south-facing (nocturnal reradiating) rock outcrops (Fig. 32A). Conversely, in the colder microenvironments of north-facing slopes and areas of cold-air drainage and accumulation, there is a high rate of freeze-caused mortality; there is little or no survival of young saguaros in such habitats (Fig. 32B).

On the upper bajadas (nonrocky, "flat" habitats), winter thermal microenvironments and freeze-caused mortality are intermediate between those of north-facing and south-facing slopes, and with increased distance from adjoining footslopes these habitats become progressively less favorable for the survival of young saguaros. Furthermore, as distance from the rocky footslopes increases, winter survival becomes increasingly dependent upon the presence of a multistoried (cold-moderating) canopy of associated shrubs and trees (Fig. 33).

Topography and slope exposure

Distinct differences in first-year saguaro survival occur in topographically different habitats of the two sections (east and west) of Saguaro National Monument. Field experiments comparing saguaro seedling survivorship in rocky habitats at the east monument clearly demonstrate that pre-winter survival on south-facing slopes is consistently higher than on adjacent north-facing slopes, and that the relationship continues throughout the first year of life (Tables 16-22; Figs. 28-30). Further, first-year survival in flat (nonrocky) habitats is lower than on south-facing slopes, but higher than on the north-facing slopes. Survival in the rolling-hills habitats is intermediate between that in flat and rocky habitats, and there, as on the steeper rocky slopes, seedling survival on the south-facing slopes is higher than on the north-facing slopes.

Due to lack of germination in some experimental plots, survivorship data from two west monument habitats are incomplete; in 1967, there was no germination at the "flats" site, and, in 1968, there was none in the open plot at the "rocks, south" site. However, synthesis of the available data for these years suggests that conditions for pre-winter seedling survival in the west monument habitats differ significantly from those of analogous habitats in the east monument. Data from the west monument (1967 experiments, and from 1968 exclosures) indicate that north-facing slopes offer a slightly more favorable environment for pre-winter survival of seedlings than do south-facing slopes. Compared to the east monument, the west monument offers a hotter and more arid environment. In that environment, relatively higher availability of moisture on north-facing slopes may well explain the higher rate of pre-winter survival in those habitats.

Fig. 31A. Sub-marginal habitat for saguaros–a north-facing slope overlooking the Cactus Forest at Saguaro National Monument (east). Saguaro seeds germinate, but young plants rarely become established in such habitats–most seedlings that survive through the warm pre-winter months die during the cold winter months of the first year of life. Thus few saguaros occur naturally on such sites. Cold air drainage from such north-facing slopes contributes to freezing conditions and resulting saguaro deaths in the Cactus Forest below. Photographed 21 Feb. 1969.

Fig. 31B. The warmer winter environment of this south-facing slope of the ridge, shown in Fig. 31A, offers more favorable conditions for saguaro establishment and survival than either the north-facing slope or the flat Cactus Forest habitat. However, this particular one is a marginal habitat for saguaros as evidenced by the freeze-caused constriction on the 2-m (6.6-ft) juvenile saguaro (left foreground) and the drooping top on the young adult plant (center right). The condition of the latter plant is the result of freezing at the site of a woodpecker nest-hole–a common cause of saguaro decapitation. Photographed 21 Feb. 1969.

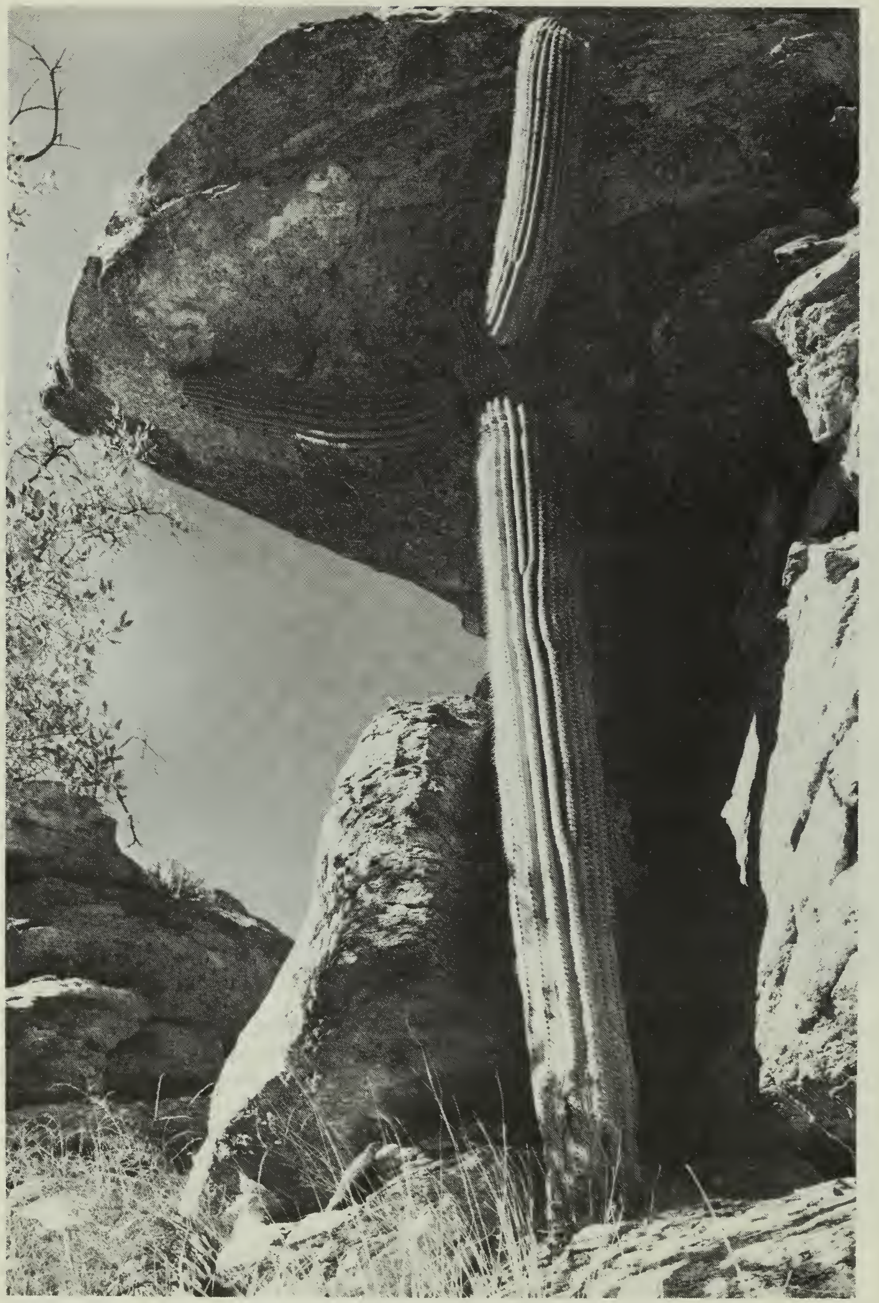

Fig. 32A. Here at the upper limits of their elevational distribution (approximately 1524 m; 5000 ft) in Saguaro National Monument and in the nearby Santa Catalina Mountains up to 1585 m (5200 ft), saguaros grow *against* winter-warm south-facing (nocturnal re-radiating) rock outcrops. Saguaro National Monument photo files.

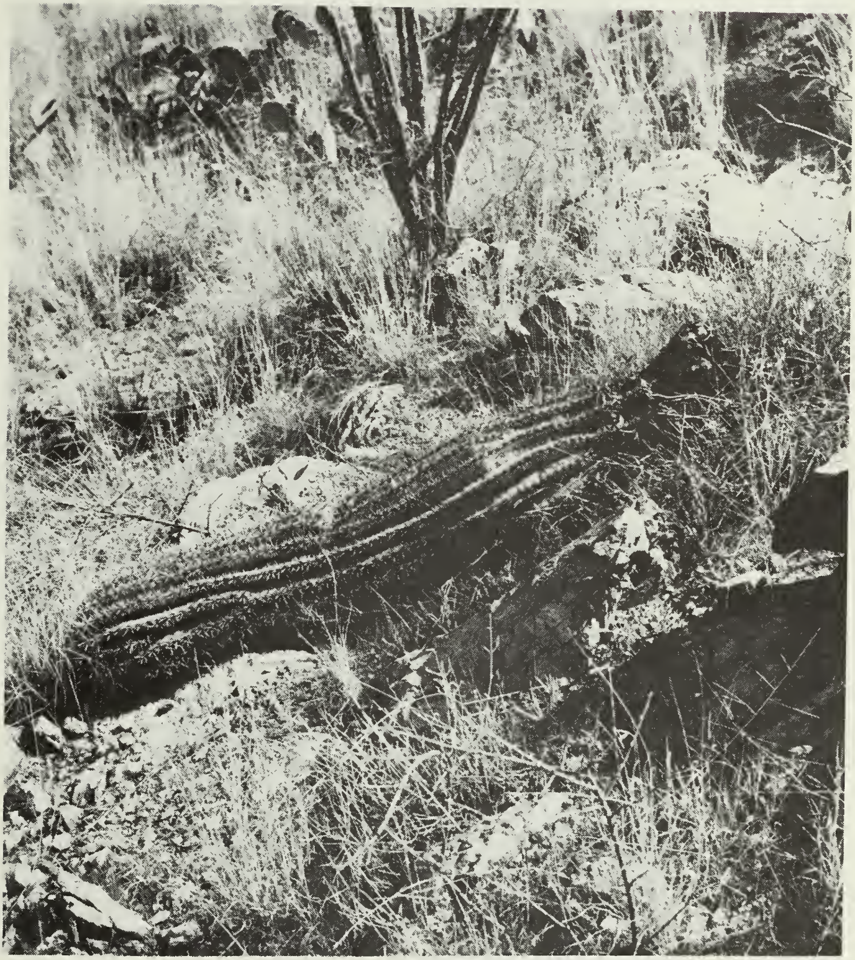

Fig. 32B. Freeze-killed 1.2-m (3.9-ft) juvenile saguaro on northeast-facing slope at Saguaro National Monument (east). The plant outgrew the adjacent rocks that protected it from freezing during the earlier years of its life. Photographed 21 Feb. 1969.

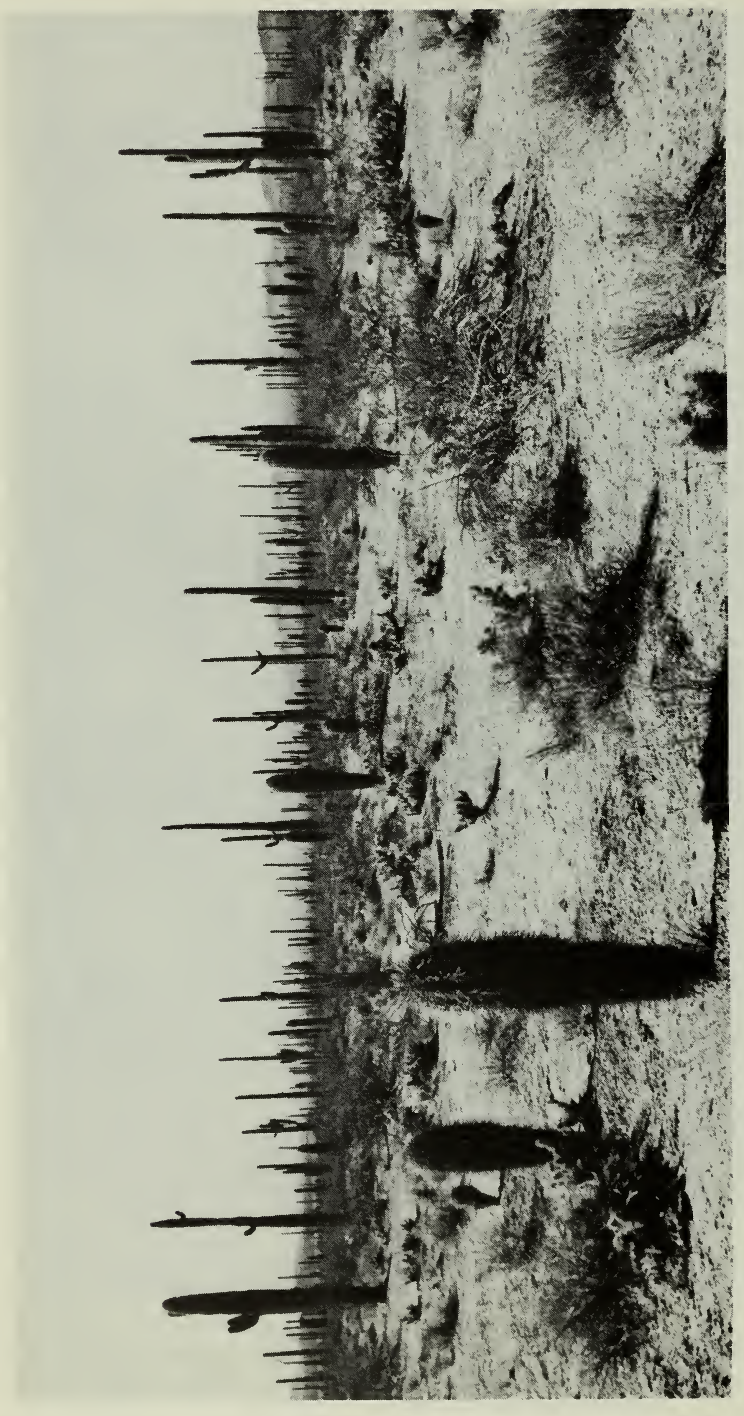

Fig. 33A. A forest of saguaros growing 53 km (33 miles) west of Sonoyta in northwestern Sonora, Mexico. Young saguaros here are associated with shrubs (primarily triangle bursage, *Ambrosia deltoidea*); note the absence of trees. In this relatively winter-warm locality, saguaros survive well without benefit of cold-moderating tree canopy. Here and in the few other flat habitats where it occurs in relative abundance, the saguaro is associated with sandy, well-drained soil. Photographed 12 Feb. 1972.

Fig. 33B. A singularly outstanding example of the association of young saguaros with "nurse-trees"—83 naturally established young saguaros are growing beneath this mesquite tree (*Prosopis velutina*) in the Altar Valley, northern Sonora, Mexico. The small shrubs are triangle bursage (*Ambrosia deltoidea*).

In nonrocky habitats in the colder portion of their distribution, association of saguaros with trees and large shrubs is intimately related to winter survival during periods of extreme cold. As the cold-limited boundaries of its range are approached, survival of the young saguaro is increasingly dependent upon the cold-moderating influence of a canopy of multistoried vegetation or massive outcroppings of rock. Photographed 18 Nov. 1969.

Soil moisture

> *The ratio of evaporation to soil moisture comprises a measurement of all the external factors which affect the water relations of plants, except the influence of radiant energy on transpiration and the possible effects of soil temperature on this function. It is accordingly unnecessary to give further consideration to rainfall, which is not in itself a factor for vegetation, at least in such a region as Arizona.* Forrest Shreve, "The vegetation of a desert mountain range as conditioned by climatic factors." 1915:93.

Drought-caused mortality of saguaro seedlings, discussed previously in this chapter, refers to death from desiccation resulting from drying of the soil to beyond the wilting point. As also discussed, such mortality is related to details of topography, slope exposure, and other soil-related features of saguaro habitats.

The plant-available soil moisture is affected importantly by the physical texture of the soil (Table 23). Nowhere is the result of this fact more striking than in the Sonoran Desert home of the saguaro, for saguaros are not found in poorly aerated soils (Shreve 1920; Kramer 1961, 1962). Coarser-textured soils primarily of gravel and rock on bajadas, fans, and rock slopes support more highly diverse desert biotic communities in which the saguaro is a major dominant and where it often forms "saguaro forests" (Fig. 34A); such coarse soils are also relatively well drained. Finer-textured soils that are relatively high in clay, silt, and sand content support fewer species, and so result in desert communities of simpler structure (Fig. 34B); such relatively fine soils are also less well drained (Yang and Lowe 1956; Kramer 1962; Whittaker and Niering 1965).

In experiments with young saguaros we have found that seedling growth stops and death eventually results from prolonged exposure to near-saturation soil moisture values in soils of all textures. In the greenhouse, rotting of young saguaros often results from daily watering during warm weather. In cultured young saguaros, Booth and Alcorn (1959) reported destruction of crowded plants by soft-rot fungi (*Fusarium* spp.).

The natural association of the saguaro with well-aerated soils and, conversely, its lack of tolerance of saturated soils under warm conditions strongly suggests that the southern limits of its distribution may be determined by interactions of soil characteristics and summer climate. The poorly aerated, predominately clayey soils that characterize the edge of the desert and coastal thornscrub southward from the vicinity north of Obregon to Navojoa may prevent the growth, establishment, and survival of young saguaros there and further southward in Mexico on the west Gulf Coast plain.

TABLE 23. Statistical comparison of soil characteristics of the two major climax vegetation types of the Sonoran Desert in Arizona (from Yang and Lowe 1956). Paloverde-saguaro (*Cercidium-Cereus*) soils are coarse-textured (high percentage of rock and gravel). Creosotebush-bursage (*Larrea-Franseria*) soils are fine-textured (high percentage of silt and sand).

Soil characteristic	*N*	*Larrea-Franseria*	*N*	*Cercidium-Cereus*	*t*	*P*
Moisture equivalent (%)	24	12.2 ± 0.61	24	6.6 ± 0.14	8.9	<0.001
Wilting coefficient (%)	24	6.6 ± 0.33	24	3.6 ± 0.08	8.8	<0.001
Moisture content[a] (%)						
Wet (approx. field capacity), summer rainfall season, July	12	9.1 ± 0.90	12	5.5 ± 0.16	7.3	<0.001
Dry, post-summer drought season, December	12	3.4 ± 0.41	12	1.4 ± 0.09	4.6	<0.001

[a] Moisture content here refers to the amount of water present in a given soil at a given time determined on the basis of a percentage of the oven-dry weight of a given sample at 105°C (221°F). For valid comparative purposes, samples were taken simultaneously at different soil stations.

Fig. 34A. The saguaro is codominant with foothill paloverde (*Cercidium microphyllum*) on this rocky southwest-facing slope in the Tucson Mountains, Saguaro National Monument. The cold-sensitive teddy bear cholla (*Opuntia bigelovi*) on the upper slope is an indicator of a winter-warm microclimate. Coarse-textured soils of gravel and rock bajadas, fans, and rock slopes support relatively diverse desert biotic communities in which the saguaro is a major dominant and where it often forms "saguaro forests." Photographed 28 April 1974.

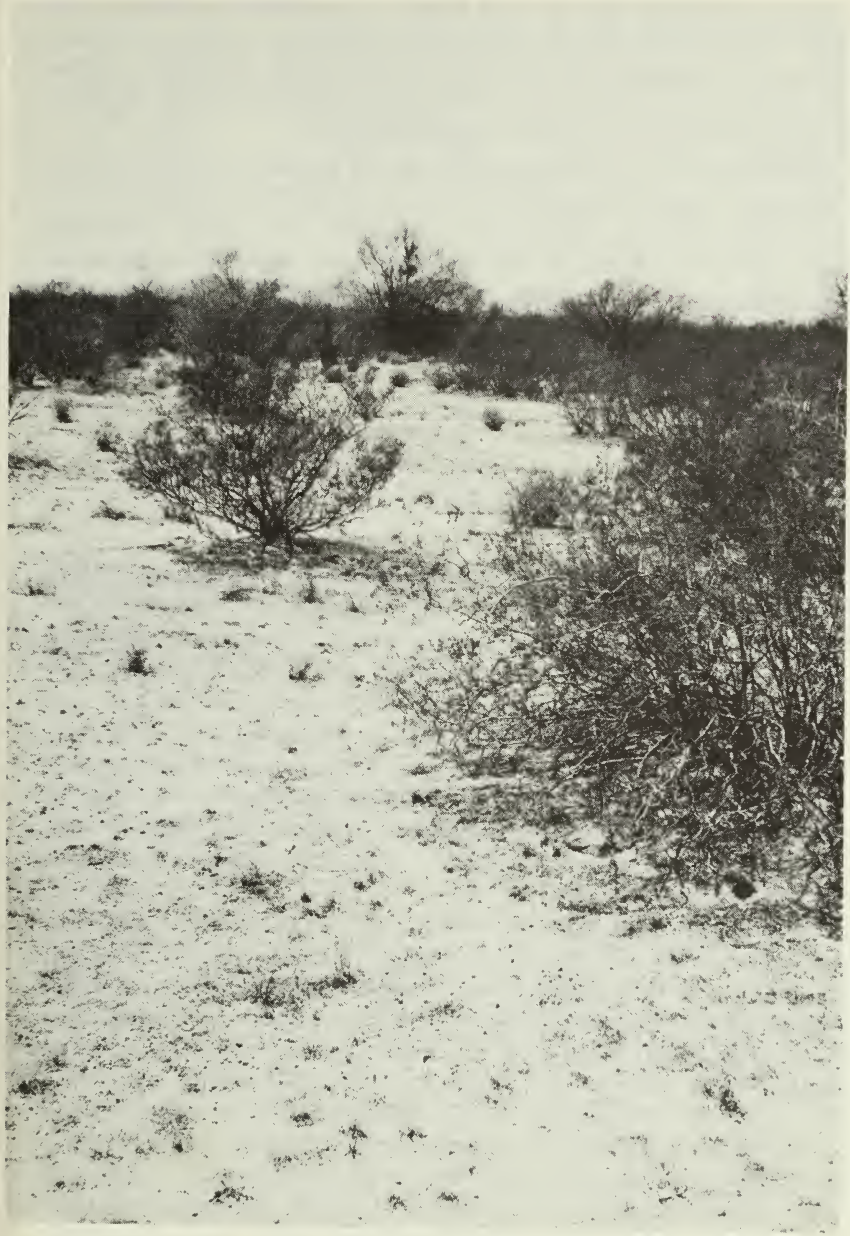

Fig. 34B. Creosotebush community in the Avra Valley northwest of Tucson. The fine-textured soils of the valley floors that are relatively high in clay, silt, and sand content support relatively few species, and so result in communities of simpler structure than those on bajadas or rocky slopes as shown in Fig. 34A. The saguaro occurs rarely when at all on such poorly aerated soils. Photographed 28 April 1974.

It is not surprising that the last saguaro populations southward are located on natural rock piles (Figs. 8, 12B, 35A). One is on Cerro Prieto east of Navojoa along the Navojoa-Alamos road and, further southward, the other is on Cerro Masiaca located northwest of Masiaca. Both populations are in extreme southern Sonora.

As demanded by the hypothesis given, the habitats of both of these southernmost saguaro populations are on disjunctively isolated rocky buttes. These isolated populations are located well above the poorly aerated, fine-textured soils of silts and clays that characterize the intervening stretches of the flood-prone coastal plain. The intervening plain is densely clothed with subtropical thornscrub ("thorn forest") maintained by a relatively high summer-warm rainfall regime (Fig. 35B).

Factor Interactions

In any year, the major portion of the current seedling crop is destroyed by a sequence of climatic and biotic factors. The operation of individual factors is associated specifically with one or more vegetative seasons as described by MacDougal (1908c, d) (Table 24): humid midsummer (July to September), arid after-summer (October and November), winter months (December to March), and arid foresummer (April to June). Most seedling deaths occur during the summer growth period. The rate of seedling mortality drops abruptly with the start of the arid after-summer in September (Tables 16-22; Figs. 28-30). Round-tailed ground squirrels estivate at that time, and insect numbers and activity decrease sharply.

There is large year-to-year variability in the rate of seedling establishment (Tables 25-27; Fig. 36). Such variability results primarily from differences in (1) summer rainfall and (2) winter minimum temperatures. During some years, exceptionally favorable conditions for germination produce an unusually large crop of seedlings; such conditions occurred at Saguaro National Monument (east) in 1964 (Steenbergh and Lowe 1969). Under those conditions many seeds germinate in exposed situations where there is little or no chance for seedling establishment. Under those circumstances a high rate of germination will be followed by high seedling mortality. Thus, a high rate of seed germination does not necessarily result in a correspondingly high rate of seedling establishment.

The relative importance of each of the several factors responsible for the destruction of young saguaros cannot be measured simply in terms of the relative mortality attributable to each cause. Rather, the relative

TABLE 24. Terms for the saguaro seasons (southern Arizona).

Period	Months	Term	Vegetative season (MacDougal 1908c)
	I. The Basic Within-year Seasons and Terms		
1. July-Aug.-Sept.	3	Summer Rain	Humid Mid-summer
2. Oct.-Nov.	2	Post-summer Drought	Dry After-summer
3. Dec.-Jan.-Feb.-Mar.	4	Winter Freeze	Winter Wet Season
4. April-May-June	3	Pre-summer Drought	Arid Fore-summer
	II. Other Periods and Terms		
1. July-Nov.	5	Pre-winter	
2. Dec.-Mar. (same as No. 3 above)	4	Winter	
3. April-June (same as No. 4 above)	3	Pre-summer	

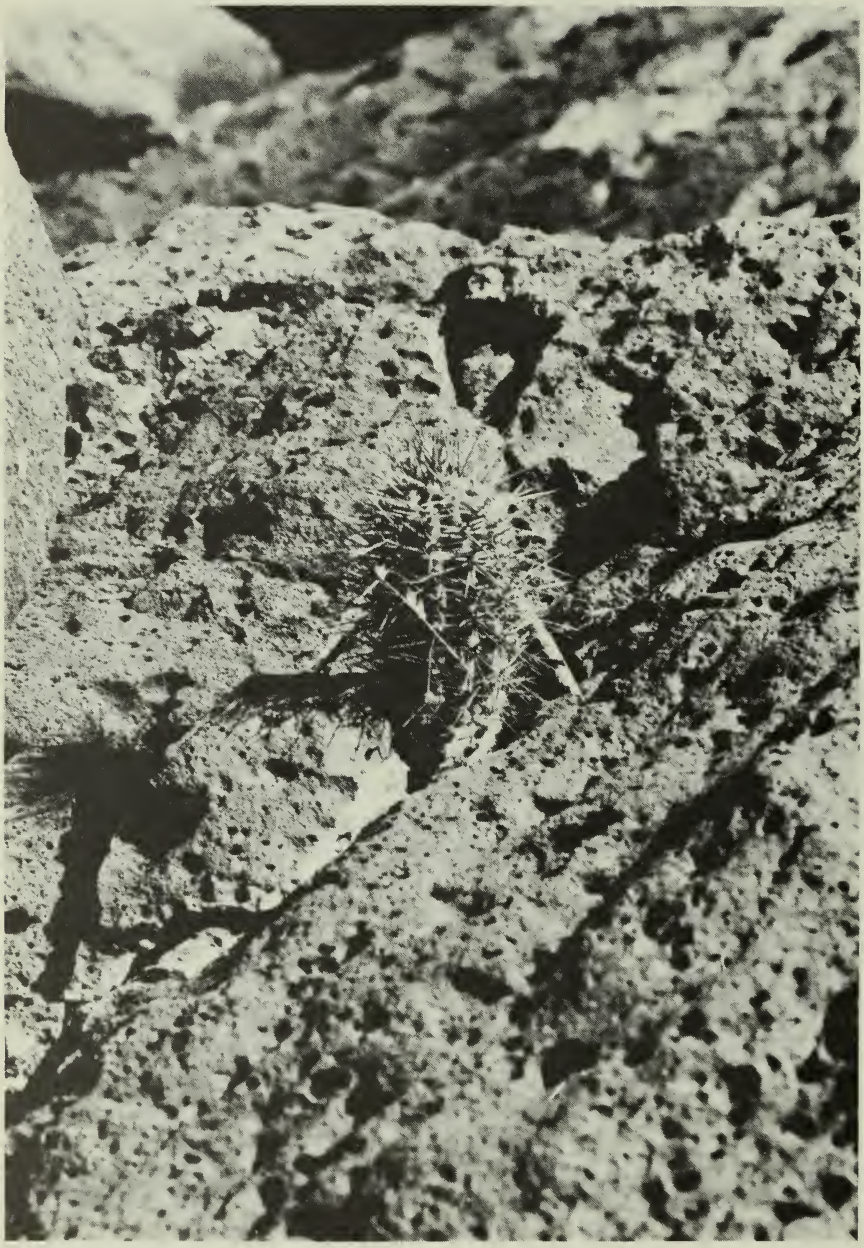

Fig. 35A. Young saguaro established in a fractured basalt boulder at Cerro Masiaca in extreme southern Sonora. The two southernmost saguaro populations, at Cerro Masiaca and at Cerro Prieto (48 km = 30 miles northward), are located *on* boulder fields of rocky buttes well above and disjunctively isolated by the intervening level plains. Photographed 27 December 1974.

Fig. 35B. Coastal thornscrub vegetation on the plains of northern Sinaloa: organpipe cactus (*Cereus thurberi*, left), hecho (*Cereus pecten-aboriginum*, center), morning-glory trees (*Ipomoea arborescens*, right), and dwarf jumping cholla (*Opuntia fulgida mamillata*, left foreground). The saguaro does not occur in these characteristic, poorly aerated, predominantly clayey soils of the thornscrub plains. The southern limits of saguaro distribution may be determined by its lack of tolerance of fine-textured and commonly saturated soils under warm conditions. Photographed 7 Jan. 1972.

TABLE 25. Summary of natural germination from broadcast saguaro seeds, Saguaro National Monument. The mean annual germination from 142,000 seeds broadcast during these experiments was 0.41% (4052 germinations per million seeds).

Pre-counted lots of seeds were broadcast within a total of 53 0.5 × 2 m (1.6 × 6.6 ft) plots during July 1965, 1966, and 1967.[a] Plots were located beneath the crowns of foothill paloverde (*Cercidium microphyllum*) trees in rocky (north-facing and south-facing slope exposures) and nonrocky (flat) habitats. The number and percentage of seedlings periodically observed to determine survivorship, and the correspondingly adjusted seed base are shown in the three right-hand columns[a] (see Table 26).

Year	Plots *N*	Seeds broadcast	Total germination		Survivorship observed		
			N	%	*N*	%	Base (seeds)
1965	28	28,000 ± 50	96	0.34	96	100.00	28,000
1966	6	19,000 ± 50	74	0.39	73	98.65	18,743
1967	19	95,000 ± 100	459	0.48	328	71.46	67,887
Total	53	142,000 ± 100	629	–	497	–	114,630

[a] In 1967 there could be no observations on survivorship in 7 of the 13 plots due to lack of germination.

TABLE 26. Cumulative first-year natural mortality and net survivorship of saguaro seedlings at Saguaro National Monument germinated from seeds broadcast during July 1965, 1966, and 1967 (see Table 25; Fig. 36).

Survivorship is expressed as survivors per million seeds disseminated. Of 497 seedlings under observation, 493 (99.2%) died within 12 months after germination; 4 seedlings (0.8%) survived to the start of the second year of life.

Date	1965 (*N* = 96)			1966 (*N* = 73)			1967 (*N* = 328)		
	Cum. dead	Surv. *N*	Surv./million seeds	Cum. dead	Surv. *N*	Surv./million seeds	Cum. dead	Surv. *N*	Surv./million seeds
Aug. 1							153	175	2,578
Aug. 6				3	70	3,735			
Aug. 8							178	150	2,210
Aug. 11	23	73	1,607						
Aug. 13				12	61	3,255			
Aug. 15							203	125	1,841
Aug. 18	59	37	1,321						
Aug. 20				21	52	2,774			
Aug. 21							213	115	1,694
Aug. 26	79	17	607						
Aug. 27				31	42	2,241			

⇨

TABLE 26.–(Continued)

Date	1965 ($N = 96$)			1966 ($N = 73$)			1967 ($N = 328$)		
	Cum. dead	Surv. N	Surv./million seeds	Cum. dead	Surv. N	Surv./million seeds	Cum. dead	Surv. N	Surv./million seeds
Sept. 1	89	7	250						
Sept. 3				35	38	2,027			
Sept. 7							247	81	1,119
Sept. 9	91	5	179						
Sept. 10				36	37	1,974			
Sept. 13	91	5	179						
Sept. 17				37	36	1,921			
Sept. 19							275	53	781
Sept. 22	92	4	143						
Sept. 25				44	29	1,547			
Oct. 2				48	25	1,334			
Oct. 3							303	25	368
Oct. 6	92	4	143						

TABLE 26.–(Continued)

Date	1965 ($N = 96$)			1966 ($N = 73$)			1967 ($N = 328$)		
	Cum. dead	Surv. N	Surv./million seeds	Cum. dead	Surv. N	Surv./million seeds	Cum. dead	Surv. N	Surv./million seeds
Oct. 18							306	22	324
Oct. 23	96	0	–	50	23	1,227			
Oct. 30				53	20	1,067			
Nov. 1				53	20	1,067	314	14	206
Nov. 6				53	20	1,067			
Nov. 13				54	19	1,014			
Nov. 15							317	11	162
Nov. 29							319	9	133
Dec. 11				55	18	960			
Dec. 13							320	8	118
Dec. 19							320	8	118
Jan. 4							322	6	88
Jan. 8				60	13	694			

⇩

TABLE 26.–(Continued)

Date	1965 ($N = 96$)			1966 ($N = 73$)			1967 ($N = 328$)		
	Cum. dead	Surv. *N*	Surv./million seeds	Cum. dead	Surv. *N*	Surv./million seeds	Cum. dead	Surv. *N*	Surv./million seeds
Jan. 10							323	5	74
Feb. 5				62	11	587			
Feb. 8							324	4	59
Feb. 21							324	4	59
Mar. 5				66	7	373			
Mar. 6							325	3	44
Apr. 4				67	6	320			
Apr. 30				68	5	267			
May 29				71	2	107			
June 26	96	0		72	1	53	325	3	44

TABLE 27. Regression equations for net first-year survivorship (from seeds) for saguaro seedlings during 3 consecutive years at Saguaro National Monument; log percent survival (Y) on log time in days (X) from 1 July by least squares. Data in Table 26, graphed in Fig. 36.

Year	N	Equation	r
1965	8	$\log Y = -3.294 \log X + 8.498$	–0.946
1966	20	$\log Y = -1.464 \log X + 6.003$	–0.933
1967	17	$\log Y = -2.012 \log X + 6.563$	–0.985
Pooled	45	$\log Y = -6.078 \log X + 6.244$	–0.939

importance of each factor is time-related. The importance of a particular factor lies in both its temporal and spatial impact upon the existing population and the life expectancy of the survivors. Furthermore, evaluation of factor importance must be concerned with the question of whether or not the particular factor operating is density-dependent and age-related.

The life expectancy of a young saguaro increases rapidly with age—it outgrows its predators and becomes increasingly able to survive the periodic hazards of the abiotic environment. However, in the case of recurring catastrophic freezes which operate without regard to population density (density-independent), survival is primarily dependent upon (1) the number of winter-favorable sites available within the habitats, and (2) the number of such sites actually occupied by young plants. Regardless of their numbers, other exposed cohorts in the population will die. Thus, near the cold-limited boundaries of its range, the number and character of physical microhabitats, as determined by the plant community together with the topographic characteristics of the habitats, are the factors that ultimately limit the survival and density of young saguaros.

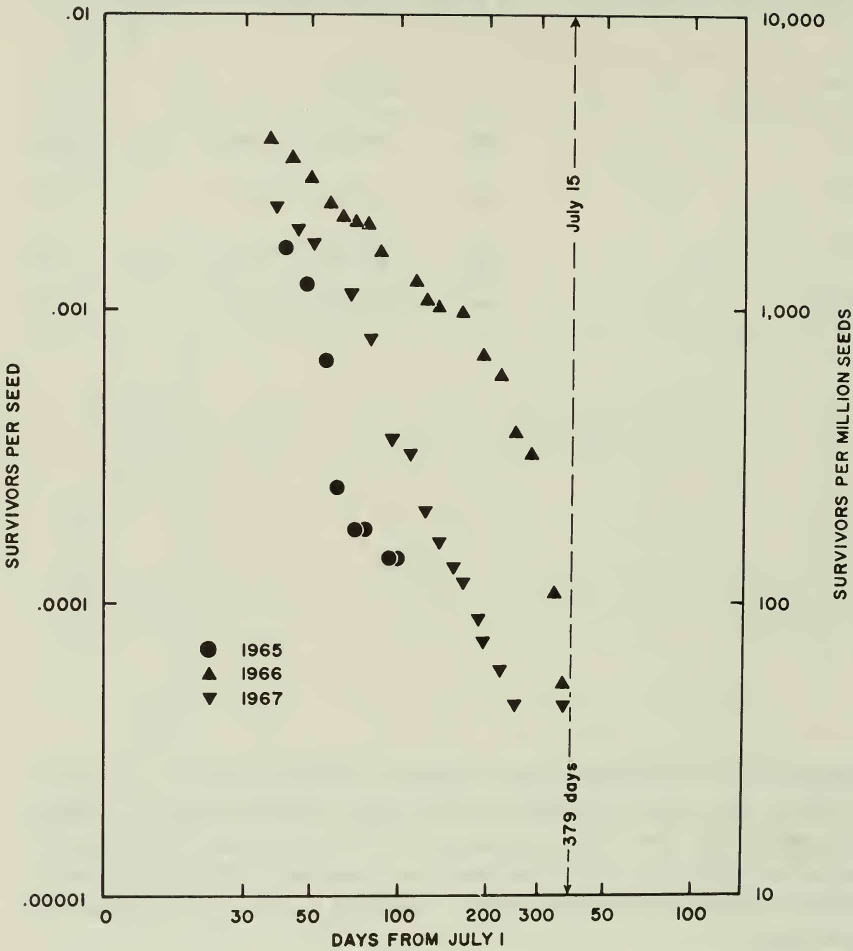

Fig. 36. Net first-year survivorship (from seeds) for 497 saguaro seedlings at Saguaro National Monument. Survivorship from 1 July is shown as seedling survivors per million seeds broadcast in representative natural habitats (Table 25); least squares regression of survivors on time in days.

Based on these data obtained during 3 consecutive years from July 1965 to June 1968, the estimated mean establishment rate (i.e., survival to 15 July of the following summer, the start of the second year of life) for saguaros in the Tucson area is 51.0 plants per million seeds (0.005%). The estimated post-germination establishment rate is 1.26%. Regression equation in Table 27, data in Tables 25 and 26.

Summary and Conclusions

For the saguaro, the greatest hazards to survival are associated with the pre-juvenile, seedling stage of life. Establishment is ordinarily reached at an age of 12-14 months.

The mean life expectancy of the newly emerged seedling is on the order of 2-6 weeks. Less than 1% of seedlings survive the first year of life to become established juvenile plants.

The end of the establishment period and the beginning of the juvenile stage is marked by the advent of monsoon rains of the summer following germination. Rapidly increasing in size and root development during that second summer of growth, the young plant attains a substantially increased drought tolerance and an increased ability to survive insect attack.

The tiny, succulent, weakly rooted saguaro seedling is highly vulnerable to destruction by a broad variety of abiotic and biotic agents. These include freezing, drought, rodents, and insects. The relative importance of each factor varies with the habitat, the season, and from year to year.

Our data indicate that *biotic factors* account for the greatest number of deaths of saguaro *seedlings*. The observations indicate that this is true in southern parts of the range (Sonora) and in the northernmost parts (Arizona). In the Tucson area and elsewhere along the northern and eastern limits of the plant's range in Arizona and Sonora, it is the extremes of the climatic environment that ultimately control the establishment and survival of *young saguaros*.

Within the absolute distributional limits imposed by the macroclimate, establishment and survival of young saguaros are dependent upon the physical protection provided by close association with other vegetation, detritus, and rocks. Acting singly or in combination, these moderate the limiting extremes of drought and winter cold and, in addition, reduce the probability of discovery and destruction by animals.

The density of young saguaros is limited by the availability within the community of suitable microhabitats as determined by the physical characteristics of the vegetation, soil type, and topography.

The probability of seedling survival increases with distance from reproductive adult saguaros and the associated activity of foraging animals. In nonrocky habitats, young saguaros rarely occur in close association with mature plants; rocks offer physical protection that permits some establishment in close proximity to mature saguaros.

Differential freeze-caused seedling mortality associated with differences in the intensity and duration of subfreezing temperatures occurs in topographically different habitats. In Saguaro National Monument and elsewhere in southeastern (and north-central) Arizona, subfreezing winter temperatures are the primary control on seedling survival.

Differential survival of seedlings occurs in rocky and nonrocky habitats, and on north- and south-facing slopes. Seedling establishment is highest on south-facing slopes, lowest on north-facing slopes, and intermediate in flat habitats.

Little or no establishment of saguaro seedlings occurs on north-facing slopes. In these habitats, higher soil moisture levels that favor pre-winter seedling survival in relatively arid environments are offset by subsequent freeze-caused winter mortality.

The southern limits of saguaro distribution may be controlled by summer climate in relation to summer soil moisture potentials. Seedlings cannot become established in poorly aerated or saturated soils.

5
Growth

> *It is difficult to find the very young Sahuaros. They are among the bushes under the palo verde and ironwood trees, and all that is to be seen of them is a gray tuft of spines. It is often ten or fifteen years before the seedling becomes large enough to be noticed, and twenty or thirty years before it begins to raise its head above the shrubbery which has sheltered its infancy. There is no direct way of telling the age of large cacti, as can be done by counting the growth rings of a leafy tree. The rate of growth of the Sahuaro is known, however, beginning at almost nothing and increasing to about four inches per year in large plants. The age of the largest ones can thus be estimated at from 125 to 175 years.*—Forrest Shreve, "The cactus and its home." 1931a:120.

Our primary concern in this report is with young saguaros so small and inconspicuous during the first years of life that they live and die virtually unnoticed in their desert microhabitats. While there have been several studies on saguaro growth, they have all quite naturally centered on relatively large, easy to find, and easy to measure individuals. While further contributing to such information, for a decade we have been studying the seedlings and juveniles in their natural habitats, and the data provided here on growth were designed to fill in the gap in the growth curve for the first critical years of the saguaro's life. In addition to analyzing the effects of environment and time on saguaro growth and growth-rate, the data reported here also permit correct age determination for young saguaros at Saguaro National Monument.

Environmental factors that influence the germination and establishment of young saguaros discussed in earlier chapters also play important roles in saguaro growth. Short of becoming limiting—i.e., short of acting as final limiting factors in the species distribution—temperature, precipitation, and soil characteristics are among the important direct and indirect environmental modifiers of growth within the species range. Accordingly, as discussed under Geographic Variation in Growth, growth rates differ in different saguaro populations in different parts of its distribution.

The Start of Growth

In the presence of continuously available moisture following germination, seedling development and growth are rapid and continuous. Within 24 hr after rupture of the seed coat, the slender, pale yellow-green seedling emerges upright. The base swells, cotyledons expand and spread to a horizontal position, and the saguaro seedling develops a light-green color—or in strong light, a pale red coloration—within one day following emergence. Stem development, with distinct areoles and spines, is evident within one week after the start of germination.

By the end of the first summer growth period, the green or reddish green seedling has 8, 12, or 16 areoles bearing well-developed spines. The total stem height is approximately 5.5 mm (0.22 inch), the diameter about 4.5 mm (0.18 inch), and the "taproot" is 1-2 cm (0.4-0.8 inch) in length. First-year stem height is ordinarily 1-2 mm (0.04-0.08 inch) greater in seedlings in flatland soils not associated with rock outcropping.

The principal growth occurs during June, July, August, and September, the period of warm summer rains, and ceases shortly after the end of those rains. Water uptake—replacement of moisture lost during the arid fall months—but no growth accompanies early winter rainfall and lower temperatures during late November, December, and January.

In years when late winter rains provide adequate soil moisture and warm temperatures prevail, a secondary and minor period of apical growth occurs as early as February and March.

In the presence of adequate moisture, some apical stem growth of seedlings (and larger saguaros as well) occurs during the arid foresummer period. On seedlings this is evidenced by the growth of new, greenish-colored apical spines and on older juvenile plants, by the lengthening and red coloration of apical spines. However, because there is water stress and stem shrinkage during this driest portion of the year, an actual decrease in stem height and diameter of saguaros of all sizes can and usually does occur.

April, May, and June are the pre-summer drought months of increasingly severe moisture stress, with increasingly warmer temperatures and scanty if any rainfall; May and June are especially hot. During that period, seedlings commonly shrink to half their original volume, and exposed small and weak individuals die.

The second year of life, the post-seedling juvenile stage, begins abruptly with the first significant summer rain (0.20 inch; 5.1 mm or more) ordinarily in early July in southern Arizona and in late June in southern Sonora. Observable water uptake can occur within 20 hr after the wetting of the soil. With adequate moisture, full turgor is quickly attained and new apical growth is evident within 8 days.

Growth and Growth Rates of Young Saguaros at Saguaro National Monument, Arizona

There have been no quantitative data available for natural saguaro growth during the seedling stage—the first year of life—and directly following early juvenile years. During these first critical years, saguaros are nearly invisible on the surface of the desert. Discovery requires work on hands and knees on the desert floor. As most one-year old saguaros are barely 5-6 mm (ca 0.25 inch) tall, and a large part of the tiny globular "stem" is underground, about all that the observant searcher can see is a small, concealing tuft of tan-colored spines.

After intensive searching, tiny saguaro seedlings and juveniles were discovered in the winter of 1965 in natural habitats under paloverde, mesquite, and bursage nurse-plants at Saguaro National Monument (see Chap. 6). The fate of these and other seedlings and young juvenile saguaros is reported by Steenbergh and Lowe (1969).

Naturally growing young saguaros at Saguaro National Monument (east) were measured to obtain data on stem form and growth rate characteristics for that population. Heights and diameters of individual, naturally established seedlings and young juvenile saguaros of known age (6-66 months) were measured in the field, the plants then removed and remeasured in the laboratory with precision calipers.

Data on the natural growth of larger juvenile plants were determined by yearly field measurements on a representative sample of the young saguaros at Saguaro National Monument (east) using permanent benchmarks and a specially designed gauge for stem height (Fig. 37) and machinist's calipers for diameter. The height and diameter of each individual was measured at one-year intervals. The difference between these consecutive annual measurements provides a series of one-year growth increments. These data provide a basis for estimating height, growth rate, and age relationships for young saguaros in this environment (Table 28; Figs. 39-41).

Fig. 37A. Height gauge used to measure apical growth of juvenile saguaros. Two aluminum legs that support the horizontal cross-bar rest on paired permanent benchmarks—steel rods set in concrete in the ground. The center measuring-rod rests on the stem tip of the young plant. The portion of the measuring-rod that projects above the horizontal crossbar is measured with a millimeter rule (measurement accuracy ± 1 mm). Apical growth increment (week, month, year) is obtained by subtracting the previous measurement; center measuring-rod is placed in the same relative position on the stem tip for successive growth measurements. Using longer legs to support the cross-bar, the same method is used to measure young plants 1-2 m (3.6-6.6 ft) tall. Photographed 21 May 1972.

Fig. 37B. Height gauge used to measure apical growth of adult saguaros. Horizontal cross-bar rests on the tip of the plant. A steel measuring tape attached to the telescoping pole (vertically oriented with a spirit level) is used to measure the distance from the horizontal cross-bar to a permanent steel benchmark at the base of the saguaro. A meter-stick resting on the benchmark allows eye-level reading to the nearest whole millimeter. The apical growth increment is obtained by subtracting the previous measurement. Photographed 10 March 1974.

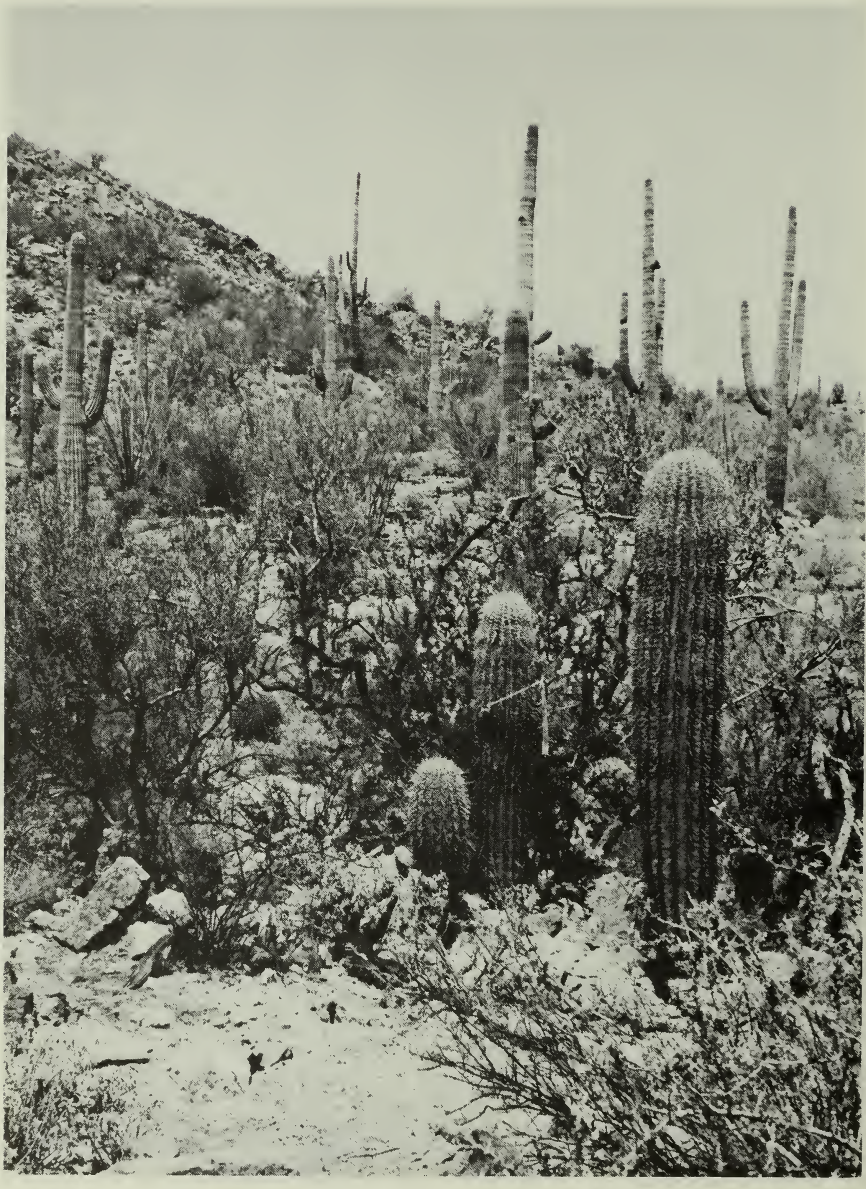

Fig. 38A. Year-to-year variation in length of saguaro spines, visible in the photographs as distinctive bands encircling the plant stem, reflects climatically related variations in summer growth. Shorter spines are associated with periods of depressed growth that result from freeze-caused injury, unusually dry summers, or other causes.

Note the change in form from the *club* shape of juvenile saguaros in the foreground to the *bottle* ("wine bottle") form of larger saguaros in the background (see text). Photographed 15 April 1971.

Fig. 38B. Saguaros in a permanent plot established in 1941 at Alamo Canyon, Organ Pipe Cactus National Monument, Arizona. Height of each individual, originally measured in 1941, was re-measured in 1967 thereby obtaining a 26-year apical growth increment (see Table 34). Accurate measurement is facilitated by permanent steel-in-concrete benchmark at the base of each plant. Photographed 11 February 1972.

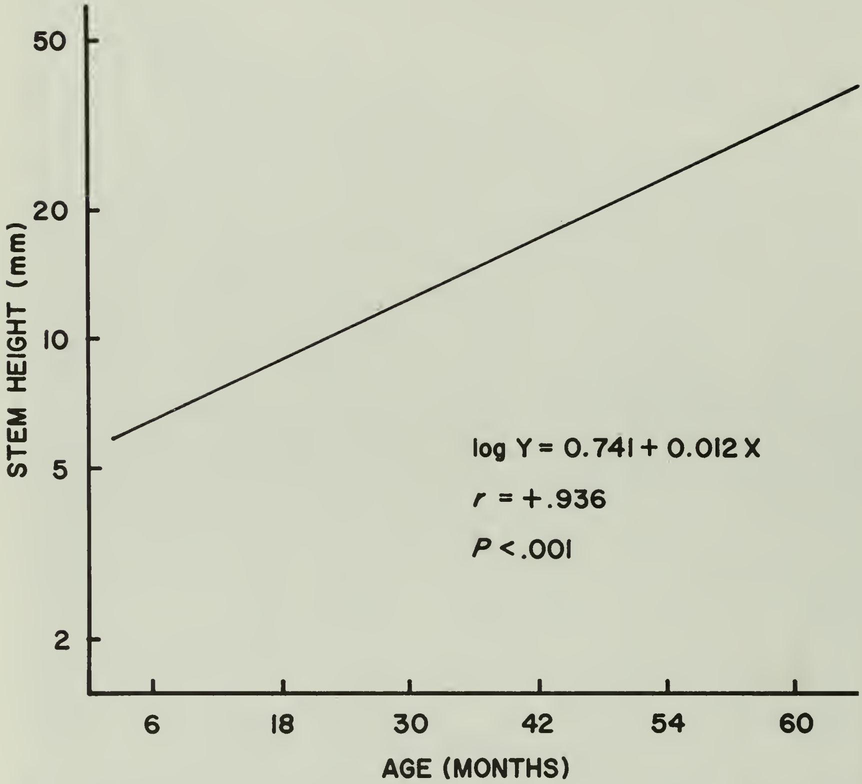

Fig. 39. Regression on semi-logarithmic coordinates of stem height on age of young saguaros (N = 30) for the first 5 years following germination in nonrocky habitats at Saguaro National Monument (east), near Tucson, Arizona. In this equation 6 months = 1 growth year, 18 months = 2 growth years, etc. See text.

The stem growth of young saguaros increases exponentially ("geometrically") with age and size. Yearly apical growth of young saguaros at Saguaro National Monument (east) is graphed in Fig. 40. The regression of one-year growth increments on stem height for 62 naturally growing seedlings and juvenile saguaros (Fig. 40) is described by equation (2) below.

The regression of yearly apical growth for wild saguaros during the first growth-year of life (seedling) and subsequent juvenile growth-years—for the first 6 years of life in flat and rolling-hill (nonrocky) habitats at Saguaro National Monument (east)—is described by

$$\log Y = 0.741 + 0.012\,X \qquad (1)$$

where Y is stem height in millimeters and X is age in months,[1] for the germinating Class of 1963 to and including the Class of 1968. The associated product-moment correlation coefficient (r) is +0.936, $N = 30$. The years involved are free of the catastrophic-kill winter freezes as recently experienced in January 1962 and January 1971 in southeastern Arizona (see Niering et al. 1963; Steenbergh and Lowe 1976).

For the seedling year (Class of 1968) of this 6-year series, the measured mean stem height of the seedlings is 6.0 mm ± 0.37 (4.8-7.6), $N = 8$. Using equation (1), the least squares calculated first-year stem height ($\hat{Y}$) is 6.5 (6.486) mm ($N = 30$), i.e., based on the growth data for all of the 6 successive years of saguaro classes (1963-68) in the study.

Accordingly, this derived best estimate for saguaro stem height attained during the first year of life at this specific locality is 0.6486 cm (0.26 inch). As it is the only natural first-year growth data in existence for the saguaro (or any other species of cactus), it might be assumed that it is applicable to saguaros elsewhere. We caution that that assumption is valid only in a highly restricted sense, for saguaro growth can and does vary significantly and widely from population to population in different environments, as well as from individual to individual in the same immediate environment. Compare, for example, the data in Tables 28-38.

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[1] In this equation, 6 months = 1 growth-year, 18 months = 2 growth-years, etc.

Age and Height

The value for first-year stem height obtained by equation (1) (0.6486 cm; 0.26 inch) provides a basis for conversion of height to age for the population studied at Saguaro National Monument (east) in the saguaro habitats on flat and moderately rolling, nonrocky surface terrain. As noted above and described below, in this population the age of a very young saguaro of a given height can be determined (i.e., estimated) using the log of 0.6486 for log X in equation (2).

The saguaro growth curve for young saguaros—saguaros <2.2 m (7.2 ft) height—illustrated in Fig. 40 is described by

$$\log Y = -0.297 + 0.991 \log X - 0.175 (\log X)^2 \tag{2}$$

where Y is a one-year apical growth increment (cm) and X is the stem height (cm) for the given plant at the start of the growth-year; the associated correlation coefficient (r) is highly significant ($r = +0.978, P < 0.001, N = 62$). As before, the data are for saguaros growing in flatland habitats at Saguaro National Monument (east) where plant-available soil moisture is relatively higher and the growth rate for most individuals is relatively faster than that for saguaros on rock outcrops and on rocky slopes with rock surfaces at Saguaro National Monument (east).

Table 28 provides age data for young saguaros (<2.2 m; 7.2 ft) at Saguaro National Monument (east) as graphed in Fig. 41. The semilogarithmic plot of height and age (Fig. 41) is described by

$$\log Y = -0.309 + 0.884 \log X + 0.609 (\log X)_2 \tag{3}$$

where Y is stem height in centimeters and X is age in years; $r = 0.997$, $P < 0.001$. The estimated Y ($\hat{Y}$) values plotted in Fig. 41 were generated by using equation (2) and the on-site mean growth during the first year of life as determined by equation (1); as explained above, the calculated subsequent one-year apical growth increment for a one-year-old plant was added to the first-year height to obtain second-year stem height and, using the same stepwise procedure, stem height was calculated for each consecutive year.

Saguaros at approximately 2 m (6.6 ft) stem height undergo a marked change in growth form. The change in form is associated with a decline in growth rate and with changes in functions associated with the onset of reproduction (see Table 29; Figs. 15, 16, 38, 40, 43, 44).

Two events occur at that stage of saguaro development: (1) the plant produces its first blooms and fruits; and (2) a transition from the "club" form of the large juvenile plant to the "wine-bottle" form of the unbranched young adult as the maximum diameter ceases to follow the upward growth of the tip (Fig. 38A).

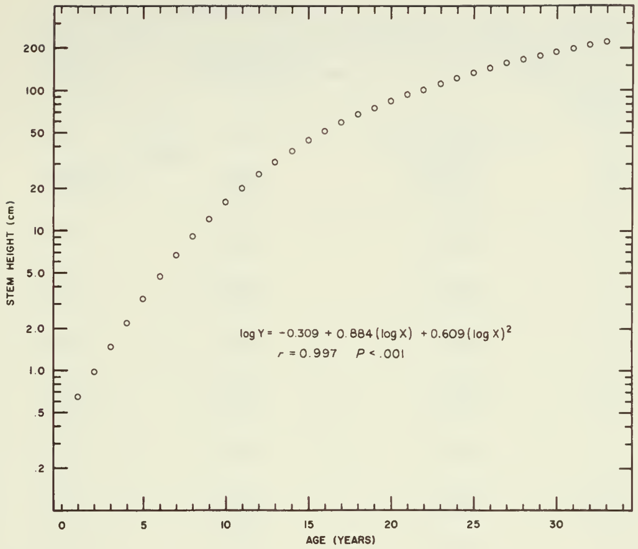

Fig. 40. Regression on logarithmic coordinates of apical growth on stem height of young saguaros (N = 62) in nonrocky (flat) habitats at Saguaro National Monument (east).

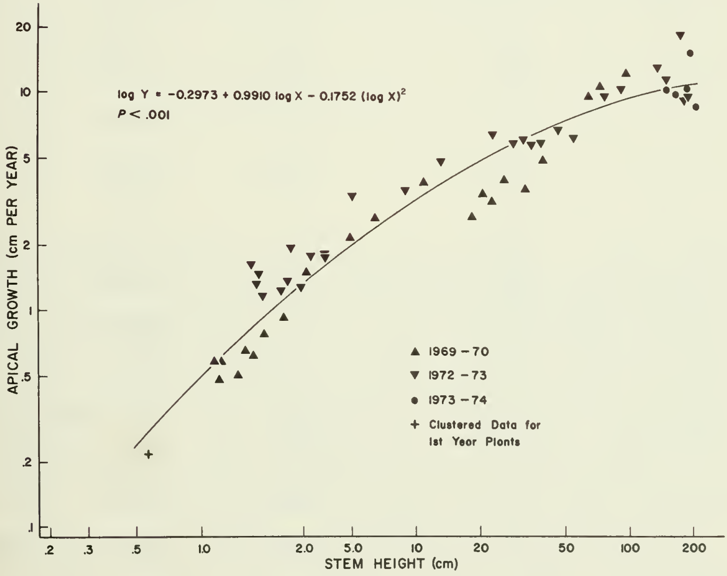

Fig. 41. Regression on semi-logarithmic coordinates of stem height on age for healthy young saguaros in flat (nonrocky) habitat at Saguaro National Monument (east). Data in Table 28; see text.

TABLE 28. Stem height-age relationship and subsequent one year apical growth of healthy young saguaros in flat (non-rocky) habitat at Saguaro National Monument (east). Graphed in Fig. 41.

Age (yrs)	Apical growth (cm/yr)	Height (cm)	Height (inches)
1	0.32	0.65	0.26
2	0.49	0.97	0.38
3	0.73	1.46	0.58
4	1.07	2.19	0,86
5	1.43	3.26	1.27
6	1.94	4.69	1.85
7	2.51	6.63	2.61
8	3.11	9.14	3.60
9	3.75	12.25	4.82
10	4.38	16.00	6.30
11	5.01	20.38	8.02
12	5.61	25.39	10.00
13	6.18	31.00	12.20
14	6.72	37.18	14.64
15	7.20	43.90	17.28
16	7.66	51.10	20.11
17	8.09	58.76	23.13
18	8.46	66.85	26.31
19	8.82	75.31	29.64
20	9.14	84.13	33.11
21	9.44	93.27	36.71
22	9.71	102.71	40.43

TABLE 28.–(Continued)

Age (yrs)	Apical growth (cm/yr)	Height (cm)	Height (inches)
23	9.96	112.42	44.25
24	10.18	122.38	48.17
25	10.40	132.56	52.18
26	10.58	142.96	56.27
27	10.76	153.54	60.43
28	10.92	164.30	64.67
29	11.07	175.22	68.97
30	11.20	186.29	73.32
31	11.33	197.49	77.73
32	11.45	208.82	82.21
33	11.55	220.27	86.72

As discussed earlier and illustrated in Chapter 2, some saguaros in southern Arizona and northern Sonora may start their reproductive life when only approximately 1.5 m (4.9 ft) in stem height. Ordinarily, 50% or more of the population in height-class 2.00-2.49 m (6.6-8.2 ft) flowers and produces seed during most years (Fig. 16). The tabular age of a young 1.5-m (4.9 ft) saguaro is 27 years, and the age range is approximately 31-36 years for height-class 2.00-2.49 m (6.6-8.2 ft). Our data thus estimate age of the 200 cm (6.6 ft) young saguaro at 31 years, and the 2.2 m (7.2 ft) mean stem height at 33 years age at Saguaro National Monument (east; flats and rolling terrain); see Table 28.

The data provided here together with our other field observations suggest that earlier changes in the apical growth rate of the young saguaro also are coincident with major changes in form. The data on the apical growth of young saguaros as graphed in Fig. 40 suggest that a reduction in apical growth rate may accompany the transition from the globose juvenile form to the "club" form of the large juvenile that occurs in the vicinity of 5-10 cm (2-4 inch) above-ground stem height. We anticipate answering this question in further investigations on growth rates and form changes in relation to saguaro survival and climatic adaptation.

Effects of Flower Bud Removal on Stem Growth

When a healthy saguaro initiates its first reproductive year of life, abruptly moving into adulthood after some 30 or more years of life in which it attains a growth up to or over approximately 2 m (6.6 ft.) in height, the energy shunted into the production of reproductive structures themselves (buds, flowers, fruits, and seeds) is energy directed away from apical stem growth. To test both the prediction and the cost of reproductive effort in terms of stem-growth increment reduction, an experimental design was structured to compare quantitatively apical growth differences between samples of treated and untreated stems of vigorous healthy saguaros.

The results for carefully paired experimental and control plants in the same stand are given in Table 29. Untreated (control) plants were allowed to complete normal development of reproductive growth. All flower buds started by experimental plants were removed each week beginning 20 April 1970. A small energy increment was required for the plant to initiate the buds that were removed, thus providing a slight underestimate in the "per cent growth change" column (Table 29). The data reveal not only that the prediction is true but also the rather dramatic disclosure that approximately 50% of the 4-5 m (13-16 ft) saguaro's potential stem growth for a given year is diverted into its yearly reproductive effort.

Freezing Effects on Growth

Freeze-caused injury depresses the subsequent rate of saguaro growth. Desiccation and volume shrinkage resulting from freeze-caused injury are expressed by decreases in stem heights and diameters (see Steenbergh and Lowe 1976). The effects of the January 1971 freeze on the height and apical stem growth of young saguaros at Saguaro National Monument (east) are shown in Tables 30, 31, and Fig. 42.

The desiccating effect of freezing is greatest on smaller juvenile plants and is evident in the stem measurements recorded in early April 1971, 3 months after the freeze. At that time, the maximum diameter of all of 14 plants over 9 cm (3.5 inches) in height showed a diameter *decrease* (rather than increase) from the size recorded one year earlier. Only 9 of

TABLE 29. Effect of flower bud removal on apical growth (cm) of unbranched saguaros in nonrocky (flat) habitat at Saguaro National Monument (east). New flower buds appearing on experimental plants (69A and 61C) were removed each week beginning 20 April 1970. Plants 69B and 69D were allowed to complete normal development of reproductive growth. Precipitation for the two summer growth seasons in Table 32.

No.	1969 ht (cm)	Apical growth and fruits				Growth change (cm)	
		1969-70		1970-71		2nd year	
		Fruits[a]	Growth	Fruits	Growth	cm	%
				EXPERIMENTAL			
69A	429.4	73	12.8	0[b]	17.2	+4.4	34.4
69C	404.0	76	10.5	0[b]	16.7	+6.2	59.0
Mean		74.5	11.65		16.95	+5.3	45.4
				CONTROLS			
69B	428.3	100	12.4	169	10.9	-1.5	-12.1
69D	449.8	40	11.2	112	12.5	+1.3	11.6
Mean	439.05	70	11.8	140.5	11.7	-0.1	-0.9
Mean Difference		4.5	-0.15		5.25	5.4	+46.3

[a] Incomplete counts taken on 8 July 1969 after start of fruit drop.

[b] Between 20 April and 25 June 1970, when the last buds developed, a total of 196 buds were removed from plant 69A, and 242 buds were removed from plant 69C.

TABLE 30. Effect of freezing on growth. Total stem height (cm) and one-year height growth increment (cm) for young saguaros ($N = 17$) in flat (nonrocky) habitats at Saguaro National Monument (east), 1969-73. Data graphed in Fig. 42.

	Stem height and annual increase (cm)							
No.	1969-70		1970-71		1971-72		1972-73	
	ht	incr.	ht	incr.	ht	incr.	ht	incr.
1	2.7	0.4	3.1	0.3	3.4	1.6	5.0	3.4
2	3.1	1.5	4.6	1.2	5.8	3.1	8.9	3.6
3	4.5	1.3	5.8	0.7	6.5	2.5	9.0	3.2
4	4.9	2.1	7.0	2.1	9.1	4.0	13.1	4.9
5	6.4	2.7	9.1	2.0	11.1	3.0	14.1	3.7
6	10.8	3.9	14.7	3.0	17.7	4.8	22.5	6.5
7	18.1	2.7	20.8	3.6	24.4	3.9	28.3	3.8
8	18.2	2.1	20.3	3.9	24.2	3.9	28.1	5.8
9	20.4	3.5	23.9	3.3	27.2	4.5	31.7	6.0
10	22.3	3.2	25.5	5.0	30.5	4.0	34.5	5.7
11	25.5	4.0	29.5	4.1	33.6	3.5	37.1	5.8
12	32.0	3.6	35.6	4.9	40.5	5.0	45.5	6.7
13	38.9	5.0	43.9	4.9	48.8	4.9	53.7	6.1
14	60.5	3.3	63.8	5.9	69.7	6.0	75.7	9.6
15	62.9	9.6	72.5	9.0	81.5	8.2	89.7	10.2
16	71.6	10.7	82.3	12.0	94.3	9.5	103.8	8.0
17	94.5	12.3	106.8	13.9	120.7	11.2	131.9	13.0

TABLE 31. Regression equations for 1-year apical growth (cm) on stem height (cm) for young saguaros ($N = 17$) at Saguaro National Monument (east). Data in Table 30, graphed in Fig. 42.

	N	Year	Regression equation	r
			INDIVIDUAL YEARS	
1	17	1969-70	$\log Y = -0.2894 + 0.6340 \log X$	+ 0.8676
2	17	1970-71	$\log Y = -0.6453 + 0.8762 \log X$	+ 0.9488
3	17	1971-72	$\log Y = 0.0559 + 0.4219 \log X$	+ 0.9110
4	17	1972-73	$\log Y = 0.1753 + 0.3964 \log X$	+ 0.9080
			2-YEAR GEOMETRIC MEANS	
5	17	1969-70, 1972-73	$\log Y = -0.0988 + 0.5358 \log X$	+ 0.9321
6	17	1970-71 1971-72	$\log Y = -0.3079 + 0.6533 \log X$	+ 0.9536

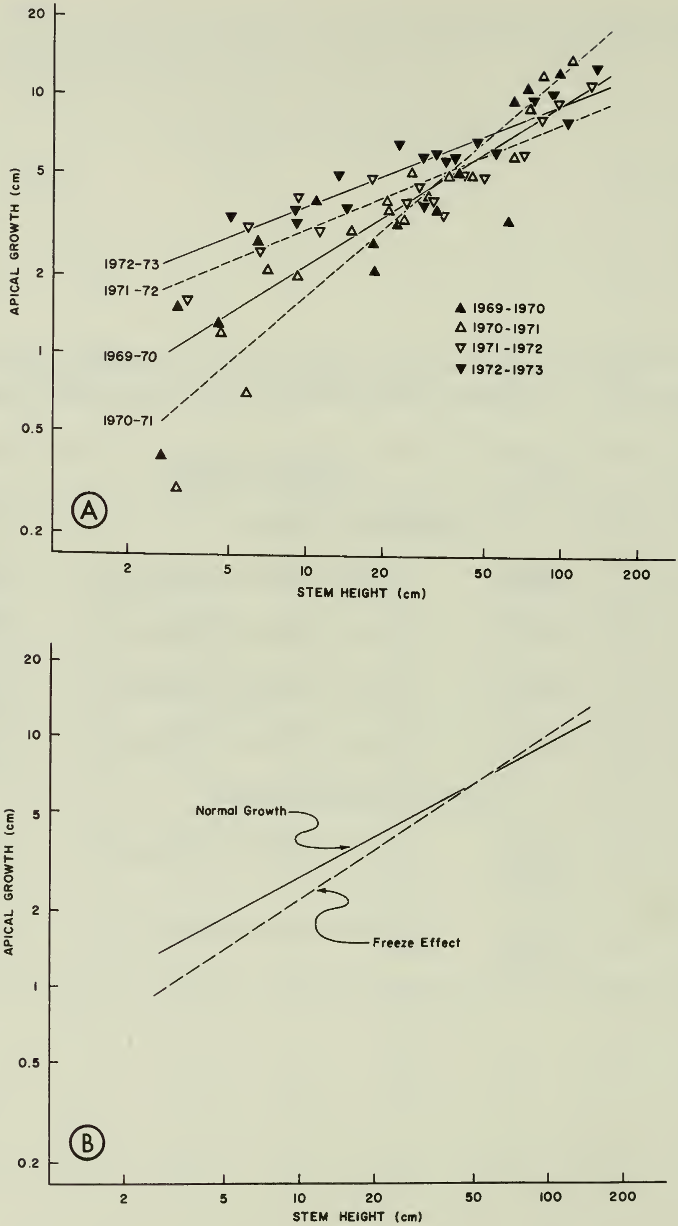

Fig. 42. Effect of freezing on apical growth of 17 young saguaros at Saguaro National Monument (east). Regression on logarithmic coordinates of apical growth on stem height. (A) Growth during 4 consecutive years, January 1969 to March 1973. (B) Geometric mean of 2 years apical growth on stem height showing normal growth (1969-70, 1972-73) and combined freeze-effect (1970-71, 1971-72) of Jaunary 1971 freeze (see text; Steenbergh and Lowe 1976). Data in Table 30, regression equations in Table 31.

the 17 plants, all more than 11.2 cm (4.4 inches) in height, showed a height increase greater than that for the previous year—the actual height growth during 1971 was partially offset and completely obscured in these measurements by shrinkage resulting from freeze-caused desiccation.

Subnormal growth following the 1971 freeze-caused injury is shown in part by the 1972 data. Even these low growth rates, however, are deceptively high, for a large portion of the indicated "apical growth" from April 1971 to April 1972 is, in fact, not growth at all but represents the recovery of freeze-caused volume loss. Thus, the effect of freezing on apical stem growth is expressed in the sum and the mean of the increments for the 2 years from 1970 to 1972 as shown in Fig. 42 and Tables 29, 30.

Geographic Variation in Growth

The rate of growth can vary significantly and even widely between saguaro populations separated by relatively short distances, especially where elevation, topography, and/or soil structure also vary greatly over short distances. For example, several different effective environments characterize different desert areas and habitats within Saguaro National Monument, and between the east and west divisions of the monument (Table 32).

Still greater differences in growth rate can be predicted for populations separated by greater distances and growing under more widely distinctive effective environments, for example, as indicated by the climatic data for Tucson, Ajo, and Yuma, Arizona (Table 33). We predict large order growth-rate differences between Tucson populations and populations in the Yuma desert (Gran Desierto) area. There the saguaros on bajadas and valley fill are essentially a desert riparian species population with low marginal density under 3.38 inches (86 mm) annual rainfall and 1.57 inches (40 mm) summer (May-October) rainfall (Green and Sellers 1964:493, Yuma; Fig. 9B).

Organ Pipe Cactus National Monument

Measurement of saguaro growth over a period of 26 years in populations at Organ Pipe Cactus National Monument provides an important sample for the study of the species that is summarized in Table 34 and graphed in Figs. 43 and 44. The curve in Fig. 44 is fitted by multiple linear regression as in the case for the Saguaro National Monument data

TABLE 32. Six-year on-site record of summer precipitation (inches; June-October) at Saguaro National Monument, east flats (SEF) and west flats (SWF).

Month	1968		1969		1970		1971		1972		1973	
	SWF	SEF	SWF	SEF	SWF	SEF	SWF	SEF	SWF	SEF	SWF	SEF
	Precipitation (inches)											
June	0[a]	0[b]	0	0	0.14[a]	0.20	0[a]	0	1.94	0.01	0.32	0.72
July	2.43	1.92	1.70	0.89	1.22	3.07	0.90	2.22	1.26	0.03	1.77	2.20
Aug.	2.76	2.77[c]	1.57	2.96	1.67	2.13	5.96	5.83	1.57	0.03	0.55	0.37[b]
Sept.	0[a]	0.12[c]	0.81	0.80	3.14	2.91	1.47	1.70	0.37	1.49	0[a]	0
Oct.	0.63	1.58	0.12	0.18	0.25	0.25	2.54	2.32	3.87	5.49	0	0.64
Cum. total	5.82	6.39	4.20	4.73	6.42	8.56	10.87	12.07	9.01	7.05	2.64	3.93

[a] Official records, Tucson Mountain District Ranger Station (west monument).

[b] Official records, Headquarters, Rincon Mountain District (east monument).

[c] Estimated temporal distribution based on official records, Monument Headquarters (east).

TABLE 33. Summary of climatic parameters for Tucson (elev. 2430 ft; 740 m), Ajo (elev. 1763 ft; 537 m), and Yuma Citrus Station (elev. 191 ft; 58.2 m), Arizona (precipitation given in inches; temperatures shown in °F).

	Tucson	Ajo	Yuma
Mean Precipitation			
Summer (May-Oct.)[a]	6.7 inches	5.0 inches	1.4 inches
Winter (Nov.-April)[a]	4.5 inches	4.0 inches	1.9 inches
Annual[b]	10.91 inches	9.10 inches	3.28 inches
Mean Temperature			
Summer (May-Oct.)[a]	79.0°	83.4°	83.7°
Winter (Nov.-April)[a]	55.9°	59.3°	60.0°
Annual[b]	67.3°	71.2°	71.9°
Maximum[b]	82.9°	84.0°	87.7°
Minimum[b]	51.6°	58.3°	56.1°
Potential Evapotranspiration[c]	41.68 inches/yr	47.19 inches/yr	47.8 inches/yr
Extreme Temperatures			
Summer maximum[b]	115° (1960)	115° (1960)[e]	119° (1957)
Winter minimum[b]	6° (1913)	17° (1937)[f]	19° (1937)[g]

TABLE 33.–(Continued)

	Tucson	Ajo	Yuma
Jan. 1937[d]	15°	17°	19°
Jan. 1962[d]	20°	25°	23°
Freeze Occurrence[h]			
Frost-free days/yr (>32°)	231	349	294
First freeze (*P* 32° = 0.50)	Nov. 14	Jan. 3	Dec. 10
Last freeze (*P* 32° = 0.50)	Mar. 28	Jan. 19	Feb. 19

[a] Green 1964.
[b] Green and Sellers 1964.
[c] Buol 1964.
[d] U.S. Weather Bureau Climatological Records.
[e] Also recorded on earlier years.
[f] No available record of temperatures prior to 1915.
[g] No available record of temperatures prior to 1920.
[h] Green and Kangieser 1967; minimum temperatures of 32°F or less.

TABLE 34. Saguaro stem height and apical growth (cm) at Organ Pipe Cactus National Monument, Arizona. Plant height in 1941 (Lightle 1941) and height of the same plants in 1967 provide a 26-yr apical growth increment. Data graphed in Figs. 43 and 44.

No.	Height (1941)	Height (1967)	26-yr growth increment
		ALAMO CANYON	
1	15.2	48.2	33.0
2	15.2	81.3	66.1
3	25.4	114.3	88.9
4	30.5	132.1	101.6
5	30.5	157.5	127.0
6	30.5	165.1	134.6
7	30.5	129.5	99.1
8	30.5	101.6	71.1
9	30.5	144.8	114.3
10	30.5	172.7	142.2
11	30.5	210.6	180.1
12	30.5	157.5	127.0
13	30.5	104.1	73.6
14	30.5	127.0	96.5
15	30.5	116.8	86.3
16	30.5	162.5	132.0
17	30.5	165.1	134.6
18	43.2	302.0	258.8
19	45.7	312.4	266.7
20	45.7	213.4	167.6
21	45.7	109.2	63.5
22	45.7	142.3	96.5

⇨

TABLE 34.–(Continued)

No.	Height (1941)	Height (1967)	26-yr growth increment
23	45.7	119.1	73.6
24	45.7	259.1	213.4
25	45.7	287.0	241.3
26	61.0	223.5	162.5
27	61.0	203.2	142.3
28	61.0	172.7	111.8
29	61.0	182.9	121.9
30	79.2	254.0	177.8
31	91.4	345.4	254.0
32	106.7	309.9	203.2
33	106.7	416.6	309.9
34	182.0	510.5	358.0
35	195.6	528.3	332.5
36	243.8	538.5	294.7
37	335.3	538.5	203.2
38	365.8	711.2	345.4
39	366.0	718.7	353.0
40	426.7	853.4	426.7
41	487.7	670.6	182.9
42	548.6	716.3	167.7
43	579.1	797.6	188.0
		DOWLING WELL	
44	30.5	101.6	71.1
45	30.5	78.7	48.2

TABLE 34.–(Continued)

No.	Height (1941)	Height (1967)	26-yr growth increment
46	30.5	134.6	104.1
47	30.5	101.6	71.1
48	45.7	106.7	61.0
49	61.0	182.8	121.8
50	61.0	160.0	99.0
51	121.9	248.9	127.0
52	182.9	340.4	157.5
53	182.9	388.6	205.7
54	182.9	348.0	165.1
55	182.9	335.3	152.4
56	195.6	373.4	177.8
57	213.4	373.4	160.0
58	213.4	462.3	248.9
59	213.4	378.4	165.0
60	213.4	408.9	195.5
61	213.4	388.6	175.2
62	213.4	388.6	175.2
63	274.3	439.4	165.1
64	274.3	469.9	195.6
65	304.8	421.6	116.8
66	365.8	513.1	147.3
67	365.8	586.7	220.9
68	365.8	551.2	185.4
69	365.8	538.5	172.7

TABLE 34.–(Continued)

No.	Height (1941)	Height (1967)	26-yr growth increment
70	365.8	518.1	152.3
71	396.2	556.3	160.1
72	426.7	609.6	182.9
73	426.7	563.9	137.2
74	426.7	589.3	162.6
75	487.7	777.2	289.5
76	487.7	647.7	160.0
77	487.7	579.1	91.4
78	518.2	640.1	121.9
79	548.6	624.8	76.2
80	548.6	685.8	137.2
81	609.6	868.7	259.1
82	609.6	853.4	243.8
83	609.6	680.7	71.1
84	670.6	823.0	152.4
85	731.5	934.7	203.2
86	731.5	787.4	55.9
87	792.5	861.1	68.6
88	792.5	990.6	198.1
89	853.4	1000.7	147.3
90	853.4	1117.6	264.2
91	853.4	1046.5	193.1
92	853.4	929.6	76.2
93	975.4	1051.6	76.2

(Fig. 40). As at Saguaro National Monument and elsewhere, the asymptote of the growth curve for Organ Pipe Cactus National Monument is at approximately 2 m (6.6 ft) stem height (Fig. 44). As noted above, important changes in form and function—and important consequences—take place in the saguaro in southern Arizona when the plant reaches a stem height on the order of 2 m (6.6 ft).

The data on apical growth of saguaros at Organ Pipe Cactus National Monument,[2] shown in Table 34 and graphed in Fig. 44, provide, for the first time, a basis for estimating mean growth rates and age-height relationships of saguaro populations whose growth rates are not under the dominant depressing influence of catastrophic freezing. Growth rates for this population, situated close to the ecological and geographic center of the species range, differ markedly from those for saguaro populations at Saguaro National Monument and elsewhere near the cold-limited boundaries of the species range.

A comparative view of a significant difference in growth rate between two saguaro populations in southern Arizona—at Saguaro National Monument (east) in southeastern Arizona and Organ Pipe Cactus National Monument in south-central Arizona—is provided in Fig. 45. The differences in growth-rate characteristics for these two populations, as shown in Fig. 45, are attributable to differences in temperature and precipitation. Gross differences in parameters of the climate at Tucson and Ajo (Table 33) relate importantly to observed differences in saguaro growth rates and to height-age relationships for saguaros in these two different climatic environments.

As compared to the climatic environment of Saguaro National Monument and the Tucson locality, the climatic environment of Organ Pipe Cactus National Monument and Ajo locality is a much warmer and drier one that results in the slower growth of *juvenile* saguaros. In its overall effects on the growth of *larger* plants, however, the warmer environment at Organ Pipe Cactus National Monument offers conditions for saguaro growth more favorable than those at Saguaro National Monument (see Hastings and Alcorn 1961). There, the effects of catastrophic freezing offset the potentially greater benefits of substantially higher plant-available moisture and lower transpiration losses.

Tempe, Arizona

Investigation of saguaro growth in a natural population of saguaros in the Phoenix, Arizona, area was conducted by Marshall and Earle (Marshall 1955) on South Hill in the Desert Botanical Garden, Tempe.

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[2] Lightle (1941) field data and re-measured in 1967 to obtain a 26-year apical growth increment.

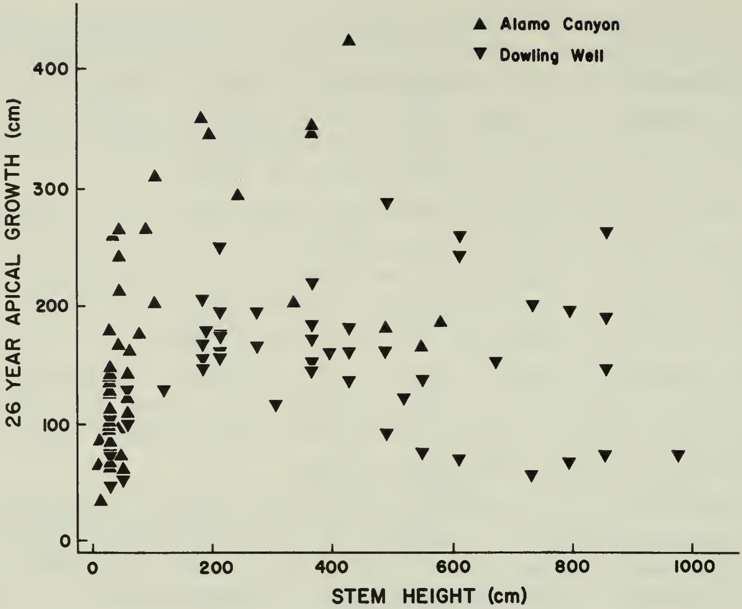

Fig. 43. Apical growth on stem height (1941) of 93 saguaros at Organ Pipe Cactus National Monument, Arizona, on uniform (arithmetic) scale. Note the reversal in the rate of growth that occurs at approximately 200 cm (6.6 ft) height. Data in Table 34.

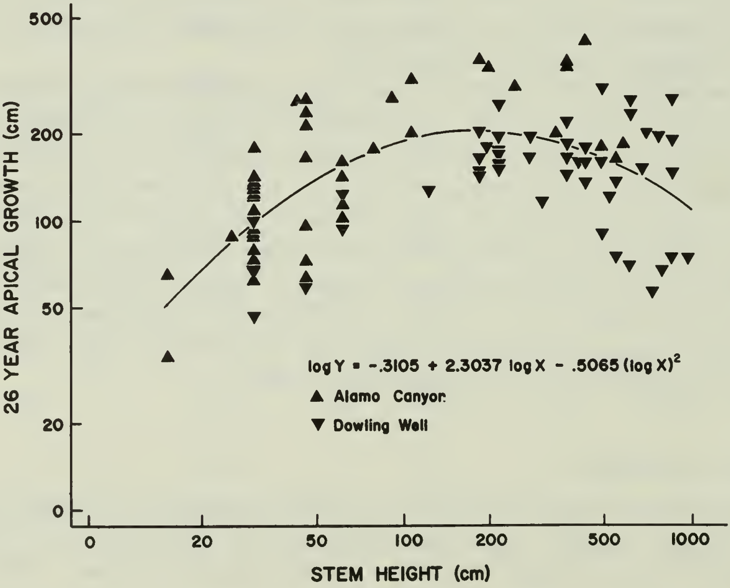

Fig. 44. Regression on logarithmic coordinates of 26-year apical growth on 1941 stem height (Lightle 1941) for 93 saguaros at Organ Pipe Cactus National Monument, Arizona. Note asymptote of curve at approximately 2 m (6.6 ft); see text. Data in Table 34.

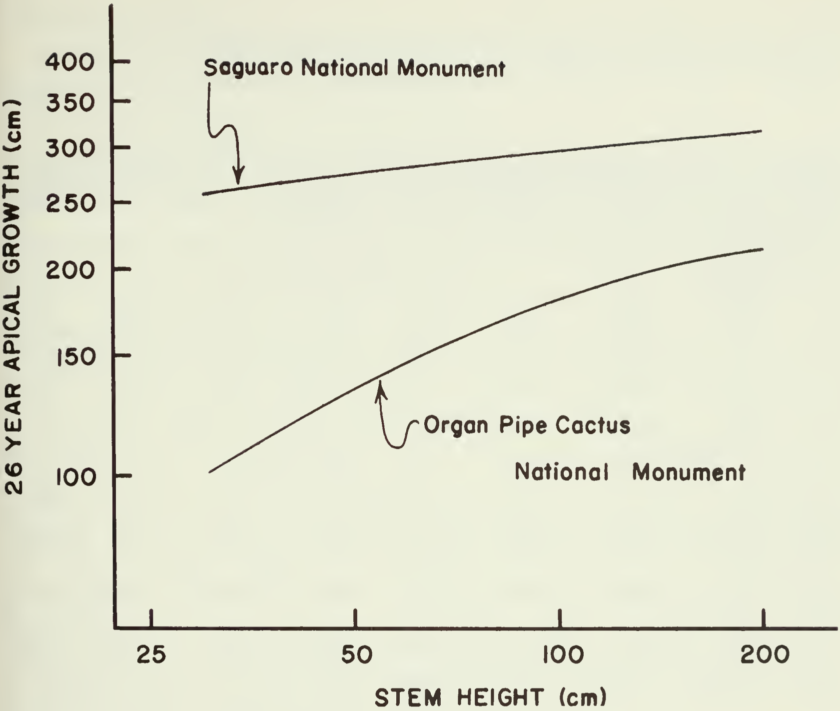

Fig. 45. Regression on logarithmic coordinates of 26-year apical growth on height for young saguaros at Saguaro National Monument (east) and Organ Pipe Cactus National Monument (see Tables 28, 33, and 34 and Figs. 38, 39, 42, and 43). See discussion in text.

Their data for 6 years (1949-54) are given in Table 35. The data appear to be in general accord with our observations and those reported by others on growth rates for young saguaros in this portion of the extreme range of the species.

TABLE 35. Height measurements (cm) and subsequent one-year apical growth increments (cm) for 14 young saguaros at Tempe, Arizona from annual measurements by W. Hubert Earle, reported by Marshall (1955:57). Original data in inches.

No.	Original height (cm)	One-yr apical growth (cm)						
		1949	1950	1951	1952	1953	1954	Mean
1	5.4	1.6	1.3	1.9	1.3	3.8	0.6	1.8
2	14.0	3.2	0.6	3.8	1.3	1.3	0.6	1.8
3	22.2	6.4	1.9	6.4	5.1	3.8	5.1	4.8
4	28.6	5.1	0.6	8.3	5.7	3.8	3.2	4.4
5	56.5	10.2	3.2	14.0	10.8	7.6	12.7	9.8
6	61.3	3.8	1.3	7.0	5.7	5.1	7.0	5.0
7	64.4	6.0	2.5	7.6	0.6	11.4	9.5	6.3
8	85.1	15.2	2.5	12.1	13.3	9.5	12.1	10.8
9	88.9	14.0	3.8	15.2	10.8	11.4	14.6	11.6
10	114.3	8.9	4.4	5.1	8.9	3.2	5.7	6.0
11	116.8	14.0	2.5	14.6	13.3	10.2	15.2	11.6
12	129.5	14.0	3.2	12.7	14.0	8.3	12.7	10.8
13	165.7	20.3	7.0	23.5	22.9	9.5	17.8	16.8
14	256.5	22.9	6.4	21.6	26.0	20.3	24.8	20.3

Tucson, Arizona

In the Tucson area, other investigations of saguaro growth have been reported by MacDougal and Spalding (1910), Shreve (1910), Hastings (1961), and Hastings and Alcorn (1961).

MacDougal and Spalding (1910) measured and reported yearly apical growth increments for individuals in a saguaro population on Tumamoc Hill in the Tucson Mountains. The data are for years 1905-8 and, though long overlooked, they are the first growth data obtained and reported for the species (see Table 36). It is a peculiarity that Shreve (1910), reporting in the same year from the same laboratory, included no reference to these important data.

The growth record provided by MacDougal and Spalding (1910:30, Table 8) contains the highest natural rate of growth ever reported for the saguaro. During the 9-month period from 23 January 1907 to 22 October 1908, one individual (No. 19) in that sample grew from a height of 244.4 cm (96.2 inches) to 301.6 cm (118.7 inches), an average of 28.6 cm (11.25 inches) per year. It is noteworthy in relation to that unusually high rate of growth that the July to September precipitation during the 1907 and 1908 summer growth periods was 8.53 inches (217 mm) (Green and Sellers 1964: Tucson) and 12.05 inches (306 mm) (MacDougal and Spalding 1910, on site), respectively. Both values are substantially above the 5.01-inch (127 mm) Tucson mean for these 3 months (Green and Sellers 1964).

Shreve (1910) provided none of the data used to obtain the age-height relationships he reported for saguaros growing on the northern slope of Tumamoc Hill in Tucson (Table 37). Using his data, a plot of height on age, however, shows an exponentially linear age-height relationship, with a distinct increase in the growth rate occurring at a height of approximately 24 cm (9.4 inches). Our results, however, do not suggest the occurrence of such a growth-rate change at that height (Tables 28, 30; Figs. 40-42).

The growth rates reported by Hastings and Alcorn (1961:Figs. 5 and 6) also showed the reversal in the annual apical growth rate occurring at a height of approximately 2 m (6.6 ft), typical of saguaro growth-form ontogeny thus far known (see Tables 34 and 38; Figs. 43 and 44).

Table 36. Original height measurements (cm) and subsequent one-yr apical growth increments (cm) for 8 saguaros on Tumamoc Hill, Tucson, Arizona, from periodic stem height measurements reported by MacDougal and Spalding (1910:Table 8).

Plant No.	Original measurement		Observed one-yr apical growth				
	Year	Height	1906	1907	1908[a]	1908[b]	Mean
24	1906	4.5	–	2.9	2.2	–	2.55
25	1906	37.4	–	6.1	8.3	15.0	9.80
21	1905	70.4	13.5	5.9	7.1	–	8.83
10	1905	86.8	5.4	0.1	6.9	–	6.47
4	1905	162.1	7.4	13.7	10.8[c]	10.8[c]	10.70
12	1905	163.8	8.6	2.0	16.2[c]	16.2[c]	10.75
19	1905	223.6	15.6	5.2	28.6[c]	28.6[c]	19.50
22	1905	230.2	10.9	13.6	14.2[c]	14.2[c]	13.25

[a] 23 Mar. 1908.

[b] 22 Oct. 1908.

[c] Means of two seasons' growth from 23 Jan. 1907 to 22 Oct. 1908.

Table 37. Height, estimated age and one-yr apical growth for saguaros on Tumamoc Hill, Tucson, Arizona; apical growth is subsequent one-yr apical growth determined by graphic analysis of height-age relationships given in Shreve (1910:237).

Height (cm)	Age (yrs)	Apical growth (cm/yr)
10	8.0	2.0
20	12.5	2.5
40	19.1	4.0
80	27.3	7.0
100	30.3	8.0
200	40.5	12.0
300	47.5	15.0
400	54.0	20.0
500	60.0	40.0

Table 38. Mean annual apical growth of saguaros in USDA sample at Saguaro National Monument 1951–59. Adjusted data in Hastings and Alcorn (1961:Fig. 5).

Height-class (ft)	Mid-point		Apical growth (cm/yr)
	(ft)	(cm)	
0-1.99	1	30.48	8.68
2-3.99	3	91.44	9.33
4-5.99	5	152.40	11.11
6-7.99	7	213.36	11.25
8-9.99	9	274.32	10.20
10-11.99	11	335.28	7.29
12-13.99	13	396.24	7.51
14-15.99	15	457.20	7.07
16-17.99	17	518.16	5.21
18-19.99	19	579.10	5.30
20-21.99	21	640.08	6.80
22-23.99	23	701.04	6.71
24-25.99	25	762.00	6.25
26-27.99	27	822.96	6.49
28-29.99	29	883.92	6.20
30-31.99	31	944.88	8.00
32-33.99	33	1005.84	9.25
34-35.99	35	1066.80	6.80

Summary and Conclusions

The saguaro is well adapted in its growth responses to the highly variable amounts and temporal distribution of summer precipitation that are characteristic of the climate of the Sonoran Desert. The shallow, widespreading root system enables the plant to utilize moisture from relatively small amounts of rainfall. It responds quickly with new growth to renewed soil moisture after a period of drought. Thus, the saguaro efficiently can utilize intermittently and briefly available moisture from infrequent summer rains.

Growth of the saguaro is distinctly seasonal and takes place during coincident periods of relatively high temperatures and plant-available soil moisture. Growth is limited by lack of moisture during the dry after-summer and arid fore-summer seasons, and by cold during the winter wet season.

The principal stem growth of the saguaro takes place during and immediately following monsoon rains in July, August, and September. Water uptake occurs and apical growth is resumed within a few hours after the start of the first saturating summer rain.

Moisture lost by transpiration during the dry after-summer is usually replaced during the early winter months. In the colder northern portions of the species distribution, water uptake without growth takes place during the period of winter rains and low temperatures in late November, December, January, and early February.

A second period of growth beginning as early as February–depending upon concurrently warm temperatures and available moisture—may occur during the late winter and early spring months. The potential increase in stem volume from such growth is offset by transpiration losses during the hot months of the arid fore-summer.

In the saguaro and other columnar cacti, there is a series of critical ontogenetic growth-form changes. In young saguaros, the first of these changes takes place when the young plant reaches a height of approximately 5.5 cm (2.2 inches), and the second change occurs when the plant reaches a height of approximately 200 cm (78.7 inches).

The annual growth increment of juvenile saguaros increases exponentially with age and increased size up to the age of first flowering. As much as 50% of the potential stem growth of adult saguaros is diverted into yearly reproductive growth.

The total summer growth of the saguaro is dependent upon the cumulative duration of periods of plant-available soil moisture. The annual increment of stem growth, therefore, is determined not only by the amount of precipitation, but in large measure, by its temporal distribution.

Growth rates of the saguaro are highly variable. Genetic variation and/or microenvironmental differences commonly result in a twofold (or larger) difference in annual height growth between individuals growing in the same immediate locality and topographic habitat. Similarly large variations in annual growth increments occur and are associated with year-to-year variation in summer precipitation and winter temperatures.

Significant differences in saguaro growth rates occur in different topographic habitats under the same general climate. These differences are directly related to the influence of slope and exposure upon temperature and plant-available moisture, and to different moisture relationships that result from differing physical characteristics of the associated soils.

The rate of saguaro growth differs widely from population to population in response to the broad range of climatic environments present within the extensive geographic range of the species. Generally, rates of saguaro growth increase along a gradient (1) of increasing summer precipitation from west to east, and (2) higher winter minimum temperatures that occur from high to low elevations, and from north to south latitudes.

Freezing depresses the growth rate of both juvenile and adult saguaros. Severe freeze-caused injury to the crowns of juvenile saguaros reduces growth for a period of 2 or more years following the freeze. Freeze-caused reduction in the growth rate of adult saguaros can continue for several years after injury.

For adult saguaros situated near the cold-limited northeastern boundary of its distribution, the growth-limiting effect of recurring catastrophic freezes offsets the advantage of relatively favorable moisture conditions. In these winter-cold environments the average growth of large saguaros is less than in some more arid but warmer environments.

Height-age relationships of saguaros growing in different portions of the species range vary not only with differences in precipitation and related availability of moisture but also are controlled by the frequency and intensity of subfreezing temperatures. Established height-age relationships for a saguaro population growing in one locality cannot be applied to populations growing in other locations without consideration of both of these controlling climatic variables.

Over a major portion of the saguaro species distribution, winter cold determines not only the growth rate but also quantitative aspects of its reproductive success, local and absolute limits of distribution, population density, and age-class structure, as well as the timing of the critical events in the life cycle of the saguaro.

6
Overview and Outlook

> *It is bootless at this time to attempt to explain the apparent decadence of the Giant Cactus. A fuller knowledge of its germination and the behavior of its seedlings, together with a more complete knowledge of the periodicity of certain climatic elements within its range will be sure to throw light on the fall in its rate of establishment.*—Forrest Shreve, "The rate of establishment of the giant cactus." 1910:240.

Now that we have established the nature and operation of the factors that control germination, establishment, and survival of young saguaros in Saguaro National Monument and elsewhere in this more northerly portion of their range, it is possible to draw conclusions concerning the current status of these populations in relation to past conditions, events, and activities, and in some measure to predict their future course.

Commerce and Conservation: The Human Factor

> *Coming down the northern point of the mountain and out westward into the plain, we transferred ourselves in a few hours from the temperate to the torrid zone. In the foot-slopes we passed through an ardent grove of giant cacti, called by Mexicans 'Sahuaros,' some of them fifty feet high. Among these prickly horrors grew a variety of lesser ones, more or less closely related to them.*—Lt. John Bigelow, Jr., "After Geronimo." 1887:522.

This oldest known observation on the stands of saguaro cactus at Saguaro National Monument—1886, quoted above—contains just enough information to whet the appetite of curiosity and to stir speculation on the condition of that saguaro forest nearly 100 years ago. Unfortunately, for purposes of understanding the present condition of the saguaro populations within the monument in relation to historical uses and abuses of the land, known references are few and nonspecific.

Further, we must add that the scattered available records are in need of much additional search and evaluation to provide detail on historic activities that relate to the past and present condition of the saguaro populations. Our present knowledge of historical conditions and factors that may relate to the past and present condition of saguaro populations in Saguaro National Monument is limited largely to the information that the various noted activities did take place, and to the approximate time and location of their occurrence.

The absence of specific information, i.e., numbers, names, dates, and precise locations of historic activities within the monument, does not allow us to ignore the fact or possible significance of their occurrence. Neither does it preclude generalized evaluation of the effects of these kinds of activities on saguaro establishment and survival. It is not our intention to document here in great detail the period or extent of any of the historic activities that may have influenced the subsequent condition of saguaro populations within Saguaro National Monument. Rather, we concern ourselves with the question of the relationship of these kinds of activities to known natural factors affecting the germination, establishment, and survival of *young* saguaros.

Cactus pirates

During the early part of this century, large numbers of young saguaros in the Tucson vicinity were removed for sale to cactus fanciers and for landscaping purposes; the practice continues although not in the monument area. Former residents of the east monument area state that, prior to 1933, cactus merchants were active in the Cactus Forest area, and that large numbers of young plants were removed by these operators.

There is no reliable basis for estimating the number of saguaros removed during these operations. That young saguaros were present in numbers sufficient to support such operators, however, is significant. The presence at that time of these young plants leaves no question that conditions were favorable for saguaro establishment, and for their survival to a size and age suitable for "harvest." It is likely that most of the saguaros sought and removed were the easily transplantable sizes of the 10- to 30-year-old age group.

Plants of that age class have a high natural life expectancy. They have grown beyond the age of high vulnerability to the principal agents of young saguaro mortality, and are entering a long period of growth when they are least vulnerable to the climatic factors that kill large adult plants. Thus, it is not unreasonable to assume that, in the absence of human intervention, a large proportion of those plants removed by cactus merchants would be alive today as intermediate-size adult saguaros—the age-group largely missing in the Cactus Forest now and from the time the original monument was established.

Woodcutting

A portion of the east monument, mainly including the Cactus Forest area, was included within the Fort Lowell military reservation and served as a source of lime during construction of the fort. Remains of limestone kilns are still present near the northeast edge of the Cactus Forest area. The green wood of paloverde trees was used to fire the kilns. However, because of the rapidity with which the wood of this species decomposes, no stumps remain to indicate the number of paloverde trees removed for this use.

Mesquite (*Prosopis juliflora*), a preferred firewood species, was cut intensively within the area. The durable dead stumps of this species are abundant in the Cactus Forest area, and most of the living mesquite trees are sprouted from old stumps (Fig. 46).

Activities of woodcutters affect the fate of young saguaros growing beneath the trees they remove. Not only are such plants liable to mechanical destruction by the woodcutters themselves, the survivors are fully exposed to trampling by cattle, and to the full decimating impact of the biotic and abiotic environment. In addition to such direct destruction of established saguaros, woodcutting also reduced the number of favorable sites for subsequent saguaro establishment. Without the modifying influence of protective plant cover, the associated microhabitats were no longer suitable for the establishment of saguaros.

Grazing

In some portions of Saguaro National Monument, saguaro habitats have been subjected to intensive grazing by cattle for more than three-quarters of a century. In some localities, particularly the Cactus Forest area of the east monument, this has had an unquestionably detrimental effect on the germination, establishment, and survival of young saguaros (Figs. 47-50).

Direct destruction of young saguaros has resulted from the long-continued trampling of cattle seeking shade and forage beneath the crowns of desert trees, mainly paloverde and mesquite (Figs. 47A, 50A). This degradation of microenvironments favorable to saguaro establishment and survival continued for a period of many decades and has resulted in a correspondingly reduced density of saguaros surviving from the year-classes of that period.

An even more significant effect of cattle grazing has been the impact of continued grazing pressure upon the physical structure of the plant community (Figs. 47-50). The resulting deterioration of the natural multistoried tree and shrub cover and the modification of associated microenvironments seriously reduced the number and quality of sites available for the germination, establishment, and survival of young saguaros.

Livestock grazing has had its greatest impact in nonrocky habitats where the germination, establishment, and survival of young saguaros are most directly dependent upon the physical protection of other vegetation (Figs. 47A, 48A, and 50A). In these habitats a multistoried canopy of overhanging tree branches together with shrubs provides concealment from destructive animals and effectively moderates extremes of drought and subfreezing temperatures (Fig. 50B).

In rocky habitats, livestock grazing has had far less impact upon young saguaros. There, as in nonrocky habitats, the protective cover of associated vegetation contributes to the germination, establishment, and survival of young saguaros. However, the deteriorating effect of livestock grazing in these habitats decreases in importance as the fate of young saguaros becomes increasingly related to their association with protective rock outcrops. Thus, despite the seriously destructive effect of grazing upon the other vegetation in these habitats (Fig. 49A), the age-class structure and the density of young saguaros in these populations have been affected much less by livestock grazing than those in nonrocky habitats.

In summary, the primary role of historic livestock grazing has been to reduce the *density* of affected saguaro populations by decreasing the number of sites suitable for germination and establishment of young plants by increasing exposure to natural mortality-causing factors. Differential impact, i.e., differential mortality, has been associated with differences in the intensity and duration of grazing and the physical characteristics (rockiness) of the terrain. Mortality is highest in intensively grazed, relatively flat, nonrocky terrain, and lowest in less intensively grazed, steep slopes with extensive rock outcrops. Natural regeneration of vegetation is occurring (Figs. 47B, 48B, and 49B) and natural rates of germination, establishment, and survival of young plants are now occurring in habitats under National Park Service protection that were heavily grazed earlier in the century.

Fire control

Fire is a natural cause of mortality of young saguaros near the upper elevational limits of their distribution. The relative importance of this factor under natural conditions is not known. However, our observations on natural fire-caused saguaro deaths in the Coronado and Tonto national forests in Arizona indicate that fire is a density-controlling factor in ungrazed habitats where grasses and other low-growing plant species provide a sufficiently continuous cover of combustible fuel to permit the

Fig. 46A. Stumps of mesquite (*Prosopis juliflora*), a preferred firewood species, are abundant in the Cactus Forest at Saguaro National Monument (east). Activities of woodcutters during the early part of this century reduced the number and favorability of sites for subsequent establishment of saguaros. In addition, the removal of trees undoubtedly contributed to the destruction of established saguaros. Photographed 19 June 1968.

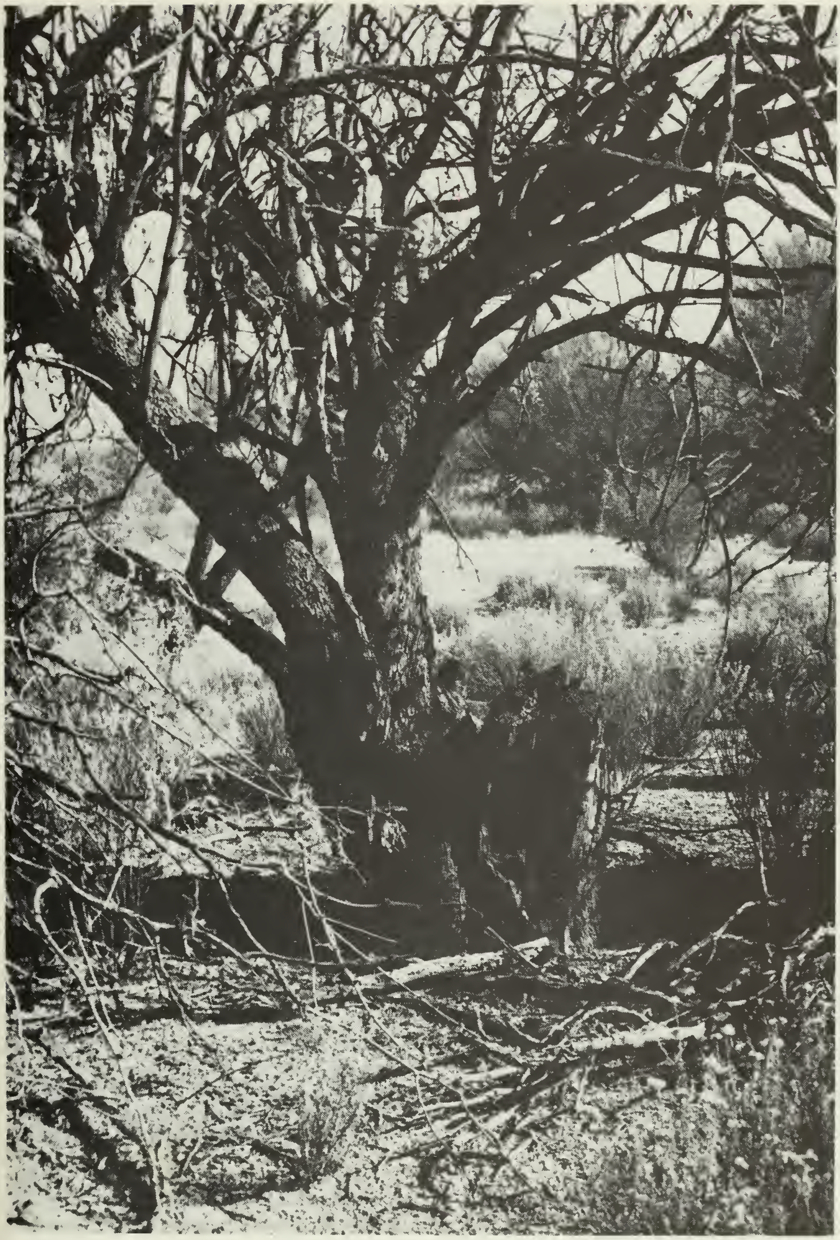

Fig. 46B. Mesquite trees (*Prosopis juliflora*) resprouted from cut stumps are common in the Cactus Forest, Saguaro National Monument (east). Young saguaros established within the last 10-15 years now occur beneath a large proportion of such resprouted mesquite trees. Photographed 20 January 1971.

Fig. 47A. Actively grazed paloverde-saguaro (*Cercidium microphyllum-Cereus giganteus*) community adjacent to Saguaro National Monument (east). Note the sparsity of shrubs and grasses. Beneath the trees, fallen limbs that would offer protection for young saguaros have been pulverized by trampling cattle. Photographed 7 August 1969.

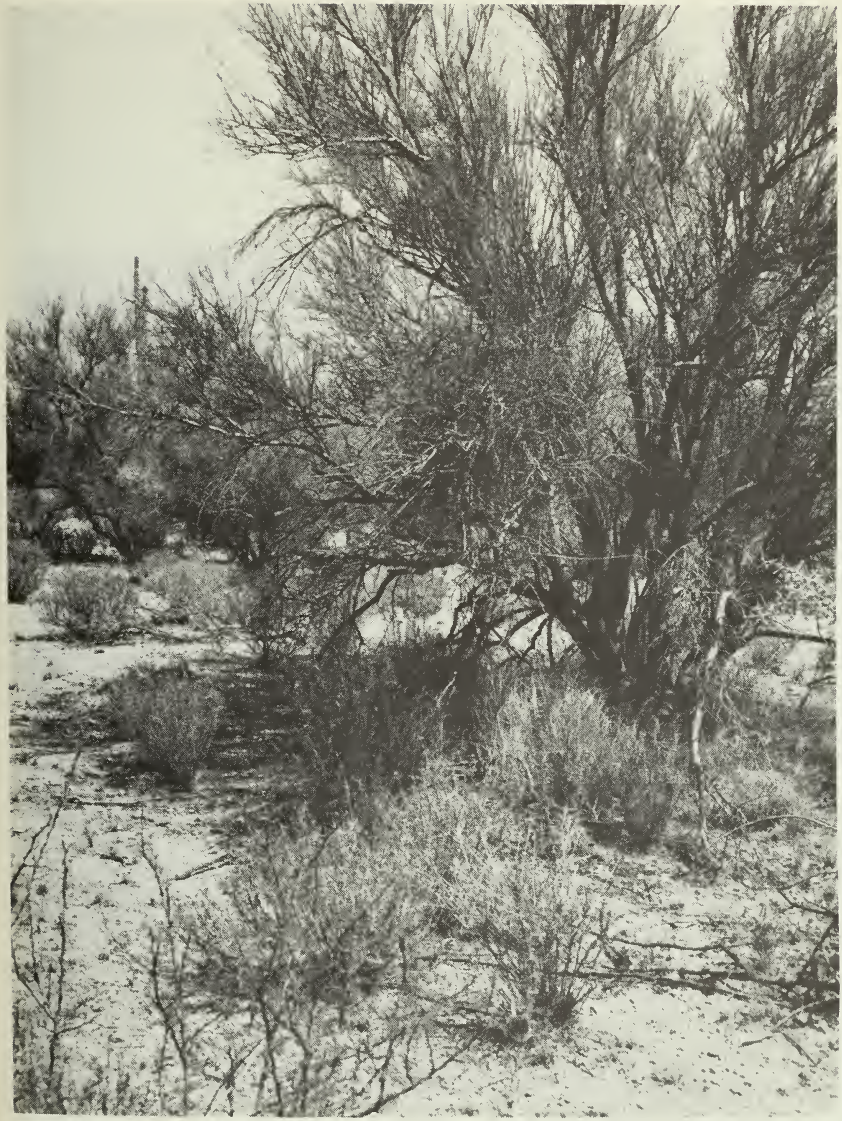

Fig. 47B. Paloverde-saguaro (*Cercidium microphyllum-Cereus giganteus*) community after 11 years' protection from cattle grazing. Compare with adjacent site shown in Fig. 47A. The multistoried canopy of shrubs and overhanging tree branches provides young saguaros with concealment from destructive animals and effectively moderates extremes of drought and subfreezing temperatures. Young saguaros now commonly occur in such regenerated microenvironments. Photographed 7 August 1969.

Fig. 48A. Closely cropped desert zinnia (*Zinnia pumila*, a low desert shrub), and desert fluffgrass (*Tridens pulchellus*) at the actively grazed site shown in Fig. 47A. Fountain pen (center) provides scale. Compare with Fig. 48B. Not only grasses, but many species of shrubs and even portions of some trees (flowers, fruits, leaves, and succulent new branches) are heavily utilized by desert cattle. Photographed 7 August 1969.

Fig. 48B. Natural regeneration of desert zinnia (*Zinnia pumila*) and fluffgrass (*Tridens pulchellus*) at Saguaro National Monument (east); same site as Fig. 48A. Fountain pen (center) provides scale. In this environment, young saguaros are commonly found under trees growing in close association with such "nurse-plant" shrubs. Photographed 7 August 1969.

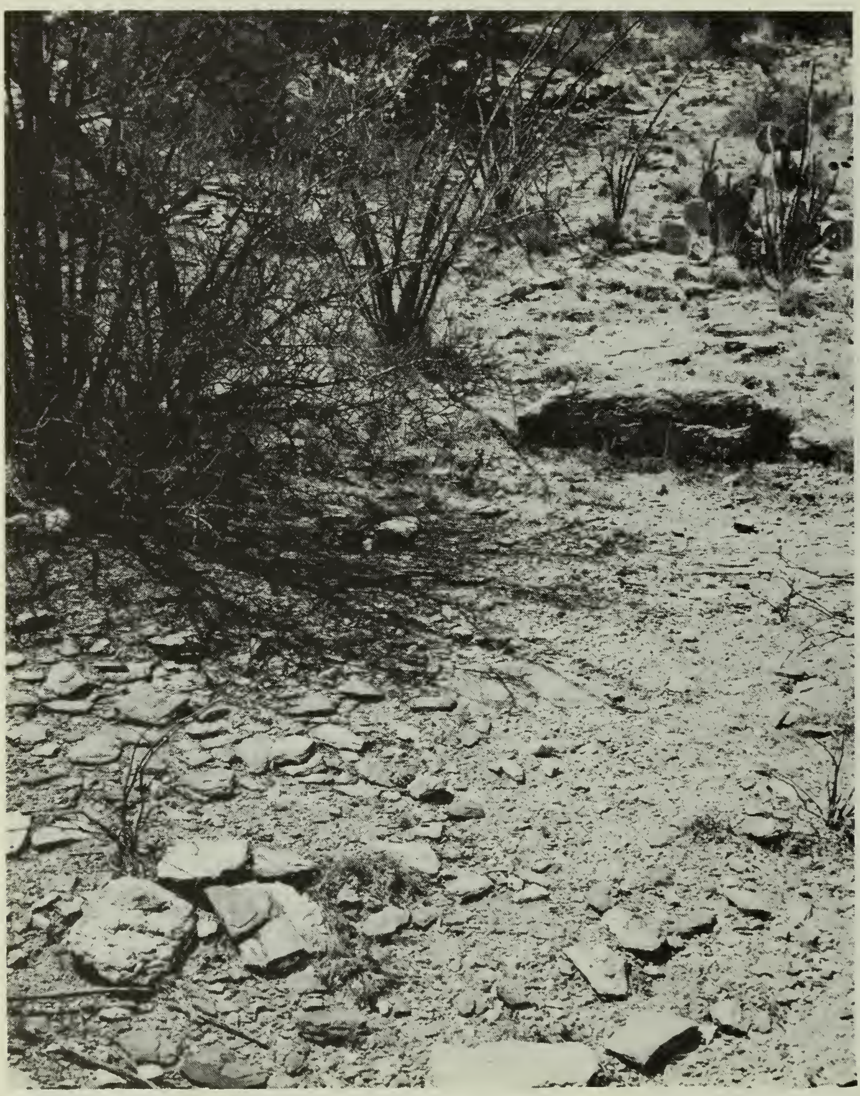

Fig. 49A. Intensively grazed rocky footslope of the Rincon Mountains, Saguaro National Monument (east). Sparse ground cover greatly increases the severity of heat, cold, and drought. Perennial vegetation includes foothill paloverde (*Cercidium microphyllum*), ocotillo (*Fouquieria splendens*), sangre-de-drago (*Jatropha cardiophylla*), and pricklypear cactus (*Opuntia engelmanni*). Photographed 22 May 1969.

Fig. 49B. Natural regeneration of vegetation on rocky footslopes following exclusion of cattle in Saguaro National Monument; same immediate locality as Fig. 49A. Eleven years' protection from livestock grazing has resulted in the development of extensive grass cover: side oats grama (*Bouteloua curtipendula*), slender grama (*Bouteloua filiformis*), bush-muhly (*Muhlenbergia porteri*), and Arizona cottontop (*Trichachne californica*). Photographed 22 May 1969.

Fig. 50A. The area surrounding this mesquite tree (*Prosopis juliflora*) at Organ Pipe Cactus National Monument has been denuded by grazing and shade-seeking cattle. Consumption and trampling by cattle has eliminated nearly every living plant at this intensively used site. Continued use precludes establishment of new plants. Photographed 8 December 1969.

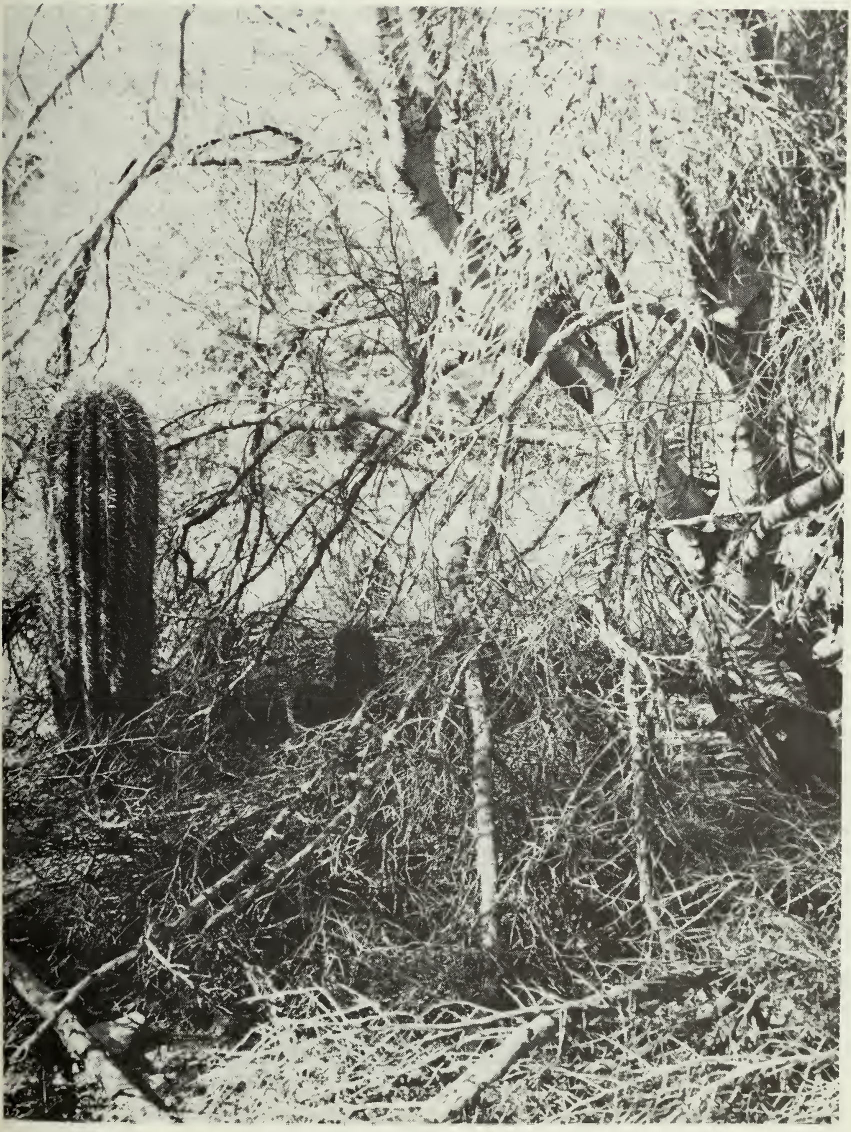

Fig. 50B. A short distance from the site shown in Fig. 50A there are seven juvenile saguaros growing among the cast limbs beneath the dense crown of this foothill paloverde tree (*Cercidium microphyllum*). Cattle have avoided this site which produces little or no forage and is protected by low, overhanging tree limbs. Photographed 8 December 1969.

spread of natural fire (Fig. 51). In such habitats, saguaros closely associated with combustible plant material—in grass, "amole" (*Agave schotti*), low shrubs, or litter beneath trees—are highly vulnerable to fire-kill. However, saguaros situated in relatively barren rock outcrops survive fire with little or no damage.

There is no known instance of fire-caused saguaro deaths within Saguaro National Monument. This is a result not only of a strict policy of controlling all fires but even more directly a consequence of cattle grazing. Grasses that naturally would form a more-or-less-continuous ground cover on the rocky footslopes have been closely cropped, and their density has been drastically reduced by long-continued cattle grazing (Fig. 49A). Fires can neither start nor spread in these denuded, grossly altered environments. In that limited and local sense it might be said that cattle grazing may have benefited saguaro survival in the monument.

Fig. 51A. Fire-killed saguaros and foothill paloverde trees (*Cercidium microphyllum*) in Tonto National Forest approximately 56 km (35 miles) northeast of Phoenix, Arizona. Seventeen of the 19 saguaros in the photograph were killed by an intense ground fire in the dry autumn of 1973, following the unusually heavy production of annual forbs and grasses earlier in that year. Fires start and spread readily through the ground level accumulation of dead, dry forbs and grasses produced in desert scrub by unusually heavy winter, spring, and/or summer rains. Photographed 18 June 1974.

Predator control

Predator control within and adjacent to both sections of Saguaro National Monument continued into the last decade cannot, with certainty, be related to the past and present condition of saguaro stands within the boundary. The whole question of the effect of predator control on fluctuations in rodent populations seems inseparably related to a host of other factors ultimately of equal or greater importance in the dynamics of desert rodent populations. These include food and water supply, habitat modifications produced by livestock grazing, climatic cycles, and the resulting complex interactions including predation.

Ultimately, it seems that the most that can be said with regard to predator control is that to some degree it may have allowed populations of some prey species to increase until some other environmental factor became limiting on their numbers. There are no data that show that an increase in rodent predators on young saguaros actually resulted from predator control, that rodent populations were maintained at unnaturally high levels, or that the establishment of young saguaros was unnaturally limited by high populations of rodents resulting from the control of predators.

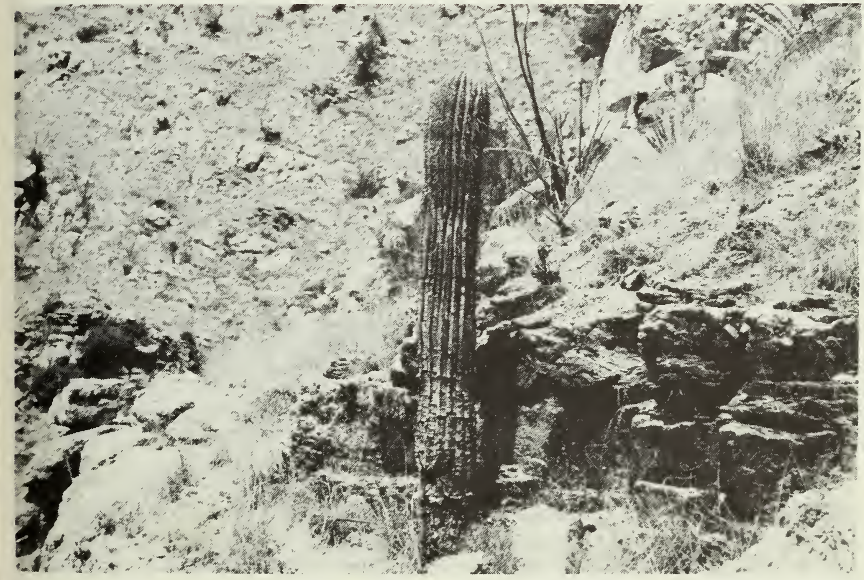

Fig. 51B. A fire-scarred saguaro, survivor of a July 1968 lightning-caused fire on the ungrazed slopes of the Santa Catalina Mountains, Coronado National Forest northeast of Tucson, Arizona. In such habitats, saguaros closely associated with an abundance of dry fuel—dense grass, shrubs, and other plants, or accumulated litter beneath trees—are highly vulnerable to fire-kill. However, saguaros often survive in relatively barren outcrops where there is little or no fuel to support the ground fire. Photographed 4 August 1969.

Except for the small effect of a limited amount of hunting outside the boundaries, the level of predator populations today appears essentially as before within the two units of the monument. Whatever the previous consequences of predator control on these saguaro populations, the present condition is that of an essentially natural relationship.

Other decimating factors

Since the establishment of Saguaro National Monument, some lack of saguaro establishment and survival must be attributed to the actions of monument users, and to certain management activities of the National Park Service itself. This has resulted not only from the direct destruction of many young saguaros but also from the inadvertent creation of environments in which the saguaro cannot become established or survive. These factors, briefly discussed here, are further detailed in Appendix I, Management Recommendations.

The construction and maintenance of roads, parking facilities, and related drainage control devices through the heart of the most spectacular saguaro stands in both sections of the monument have involved the direct removal of young (and some old) plants (Figs. 52 and 53). These developments have also eliminated a substantial area of formerly prime saguaro habitat.

Both causes and rates of saguaro mortality increase with proximity to roadways and parking areas (Figs. 52 and 55B). Easy access and intensive use are accompanied by higher rates of vandalism on saguaros of all sizes. Saguaros attract and are highly vulnerable objects of vandalism (Fig. 53B); small plants are easily removed completely. Younger plants are especially subject to injury, destruction, and removal, and deterioration of saguaro habitat occurs with intensive use of areas adjacent to parking sites.

Saguaros immediately adjacent to roadways are left with only partially functional root systems, the shallow roots either severed or covered with pavement or compacted soil (Fig. 52). The vigor of such plants is impaired by reduced water-uptake capability, and vulnerability to windthrow is greatly increased.

Freeze-caused mortality is increased by close proximity to unpaved roadways (Fig. 55A). During cold winter nights, the greatest extremes of low temperatures are associated with the high rates of nocturnal reradiation from these barren surfaces. The lack of protective vegetation further increases the vulnerability of roadside saguaros to freezing (Lowe and Hinds 1971; Steenbergh and Lowe 1976; Fig. 55B).

Picnic areas, without exception, have been developed in prime saguaro habitats; generally, most of the decimating factors associated with roadways apply to the establishment and survival of saguaros at and near these locations (Fig. 53). Vandalism, destruction of vegetation, and soil compaction have virtually precluded the establishment and survival of young saguaros, have caused the death of many of the older saguaros, and with continued use, will in time eliminate the remaining large saguaros at these locations. Furthermore, the areas surrounding these sites are subject to intensive use and associated vandalism and removal of young saguaros (Fig. 53B).

The "bacterial necrosis disease" as an historical factor

The long-continued commitment to the "bacterial necrosis disease" hypothesis and the medical approach to the problem of saguaro population decline, reviewed in Chapter I, have had a number of unfortunate consequences for the public, the National Park Service, and the scientific community.

The National Park Service, in the acceptance of that hypothesis, contributed heavily to futile efforts to control the supposed disease. They also supported pathology-oriented research that sought unsuccessfully to explain the lack of seedling establishment and survival. Substantial effort and money were expended to develop management programs to correct a condition of undetermined cause. Much important information was gained from these efforts, but the primary question remained unanswered and appropriate management programs could not be developed or implemented without the answers to the question of cause.

With the acceptance of the ecologically untenable "disease" hypothesis in 1941, the primary cause of the observed saguaro deaths—freezing—passed completely unrecognized, as did the controlling relationship between that factor and the establishment and survival of young saguaros. As a consequence, the critical questions on the role of freezing weather in these populations remained unasked for nearly two more decades.

For the public and the National Park Service, a most unfortunate consequence of the emotionally appealing hypothesis was the widely accepted and now firmly entrenched belief in a devastating, but hopefully curable, "disease" that supposedly threatened the saguaro with early extinction.

Fig. 52A. Dead, roadside saguaro, Tucson Mountains, Saguaro National Monument (west). High mortality of saguaros immediately adjacent to graded roads is primarily attributable to conventional road maintenance practices (see Fig. 52B). Photographed 29 November 1973.

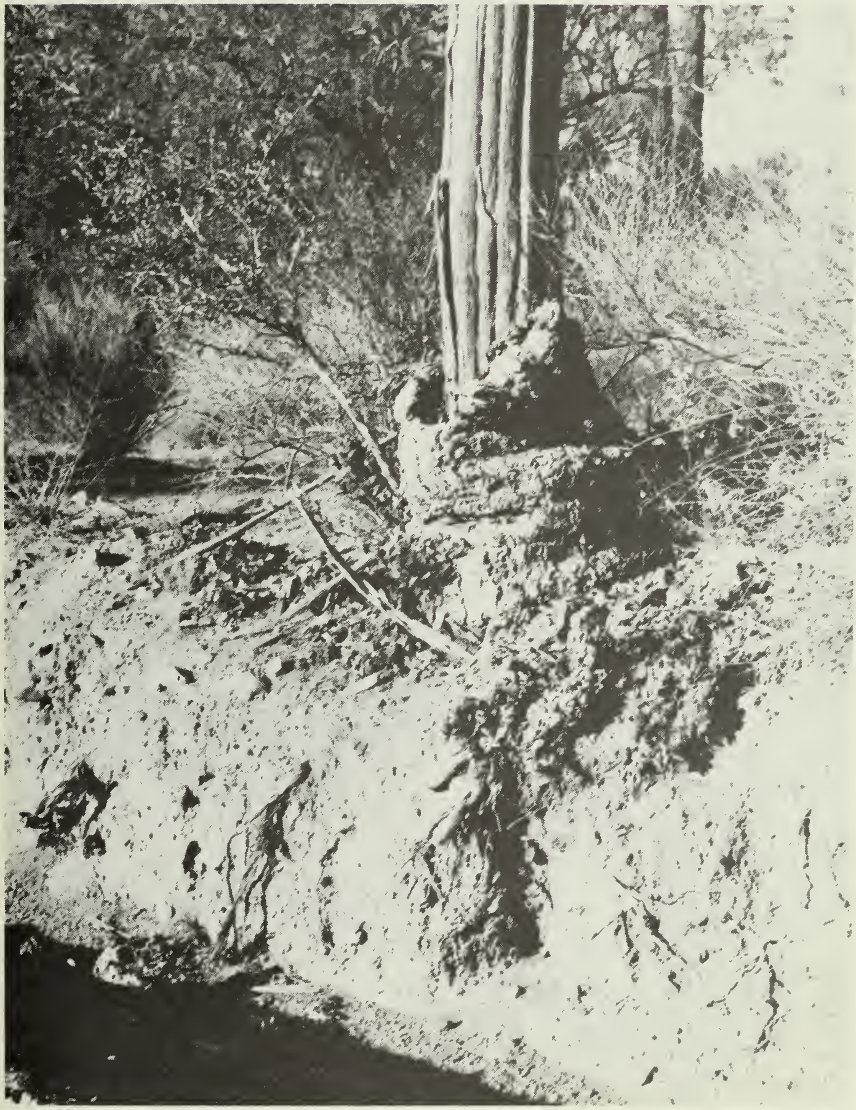

Fig. 52B. Closeup showing saguaro roots severed by roadgrader (saguaro shown in Fig. 52A). The primary root system of the saguaro lies within 2 ft (0.6 m) of the soil surface. This plant has lost nearly half of its root system. Such injury results not only in loss of plant vigor but greatly increases vulnerability to freezing and windthrow. Photographed 29 November 1973.

Fig. 53A. Concentrated visitor use—as in this picnic area—hastens the death of living saguaros and precludes the establishment of new individuals. Vandalism and soil compaction reduces the vigor of old plants. Establishment of young saguaros cannot occur on barren, intensively used sites. Continued intensive use of these sites will lead to the eventual elimination of their two principal attractions—saguaros and shade. Photographed 1 December 1969.

Fig. 53B. Vandalized young saguaro adjacent to picnic area shown in Fig. 53A. Vandalism on standing saguaros, large and small, and the removal of easily uprooted small saguaros is most severe in the immediate vicinity of intensively used recreational facilities and roads. Photographed 22 May 1969.

History in Perspective—Ecology or Pathology?

Our investigations and the work of others leave no doubt that natural environmental factors are the underlying cause of the dramatic changes that have occurred within the saguaro populations at Saguaro National Monument since its establishment. The historical activities of man and his domestic animals have been superimposed upon the natural environmental factors that limit the natural distribution of the saguaro and, within those limits, control its germination, establishment, and survival.

Responses of an abused environment

The role of historical factors has been *not* to act as new and overriding controls ; rather, historical factors have acted to intensify or mitigate the operation of natural regulating factors. Acting primarily in an indirect manner, the overall effect has been to decrease the number and suitability of sites for germination, establishment, and survival of young saguaros. Within Saguaro National Monument, the saguaro has not been eliminated from any of its former habitats by these activities, but rather, in some habitats, the density of large juvenile and young adult plants is below the expected level for these habitats.

There is no cause to believe that historical factors have created irreversible deterioration of any of the primary habitats of the saguaro at Saguaro National Monument. Where elimination of adverse uses has been accomplished, it has been followed by natural regeneration of the plant community, and by the establishment of large numbers of juvenile saguaros.

Termination of grazing or other actions that similarly degrade those desert habitats and environments is followed by regenerative "non-succession." It is not, however, the generally known plant succession that occurs in more mesic environments where seral stages of different sets of species replace others in a successive series of different communities. In the desert environment where moisture, rather than light, is limiting, interspecies competition takes place almost entirely within the root zone (see Cannon 1909, 1911, 1912). Thus, as in the case of the saguaro, plant species that require physical protection for their establishment and early survival follow the development of moderated microenvironments created by the canopy of trees and shrubs. These microhabitats offer protection from extremes of drought, heat, light, and cold, and in addition provide concealment and physical barriers that effectively reduce destruction by animals.

The sparsity of large juvenile and young adult saguaros in some habitats is indirectly attributable to past abuses of these environments. That is the irrevocable condition of these populations that absolutely insures that for many decades to come, as natural die-off of large, old saguaros continues, the spectacular qualities of these stands will continue to decline.

In contrast to the condition reported only a few years ago, and still presumed by many to be the situation, *there are today in each of the two sections of Saguaro National Monument thousands of young saguaros less than a half-meter (20 inches) tall.* These occur not only on the rocky footslopes of the Rincon and Tucson mountains—where the presence of substantial numbers of large juvenile and young adult saguaros indicates continued establishment and survival of young saguaros in these habitats—but notably in the nonrocky, flat habitats of the Cactus Forest area, and the lower bajadas of the respective east and west sections of the monument.

The unstable nature of saguaro populations within Saguaro National Monument is neither a recent nor an unnatural development. The unbalanced age-class structure evidenced by the present conspicuous lack of large juvenile and small and intermediate sizes of adult saguaros within certain of these monument stands long predates the establishment of the monument in 1933.

Both the dramatic die-off of large, old plants and the lack of younger replacements in these populations are the inevitable response to climatic events—recurring catastrophic freezes—that are a normal characteristic of the region. The particular populations in question are those which occupy marginal saguaro habitats—topographic situations where subfreezing temperatures are intensified by cold air drainage and accumulation.

Requiem for a myth

> *In 1838, I published . . . in an article on the intense cold of January, 1838, the following remarks—". . . cold does not kill vegetation by a mechanical action proceeding from the congelation of the liquid as some naturalists pretend. We must recognize rather a physiological action; that the vitality of the tissue is destroyed by a certain degree of cold followed by a certain degree of heat, according to the peculiar nature of each plant. The vegetable and animal kingdom, according to this view, will act alike. In the same manner as the gangrene that sets in after the thawing of a frozen part causes the death of an animal tissue, so the change or putrefaction which follows a rapid thawing will be the principal cause of the death of the vegetable tissue."*—M. A. de Candolle, "On the freezing of vegetables." 1852:445-446.

Bacterial rot is the long understood, *subsequent*, and ecologically important process of natural decomposition that aids the final breakdown of the soft tissues of saguaros that are killed outright or rendered physiologically dysfunctional by mechanical factors, primarily freezing and lightning (see Lowe 1964, 1966; Steenbergh 1972; Steenbergh and Lowe 1976).

Our observations, and the numerous investigations and reports of others, have established the nature of the principal causes of death of saguaros. Bacterial disease is *not* among these confirmed causes of mortality in natural saguaro populations, and *no* significant number of saguaro deaths remains to be explained by additional or unknown causes. Our ecological investigations over the last 23 years on naturally growing field populations of saguaros have resulted in no evidence that any pathogenic microorganism is, or ever has been, a significant cause of the death of saguaros—or that any death of healthy saguaros, young or old, can be attributed properly to bacterial action.

As the appointed custodian and official ecological interpreter of the best-known saguaro populations in the world, the National Park Service is heir to a difficult task. The ecologically unsupportable myth of the "bacterial necrosis disease" must be supplanted by a possibly less appealing, but ecologically realistic, interpretation: the decline of once spectacular saguaro populations at Saguaro National Monument and elsewhere in Arizona is an inevitable and continuing response of these populations to uncontrollable climatic events.

Diverse Records: Populations in Response to Climatic Events

Diverse records on saguaro populations (and other warm-desert plant populations) and climatic events clearly tell the story of a population in trouble since the middle of the last century. The relative sparsity of young saguaros in some populations and the relationship of that condition to saguaro population fluctuations have long been a matter of record and concern.

Populations in trouble

Dense populations of saguaros near the northeast base of the Rincon Mountains east of Tucson are indicated by the previously quoted observations of Bigelow (1887). Hubbard (1899) provided observations on the condition of saguaro populations near Tucson at the end of the 19th century. Hubbard's (1899:6) 1897 observation was particularly significant:

> The entire mesa at the foot of the Sta. Catalina Mountains near Sabina cañon, about 18 miles northeast of Tucson, is covered for miles and miles with immense giant cactus, in one unbroken army, as thick mullein stalks in an eastern cattle pasture. Out of these thousands of cacti I did not discover a single plant that was diseased or rotting. . . .

MacDougal (1908b) commented generally on the difficulty of finding young saguaros, but remarked that ". . . the great valley lying between the Carobabi and Quijotoa Mountains, was found to be densely inhabited by this plant, represented by individuals in all stages of development, the plantlets being so numerous in places as to form clumps."

Shreve (1910) offered the first numerical data on saguaro populations and concluded that ". . . it is not maintaining itself in either of two situations, one of which offers the highest average water-content of any desert soil away from stream beds, and the other the temperature and other conditions which have brought about in it the densest Giant Cactus population that can be found in any habitat." In that report, he further recognized that "mechanical factors" are the principal cause of saguaro death.

Shreve (1911) subsequently established the role of freezing weather as a critical determinant of the elevational and geographic limits of saguaro distribution. Surprisingly, however, Shreve apparently did not then or later recognize the further relationship of his work on freezing to causes of saguaro death, and the observed decline of certain saguaro populations: *In establishing the relationship between subfreezing temperatures and saguaro survival, Shreve (1911) had answered his own important question on the primary factor responsible for the observed fall in the rate of saguaro establishment, and had delineated the primary cause of saguaro deaths in populations near the cold-limited boundaries of its distribution* (also see Thornber 1916; Lowe 1959, 1964; Steenbergh and Lowe 1976).

The saguaro population in portions of Saguaro National Monument (east) was in a long-standing state of decadence at the time of the establishment of the monument in 1933. In the photographs by Homer Shantz (Fig. 3A; also see Hastings and Turner 1965), there is an abundance of large, old saguaros, and a conspicuous sparsity of juvenile and young adult saguaros. The very characteristic that inspired Shantz (1932) to say, "Nowhere in the world is there so fine a stand of giant sahuara (*Carnegia gigantia*) as in the University Cactus Forest." was the irrevocable condition that was to lead to the subsequent and inevitable dramatic decline of that same stand.

The first quantitative evidence on the declining condition of the east monument saguaro population was supplied by Wilder and Wilder (1939) and Wilder (1940). They not only pointed out that the saguaro was not maintaining itself in the "Lower Desert Floor" (i.e., flat habitat), but importantly concluded (Wilder and Wilder 1939) that "They are, apparently, reproducing satisfactorily in level-floored pockets just below the foothills and on the foothills (or mesas leading up to the Tanque Verde Mountains)."

Following massive die-offs of saguaros that occurred in 1939 and 1940 (Gill 1951), systematic sampling of saguaro populations at

Saguaro and Organ Pipe Cactus national monuments was initiated in conjunction with "Cactus Disease Investigations" by the USDA Bureau of Plant Industry (Gill and Lightle 1942, 1946; Gill 1951; Mielke 1944; also see Steenbergh and Lowe 1976). That study included data on 12,698 saguaros in the Saguaro Monument (east) flats habitat, the largest single saguaro population sample ever taken.

The results of those investigations support the earlier observations of Wilder and Wilder (1939) and Wilder (1940) that the number of young saguaros in the east monument flats stand had long been insufficient to maintain the stand, and that the highest densities of saguaros occurred on the rocky footslopes. Further, these studies showed that at Organ Pipe Cactus National Monument there was a relatively low rate of die-off of large saguaros (7%) and, significantly, that a high proportion (33.6%) of the saguaros in that population were healthy individuals 3 ft (91 cm) or less in height (Gill and Lightle 1942). In 1941, the saguaro population at Organ Pipe Cactus National Monument exhibited, and—based on recent reexamination by the authors—continues to exhibit on the whole a relatively stable age distribution.

Investigations in 1962 (Niering et al. 1963; Niering and Whittaker 1965) on saguaro populations in the vicinity of Tucson further confirm earlier observations that saguaro establishment and survival rates in rocky habitats are higher than in the finer soil of nonrocky habitats (also see Kramer 1962; Bingham 1963). More important, these studies further support the earlier observation by Thornber (1916) that massive die-off of saguaros is associated with catastrophic freezing, and explain the relationship of freezing weather to higher survival rates in rocky habitats. From the data in those reports, it also can be seen that freeze-caused saguaro mortality decreases from east to west along a gradient of increasingly warmer winter climate.

Further data on saguaro populations in Saguaro National Monument and the relationship of saguaro size and habitat to freeze-caused mortality are reported by Steenbergh and Lowe (1976). In that report, we concluded that catastrophic freezing selectively structures saguaro populations, removing the smallest (youngest) and the largest (oldest) plants, leaving a high percentage of large juvenile and unbranched young adult saguaros with heights from 0.46 to 3.80 m (1.5-12.5 ft).

Catastrophic freezes

Daily weather observations provide a record of minimum temperatures in Tucson since 1895 (see Steenbergh and Lowe 1976, Fig. 25). Other diverse records of these climatic events and the response of saguaro populations and other cold-sensitive plant populations are scattered throughout the literature (Thornber 1912, 1916; Wiggins 1937; Turnage and Hinckley 1938; Niering et al. 1963) and are, in fact, recorded in the responsive plant populations themselves.

Saguaro populations in the Tucson vicinity are an unexamined record of catastrophic freeze occurrence that long predates the oldest written weather records (Figs. 54 and 55). The size-class structure of these and other saguaro populations is an indication of past winter climate (Fig. 55A). In many northern saguaro populations, constrictions near the base of the stem tell the story of previous catastrophic freezes. These constrictions result from freeze-caused crown-kill. In some habitats at Saguaro National Monument, such scars, present on nearly every large juvenile and adult saguaro, provide a continuous record of recurring catastrophic freezes as old as the plants themselves (Fig. 54). Based on the estimated age of larger saguaros in these habitats, recurring catastrophic freezes have been a *normal* part of these environments for more than 150 years.

The lack of rotting saguaros noted by Hubbard (1899) reflects the occurrence of mild winters with relatively little freeze-kill of saguaros toward the end of the 19th century. However, low temperature readings in Tucson recorded during the first decade of this century were followed by MacDougal's (1908b) observations of rotting saguaros, and by Shreve's (1910) observation on the ". . . abundance of fallen skeletons. . . ."

The most noteworthy record of low temperature, however, is the 6°F (−14.4°C) Tucson temperature recorded on 13 January 1913. As the first report on catastrophic freeze-kill of saguaros, Thornber's (1916) observations on the devastating effects of that freeze are particularly significant:

> . . . during the very cold winter of 1912-13 thousands of small giant cactus plants growing near their greatest altitudinal limits were killed outright. Many other species also suffered great damage.

The Shantz photographs suggest that for a period from the mid-1920s to 1937, there was little or no freeze-caused death of saguaros in the populations at the Saguaro National Monument (east) location. There are no rotting plants, and few skeletons of dead saguaros in any of those photographs (see Fig. 3A).

The catastrophic freeze that occurred in January 1937, and resulting severe damage to warm-desert plants, was the subject of a comprehensive report by Turnage and Hinckley (1938). Although damage to saguaros was not noted in that report, damage to all other species of columnar cacti native to the Sonoran Desert was reported.

Fig. 54A. Constricted upper stem of a young, 93-cm (37-inch) saguaro at Saguaro National Monument (east) is a result of a January 1971 freeze-caused crown-kill. Four other scars (arrows) visible below the mid-point of the stem are the result of a series of freezes that occurred during the earlier years of the plant's life. Photographed 14 July 1974.

Fig. 54B. Constrictions near the base of the stem of saguaros provide a record of previous catastrophic freezes that endures throughout the life of the plant. In some habitats at Saguaro National Monument, the presence of such scars on nearly every saguaro indicates that catastrophic freezes have been a *normal* part of the local climatic environment for more than 150 years. Photographed 26 June 1973.

Wiggins (1937) reported severe injury to organpipe cacti at Organ Pipe Cactus National Monument and noted evidence of similar injuries sustained during prior freezes. Additional reports of freeze-caused damage to plants are contained in the compiled reports of the National Park Service for that period (USDI 1937).

Although there is no record of damage to or death of saguaros immediately following the January 1937 freeze, subsequent events leave no doubt that it was among the species most severely damaged by that freeze. The spectacular die-off of saguaros first noted in 1939 and continuing into the 1940s (Gill and Lightle 1942, 1946; Mielke 1944; Gill 1951) was the delayed response to the subfreezing temperatures of January 1937, the coldest period in 24 years (Turnage and Hinckley 1938).

It is well known that not all parts of a plant die at the same moment. This time scale of organ death is greatly exaggerated in the saguaro giant cactus. As many as 9 years may elapse between lethal injury and collapse of a freeze-damaged saguaro (Figs. 4B, 14B, and 55A). Thus, the death of large saguaros lethally injured in 1937 escaped recognition until 1939 and later when, with their decay and collapse, death became obvious.

Saguaro die-off in response to catastrophic freeze followed by rapid thawing conditions in 1962, reported by Niering et al. (1963) and Lowe (1964), was followed by rapid collapse of many of the stricken individuals (see de Candolle 1852). However, as in the case of the 1937 freeze, the death of many plants did not become evident for one or more years after the freeze. The 1962 freeze also damaged plants at Organ Pipe Cactus National Monument where we observed resulting severe injury to senita and organpipe cacti as well as to other cacti, elephant trees (*Bursera microphylla*), and other subtropical shrubs.

The initial response of saguaro populations to the freeze of January 1971 is described by Steenbergh and Lowe (1976) and the resulting collapse of saguaros has continued into 1974. We also observed, as a result of the 1971 freeze, damage to organpipe and senita cacti at Organ Pipe Cactus National Monument and, near Tucson, the death of other species of cacti, namely, bisnaga (*Ferocactus wislizeni*) and the chain-fruit cholla (*Opuntia fulgida*) (Figs. 56-58). In the Tucson vicinity, we observed severe damage to desert ironwood and foothill paloverde that in some localities resulted in the subsequent death of numerous individuals of both species (Fig. 58B).

From our observations, it is clear that the population fluctuations of chain-fruit cholla populations long observed by many ecologists (see Tschirley and Wagle 1964) and similar population fluctuations of other cactus species are attributable to freezing. Similarly, it is probable that several of the vegetation changes noted in Hastings and Turner (1965) are attributable to catastrophic freezing.

The Outlook

The outlook for the future of saguaros at Saguaro National Monument is not an optimistic one. Neither, however, does it conform to the grim predictions of early extinction that some have offered. Barring unlikely sudden environmental changes in the habitats of its major occurrence within the monument, the saguaro will continue to survive long after our concern with the question is terminated.

There are today thousands of young saguaros at Saguaro National Monument, many of which will survive beyond a human lifetime. Many more of these, however, will perish during that time. Certainly, there will not be in our time—and perhaps never again—a return to the condition that inspired Homer Shantz (1932) to describe it as the finest stand of the giant saguaro in the world.

Generally, even in the absence of further adverse influences of man, we can expect that the density of large saguaros in most, if not all, habitats within the monument will be lower than in the recent past. In some habitats, however, we can expect that with the complete elimination of livestock grazing an increase in the density of young saguaros will accompany a natural regeneration of the damaged plant communities.

Within the monument, continuing short-term climatic variations can be expected to produce corresponding fluctuations of saguaro populations but not to cause their early extirpation. Generally, this will effect changes in density, with unfavorable winter temperatures eliminating young plants from the least favorable microsites.

Here at the cold-limited margin of its range, saguaro density is limited ultimately by the number of available sites suitable for the survival of young plants during critical freezing periods. During a series of favorable winters when there are no prolonged periods of subfreezing temperatures, young plants will become established in relatively large numbers, occupying microhabitats offering varying degrees of protection from freezing. The subsequent occurrence of a catastrophic freeze will then eliminate those individuals that become established on relatively unprotected sites. The survivors will be those occupying sites offering the greatest protection from freezing.

The number of sites suitable for germination and initial growth of the seedling far exceed those suitable for its survival through the first winter of life. During its first years of life, the probability that a young plant will survive is dependent mainly upon the winter-cold moderating effec-

Fig. 55A. Recent and historic evidence of a saguaro population in trouble. The sparsity of small and intermediate-sized saguaros in this population at Saguaro National Monument (east) is a record of response to past environments. The missing size-classes have been eliminated by past events, namely, catastrophic freezes. The foreground saguaro, bearing its last crop of fruits—despite the death of the lower stem—nears final collapse as a result of lethal freeze-caused injuries received 7 years earlier in 1962. Photographed 30 June 1969.

Fig. 55B. Road-associated 1971 freeze-caused saguaro deaths, Saguaro National Monument (west). Vulnerability of saguaros to freeze-caused death is increased by proximity to unpaved roads. The greatest extremes of low temperatures are associated with high rates of nocturnal re-radiation from large areas of barren earth.

Drooping arms on dying saguaro in foreground are the result of long pre-existing freezing injury. Photographed 9 August 1971.

tiveness of its physical environment. Further, as the plant increases in size, the size of the effective microenvironment needed by the plant also increases, i.e., the plant grows out of its original microenvironment—pebble, dead branch, or small shrub. Its survival then depends upon the presence of a larger protective canopy—a rock, larger shrub, or tree.

As the cold-limited boundaries of its range are approached, survival of the young plant to the age of first flowering is increasingly dependent upon the presence of multistoried vegetation or massive outcroppings of rock. Conversely, it may be observed that in the warmer portions of its range, in southwestern Arizona and in Sonora, the saguaro increasingly occurs in association with low shrubs, without benefit from or dependence upon tree canopy.

Fig. 56A. Jumping cholla (chain-fruit cholla, *Opuntia fulgida*) photographed immediately following critical subfreezing temperatures in January 1971. At that time, characteristic symptoms of freeze damage—discolored, watery appearance of softened fruits, and the drooping terminal joints—were widely evident. Within 3 months after the freeze, all but a few withered joints had dropped to the ground. Compare with Fig. 56B. Photographed 19 January 1974.

Climatic trends

A small but significant climatic change toward somewhat warmer and drier conditions is "written" into diverse records (see Kincer 1946; McDonald 1956; Schulman 1956). A long record of catastrophic freezes accompanying this change during the last century is "written" into the existing age-class structure of the saguaro populations in the northern portions of the Sonoran Desert, and indeed, in the form of freeze-caused scars, in the plants themselves.

The continued occurrence of catastrophic freezes does not, as it might appear, conflict with the observed trend toward "warmer and drier conditions" previously noted. Rather, there may be an overall trend, at least in this region, toward an increasingly continental climate, and conversely, a decrease in the maritime influence upon the climate of the region.

Fig. 56B. Rephotograph of the cholla shown in Fig. 56A, taken approximately 3 years after lethal freeze-caused injury. The plant is dead. Photographed 29 November 1973.

While it is not evident in this stage of our on-going analysis of the freeze-scar record in saguaro populations that a climatic trend is recorded in those scars, it is clear that recurring catastrophic freezes are a long-standing characteristic of the climatic environment of this northern portion of the Sonoran Desert. Observed changes in the age-class structure of these populations may indicate a climatic trend. A continued decline of these saguaro populations would suggest a shift toward increasingly frequent and/or severe extremes of winter cold. In view of the relatively brief length of the climatic record, and long life span of the saguaro—approximately twice the length of the climatic record—such a conclusion is highly tenuous.

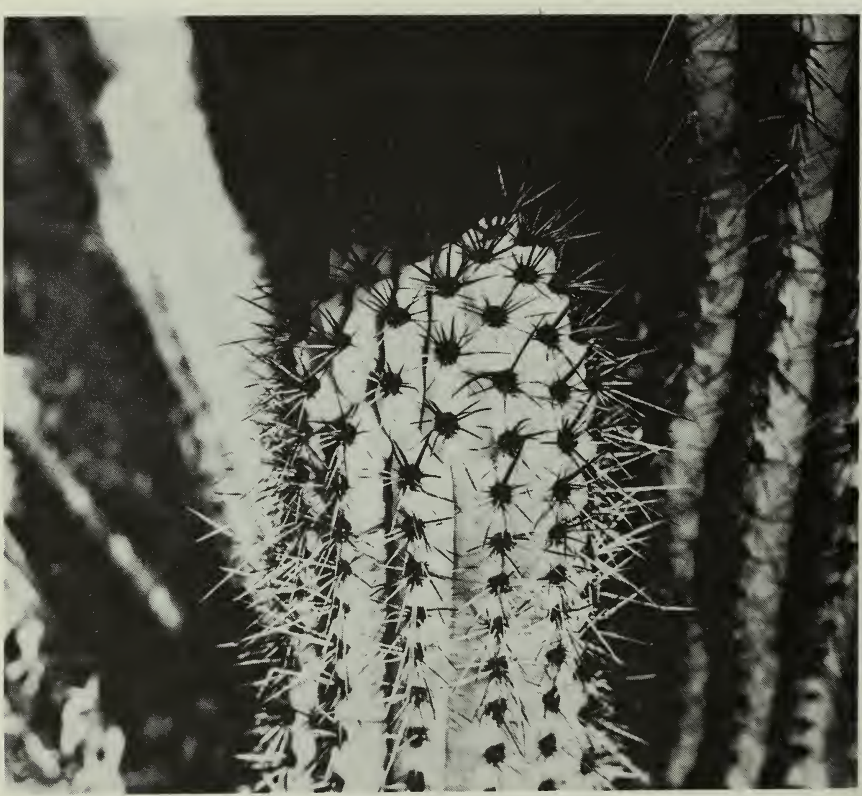

Fig. 57A. Freeze-caused injury in 1971 to organpipe cactus (*Cereus thurberi*) at Organ Pipe Cactus National Monument. Pale yellow coloration is evidence of severe injury at the stem tip. Resulting constrictions that produce "jointed" stems appear on nearly every organpipe cactus in this northern portion of its range. Investigations of organpipe deaths within the Organ Pipe Cactus National Monument reveal that the damage produced by the 1971 freeze was lethal to a substantial number of individuals in that population. Similar injuries and the subsequent death of organpipe cacti (and other cold sensitive species) were observed following the catastrophic freeze in January 1962. Photographed 3 February 1971.

Fig. 57B. Freeze-caused injury in 1971 to senita cactus (*Cereus schotti*) at Organ Pipe Cactus National Monument. Constriction below the blackened, recently frozen tip is the result of a previously occurring freeze. Similar injuries to stem tips were observed immediately following the severe freeze in January 1962. Photographed 3 February 1971.

Fig. 58A. Freeze-killed barrel cactus (*Ferocactus wislizeni*) in 1971 at Saguaro National Monument (east). Numerous other individuals of this species, not killed, received some damage to tissues on the upper portion of the plants. All species of barrel cactus are frost-sensitive. The catastrophic freeze of January 1962 killed more barrel cacti than saguaros on some sites at the upper edge of the desert (1070-1240 m; 3500-4000 ft elevation) on the Santa Catalina and Rincon mountains bordering Tucson on the north and east, respectively.

Fig. 58B. Freeze-killed foothill paloverde (*Cercidium microphyllum*) in 1971 at Saguaro National Monument (east). In addition to freeze-caused deaths, extensive die-back of the foothill paloverde occurred in many localities in southern Arizona and adjacent Sonora, Mexico, following the severe January freezes of 1962 and 1971. In the Tucson Mountains, similar die-back and complete kill of the desert ironwood (*Olneya tesota*) was evident within a few weeks following the freezes. Photographed 25 June 1974.

Population trends

> *. . . on passing from lower to higher latitudes or altitudes the number of consecutive hours of freezing becomes gradually greater until the point is reached at which days without a mid-day thaw are first encountered; there is then a sudden rise from about 22 hours of frost to from 36 to 42 hours, according as the fall and subsequent rise of temperature are abrupt or gradual. In other words this factor is unique in that the curve expressing its changes of intensity possesses a sudden vertical rise, or indeed a number of such rises. The line along which this takes place in the severest of winters is bound to be an important limit of plant distribution, at least it is so along the line of sudden rise which lies nearest the absolute frost line.*—Forrest Shreve, "The influence of low temperatures on the distribution of the giant cactus." 1911:139.

Regardless of any other changes that may occur, this statement by Forrest Shreve describes the single most important natural environmental factor—past, present, and future—affecting saguaro populations at Saguaro National Monument and elsewhere in the colder portions of its natural distribution in Sonora and Arizona.

Saguaro populations and other cold-limited Sonoran Desert plant species will continue to be controlled by recurring catastrophic freezes (see Steenbergh and Lowe 1976). Any changes in the frequency, intensity, or duration of these recurring catastrophic freezes will result in a response by the affected populations. Any trend in these populations will follow the trend of those particular parameters of the winter climate that exert the greatest effect on the youngest members of the plant populations.

A continued trend toward an increasingly continental climate would be accompanied by a continued response in saguaro and other warm-desert plant populations in the colder portions of their geographic distribution: (1)shrinking the absolute limits of their occurrence along the cold-limited boundaries of their distribution; (2) eliminating populations now occupying habitats with marginally cold winter environments; and (3) reducing the density of populations occupying habitats with warmer, more favorable winter environments. In each instance the response would decrease along an environmental gradient from the coldest to the warmest winter environments of the species' distribution and as the distributional limits imposed by other factors are approached.

Our grossly inadequate knowledge either of climatic trends or the long-term dynamics of saguaro populations, however, justifies no such long-term projections concerning future saguaro populations.

Long-term climatic trends, however, are not necessarily the only or most plausible explanation for observed changes in saguaro populations. It is clear that the dramatic fluctuations of saguaro populations in the colder portions of their range that have been observed during this century are unquestionably attributable to catastrophic freezes. However, we have no information indicating that such climatic events are not a long-standing, "normal" characteristic of the regional climate that has similarly affected many past generations of saguaros in the same habitats where they presently occur.

With its high reproductive potential and long life span, the saguaro is well adapted to maintain itself in an environment in which occasional freezes that result in catastrophic die-off are followed by regeneration of the population during intervening periods of climatic remission. It is entirely possible that we have observed in these saguaro populations but one phase of the normal fluctuation of populations whose stability must be measured not in years, but in generations.

It may well be that the "problem" that we have observed—the "decline" of specific saguaro populations—is but a limitation imposed by our life span, too brief to permit our recognition of an adaptive strategy of a longer-lived species that by natural selection has evolved a near-perfect system for survival in an environment of recurring catastrophic climatic events. If that likely explanation is correct, then the real "problem" is neither in biology nor management, but in a limited perspective, and the only "solution" lies in the perspective offered by the time scale of evolution.

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APPENDIX I

Management Recommendations

The choice among alternatives for management of the saguaro is contingent upon the questions of purpose and significance. The available alternatives fall into two basic categories determined either by (1) a commitment to an arbitrary and idyllic concept of nature involving controlled environments and cultivated populations, or (2) acceptance of the natural response of these populations to the continuing climatic control of their numbers and distribution.

The first category of alternatives would create an artificial environment inconsistent with the legislated purpose of the National Park Service, and will be considered no further here. The second category of alternatives, however, includes a powerful opportunity for fulfillment of the National Park Service's obligation to contribute to the understanding of basic ecological relationships.

Applicability

Management recommendations offered here incorporate and supplement the recommendations contained in our earlier (1976) report, *Ecology of the saguaro I: The role of freezing weather in a warm-desert plant population.* Although developed specifically for National Park Service consideration for application to the management of saguaro populations within Saguaro National Monument, these recommendations and the findings upon which they are based have a much broader applicability. Our recommendations apply in important degree to the management of saguaros—and other warm-desert plant populations—at Casa Grande National Monument, Tonto National Monument, and Organ Pipe Cactus National Monument.

At Organ Pipe Cactus National Monument, many of the recommendations are specifically applicable to the management of the senita (*Cereus schotti*) and organpipe (*Cereus thurberi*) cacti, the two other species of large columnar cacti whose distribution extends north of the United States-Mexico border.

At Organ Pipe Cactus National Monument, the organpipe cactus, less cold-tolerant than the saguaro, closely approaches the cold-limited northern and eastern boundaries of its geographic distribution. The even more cold-sensitive senita reaches the absolute limits of its northern distribution within the monument which contains the entire United States population of approximately 500 plants.

In a manner similar in many ways to that of the saguaro in slightly colder environments, the organpipe cactus and the senita cactus are responding to the same climatic events—recurring catastrophic freezes. At best, the future of these populations is precarious, and the National Park Service should be concerned with the present and future status of these populations, and as well, with the status of other plant species that reach or closely approach the northern limits of their distribution within Organ Pipe Cactus National Monument. Their numbers should be carefully guarded, and their continuing status closely observed.

Purpose, Significance, and Ecological Perspectives

> *Whereas a certain area within the Catalina Division of the Coronado National Forest in the State of Arizona and certain adjacent lands are of outstanding scientific interest because of the exceptional growth thereon of various species of cacti, including the so-called giant cactus, it appears that the public interest will be promoted by reserving as much land as may be necessary for the proper protection thereof as a national monument.*— Herbert Hoover, Presidential Proclamation of 1 Mar. 1933.

Under the authority of the Antiquities Act of 8 June 1906, Saguaro National Monument was set aside because of its *scientific interest*—specifically for the intrinsic interest of the natural vegetation therein.

The primary significance of Saguaro National Monument, therefore, lies in the natural associations of the vegetation found within its boundaries. The monument includes the last remaining example of an essentially undisturbed continuum of natural warm-desert to mountain-forest biotic associations in the southwestern United States. The singular rarity of this resource clearly indicates the importance of maintaining the integrity of the natural associations and relationships within Saguaro National Monument.

It is upon consideration of (1) the legislated purpose; (2) the intrinsic natural significance of the area; and (3) the scientific and cultural values of the resources that our management recommendations are based. The instability of saguaro populations at Saguaro National Monument is a natural and primary characteristic of those populations. There is little or nothing that can, or appropriately should, be done to control that condition, for it is the expression of the naturally evolved, genetically controlled response of the species to natural fluctuations in the climatic environment. Our recommendations are directed toward the development of a better understanding of the evolution and function of natural ecological relationships, and to the reduction or elimination of past and present human influences upon these relationships. It is within the framework of the foregoing ecological perspective and considerations of purpose and significance that we offer the following management recommendations:

I. Exclude developments and associated intensive use from highly responsive, uncommon, or rare habitats and natural communities. All use causes some deterioration of saguaro and other habitats. The question of what constitutes an acceptable level of destruction must be answered with every decision to accomodate such monument use.

  1. Reevaluate programs relating to roads—their locations, design, construction or reconstruction, maintenance practices, and public use. The physical influence of the roads themselves, road maintenance practices, and public activities associated with road use destroy or degrade saguaro habitat and contribute to the death of adjacent saguaros and other vegetation.

    A. Eliminate roads and associated developments from high density saguaro stands in nonrocky habitats. Access to these stands can be accomplished by the development of high standard walking trails originating near the periphery of these stands. The users of such trails could enjoy the benefit of the more intimate experience offered by a nonmechanized environment.

    B. Redesign to a low standard and, where necessary, relocate and pave roadways for public use. The narrow, unobtrusive Cactus Forest Drive, constructed with minimum disturbance to vegetation and natural drainage patterns, provides an excellent model for the design of ecologically compatible and aesthetically pleasing roadways. The wide, intensively maintained roads of the Tucson Mountain section of the monument, on the other hand, have grossly altered natural drainage patterns, are increasingly deepening erosion channels, and their presence, maintenance, and use contribute substantially to the deterioration and death of adjacent vegetation.

    C. Develop a program of minimal maintenance for unpaved roads. With the application of a grader, motor vehicle trails that have been used for decades without significant erosion channels now require grading with ever-increasing frequency. Ditching to control runoff further establishes erosion channels and damages the root systems of adjacent shallow-rooted saguaros and other plants.

D. ''De-construct'' rather than ''obliterate'' abandoned roadways. The first—and most important—step in aiding the natural regeneration of vegetation on abandoned roadways is the restoration of natural microtopography and drainage patterns. In some instances this will entail removal of berms and dikes, recovery of fill, refilling of cuts, and replacement, in kind, of eroded soil. The practice of scarifying, particularly where it follows the slope, can contribute to further erosion and, at best, is a questionably beneficial practice. ''Pitting,'' used in preference to scarifying, effectively reduces erosion and creates sites favorable for natural reestablishment of perennial vegetation.

2. Eliminate picnic areas from saguaro habitats. Soil compaction, destruction of vegetation, wood-gathering, vandalism, and removal of young saguaros associated with these developments all contribute to the degeneration of the site and adjacent habitat, ultimately leading to the death of existing saguaros and precluding the germination, establishment, and survival of young plants.

3. Limit further developments within saguaro habitats to those that will not attract destructive use and cannot be located elsewhere.

II. Develop management programs to provide more effective control of activities that are directly destructive to natural populations, communities, and habitats.

1. Control uses that are destructive to saguaro habitat such as off-pavement vehicle parking and off-trail foot and horse travel. Where necessary, provide and direct the use of appropriate facilities for such activities.

2. Intensify management programs to control increasing vandalism and removal of saguaros. Old plants destroyed will not be replaced in a human lifetime. Young plants destroyed are those few that have survived the many hazards of the first critical years of life.

III. Continue programs to eliminate all cattle-grazing. Continuing consumptive use by these exotic animals has a devastating impact upon the biotic as well as the aesthetic environment. Grazing intensifies detrimental actions of natural environmental factors.

IV. Continue research designed to obtain basic information on population and community dynamics and institute new programs to facilitate related studies.

1. Continue on-going saguaro population studies and institute additional studies on related communities. The response of saguaro populations and the associated biotic communities—past, present, and future—provide a valuable measure of climatic change and the resulting effects.

2. Institute additional studies to inventory and estimate the status and trend of saguaro populations and other key species in characteristic and topographically dissimilar habitats.

3. Establish weather stations and maintain accurate and consistent weather records, using standard calibrated instruments and recognized procedures. Lack of reliable on-site climatic data has been a major handicap in efforts to relate environmental factors to saguaro population changes.
4. Map and identify all transplanted saguaros surviving from previous research activities. The absence of such identification precludes the obtaining of accurate information on natural survival at those locations.

V. Encourage and facilitate nondestructive independent scientific research activities appropriate to the purpose and significance of the area.

VI. Incorporate research findings into the interpretive program, stressing natural evolution and physical environment in relation to natural populations and communities.

VII. Allow continuation of natural regenerative processes in saguaro habitats from which adverse use has been eliminated. Avoid interference with these processes by avoiding the introduction of horticultural and other programs that will unbalance on-going natural recovery of deteriorated habitats.

APPENDIX II

The Saguaro Giant Cactus: A Bibliography

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Preface

This bibliography is a revision of "The saguaro giant cactus: A bibliography" Steenbergh (1974), and includes titles that have come to our attention since that bibliography was originally compiled in 1972.

Since the time of their first arrival in the Sonoran Desert, explorers and naturalists have been intrigued by the saguaro giant cactus (*Cereus giganteus* Engelm., *Carnegiea gigantea* [Engelm.] Britt. and Rose). As a major plant dominant in this subtropical desert, the saguaro has been the subject of continuing observations and reports, and in many ways it has proved to be an excellent organism for experimental research.

We offer here a compilation of references that have come to our attention in the course of our investigations on the ecology of the saguaro for the use of researchers, interpreters, natural resource managers, and others who have an interest in the extensive literature on the saguaro.

We have endeavored to provide a comprehensive list of the scientific literature on the saguaro. In addition, we have included selected historical and nontechnical reports containing original observations on the species.

The list also includes a selected representation of the numerous more recent, nontechnical and interpretive articles that have appeared in popular magazines. We have not, however, attempted to provide a comprehensive compilation of such titles.

An asterisk indicates references that we have been unable to obtain for examination but which seem likely to contain basic information or interesting commentary.

The literature on the saguaro is widely scattered and may well include important references that we have overlooked. The authors will greatly appreciate advice of any such omissions that may be recognized by the users of this bibliography.

Acknowledgments

The development of this bibliography has depended heavily upon the efforts of numerous organizations and individuals. These importantly include Mary Sherman Caldwell, Patricia Paylore, and other members of the staff of the University of Arizona Office of Arid Lands Studies who generously shared information resulting from their research.

We are grateful to the staff members of the University of Arizona Reference Library who were always ready to provide helpful suggestions in our search for material which proved difficult to locate.

We thank Charles H. Lowe for directing our attention to numerous important references that he has identified during the course of his continuing investigations on the ecology of the saguaro cactus.

We are indebted to Larry W. Mitich and Jan G. Bruhn for generously allowing us to examine a prepublication draft of their independently developed bibliography on the saguaro cactus, for calling our attention to references not included in the original edition of this bibliography on the saguaro, and for providing copies of difficult to obtain publications.

The assistance of the superintendents and staff members of Saguaro and Organ Pipe Cactus national monuments is gratefully acknowledged. To the National Park Service, we are indebted for the support of this project.

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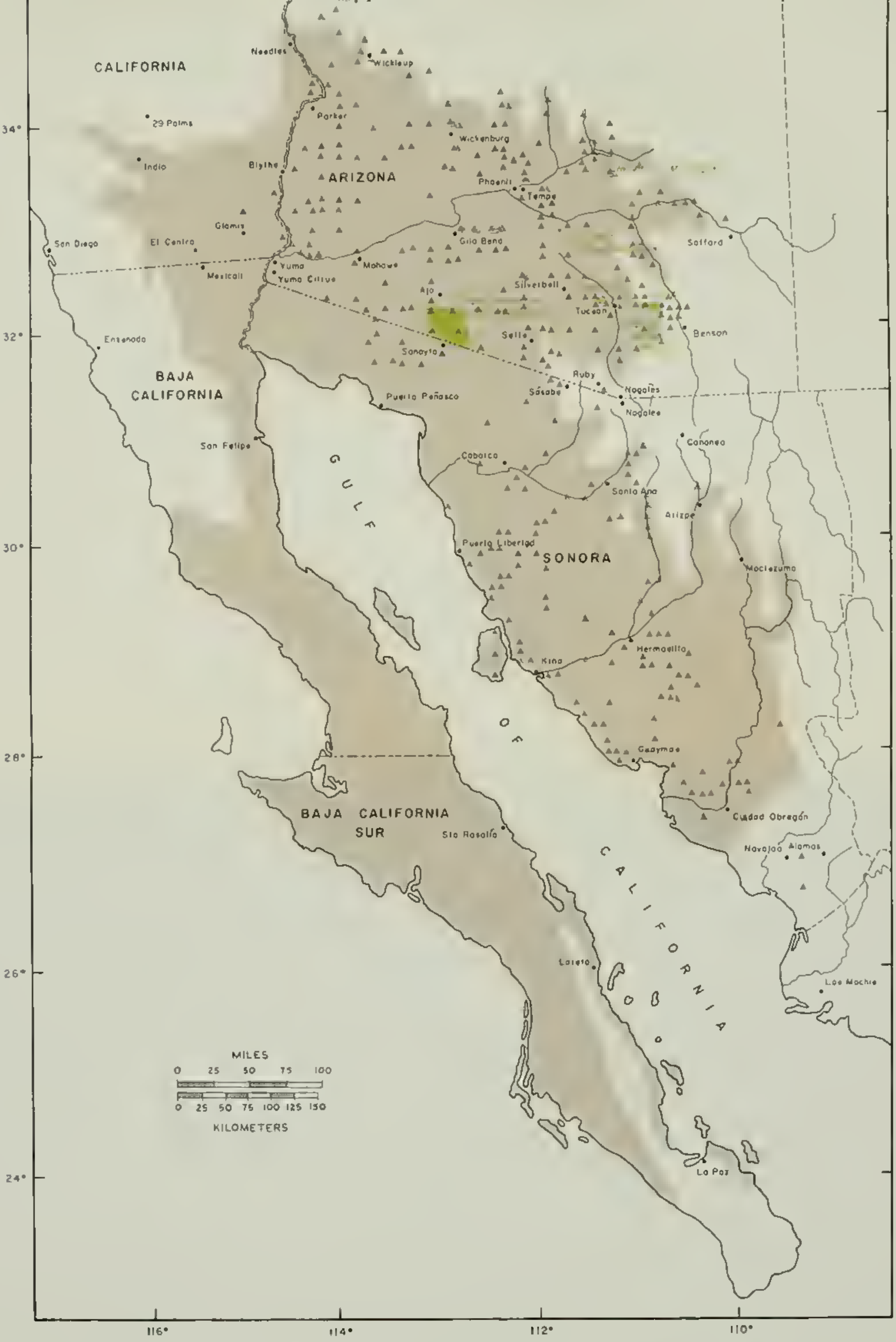

Fig. 1. Geographic distribution of the saguaro (*Cereus giganteus*) in the Sonoran Desert region. Triangles indicate saguaro observations. In addition to our own observations, these include distributions reported by Benson (1940, 1950, 1969), Shreve (1951), Soule and Lowe (1970), and Hastings, et al. (1972). Boundary of the Sonoran Desert from Shreve (1951). Some major islands are not shown.

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