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Ecology of the Saguaro: III

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ECOLOGY OF THE SAGUARO: III

Growth and Demography

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U.S. Department of Interior
National Park Service
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As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. administration.

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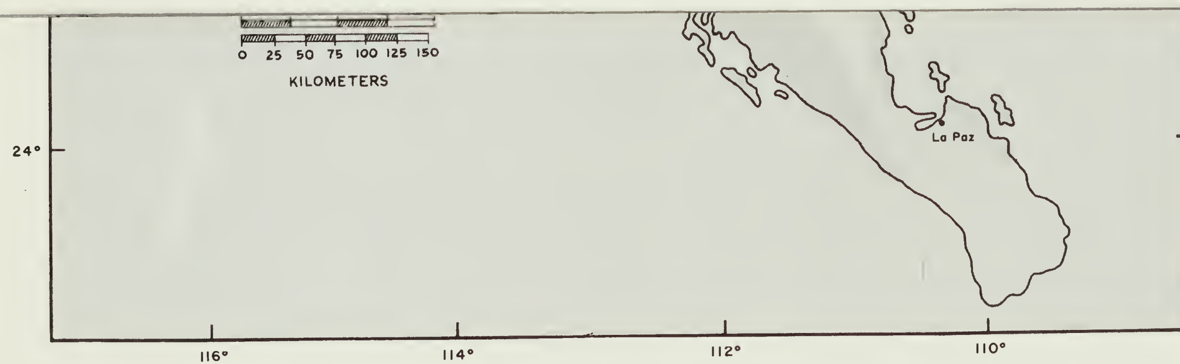
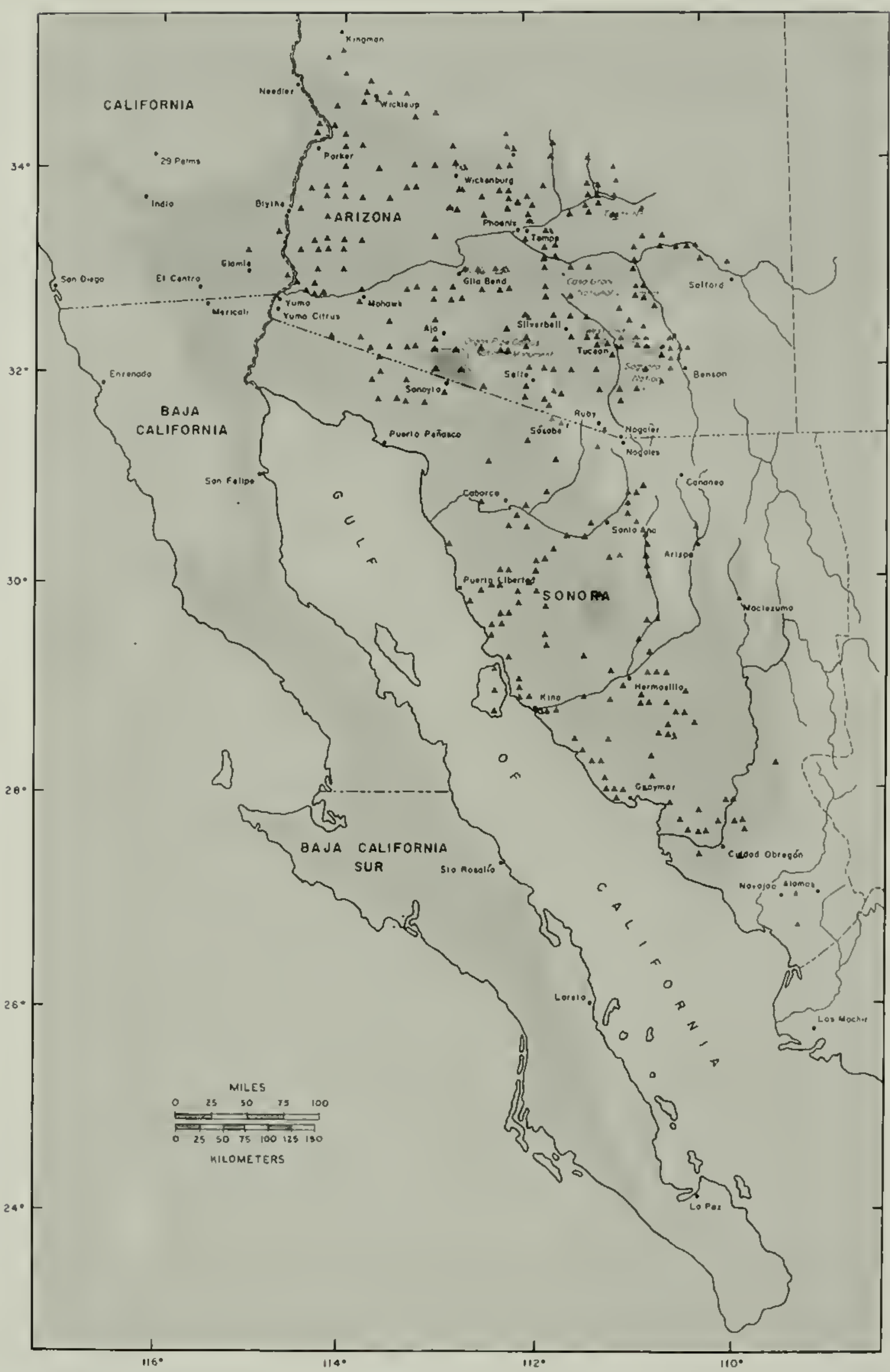


Frontispiece. Geographic distribution of the saguaro *(Cereus giganteus)* in the Sonoran Desert region. Triangles indicate saguaro observations. In addition to our own observations, these include distributions reported by Benson (1940, 1950, 1969), Shreve (1951), Soule and Lowe (1970), and Hastings,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



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To "Davey" Jones, Paul A. Judge, Robert M. Linn, George Sprugel, and Lowell Sumner, who cleared the way.

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Preface

The saguaro is a long-lived tropically derived species with relatively recent evolutionary origin. Under the powerful selective pressure of an ever-changing climate the species is still actively evolving. Dramatic fluctuations in certain of its populations, witnessed during this century, are a critically important, wholly natural, and widely misunderstood part of this dynamic process.

In this third volume in the National Park Service series of reports on our investigations on the ecology of the saguaro, we integrate some of the results of our previously reported investigations with more recently acquired data on these and other populations. In this report we explore the relationship of these results to questions on adaptive strategies, natural selection, and the continuing evolution of the species.

Within the perspective of the evolutionary time scale appropriate to the problem, we are obliged to examine these questions within a minuscule time-slice of a few decades, aided occasionally by a bit of insight stimulated by a coincidentally recorded historical note. To seek definitive answers to questions on the life history of an organism that survives to an age approximately twice that of the seeker suggests a certain degree of arrogance. If such exists at the outset of the quest, it is rapidly dispelled by the many frustrations inherent in securing appropriate data on a long-lived species.

Humility comes quickly when one is faced with attempts to interpret the present significance of unrecorded or obliquely documented events that may have occurred as much as a century or more before one's birth. Even more humbling in the face of unknowable future events are attempts at prediction. One quickly recognizes that such predictions—ultimately based on observations that, of necessity, span only a fraction of the species' normal generation time—are, at best, tenuous indeed.

Numerous journalists dedicated to the philosophy that "bad news makes good copy" have enthusiastically promoted and perpetuated the widespread popular belief that the saguaro is doomed to early extinction. Such stories have their origins in the medically oriented and ecologically untenable myth that locally spectacular saguaro die-offs—that are, in fact, a completely natural response to normally occurring climatic events—are the result of a mysterious, devastating, and incurable "disease." The myth, coupled with photographic examples of decomposing dead saguaros, constitutes the grist for scores of emotionally charged stories on the impending "demise" of the species. The following, for example, are concluding lines from an article entitled "The Desert's Declining King" (Lansford 1967):

> ". . . our great grandchildren may see the saguaros not as kings of the green desert but as a few scattered senile specimens, and their grandchildren may never see the saguaros at all, except in their picture books."

It is our hope that new information presented here will serve to relieve some of the ignorance responsible for such reports and help to dispel some of the persistent myths so long associated with this giant cactus species.

Acknowledgments

The list of those to whom we owe a debt of gratitude for assistance during the nearly three decades of our work on the saguaro is long indeed. Acknowledgment of those debts is an enjoyable and, at the same time, difficult undertaking. The "task" is pleasant in the recollection of mutually enjoyed experiences and companionship, stimulating discussions, and shared insights; difficult in that no few words, however carefully considered, can possibly express the full measure of our indebtedness, much less of our feelings. Too, there is discouragement in the realization that many others who, either by necessity or oversight, here and previously are unnamed, have contributed—directly or indirectly—in some important way to the pleasure and the accomplishment of our work. To them we offer not only our thanks, but our apologies as well.

The third volume in a series of reports on the ecology of the saguaro was supported in principal part by the National Park Service Offices of Natural Science Studies, in part by the National Science Foundation (IBP, Structure of Ecosystems), and is in part a contribution from the Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona. This report concludes research conducted under National Park Service Contract No. 14-10-0333-1303 to Charles H. Lowe.

For their early and continued commitment to National Park Service support of these investigations on saguaro ecology, we are deeply indebted to "Davey" Jones, Paul A. Judge, Robert M. Linn, George Sprugel, and Lowell Sumner.

We are indebted to numerous members of the National Park Service, past and present—the Washington office staff of the Office of the Chief Scientist, Regional Chief Scientist Dennis B. Fenn, and former Regional Chief Scientist O. L. Wallis, and others at the National Park Service Western and Southwestern Regional offices for personal encouragement and administrative support. We thank the current and past superintendents at Tonto, Saguaro, and Organ Pipe Cactus national monuments and the many members of their staffs who have contributed their support to these investigations.

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We remember most of all the saguaro trails with Claudia, with Ann, Peggy, and Paula, and with Arlene, Cal, and Cathy.

Tucson, Arizona
March 31, 1980

WARREN F. STEENBERGH
CHARLES H. LOWE

Summary

Differences in growth rates, density, size and age structure of saguaro populations growing in dissimilar climatic environments and topographic habitats provide useful insights into the natural dynamics of perennial plant species in arid lands. This investigation provides, for the first time, comparative information on growth and age relationships and related population parameters for saguaros growing in three differing climatic environments that are characteristic of a major portion of the species' distribution in Arizona and northern Sonora, Mexico.

Relationships between climatic factors, growth rates, habitat suitability, and the structure and dynamics of saguaro populations are discussed. Survivorship and the question of stable-age distribution in populations of long-lived terrestrial species growing in nonequable climates of mid-latitudes is examined.

Our observations and the observations of others on saguaro populations growing in representative Arizona habitats of the species leave no doubt that important long-term changes have occurred and will continue to occur in these populations. A decline in numbers of saguaros has occurred in each of three climatically dissimilar desert environments investigated.

In each of these environments, major differences in population age structure reflect the relative suitability of topographically dissimilar habitats. Populations growing in winter-warm habitats—rocky south-facing slopes—are relatively stable. Populations in less suitable, winter-cold habitats—north-facing slopes and nonrock, bajada and ''flats'' habitats—have insufficient numbers of young plants to maintain existing population age structure. The small proportion of young saguaros in these populations ensures that the numbers of large, old plants in these habitats must continue to decline for another half-century or more regardless of any future change in the recruitment rates.

The *number* of saguaros in a given habitat is limited by the number of microhabitats suitable for germination and seedling survival. Microhabitat suitability is determined by microtopography and the physical structure of the plant community. During the first years of saguaro life, microhabitat suitability determines the differential selective action by biotic and abiotic factors. Thus, during this early period in the selective process, chance alone may override differential fitness. In north-

ern portions of the species' range, catastrophic freezing selectively removes cold-intolerant individuals from the population, and, by differential selection on the youngest (smallest) and oldest (largest) members, selectively structures these populations.

The data on saguaro population structure support our earlier observations on the relationship of freezing temperatures to the limits, local distribution, and dynamics of saguaro populations in this portion of the species' range. Generally, the age structure of these populations is characterized by increasing density, and higher ratios of young to old plants, occurring on a gradient of increasingly favorable (i.e. warmer) winter microclimate.

Increase in habitat suitability is associated with differences in slope exposure (north to south), and rockiness of the habitat (nonrock to rock). Similarly, habitat suitability increases from low to high elevations with the moderation of winter minimum temperatures associated with thermal inversions that result from cold air drainage and accumulation in valley bottoms.

There is little doubt that domestic livestock grazing has contributed indirectly to the decline in saguaro establishment rates observed in these populations growing in winter-cold habitats; these include both rocky bajadas and flatland habitats with fine-textured soils. Grazing reduces the number and quality of sites suitable for germination; and, by the removal of protective low-level plant cover and mechanical breakdown of detritus, grazing increases vulnerability of young plants to destruction by freezing and other natural environmental hazards. There is, however, no substantive evidence that domestic livestock grazing has resulted in irreversible degradation of saguaro habitats. Neither is there conclusive evidence that grazing has resulted in significant increases in populations of rodents or other animals specifically detrimental to saguaro survival.

The results of our investigations certainly do *not* indicate that the saguaro is becoming extinct—nor do they suggest that it is "vanishing" from any of its historic habitats that have not been converted to intensive human uses. Rather, there has been, in this century, a decrease in the density of populations growing in marginal habitats, and a minor reduction in the absolute distributional limits of local populations.

Catastrophic freezes occur throughout the range of the saguaro and are an integral component of the species' environment. Such events are not "new," and do not in themselves indicate a climatic trend. Freeze-caused scars at the base of the largest saguaros provide a record of critical freezes that date back to the first half of the 19th century. Historical records of disastrous freezes in 1848 and 1870 further complement and confirm this record.

The observed fluctuations in Arizona populations of the saguaro are a natural and *expected* response to short-term variations in the critical extremes of the controlling environmental factor—recurring catastrophic freezes. Such freezes are the primary cause of adult saguaro deaths in Arizona and northern Sonora, Mexico, and are the primary control on the northern, eastern, and upper elevational limits as well as the age structure and dynamics of these populations.

Under the influence of the powerful selective pressure of recurring catastrophic freezes the species is actively evolving natural resistance to freezing. Adaptive evolution is expressed by natural selection for stem geometry and surface architecture that increase resistance to freezing.

Stable population age distribution, with regard to catastrophically selected plant species such as the saguaro, does not occur. In the presence of strong mid-latitude climatic variation—expected on an annual and/or longer term basis—such populations fluctuate in response to critical extremes of the controlling environmental factor(s). Furthermore, in such populations, the greatest fluctuations in numbers and age structure occur at the climatically limited margins of the species' distribution, where the extremes of a controlling environmental factor most frequently exceed the ecological tolerance of the plant.

The saguaro has evolved, through natural selection, a set of adaptive strategies required to survive the irregular occurrence of climatic extremes that are a normal characteristic of the saguaro environment. The "tragedy" of catastrophic die-offs observed in saguaro populations during this century is a human concept that is derived primarily from inability to relate these natural, climatically controlled events to the time scale of evolution.

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Introduction

This is the third volume in a series of National Park Service publications by the authors on the ecology of the saguaro. Part I reports on the critical role of freezing weather in the distribution and dynamics of saguaro populations in southern and northern Arizona (Steenbergh and Lowe 1976). Part II discusses reproduction, germination, establishment, growth, and survival of young saguaros to the age of first reproduction.[1]

In this volume we report on the relationship of saguaro population structure and dynamics to the broader questions of adaptive strategies, natural selection, and evolutionary significance. This report includes the results of our investigations into population structure, survivorship, reproductive dynamics, growth, and age of young and adult saguaros growing in climatic environments and topographic habitats that characterize the major portion of the species' distribution in Arizona and northern Sonora, Mexico (Figs. 1-1 to 1-7).

In this report we present growth curves and comparative height-age relationships for saguaros growing in three climatically dissimilar Arizona environments: the east (Rincon Mountains) and west (Tucson Mountains) sections of Saguaro National Monument near Tucson, Arizona, and Organ Pipe Cactus National Monument near Sonoita, Sonora, Mexico. These estimates—based on 536 precision measurements on 161 naturally growing seedling, juvenile, and adult saguaros and obtained over an 11-year period—permit, for the first time, an accurate comparison and evaluation of saguaro population age-structure in representative habitats of the species.

In connection with this investigation, we relocated and resurveyed a series of population study plots originally established at Saguaro and Organ Pipe Cactus national monuments in 1941 (Gill and Lightle 1942). These data are supplemented by density and size-class data from a series of 2-ha plots that we established from 1971 through 1975. Thus we include in this report population data on approximately 2,500 saguaros from a total plot area of 29.1 ha. These data, some of which span a period of 34 years,

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[1]The Library of Congress publication data for "Ecology of the Saguaro: II." (Steenbergh and Lowe 1977) incorrectly states that it is "The second part of a *two-part work*. . . ." [italics ours].

are for saguaros growing in representative Arizona habitats in three geographical localities.

The saguaro giant cactus (*Cereus giganteus* Engelm., *Carnegiea gigantea* [Engelm.] Britt. and Rose) is a tropically derived, cold-intolerant species whose distribution fully spans the latitudinal and elevational limits of the Sonoran Desert. In Arizona, and northern Sonora, Mexico, the eastern and northern limits of its distribution *define* the boundaries of the Sonoran Desert (Shreve 1951).

Broad spatial and temporal variability is a primary characteristic of the climatic environment in which the species has evolved through natural selection. The saguaro is a long-lived and responsive integrator of the total environment. The nautral dynamics of saguaro populations, therefore provide useful insights into the past and the present role of climatic fluctuations in the evolution of natural biotic communities in this large arid and semiarid region in the North American Southwest.

Fig. 1-1a. The Cactus Forest at Saguaro National Monument (east, flat habitat, elev. 870 m). At the time the monument was established this was considered to be the finest stand of saguaros in the world. A series of catastrophic freezes have since eliminated most of the large, old saguaros from this population. The establishment of thousands of young saguaros in this habitat during the past two decades, however, gives evidence that regeneration of this long declining population is now taking place. Photographed 26 June 1979.

The nature and causes of large-scale fluctuations in saguaro populations in Arizona have been sources of interest and speculation since the phenomenon was originally recognized during the first decade of this century. The status and probable future of saguaro populations in Arizona are a matter of concern to a number of Federal, State, and County agencies responsible for the management of lands on which the major northern populations occur. The question is of critical and continuing interest to the National Park Service, which is charged with the management and interpretation of four natural Arizona populations of the species located at Saguaro National Monument (east and west sections) and at Organ Pipe Cactus and Tonto national monuments (Steenbergh and Lowe 1969, 1976, 1977, 1979a, 1979b; Figs. 1-1 to 1-7).

Questions on the age structure and fluctuation of saguaro populations in Arizona are long standing. Shreve (1910), reporting on saguaro populations in the vicinity of Tucson, concluded that ". . . it is not maintaining itself in either of two situations, one of which offers the highest

Fig. 1-1b. Rolling hills habitat at Saguaro National Monument (east, elev. 925 m). Here, as in the Cactus Forest, the saguaro population has dwindled during the past 50 years to a sparse and unimpressive stand as a result of recurring freezes. Both populations lie in an area of cold air drainage from the slopes of the Rincon Mountains (right). Photographed 27 Feb. 1979.

Fig. 1-2a. North-facing slope habitat, Saguaro National Monument (east, elev. 960 m). The saguaro population consists of a few widely scattered individuals. Winter cold severely limits saguaro establishment and survival in this habitat. Photographed 27 Feb. 1979.

average water-content of any desert soil away from stream beds, and the other the temperature and other conditions that have brought about in it the densest Giant Cactus population that can be found in any habitat."

Subsequent investigations on saguaro population structure and dynamics have focused primarily on atypical populations growing at the edge of the desert in the extreme northwestern portion of Saguaro National Monument (east). There Wilder and Wilder (1939) and Wilder (1940) first recognized important differences in the age structure of populations growing in differing topographic habitats. They observed that saguaros ". . . 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)." They further observed ". . . that saguaros are not replacing themselves in that part of the Saguaro National Monument called in this paper the Lower Desert Floor, where at the present time the thickest stand and the largest trees are found."[2] What the Wilders were but dimly, if at all, able to recognize four decades ago, was

[2]Subsequently named "The Cactus Forest."

Fig. 1-2b. Rocky, south-facing slope habitat, Saguaro National Monument (east, elev. 975 m). Highest population densities and a relatively well-balanced age distribution of saguaros occur in these winter-warm habitats. Nocturnal reradiation from rock outcrops provides smaller saguaros with effective protection against freezing. Photographed by Paul Fugate, 9 Jan. 1976.

that the extraordinary (atypical) stand of saguaro giants, a deciding factor in the establishment of the monument, was in fact a relatively short-lived transitory, natural phenomenon.

Attention was further focused on this population with the observations in 1939-40 that catastrophic die-off was decimating the exemplary Cactus Forest stand of giant saguaros. The massive die-off—which was in fact the delayed response to critical injuries, inflicted by the intense freeze of January 1937[3] and compounded by a second deep-freeze in February 1939[4]—was mistakenly presumed to be an epidemic of organismically caused disease (Lightle et al. 1942).

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[3]It is an interesting fact that reports on the devastating winter freeze of 1937, including those of Wiggins (1937) and of Turnage and Hinckley (1938), did not mention saguaros. This comes as no surprise, however, since the characteristically delayed and readily observable diseaselike signs of such lethal freeze-caused injury did not become evident until the summer of 1939—more than two years after the 1937 freeze (see Gill 1942). Thus, the actual cause of the resulting rapid decline of saguaros at Saguaro National Monument and elsewhere remained unrecognized.

[4]February 1939 is one of the coldest months on record for Arizona and is the coldest *February* on record for the State (see USDA, Weather Bureau 1939).

Fig. 1-3. Bajada habitat, Saguaro National Monument (west, elev. 800 m). Although saguaro density is higher than in the Cactus Forest at the east monument, the proportion of young individuals present in this slightly warmer environment is insufficient to maintain the population at its present level. The population includes a large number of dead and dying freeze-damaged older plants. Photographed 15 May 1979.

That assumption was followed by pathology-oriented investigations and intensive efforts by the USDA Bureau of Plant Industry to control the supposed disease (see Appendix I; Gill 1942). In conjunction with those efforts, comprehensive, systematic surveys of saguaro populations were carried out at Saguaro National Monument (east), Organ Pipe Cactus National Monument, and in the Tucson Mountains. While the immediate "disease"-oriented objective of the investigations was incorrect, the data from those surveys clearly reveal the grossly unbalanced age structure of the Cactus Forest population, supporting the Wilders' observation that it was in a state of decline. These valuable baseline data have eventually revealed important dissimilarities in the density and age structure of populations growing in differing habitats and in differing local and regional climatic environments, a subject on which we report in the following chapters.

The Cactus Forest stand again commanded attention in 1962 with the mistaken prediction that this population would become extinct by the end

Fig. 1-4a. North-facing slope habitat, Saguaro National Monument (west, elev. 960 m). All of the large saguaros in this sparse population bear evidence of recent freeze-caused injury. Sotol *(Dasylirion wheeleri,* foreground) is a cold-tolerant plant of the Desert Grassland community. Photographed by Paul Fugate, 24 June 1975.

of the 20th century (Alcorn and May 1962). In a first response to that prediction, the National Park Service developed plans for, and began implementation of, a large-scale saguaro reforestation project. The project, never fully implemented, was finally abandoned in the mid-1960's when it was recognized that "reforestation" was based on an unsound dire prediction and was neither ecologically sound nor consistent with National Park Service administrative policy.

Height-age estimates for saguaros at Saguaro National Monument (east) reported by Hastings and Alcorn (1961) were subsequently used for status evaluation of saguaro populations in the Cactus Forest and elsewhere.[5] Hastings (1961) attempted to provide a broader view of differences in saguaro population structure in different geographic locations with dissimilar climatic environments. Niering et al. (1963) surveyed and compared the structure of saguaro populations growing at Saguaro National Monument and elsewhere in the vicinity of Tucson, Arizona. They

[5]See Steenbergh and Lowe (1977) for a comprehensive summary of investigations on the saguaro.

Fig. 1-4b. Rocky, south-facing slope habitat, Saguaro National Monument (west, elev. 920 m). This saguaro population, situated on the southwest slopes of Wasson Peak in the Tucson Mountains, is the most vigorous of any examined during this investigation. Saguaro density and the proportion of young saguaros growing in this habitat are greater than was found in any of the other populations surveyed. Photographed by Paul Fugate, 24 June 1975.

concluded that the population was reproducing well on rocky slopes and some bajada communities, but was failing to reproduce on the finer soils of bajadas affected by grazing.

Except for Soule and Lowe's (1970) investigations, conducted over the full latitudinal range of the species' distribution, and work on populations located near Ventana Cave in central Pima County, Arizona, and in McDougal Crater in northwestern Sonora—both of which were studied by several Tucson ecologists in the 1950's and reported by Hastings (1961)—most studies have centered on saguaro populations in the vicinity of Tucson, Arizona. The Tucson populations are growing at the northeastern and upper elevational limits of the species' distribution (see Steenbergh and Lowe 1977; Figs. 1 and 2). In view of that fact, the large-scale fluctuations observed in these populations during this century are not surprising. Rather, as Harper (1967, 1977) and others have pointed out, major fluctuations are an *expected* characteristic of plant populations subject to varying extremes of the principal environmental factor(s) determining the absolute limits of the species' distribution.

Fig. 1-5a. Bajada habitat near the mouth of Alamo Canyon, Organ Pipe Cactus National Monument (elev. 680 m). Highest saguaro densities are associated with rocky soil immediately adjacent to the western base of the Ajo Mountains. Density decreases with progressively finer soil textures that occur from the base of the mountains to the center of the broad valley in the distance. Photographed 5 Mar. 1979.

We begin the data analysis in this volume by providing in chapter 2 a detailed account of saguaro growth in populations located across extreme southern Arizona that are representative of saguaro growth in Sonoran Desert habitats in southern Arizona and northern Sonora, Mexico. Unless one is or has been involved in such work, it is difficult to appreciate the difficulty in obtaining precise and meaningful physiological growth data in the field, especially for developing stem growth equations for populations of long-lived plant species.

Growth data are determined in a long and arduous process, in the field. Such investigation involves a series of precise stem and other measurements conducted over many years on marked individuals of all sizes and ages. Among the many associated problems are those of obtaining data on growth and survival of the tiny plants during the earliest years of life. At germination, the widely dispersed, inconspicuously colored, and often concealed saguaro seedlings are barely larger than a grain of sand and can be found only by intensive hands-and-knees search with the

Fig. 1-5b. Desert riparian habitat at Senita Basin, Organ Pipe Cactus National Monument (elev. 490 m). A vigorous saguaro population is intermixed with organ-pipe and senita cacti. Topographic features concentrate water runoff, and, in combination with the low elevation, moderate winter cold and provide a habitat which supports one of the northernmost populations of the cold-intolerant senita cactus. Photographed 7 Feb. 1979.

aid of a magnifying lens. The size of the young plant increases only a few millimeters per year, and the original sample is rapidly diminished by a large assortment of decimating agents, thus severely limiting opportunities for sequential measurements on stem growth.

Another of the more difficult problems in these ecological investigations is ensuring that, for larger plants, growth data are for healthy, not moribund, individuals. This requires recognition and elimination (or nonelimination, as the special case may be) of green, standing yet moribund, individuals that may grow at a slow-to-negligible rate for a few years after serious damage to the stem or root systems—as usually occurs after one or more badly damaging freezes in a winter(s) past. Data for failing saguaros mask the normal rates of growth for the populations studied.

Why the great concern about physiological growth and its accurate assessment, from locality to locality, and the derivation of growth equations that cover one to two centuries of the natural stem growth of large

Fig. 1-6. Rocky, south-facing slope habitat, Ajo Mountains, Organ Pipe Cactus National Monument (elev. 730 m). Organpipe cacti (foreground) outnumber saguaros in this relatively arid habitat. Saguaro density is higher in the adjoining bajada habitat. Photographed 30 Jan. 1976.

samples of individual saguaros? In addition to being of much interest to plant physiology for its own sake, physiological plant growth and the operation of its controls provide crucial information needed to determine many other important aspects of saguaro population ecology. Growth data provide the age data. Such growth-derived age data provide the basis for determining population age structure, survivorship, and related population parameters. Accurate age data permit us to prepare life tables for saguaro populations and to calculate life expectancy, generation time, reproductive rates, etc., and to theorize on the kinds of selection potentially operating on and limiting saguaro and some other native perennial plant populations in the Sonoran Desert.

Such population identities allow us to predict population success and failure in differing microenvironments within the saguaro's geographic distribution—throughout the latitudinal and elevational limits of the Sonoran Desert, and slightly beyond it into the moister ecotones with thornscrub at the south, chaparral on the west, grassland on the east, and Mohave desertscrub in the north.

Fig. 1-7. Rocky south-facing slope habitat at Tonto National Monument (elev. 850 m). Mean annual precipitation of approximately 350 mm supports an ecotonal association of desert and desert grassland plant species. In this habitat with a more or less continuous ground cover of combustible grasses, the saguaro population is subject to occasional lightning-caused fires. Photographed 18 July 1978.

2
Growth and Age

Saguaro growth rates provide a basis for determination of size-age relationships and thus permit evaluation of population age structure, survivorship, life expectancy, and related demographic parameters. Our earlier investigations show that large-order differences in saguaro growth rates exist in climatically different areas of the species' distribution (Steenbergh and Lowe 1977). Thus, saguaro height-age relationships established for one locality cannot be applied to populations growing elsewhere, in a different growth environment. This report provides comparative information on growth rates and age-height relationships for saguaro populations growing in three differing climatic environments characteristic of the major portion of the species' distribution in Arizona and northern Sonora, Mexico (Table 2-1; also see Steenbergh and Lowe 1977, Table 33).

Reported here are data on natural growth of seedling, juvenile, and adult saguaros at each of the two sections of Saguaro National Monument (east and west) near Tucson, Arizona, and at Organ Pipe Cactus National Monument, near Sonoita, Sonora, Mexico, and Ajo, Arizona. These data, obtained over an 11-year period from 1967-1977, supplement previously

TABLE 2-1. Comparison of mean summer (July-September) and annual (January-December) precipitation at saguaro growth study sites, 1968-1976.

Location	Precipitation			
	Summer		Annual	
	mm	in	mm	in
Saguaro N. Mon.				
east	134	5.29[a]	312	12.30
west	113	4.44[a]	261	10.27
Organ Pipe Cactus N. Mon.				
headquarters	102	4.02	192	7.56

[a] On-site field station. All other values from official National Park Service station records.

reported data on the growth of young saguaros at Saguaro National Monument (east) by Steenbergh and Lowe (1977).

Saguaro National Monument

Growth rates and estimated total stem-height/age relationships for naturally growing, healthy young saguaros to 2.2 m in height at Saguaro National Monument (east) are provided in Steenbergh and Lowe (1977). Supplemental growth measurements of naturally growing saguaros were obtained from 1968 to 1977 using the methods described in that report. Data reported here include the above (1977) data together with additional yearly measurements on a representative sample of adult plants as well as seedlings (first year) and juvenile saguaros in both east and west sections of the monument. These data provide a basis for further evaluating the effects of environment and time on saguaro growth and growth rates in dissimilar habitats. They further permit more accurate age determination for adult as well as seedling and juvenile saguaros growing in these two flatland habitats.

Growth curves

Field measurements taken with precision calipers were used to obtain aboveground stem heights for individual known-age, naturally growing young saguaros (age-classes 1 to 8 years) in each of two sections of the monument. A portion of the individuals was then removed and confirming precision measurements were made in the laboratory. Regression analysis of aboveground stem height on known year-class (Tables 2-2 and 2-3) was used to derive preliminary estimates of mean aboveground stem height and subsequent 1-year apical (height) growth increments for young saguaros in each of the two sections of the monument. These data are shown in Tables 2-5 and 2-6, and graphed in Figs. 2-1, 2-2, and 2-3; regression equations are given in Table 2-4.

Growth curves for saguaros growing in flatland habitats in each of the two (east and west) sections of Saguaro National Monument are shown in Figs. 2-2 and 2-3. The curves were individually generated by stepwise multiple regression analysis (successive powers of X) of log-transformed data as described by Kim and Kohout (1975) using SPSS program version 6.5.3. (Vogelback Computing Center 1977). The data are aboveground stem height (X) and subsequent 1-year apical growth increments (Y; Appendices II and III) pooled with mean height (X) and 1-year growth increments (Y, weighted "N" times for each year-class) for known-age young saguaros (Tables 2-5 and 2-6). Equations and regression statistics for the two resulting growth curves are shown in Table 2-7. In these equations, Y is a 1-year apical growth (height) increment (cm), and X is the aboveground stem height (cm) for the plant at the start of the growth year.

TABLE 2-2. Aboveground stem height (cm) of known-age (year-class) juvenile saguaros ($N = 34$) at Saguaro National Monument (east).

	Aboveground stem height							
	1 Yr	2 Yr	3 Yr	4 Yr	5 Yr	6 Yr	7 Yr	8 Yr
1[a]	0.36	0.51	0.74	1.92	2.08	2.40	2.88	3.50
2	0.20	0.41	0.50	0.53	1.20	2.40		
3	0.22	0.45	1.23	0.65		2.57		
4	0.25	0.47	1.30	0.84				
5	0.40	0.48		1.00				
6	0.42	0.51		1.14				
7	0.46	0.55						
8	0.46	0.56						
9	0.53							
Total	3.30	3.94	3.77	6.08	3.28	7.37	2.88	3.50
Mean	0.37	0.49	0.94	1.01	1.64	2.46	2.88	3.50
N	9	8	4	6	2	3	1	1

[a] Sequential measurements.

TABLE 2-3. Aboveground stem height (cm) of known-age (year-class) juvenile saguaros ($N = 33$) at Saguaro National Monument (west).

	Aboveground stem height[a]						
	1 Yr	2 Yr	3 Yr	4 Yr	5 Yr	6 Yr	7 Yr
1					1.68	1.78	2.54
2		0.30	0.31	0.48	0.54	0.88	
3		0.52	0.67	1.06	1.02	1.72	
4		0.75	0.73	0.69	0.77	1.10	
5		0.29	0.51				
6		0.33	0.50				
7	0.18	0.24	0.46	0.48	0.70		
8	0.29	0.28	0.30	0.40	0.40		
9		0.18					
10	0.33						
Total	0.98	2.70	3.48	3.11	4.71	5.48	2.54
Mean	0.24	0.37	0.50	0.51	0.94	1.37	2.54
N	4	7	7	5	5	4	1

[a] Sequential measurements.

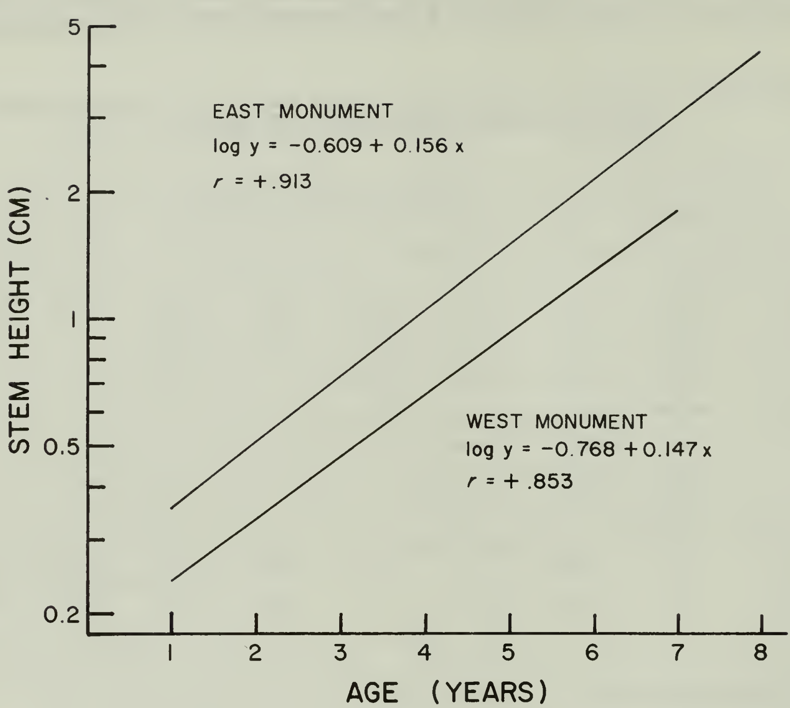

Fig. 2-1. Regression on semilogarithmic coordinates of aboveground stem height on age (year-class) of naturally growing young saguaros for the first 7-8 years following germination in nonrocky habitats at Saguaro National Monument (east, $N = 34$; west, $N = 33$). The difference in the elevation of the curves is highly significant ($p < 0.005$); differences in slope are not significant ($p > 0.06$). Data in Tables 2-2, 2-3, 2-5, and 2-6. Regression equations in Table 2-4.

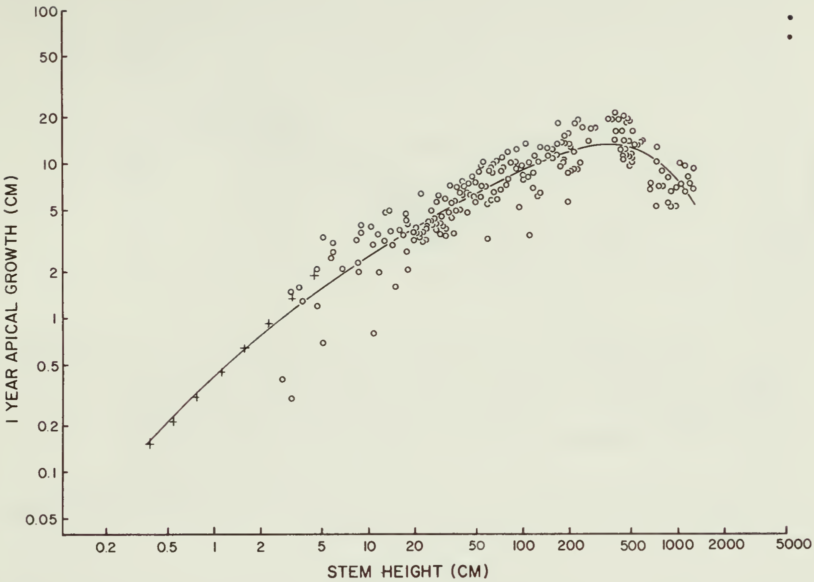

Fig. 2-2. Regression on logarithmic coordinates of 1-year apical growth (open circles) on aboveground stem (trunk) height of saguaros (N = 244) in nonrocky habitat at Saguaro National Monument (east). Plus symbols are mean 1-year apical growth increments for known-age seedlings and young juvenile saguaros (N = 34) shown in Table 2-5. Data for larger plants in Appendix II. Regression statistics summary in Table 2-7 (equation 1).

Solid circles (upper right) are *total* 1-year apical growth increments (N = 2, trunk plus branches) on *total* height for single 10-branched plant. Data in Table 2-8. See discussion in text.

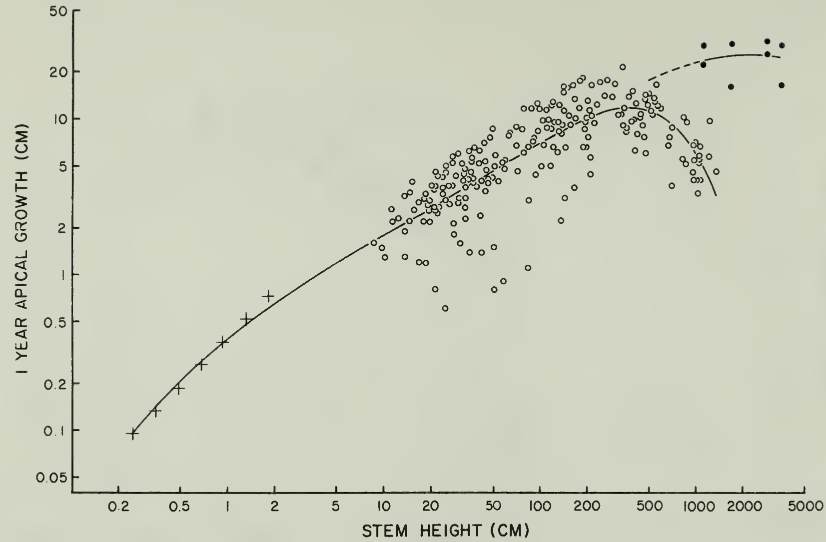

Fig. 2-3. Regression on logarithmic coordinates (lower curve) of 1-year apical growth (open circles) on aboveground stem (trunk) height of saguaros ($N = 248$) in nonrocky habitat at Saguaro National Monument (west). Plus symbols are mean 1-year apical growth increments for known-age seedlings and young juvenile saguaros ($N = 33$) shown in Table 2-6. Data for larger plants in Appendix III. Regression statistics summary in Table 2-7 (equation 2).

The upper curve (right, solid circles) is the regression of *total* 1-year apical growth increments ($N = 8$, trunk + branches) on *total* height. The equation for the line is:

$$\log Y = -3.353 + 2.837 \log X - 0.423 (\log X)^2; \; r = 0.074.$$

Data in Table 2-9. See discussion in text.

TABLE 2-4. Regression equations for aboveground stem height on age (year-class) of known-age juvenile saguaros in nonrocky habitats at Saguaro National Monument (east = SE; west = SW). Data in Tables 2-2, 2-3, Graphed in Fig. 2-1.

	Monument	N	Regression equation	r
1	SE	34	$\log Y = -0.6088 + 0.1562\,X$	+0.9132
2	SW	33	$\log Y = -0.7685 + 0.1466\,X$	+0.8528

TABLE 2-5. Age (yrs), calculated aboveground stem height (cm), and subsequent 1-year height growth increment (cm) for known-age seedlings and young juvenile saguaros (N = 34) at Saguaro National Monument (east) by regression equation (1) in Table 2-4. Graphed in Figs. 2-1 and 2-2.

Age	N	Height	Growth
1	9	0.353	0.153
2	8	0.505	0.219
3	4	0.724	0.313
4	6	1.037	0.449
5	2	1.486	0.643
6	3	2.129	0.921
7	1	3.050	1.320
8	1	4.370	1.891

TABLE 2-6. Age (yrs), calculated aboveground stem height (cm), and subsequent 1-year height growth increment (cm) for known-age seedlings and young juvenile saguaros (N = 33) at Saguaro National Monument (west) by regression equation (2) in Table 2-4. Graphed in Figs. 2-1 and 2-3.

Age	N	Height	Growth
1	4	0.239	0.096
2	7	0.335	0.134
3	7	0.469	0.188
4	5	0.657	0.264
5	5	0.921	0.370
6	4	1.291	0.519
7	1	1.810	0.727

TABLE 2-7. Summary statistics, stepwise multiple regression of log transformation of saguaro cactus apical growth (Y, cm) on stem height (X, cm) at Saguaro National Monument east (SNME; N = 244), Saguaro National Monument west (SNMW; N = 248), and Organ Pipe Cactus National Monument (OPCNM; N = 30). Data in Tables 2-5, 2-6; Apps. II, III, and IV. Equations graphed in Figs. 2-2, 2-3, and 2-5.

No.	Habitat	Step	Variable	Coefficient (± SE)	Cum. r^2	F	P
1	SNME[a]	1	$\log X$	0.92095 ± 0.04452	0.811	427.982	<.001

No.	Habitat	Step	Variable	Coefficient (± SE)	Cum. r^2	F	P
1	SNME[a]	1	$\log X$	0.92095 ± 0.04452	0.811	427.982	<.001
		2	$(\log X)^5$	0.00558 ± 0.00263	0.936	4.511	0.035
		3	$(\log X)^2$	−0.14860 ± 0.03752	0.937	15.688	<0.001
		4	$(\log X)^7$	−0.00069 ± 0.00020	0.940	11.404	0.001
		Constant		−0.36894 ± 0.02133		299.088	<0.001
2	SNMW[a]	1	$\log X$	0.82044 ± 0.06306	0.761	169.269	<0.001
		2	$(\log X)^8$	−0.00017 ± 0.00003	0.883	31.209	<0.001
		3	$(\log X)^2$	−0.21866 ± 0.10161	0.883	4.632	0.032
		4	$(\log X)^3$	0.06674 ± 0.03290	0.885	4.115	0.044
		Constant		−0.41711 ± 0.04509		85.566	<0.001
3	OPCNM[b]	1	$\log X$	2.11375 ± 1.32243	0.101	2.555	0.122
		2	$(\log X)^4$	−0.03753 ± 0.03996	0.530	0.882	0.356
		3	$(\log X)^8$	0.00005 ± 0.00022	0.531	0.058	0.812
		Constant		−1.91272 ± 2.08861		0.839	0.368

[a] 1-year increments.
[b] 10-year increments (1967-77).

Age and height

Age determinations for saguaros growing in flat and moderately rolling nonrocky terrain at Saguaro National Monument (Tables 2-10 and 2-11) are graphed in Fig. 2-4. Values for the east monument (Table 2-10) were generated by the following stepwise computation of successive 1-year growth increments:

1. The mean aboveground stem height attained by saguaros during the first year of life is 0.353 cm (Table 2-5) as estimated from our data for field years 1961-1969. By substitution of this value for X (equation 1, Table 2-7), the estimated subsequent 1-year growth increment ($\hat{Y}$, growth during the second year of life) is 0.153 cm.

2. By addition (initial height + second-year growth), the second-year stem height is 0.506 cm.

3. By use of the same two-step procedure, the subsequent 1-year apical growth ($\hat{Y}$) and stem height were calculated for each consecutive year.

Values for the west monument (Table 2-11) were generated in the same manner, by substitution of the mean first-year stem height (0.239 cm) at that location (Table 2-6) for X (equation 2, Table 2-7).

As shown in Appendices II and III, the upper limits of the field data on stem height growth at the east and west monuments are 1,292.7 cm and 1,363.4 cm, respectively. Regression values for saguaros of greater height are shown in Tables 2-10 and 2-11 and Fig. 2-4 (dashed lines).

Organ Pipe Cactus National Monument

Data on the growth of saguaros at Organ Pipe Cactus National Monument obtained from 1967 to 1977 provide a basis for estimation of growth rates and the first determinations of age-height relationships for saguaros at that location. The monument is in southwestern Arizona directly across (north) the international boundary line from Sonoita, Sonora, Mexico (see Steenbergh and Lowe 1977, Fig. 1).

The growth curve

The 10-year growth curve for saguaros at Organ Pipe Cactus National Monument (Fig. 2-5) is a composite curve based on (1) multiple regression analysis of 10-year data for on-site growth from 1967 to 1977 (upper, solid line; heights greater than 83.8 cm, Appendix IV), (2) first-year on-site seedling growth data (Table 2-12; Fig. 2-6), and (3) proportional estimate of growth for young saguaros (lower, dashed line; heights to 83.8 cm).

Data on the growth of older saguaros in a sample population growing in a bajada (flatland) habitat near the mouth of Alamo Canyon were obtained by consecutive measurements in the manner described for Saguaro National Monument. The aboveground stem heights of all individuals in the sample were measured during the spring of 1967. The same individuals were measured again in March 1977 to obtain a 10-year record of growth in that environment (Appendix IV).

The 10-year growth curve for saguaros greater than 83.8 cm in height (Fig. 2-5, upper segment, solid line) was derived by stepwise multiple regression as described for the Saguaro National Monument growth sample, using log-transformation of the data in Appendix IV. Regression statistics are shown in Table 2-7, equation 3. In this equation Y is a 10-year apical growth (height) increment (cm), and X is the 1967 aboveground stem height (cm).

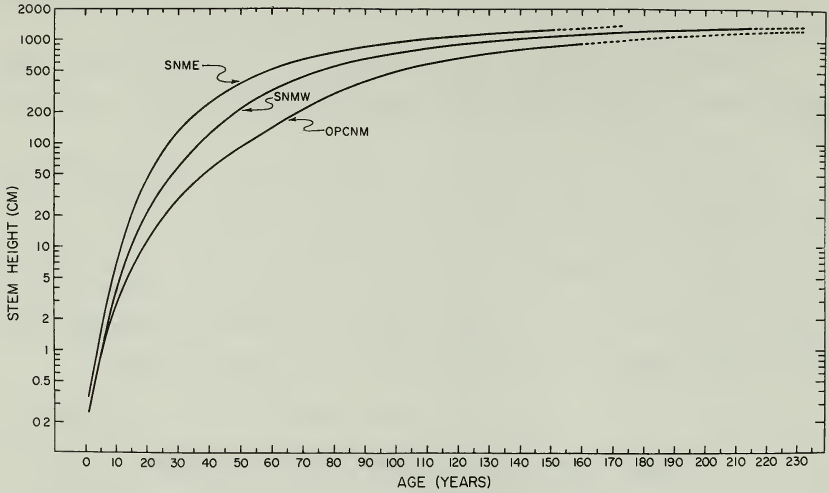

Fig. 2-4. Aboveground stem height (cm) on age (years) on semilogarithmic coordinates for saguaros at Saguaro National Monument (east = SNME, upper line; west = SNMW, middle line) and Organ Pipe Cactus National Monument (OPC-NM, lower line). Dashed lines are extrapolated values by regression. Data in Tables 2-10, 2-11, and 2-13 (see text).

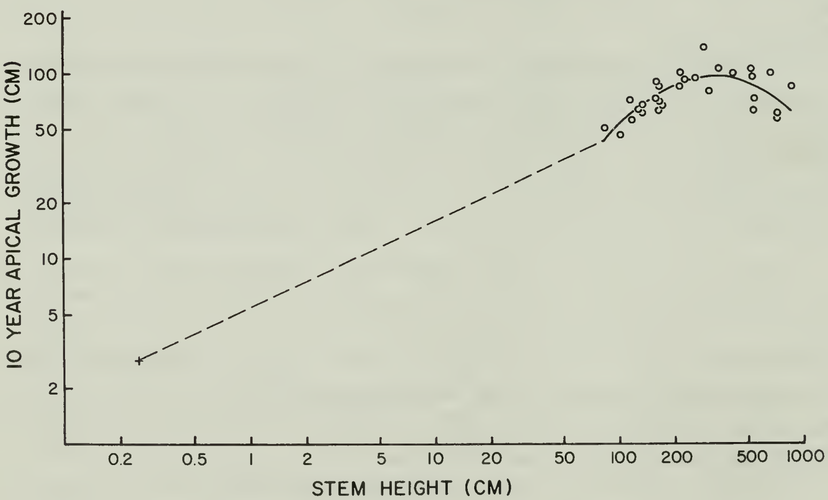

Fig. 2-5. Regression on logarithmic coordinates of 10-year apical growth (cm), 1967-1977, on height (cm) of saguaros (N = 30) at Organ Pipe Cactus National Monument. Data in Appendix IV. Regression statistics summary in Table 2-7 (equation 3). Dashed line is a proportional estimate of the 10-year growth rate for juvenile saguaros based on comparative analysis of on-site growth data and growth rates of juvenile saguaros at Saguaro National Monument (west; see text).

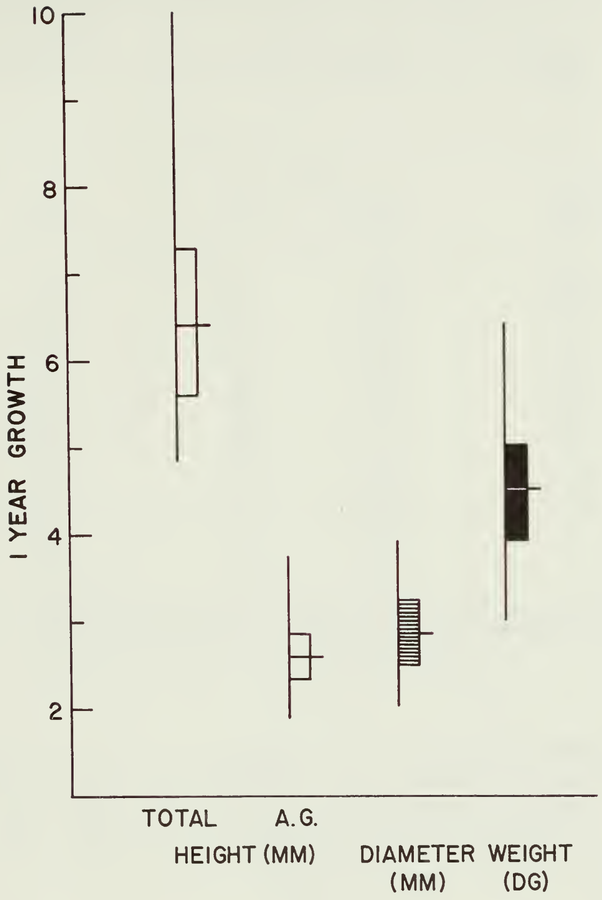

Fig. 2-6. Total height (mm), aboveground (A.G.) height (mm), stem diameter (mm), and weight (dg) for naturally growing first-year saguaro seedlings at Organ Pipe Cactus National Monument (N = 14). Mean, range, and 95% confidence interval. Data in Table 2-12.

TABLE 2-8. Total apical growth of a single-branched saguaro at Saguaro National Monument (east) 1975-1977. Stem height (trunk; cm), vertical measurement from base of branch to tip of branch, and subsequent 1-year apical growth increment (cm). Graphed in Fig. 2-2.

Plant no.		1975		1976	
Stem	Branch	Height	Growth	Height	Growth
7521	(trunk)	1,051.6	7.5	1,059.1	10.1
	A	398.1	6.3	494.4	7.1
	B	347.4	5.5	352.9	7.4
	C	388.6	5.2	393.8	9.6
	D	353.1	6.9	360.0	8.7
	E	379.5	7.0	395.9	9.4
	F	50.6	3.3	60.5	6.6
	G	270.1	4.5	278.4	3.8
	H	305.8	5.8	311.6	6.7
	I	358.8	4.9	363.7	7.2
	J	496.6	6.0	412.6	7.4
Total		4,310.2	62.9	4,457.1	84.0

TABLE 2-9. Total apical growth of branched saguaros ($N = 4$) at Saguaro National Monument (west) 1975-1977. Stem height (cm), vertical measurement from base of branch to tip of branch, and 1-year subsequent apical growth increment (cm). Graphed in Fig. 2-3.

Plant no.		1975		1976	
Stem	Branch	Height	Growth	Height	Growth
7162	(trunk)	676.1	6.7	682.8	7.5
	A	265.4	4.7	270.1	8.9
	B	182.6	5.9	188.5	7.4
	C	156.7	4.7	161.4	5.8
Total		1,280.8	22.0	1,302.8	29.6
7523	(trunk)	994.8	4.1	998.9	5.4
	A	513.7	4.3	518.0	6.5
	B	440.8	4.7	445.5	6.1
	C	418.4	4.7	423.1	6.0
	D	438.1	5.0	443.1	4.2
	E	148.7	3.8	152.5	4.0
Total		2,954.5	26.6	2,981.1	32.2

TABLE 2-9—*continued*

Plant no.		1975		1976	
Stem	Branch	Height	Growth	Height	Growth
71116	(trunk)	1,001.3	4.1	1,005.4	7.1
	A	435.5	4.0	439.5	8.5
	B	97.2	4.0	101.2	5.3
	C	195.3	3.9	199.2	9.1
Total		1,729.3	16.0	1,745.3	30.0
7525	(trunk)	1,356.4	2.4	1,358.8	4.6
	A	37.1	1.8	38.9	3.8
	B	627.5	3.6	631.1	3.9
	C	679.3	3.2	682.5	5.9
	D	289.5	2.4	291.9	4.6
	E	669.0	3.2	672.2	6.5
Total		3,658.8	16.6	3,675.4	29.3

TABLE 2-10. Age, aboveground stem height (cm), and subsequent 1-year apical growth (cm) of saguaros in nonrocky habitats at Saguaro National Monument (east). Graphed in Fig. 2-4.

Age (yrs)	Height (cm)	Apical growth (cm/yr)
1	0.35	0.15
2	0.51	0.22
3	0.73	0.32
4	1.04	0.44
5	1.49	0.61
6	2.10	0.82
7	2.92	1.06
8	3.98	1.35
9	5.33	1.67
10	7.00	2.02
11	9.03	2.39
12	11.42	2.79
13	14.21	3.20
14	17.40	3.62
15	21.02	4.04
16	25.06	4.48
17	29.55	4.92
18	34.47	5.37
19	39.83	5.81
20	45.65	6.26

TABLE 2-10—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
21	51.90	6.70
22	58.61	7.14
23	65.75	7.58
24	73.33	8.01
25	81.35	8.44
26	89.78	8.85
27	98.63	9.25
28	107.88	9.64
29	117.52	10.01
30	127.53	10.37
31	137.90	10.71
32	148.62	11.04
33	159.66	11.34
34	171.00	11.63
35	182.63	11.89
36	194.52	12.14
37	206.66	12.36
38	219.03	12.57
39	231.59	12.75
40	244.34	12.91
41	257.25	13.05
42	270.30	13.17
43	283.47	13.27
44	296.74	13.36
45	310.10	13.43
46	323.53	13.48
47	337.00	13.51
48	350.51	13.53
49	364.04	13.53
50	377.57	13.53
51	391.10	13.51
52	404.61	13.48
53	418.08	13.43
54	431.52	13.38
55	444.90	13.32
56	458.22	13.26
57	471.48	13.18
58	484.66	13.10
59	497.76	13.01
60	510.77	12.92
61	523.69	12.82
62	536.51	12.72
63	549.23	12.62
64	561.85	12.51
65	574.36	12.40
66	586.76	12.29

TABLE 2-10—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
67	599.05	12.17
68	611.23	12.06
69	623.28	11.94
70	635.23	11.83
71	647.05	11.71
72	658.76	11.59
73	670.35	11.47
74	681.82	11.35
75	693.17	11.23
76	704.41	11.12
77	715.52	11.00
78	726.52	10.88
79	737.40	10.77
80	748.17	10.65
81	758.82	10.54
82	769.36	10.42
83	779.78	10.31
84	790.09	10.20
85	800.30	10.09
86	810.39	9.98
87	820.37	9.88
88	830.25	9.77
89	840.02	9.67
90	849.68	9.56
91	859.25	9.46
92	868.71	9.36
93	878.07	9.26
94	887.33	9.16
95	896.50	9.07
96	905.56	8.97
97	914.54	8.88
98	923.42	8.79
99	932.20	8.70
100	940.90	8.61
101	949.51	8.52
102	958.03	8.43
103	966.46	8.35
104	974.81	8.26
105	983.07	8.18
106	991.25	8.10
107	999.35	8.02
108	1,007.37	7.94
109	1,015.31	7.86
110	1,023.17	7.79
111	1,030.96	7.71
112	1,038.67	7.64

TABLE 2-10—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
113	1,046.31	7.56
114	1,053.87	7.49
115	1,061.36	7.42
116	1,068.78	7.35
117	1,076.13	7.28
118	1,083.42	7.21
119	1,090.63	7.15
120	1,097.78	7.08
121	1,104.86	7.02
122	1,111.88	6.96
123	1,118.84	6.89
124	1,125.73	6.83
125	1,132.56	6.77
126	1,139.33	6.71
127	1,146.04	6.65
128	1,152.69	6.59
129	1,159.29	6.54
130	1,165.82	6.48
131	1,172.31	6.43
132	1,178.73	6.37
133	1,185.10	6.32
134	1,191.42	6.26
135	1,197.69	6.21
136	1,203.90	6.16
137	1,210.06	6.11
138	1,216.17	6.06
139	1,222.23	6.01
140	1,228.24	6.96
141	1,234.21	5.92
142	1,240.12	5.87
143	1,245.99	5.82
144	1,251.81	5.78
145	1,257.59	5.73
146	1,263.32	5.69
147	1,269.00	5.64
148	1,274.65	5.60
149	1,280.25	5.56
150	1,285.80	5.51
151	1,291.32[a]	5.47
152	1,296.79	5.43
153	1,302.22	5.39
154	1,307.62	5.35
155	1,312.97	5.31
156	1,318.28	5.27
157	1,323.56	5.24
158	1,328.79	5.20

TABLE 2-10—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
159	1,333.99	5.16
160	1,339.15	5.12
161	1,344.28	5.09
162	1,349.36	5.05
163	1,354.42	5.02
164	1,359.43	4.98
165	1,364.41	4.95
166	1,369.36	4.91
167	1,374.27	4.88
168	1,379.15	4.85
169	1,384.00	4.81
170	1,388.81	4.78
171	1,393.60	4.75
172	1,398.35	4.72
173	1,403.06	4.69

[a] Growth data limit (ht 1,292.7 cm). Subsequent values by regression.

Branching and total height growth

Tables 2-8 and 2-9 provide data on the growth of individual branches ("arms") and total apical growth of branched adult saguaros. From permanent benchmarks set directly beneath the tip of each branch and at the base of the stem, yearly height measurements were made with pole calipers to obtain annual height-growth increments. The initial height of each branch was determined by measuring the vertical distance from the base of the branch (juncture with the stem) to the branch tip.

The sum of stem and branch heights and total apical growth (stem + branches) for each individual are graphed in Figs. 2-2 and 2-3 (solid circles, upper right). As shown in those two graphs, *the total height growth of adult saguaros continues to increase exponentially by the growth of branches until mechanical injury or senescence finally becomes limiting on growth of large individuals.*

TABLE 2-11. Age, aboveground stem height (cm), and subsequent 1-year apical growth (cm) of saguaros in nonrocky habitat at Saguaro National Monument (west). Graphed in Fig. 2-4.

Age (yrs)	Height (cm)	Apical growth (cm/yr)
1	0.24	0.09
2	0.33	0.14
3	0.47	0.19
4	0.66	0.27
5	0.93	0.36
6	1.29	0.47
7	1.76	0.59
8	2.35	0.73
9	3.08	0.87
10	3.95	1.02
11	4.97	1.18
12	6.15	1.34
13	7.48	1.50
14	8.99	1.68
15	10.66	1.85
16	12.52	2.03
17	14.55	2.22
18	16.76	2.41
19	19.17	2.60
20	21.77	2.80
21	24.57	3.01
22	27.58	3.22
23	30.79	3.43
24	34.23	3.65
25	37.88	3.88
26	41.76	4.12
27	45.88	4.35
28	50.23	4.60
29	54.83	4.85
30	59.67	5.10
31	64.77	5.36
32	70.13	5.62
33	75.74	5.88
34	81.62	6.15
35	87.77	6.41
36	94.18	6.68
37	100.87	6.95
38	107.82	7.22
39	115.04	7.49
40	122.54	7.76
41	130.29	8.02
42	138.31	8.28
43	146.59	8.53
44	155.12	8.78

TABLE 2-11—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
45	163.90	9.02
46	172.92	9.25
47	182.17	9.48
48	191.65	9.69
49	201.34	9.89
50	211.23	10.09
51	221.32	10.27
52	231.59	10.44
53	242.03	10.60
54	252.63	10.74
55	263.37	10.87
56	274.24	10.99
57	285.24	11.10
58	296.33	11.19
59	307.53	11.27
60	318.80	11.34
61	330.14	11.40
62	341.53	11.44
63	352.97	11.47
64	364.44	11.49
65	375.93	11.50
66	387.43	11.50
67	398.94	11.49
68	410.43	11.47
69	421.90	11.44
70	433.34	11.41
71	444.75	11.37
72	456.12	11.32
73	467.44	11.26
74	478.70	11.20
75	489.89	11.13
76	501.03	11.06
77	512.08	10.98
78	523.06	10.90
79	533.97	10.82
80	544.78	10.73
81	555.51	10.64
82	566.15	10.55
83	576.70	10.45
84	587.15	10.35
85	597.50	10.26
86	607.76	10.16
87	617.92	10.06
88	627.97	9.96
89	637.93	9.86
90	647.79	9.75

TABLE 2-11—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
91	657.54	9.65
92	667.19	9.55
93	676.74	9.45
94	686.19	9.35
95	695.53	9.24
96	704.78	9.14
97	713.92	9.04
98	722.97	8.94
99	731.91	8.85
100	740.76	8.75
101	749.50	8.65
102	758.15	8.55
103	766.71	8.46
104	775.17	8.37
105	783.53	8.27
106	791.81	8.18
107	799.99	8.09
108	808.08	8.00
109	816.08	7.91
110	823.99	7.83
111	831.82	7.74
112	839.56	7.65
113	847.21	7.57
114	854.78	7.49
115	862.27	7.41
116	869.68	7.33
117	877.01	7.25
118	884.26	7.17
119	891.43	7.09
120	898.52	7.02
121	905.54	6.94
122	912.48	6.87
123	919.35	6.80
124	926.15	6.73
125	932.88	6.66
126	939.54	6.59
127	946.13	6.52
128	952.65	6.46
129	959.11	6.39
130	965.50	6.33
131	971.83	6.26
132	978.09	6.20
133	984.29	6.14
134	990.43	6.08
135	996.51	6.02
136	1,002.53	5.96
137	1,008.49	5.90

TABLE 2-11—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
138	1,014.39	5.85
139	1,020.23	5.79
140	1,026.02	5.73
141	1,031.76	5.68
142	1,037.44	5.63
143	1,043.07	5.57
144	1,048.64	5.52
145	1,054.16	5.47
146	1,059.64	5.42
147	1,065.06	5.37
148	1,070.43	5.32
149	1,075.76	5.28
150	1,081.03	5.23
151	1,086.26	5.18
152	1,091.45	5.14
153	1,096.58	5.09
154	1,101.68	5.05
155	1,106.72	5.00
156	1,111.73	4.96
157	1,116.69	4.92
158	1,121.61	4.88
159	1,126.48	4.84
160	1,131.32	4.80
161	1,136.12	4.76
162	1,140.87	4.72
163	1,145.59	4.68
164	1,150.26	4.64
165	1,154.90	4.60
166	1,159.51	4.56
167	1,164.07	4.53
168	1,168.60	4.49
169	1,173.09	4.46
170	1,177.54	4.42
171	1,181.96	4.39
172	1,186.35	4.35
173	1,190.70	4.32
174	1,195.02	4.28
175	1,199.31	4.25
176	1,203.56	4.22
177	1,207.78	4.19
178	1,211.97	4.16
179	1,216.12	4.13
180	1,220.25	4.09
181	1,224.34	4.06
182	1,228.41	4.03
183	1,232.44	4.01
184	1,236.45	3.98

TABLE 2-11—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
185	1,240.42	3.95
186	1,244.37	3.92
187	1,248.29	3.89
188	1,252.18	3.86
189	1,256.05	3.84
190	1,259.88	3.81
191	1,263.69	3.78
192	1,267.48	3.76
193	1,271.24	3.73
194	1,274.97	3.71
195	1,278.67	3.68
196	1,282.35	3.66
197	1,286.01	3.63
198	1,289.64	3.61
199	1,293.25	3.58
200	1,296.83	3.56
201	1,300.39	3.54
202	1,303.93	3.51
203	1,307.44	3.49
204	1,310.93	3.47
205	1,314.40	3.44
206	1,317.84	3.42
207	1,321.26	3.40
208	1,324.66	3.38
209	1,328.04	3.36
210	1,331.40	3.34
211	1,334.74	3.32
212	1,338.06	3.30
213	1,341.35	3.28
214	1,344.63	3.26
215	1,347.88	3.24
216	1,351.12	3.22
217	1,354.33	3.20
218	1,357.53	3.18
219	1,360.71[a]	3.16
220	1,363.87	3.14
221	1,367.01	3.12
222	1,370.13	3.10
223	1,373.23	3.08
224	1,376.31	3.07
225	1,379.38	3.05
226	1,382.43	3.03
227	1,385.46	3.01

TABLE 2-11—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
228	1,388.47	3.00
229	1,391.47	2.98
230	1,394.45	2.96
231	1,397.41	2.95
232	1,400.36	2.93

[a] Growth data limit (ht 1,363.4 cm). Subsequent values by regression.

Data on natural seedling growth (Table 2-12 and Fig. 2-6) were obtained from a sample of 14 first-year plants naturally germinated on-site during the summer of 1974. Seedlings were removed to the laboratory in mid-March 1975 for precision measurement of aboveground stem height (height above cotyledon juncture), total stem height (stem + cotyledon), maximum stem diameter, and weight of each individual. The measured mean first-year aboveground height for these naturally growing saguaros is 0.260 cm ± 0.012 SE (range 0.188-0.375), $N = 14$.

As shown in Appendix IV, there were no usable on-site 10-year growth data for juvenile plants less than 83.8 cm in height. A proportional estimate of growth rates, therefore, was used to complete the lower portion of the growth curve.

As described below, the lower segment of the growth curve (dashed line in Fig. 2-5) is based on on-site seedling growth data (Table 2-12) and the relative rates of growth of larger juvenile plants on-site, and at Saguaro National Monument (west)—a site with similar growth data for smaller juvenile saguaros. In the absence of further definitive on-site data, a usual logarithmic (straight-line) relationship for this portion of the growth curve is assumed (Fig. 2-5).

The following steps were employed to estimate the 10-year growth curve for juvenile saguaros less than 83.8 cm height:

1. Logarithmic regression of mean 10-year growth increments ($N = 2$) for saguaros less than 83.8 cm initial height derived from values in Table 2-11 ($X_1 = 0.239$ cm, $Y_1 = 4.730$ cm; $X_2 = 81.622$ cm, $Y_2 = 73.500$ cm) was used to calculate the linear equation for 10-year growth (Y) on height (X) at Saguaro National Monument (west). The resulting equation is

$$\log Y = 0.967 + 0.470 \log X \qquad (1)$$

2. By use of equation 3 (Table 2-7), the 10-year growth increment ($\hat{Y}$) for a saguaro of the same height ($X = 81.622$) at Organ Pipe Cactus National Monument is 43.307 cm.

3. By substitution of log of 43.307 ($\hat{Y}$ from step 2) for log Y and X = 81.622 in equation (1) of the first step above, the Y intercept is obtained. The derived equation for proportional 10-year growth of young saguaros at Organ Pipe Cactus National Monument is

$$\log Y = 0.737 + 0.470 \log X \qquad (2)$$

Equation (2) describes the lower segment (dashed line) of the curve shown in Fig. 2-5.

Within the limitations imposed by the data, the composite growth curve as described above represents the best available estimate of saguaro growth rates in this population. We expect continuing on-site investigations on the growth of young saguaros to provide a more precise estimate of saguaro growth and age in this environment.

Age and height

Age data for saguaros at Organ Pipe Cactus National Monument (Table 2-13) are graphed in Fig. 2-4. The age estimates provided are based on the composite growth curve shown in Fig. 2-5, and are, therefore, sub-

TABLE 2-12. Stem measurements for naturally growing first-year saguaro seedlings (N = 14) at Alamo Canyon, Organ Pipe Cactus National Monument. Graphed in Fig. 2-6.

No.	Height(cm)		Diameter	Weight
	Total	A.G.	(cm)	(gm)
1	0.484	0.239	0.257	
2	0.502	0.200	0.201	0.030
3	0.535	0.251	0.323	0.040
4	0.535	0.271	0.313	0.049
5	0.536	0.311	0.374	0.052
6	0.584	0.257	0.234	0.037
7	0.585	0.261	0.284	0.040
8	0.620	0.281	0.392	0.064
9	0.652	0.279	0.252	0.055
10	0.653	0.375	0.391	0.057
11	0.694	0.188	0.278	0.045
12	0.771	0.221	0.239	0.042
13	0.847	0.258	0.280	0.044
14	1.000	0.246	0.203	0.039
Total	8.998	3.638	4.021	0.625
Mean	0.643	0.260	0.287	0.045
SE	±.039	±.012	±.017	±.003

ject to the limitations imposed by estimation of the lower segment of the growth curve as noted previously.

The equations describing each of the two segments of the saguaro growth curve at Organ Pipe Cactus National Monument were used separately to generate successive 10-year growth increments ($\hat{Y}$ values) and stem heights at consecutive 10-year intervals by the stepwise computation procedure described for Saguaro National Monument. Equation (2) above was used to derive 10-year increments and age values for saguaros less than 83.8 cm in height. The mean first-year aboveground stem height, 0.260 cm (Table 2-12), was used as the initial (X) value to calculate the subsequent 10-year growth increment ($\hat{Y}$) and, by stepwise computation, to estimate stem heights at successive 10-year intervals. Intermediate year values to age 48 years (82.5 cm ht) were then determined by graphic analysis.

Values for larger plants were generated in the same manner, using 82.5 cm (age 48 years) as the initial height (X) in equation 3 (Table 2-7). Intermediate year values were determined by graphic analysis. Regression values for saguaros greater than 939.5 cm in height, the upper height limit of our field growth data (Appendix IV), are shown in Table 2-13 and graphed in Fig. 2-4 (dashed line).

TABLE 2-13. Age, aboveground stem height (cm), and subsequent 1-year apical growth (cm) of saguaros at Organ Pipe Cactus National Monument. Graphed in Fig. 2-4.

Age (yrs)	Height (cm)	Apical growth (cm/yr)
1	0.26	0.09
2	0.35	0.14
3	0.49	0.18
4	0.67	0.22
5	0.88	0.26
6	1.14	0.30
7	1.44	0.35
8	1.79	0.40
9	2.19	0.46
10	2.64	0.52
11	3.2	0.6
12	3.8	0.7
13	4.5	0.8
14	5.2	0.8
15	6.0	0.9
16	6.9	1.0

TABLE 2-13—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
17	7.9	1.0
18	8.9	1.1
19	10.1	1.2
20	11.3	1.3
21	12.5	1.4
22	14.0	1.5
23	15.4	1.6
24	17.0	1.7
25	18.7	1.8
26	20.4	1.8
27	22.3	1.9
28	24.2	2.0
29	26.2	2.1
30	28.3	2.2
31	30.5	2.3
32	32.8	2.4
33	35.2	2.5
34	37.7	2.6
35	40.3	2.7
36	43.0	2.8
37	45.7	2.9
38	48.6	3.0
39	51.5	3.1
40	54.6	3.2
41	57.8	3.3
42	61.0	3.3
43	64.3	3.4
44	67.8	3.5
45	71.3	3.6
46	74.9	3.7
47	78.7	3.8
48	82.5	3.5
49	86.0	3.7
50	89.7	3.9
51	93.5	4.1
52	97.6	4.3
53	101.8	4.5
54	106.3	4.7
55	111.0	4.9
56	115.9	5.1
57	121.0	5.3
58	126.3	5.5
59	131.8	5.8
60	137.6	6.0
61	143.6	6.2
62	149.8	6.5
63	156.2	6.7

TABLE 2-13—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
64	162.9	6.9
65	169.9	7.2
66	177.0	7.4
67	184.4	7.6
68	192.0	7.8
69	199.8	8.0
70	207.7	8.2
71	215.9	8.3
72	224.2	8.5
73	232.8	8.7
74	241.5	8.9
75	250.3	9.0
76	259.3	9.1
77	268.5	9.3
78	277.7	9.3
79	287.0	9.4
80	296.4	9.5
81	305.9	9.5
82	315.4	9.6
83	325.0	9.7
84	334.7	9.7
85	344.4	9.8
86	354.2	9.8
87	364.0	9.8
88	373.7	9.7
89	383.4	9.7
90	393.2	9.7
91	402.8	9.7
92	412.5	9.7
93	422.2	9.6
94	431.8	9.6
95	441.4	9.6
96	451.0	9.5
97	460.6	9.5
98	470.1	9.4
99	479.4	9.3
100	488.8	9.3
101	498.0	9.2
102	507.3	9.2
103	516.4	9.1
104	525.6	9.1
105	534.6	9.0
106	543.6	9.0
107	552.6	8.9
108	561.5	8.8
109	570.2	8.7
110	578.9	8.6

TABLE 2-13—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
111	587.6	8.6
112	596.1	8.5
113	604.6	8.5
114	613.1	8.4
115	621.5	8.4
116	629.8	8.3
117	638.1	8.2
118	646.3	8.1
119	654.4	8.0
120	662.5	8.0
121	670.4	8.0
122	678.4	7.9
123	686.2	7.8
124	694.0	7.8
125	701.8	7.7
126	709.5	7.7
127	717.2	7.6
128	724.7	7.5
129	732.2	7.4
130	739.7	7.4
131	747.0	7.3
132	754.4	7.3
133	761.6	7.2
134	768.9	7.2
135	776.0	7.1
136	783.2	7.1
137	790.3	7.0
138	797.3	6.9
139	804.2	6.9
140	811.1	6.8
141	818.0	6.8
142	824.8	6.8
143	831.5	6.7
144	838.2	6.7
145	844.9	6.6
146	851.5	6.6
147	858.1	6.5
148	864.7	6.5
149	871.2	6.4
150	877.6	6.4
151	883.9	6.3
152	890.3	6.3
153	896.6	6.3
154	902.9	6.2
155	909.1	6.2
156	915.3	6.2
157	921.5	6.1

TABLE 2-13—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
158	927.6	6.1
159	933.6	6.0
160	939.7[a]	6.0
161	945.6	5.9
162	951.6	5.9
163	957.5	5.9
164	963.4	5.9
165	969.2	5.8
166	975.0	5.8
167	980.8	5.8
168	986.6	5.7
169	992.3	5.7
170	997.9	5.6
171	1,003.6	5.6
172	1,009.2	5.6
173	1,014.7	5.5
174	1,020.3	5.5
175	1,025.8	5.5
176	1,031.3	5.5
177	1,036.7	5.4
178	1,042.2	5.4
179	1,047.5	5.3
180	1,052.9	5.3
181	1,058.2	5.3
182	1,063.5	5.3
183	1,068.7	5.2
184	1,074.0	5.2
185	1,079.2	5.2
186	1,084.4	5.2
187	1,089.6	5.2
188	1,094.7	5.1
189	1,099.8	5.1
190	1,104.9	5.0
191	1,109.9	5.0
192	1,114.9	5.0
193	1,119.9	5.0
194	1,124.9	5.0
195	1,129.9	4.9
196	1,134.8	4.9
197	1,139.7	4.9
198	1,144.6	4.8
199	1,149.5	4.8
200	1,154.3	4.8
201	1,159.1	4.8
202	1,163.9	4.8
203	1,168.6	4.7
204	1,173.4	4.7

TABLE 2-13—*continued*

Age (yrs)	Height (cm)	Apical growth (cm/yr)
205	1,178.1	4.7
206	1,182.8	4.7
207	1,187.5	4.7
208	1,192.2	4.6
209	1,196.8	4.6
210	1,201.4	4.6
211	1,205.9	4.6
212	1,210.5	4.6
213	1,215.1	4.5
214	1,219.6	4.5
215	1,224.1	4.5
216	1,228.6	4.5
217	1,233.1	4.5
218	1,237.5	4.4
219	1,242.0	4.4
220	1,246.4	4.4
221	1,250.7	4.4
222	1,255.1	4.4
223	1,259.5	4.3
224	1,263.8	4.3
225	1,268.1	4.3
226	1,272.4	4.3
227	1,276.7	4.3
228	1,281.0	4.2
229	1,285.3	4.2
230	1,289.5	4.2
231	1,293.7	4.2
232	1,297.8	4.2

[a] Growth data limit (ht 939.7 cm). Subsequent values by regression.

Growth Rates, Form, and Phenological Events

Size-related changes in saguaro growth rates occur coincidently with 1) changes in form and 2) phenological events. These events are expressed by changes in the slope of growth curves as shown in Figs. 2-2, 2-3, and 2-5.

The first of such events (which occurs in the range of 1.5-6.0 cm height) is a transition from the globose stem form of the young juvenile plants to the "club" form of older juveniles (Figs. 2-7a and 2-7b).

A second change in stem form begins with the initiation of reproductive growth (buds, flowers, fruits, and seeds) when the juvenile saguaro reaches a height of approximately 200 cm (Steenbergh and Lowe 1977).

Fig. 2-7a. Juvenile saguaro, globose stem form (height 2.0 cm). Approximately 40% of the plant stem is situated *in* the soil. At this stage of development annual increments of stem height and diameter growth are approximately equal. Development of ribs (flutes) occurs with the vertical alignment of tubercles when the stem attains an aboveground height of approximately 3 cm. Photographed 11 Jan. 1974.

Stem form becomes increasingly ellipsoidal as the upward shift of the maximum stem diameter ceases to coincide with upward growth of the tip, ultimately assuming the "bowling-pin" (= "wine bottle") form of the unbranched adult (Figs. 2-8 and 2-9a).

The maximum rate of saguaro stem growth occurs during the transition stage from the unbranched to the branched adult form. The asymptote of the growth curve which occurs in the range of 350-400 cm in height (Figs. 2-3, 2-4, and 2-5) represents the point at which half of the energy of the plant is diverted into growth of reproductive structures (Fig. 2-10). Beyond this point, the curve of stem growth gradually falls as an increasing proportion of the available energy is diverted into additional reproductive growth.

The ultimate stage of saguaro development, the branched adult form, begins with the initiation of branch growth at approximately 450-500 cm in stem height (Fig. 2-9b). Beyond this point, an exponentially increasing proportion of the plant's energy is committed to the growth of branches and additional associated reproductive effort (Fig. 2-11).

Fig. 2-7b. Juvenile saguaro, ''club'' stem form (N = 12, height 15-40 cm), growing beneath the crown of a single velvet mesquite *(Prosopis juliflora),* Cactus Forest (flats) at Saguaro National Monument (east). A decrease in the slope of the growth curves shown in Figs. 2-2 and 2-3 accompanies the transition from the globose stem form (Fig. 2-7a) to the columnar ''club'' form. Photographed 26 June 1979.

Fig. 2-8. Young adult saguaro, ellipsoidal stem form (foreground, height 3 m). Transition from the club form (smaller saguaro behind) begins with initiation of reproductive growth at approximately 2 m in height. A progressive decrease in the slope of the height growth curves (Figs. 2-2 and 2-3) occurs with this diversion of energy into reproductive structures. Photographed 23 Mar. 1979.

Fig. 2-9a. Unbranched adult saguaro, "bowling-pin" (= "wine-bottle") form, height 4.2 m. The asymptote of the saguaro height growth curve (Figs. 2-2, 2-3, and 2-5) coincides with the point at which half the energy of the plant is directed into the growth of flowers, fruits, and seeds. Photographed 23 June 1978.

Fig. 2-9b. Adult saguaro (height 4.5 m) with emerging branch ("arm") buds. First branches normally emerge approximately 1.5-2.0 m below the stem apex, the point of greatest stem diameter. Initiation of branch growth is controlled by apical dominance. Photographed 18 May 1979.

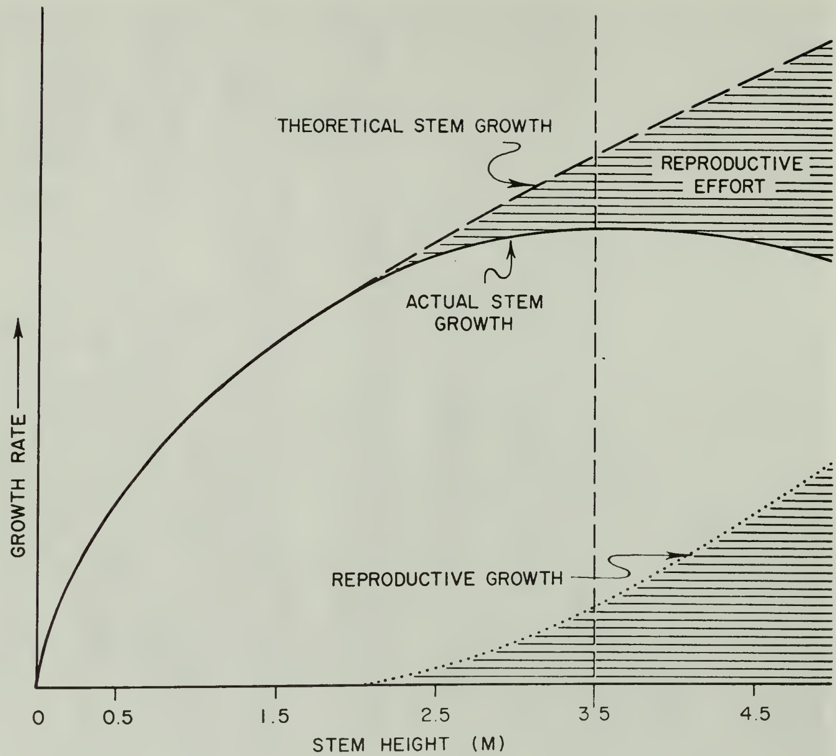

Fig. 2-10. Model of energy partitioning between reproductive effort and stem growth of unbranched saguaros. The uppermost (dashed) line represents the theoretical curve of stem growth unlimited by reproductive effort. The solid line is the actual growth curve. The lower (dotted) line represents energy expenditure for reproductive growth.

The asymptote form of the stem growth curve is an expression of the diversion of energy from stem growth into reproductive growth. Exponentially increasing reproductive growth is initiated when the plant reaches a height of 2.0 to 2.5 m. The maximum rate of stem growth—the asymptote of the actual growth curve at 3.5 to 4.0 m—occurs at the point where the proportional commitment of energy to reproductive growth begins to excecd the commitment to stem growth. The shaded area between the curves of theoretical and actual stem growth represents energy diverted from potential stem growth into reproductive effort.

Fig. 2-11a. Mature adult saguaros with multiple branches (height 11-12 m), the ultimate form of the saguaro. The function of branches on the saguaro is to increase the reproductive potential of the plant. Each additional branch increases, by approximately doubling, tripling, etc., the number of fruits produced, thereby increasing the annual seed production of the individual. Photographed 31 Jan. 1979.

Fig. 2-11b. Tallest saguaro. The 1,600.5-cm height of this old giant is the greatest measured height ever reported for a saguaro. The location is the south-facing slope of Safford Peak in the Tucson Mountains northwest of Tucson, Arizona. The plant, broken off at the base by a windstorm, was dead two months after the photograph was taken.

The telescoping aluminum pole-caliper shown was used for periodic height measurements to determine growth increments for adult saguaros over 240 cm tall. A steel measuring tape suspended from the top of the pole permits direct measurement of height from the horizontal crossbar, which rests on the stem apex, to a steel benchmark permanently installed at the base of the plant. Photographed by Paul Fugate 30 June 1975.

Saguaro populations growing in dissimilar climatic environments exhibit large order differences in branching characteristics. As shown in Table 2-14, the frequency of branched stems and the number of branches per stem increases across the species' distribution from west to east.

The production of branches increases with faster rates of stem growth associated with the gradient of increasing summer precipitation from west to east and greater plant-available soil moisture during the principal period of saguaro growth (Table 2-1; Fig. 2-12). Differences in the number of branches (''arms'') produced by the saguaro is a function of differential growth rates; faster growing plants produce the greatest number of branches.

The ultimate function of branches on the saguaro stem is to increase the reproductive potential of the plant (Fig. 2-13). Branches increase the number of fruits, thereby increasing, by thousands to hundreds of thousands, the total number of seeds per year that are produced by the individual. Natural selection has favored those saguaro genotypes that provide greater differential reproduction and survival, i.e., the more greatly branched plants over the less productive, less branched and unbranched plants. In this case a result of selection for greater reproductive effort is, among other things, a branched columnar cactus.

Stem branching, which ultimately provides greater reproductive effort, is a function of growth rate. Selection for the branched form, which provides greater differential survival, thereby concomitantly selects for higher growth rate potential.

Growth and Climatic Factors

Precipitation and seasonal growth

Seasonal growth and response of adult saguaros to precipitation (Fig. 2-14) closely follow the pattern reported for the growth of young saguaros (Steenbergh and Lowe 1969, 1977). Periodic stem height measurements of adult saguaros growing at Saguaro National Monument (east) were made over a 15-month period from January 1970 to April 1971. Permanent benchmarks, installed adjacent to the base of the stem, and specially designed pole-calipers for stem height measurements were used as Steenbergh and Lowe described (in 1977). The growth data together with concurrently measured on-site precipitation are shown in Table 2-15.

As shown in Fig. 2-14, the principal stem growth of adult saguaros coincides with the July-September period of warm summer rains, with minor apical growth following precipitation in April and May. In these winter-cold northern environments there is water uptake, as evidenced by increased stem turgor (diameter increase), but little or no height growth in response to late fall and winter rains (October-March). It is likely, however, that some growth does occur in response to winter rains in the warmer southern portions of the species range in southern Sonora.

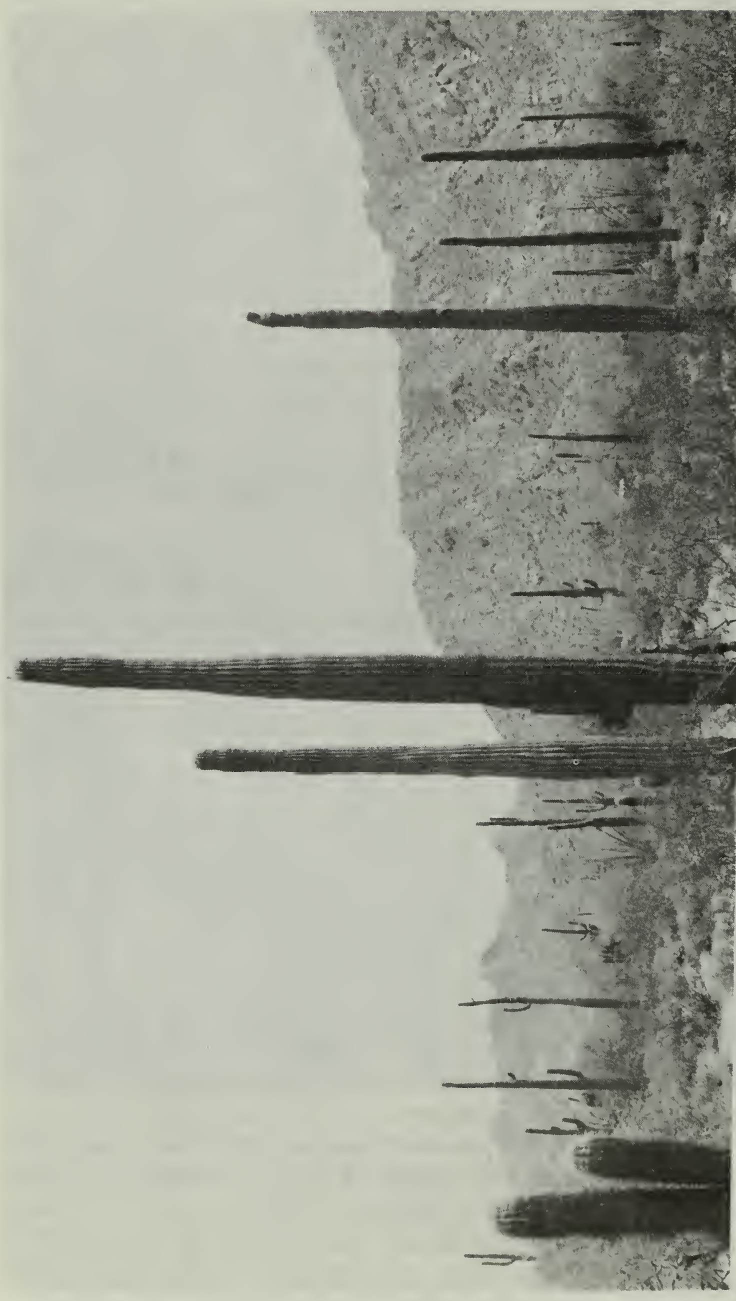

Fig. 2-12a. Saguaro population growing 16 km southwest of Sonoita, Sonora, Mexico (elevation approximately 365m). This population of slow-growing plants is situated near the moisture-limited western boundary of the species' distribution. Estimated mean annual precipitation at this location is less than 230 mm per year. Note the slender stem form and low frequency of branched individuals. Compare with Fig. 2-12b. Photographed 4 Sept. 1978.

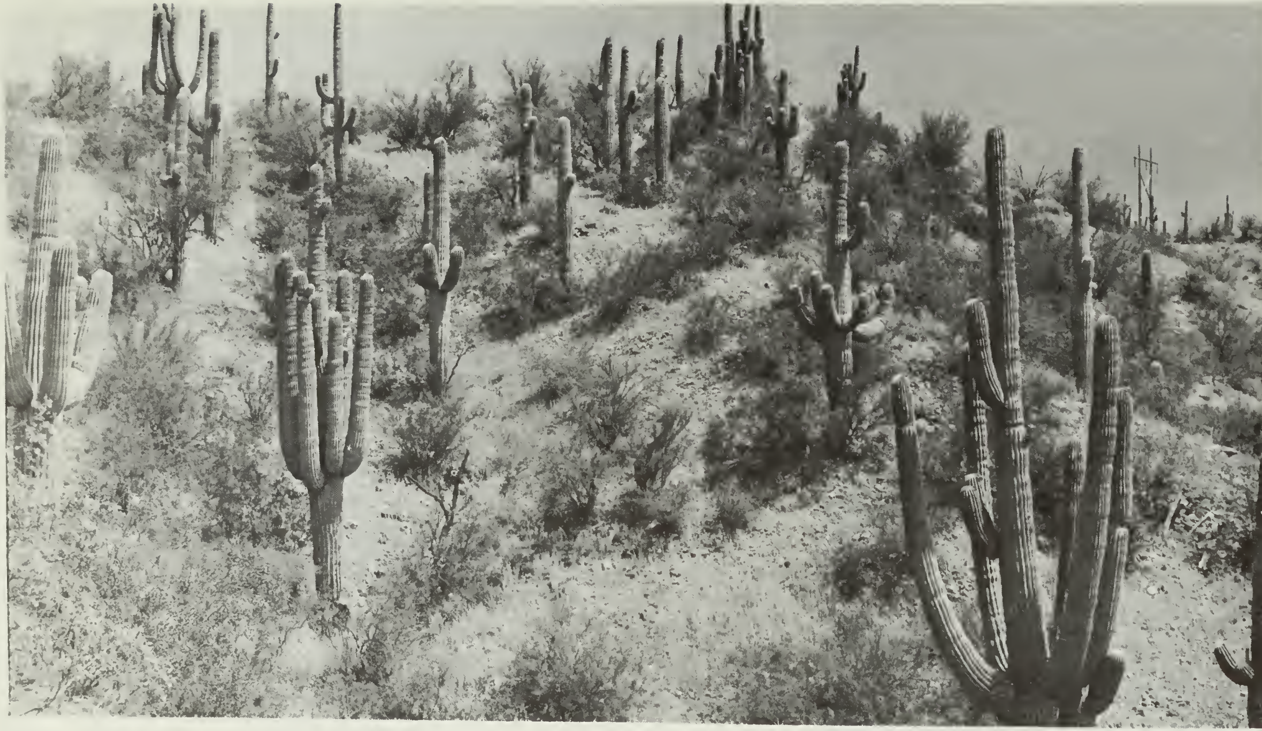

Fig. 2-12b. Saguaro population growing on a south-facing slope 29 km south of Winkleman, Arizona (elevation approximately 760 m). This population is growing near the cold-limited northeastern boundary of the species' distribution. Prolific branching and stout stems are associated with faster growth that occurs in response to relatively high annual precipitation (approximately 320 mm per year). The stout form aids resistance to freezing. The frequency of branched stems and the number of branches per stem is a function of growth rate.

Fig. 2-13a. Regeneration of branches on the 2.5-m stump of a freeze-damaged adult saguaro. The original branches and the upper stem of this plant were destroyed by the freeze of January 1971. When apical dominance is interrupted by decapitation, water and nutrients supplied by the undamaged root system are utilized for rapid generation of new branches. Photographed 23 Mar. 1979.

Fig. 2-13b. Decapitated saguaro with regenerated branches. The reproductive function of the plant has been restored by the growth of new branches. Natural selection favors those saguaro genotypes that provide greater differential reproduction, i.e., the more productive multiple-branched individuals. Photographed 23 June 1978.

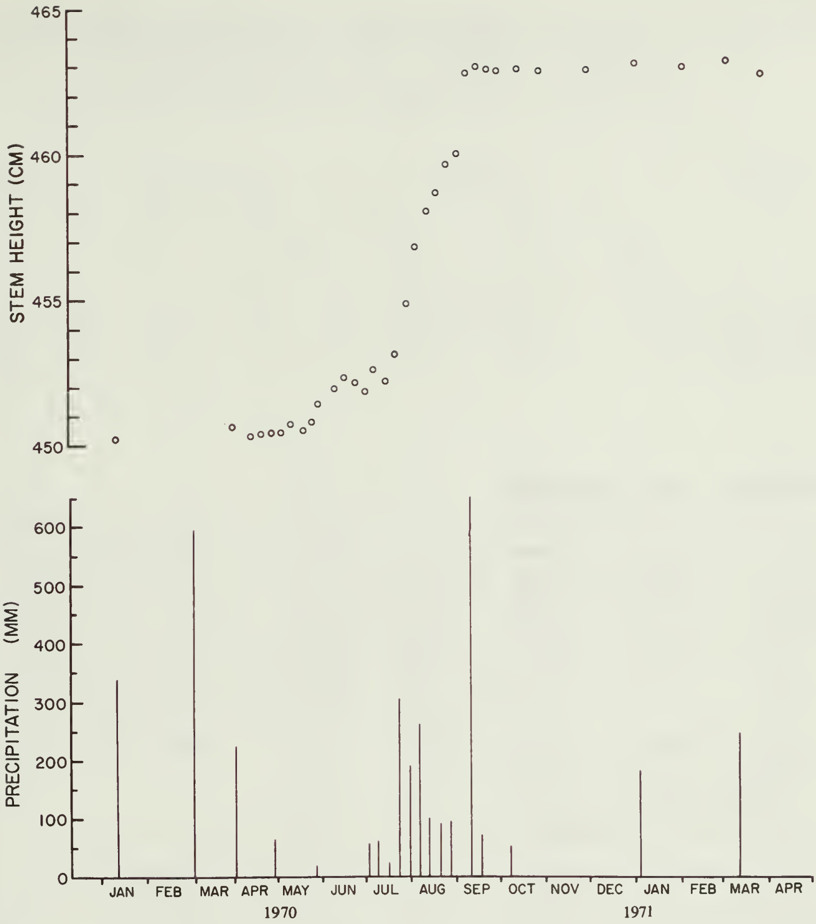

Fig. 2-14. Precipitation and seasonal stem height growth of adult saguaros (N = 2) in nonrocky habitat at Saguaro National Monument (east). Data in Table 2-15.

The principal stem growth of adult saguaros in this environment is initiated with the arrival of monsoon rains in late June or early July. Growth continues during the hot months of July, August, and September, the summer rain season, and ends during the post-summer, October-November, drought period.

TABLE 2-14. Comparison of branching characteristics of adult saguaros growing in three different climatic environments. Frequency (%) and number of branches per plant for adult saguaros 4-10 m height in bajada (nonrocky) habitats, three 2-ha plots at each location.

Location	Elevation		*N*	Branched stems		No. branches	
	(m)	(ft)		No.	%	Total	Mean
Saguaro N.M. (east)	856-878	2810-2880	94	79	84.04	317	3.37
Saguaro N.M. (west)	693-792	2275-2600	226	141	62.39	410	1.81
Organ Pipe Cactus N.M.	646-735	1970-2240	91	34	37.36	82	0.90

Freezing, vigor, and growth

Large order differences in the growth rates of saguaros growing in the same environment are associated with readily observable differences in the form of healthy and freeze-damaged plant stems (Figs. 2-15 to 2-20). As shown in Fig. 2-19, low vigor of adult saguaros is clearly evidenced by lack of turgor (flaccid, radially compressed stem and branches) and shriveled crowns on stem and branches. Such individuals also exhibit markedly reduced reproductive growth (numbers of flowers and fruits produced). Both conditions are a characteristic result of freeze-caused injury (see Steenbergh and Lowe 1976, 1977).

Height and 1-year growth increments (1975-1976) for a sample of vigorous (normal, healthy plants, $N = 11$) and nonvigorous (flaccid, $N = 7$) adult saguaros growing in the same environment at Saguaro National Monument (east) are shown in Table 2-16. The difference in the resulting means that are graphed in Fig. 2-21 is highly significant ($P < 0.001$). We found that *the mean growth rate of nonvigorous (flaccid) saguaros was approximately one-half the growth rate of normal (healthy) plants growing in the same environment*—the flaccid plants are moribund. Such moribund plants, surviving mainly or entirely on diminishing water and energy reserves, have a relatively short remaining life expectancy.

Age and Growth Rates in Different Environments

The height-age curves shown in Fig. 2-4 and the growth curves for healthy saguaros shown in Figs. 2-2, 2-3, and 2-5 provide a comparison of growth rates and age in three different climatic environments that are characteristic of the major portion of the species' distribution in Arizona and northern Sonora. Comparison of the three curves for saguaros growing in similar topographic habitats clearly shows an increase in saguaro

TABLE 2-15. On-site precipitation (mm) and seasonal height growth (incr., cm) of unbranched adult saguaros (N = 2) at Saguaro National Monument (east), 12 January 1970 to 2 April 1971. Graphed in Fig. 2-14.

Date	Precip.[a] (mm)	Plant no. 69B Ht. (cm)	Plant no. 69B Incr. (cm)	Plant no. 69D Ht. (cm)	Plant no. 69D Incr. (cm)	Mean ht. (cm)
1970						
Jan. 12	34[b]	440.4		460.1		450.25
Feb. 1	0					
Mar. 5	59					
Apr. 2	224	440.7	+0.3	461.0	+0.9	450.85
Apr. 15	0	440.4	−0.3	460.3	−0.7	450.35
Apr. 22	0	440.5	+0.1	460.3	0.0	450.40
Apr. 29	6	440.5	0.0	460.4	+0.1	450.45
May 6	0	440.4	−0.1	460.5	+0.1	450.45
May 12	0	440.3	−0.1	461.2	+0.7	450.75
May 21	0	440.6	+0.3	460.5	−0.7	450.55
May 27	2	440.7	+0.1	461.0	+0.5	450.85
June 4	0	440.8	+0.1	462.1	+1.1	451.45
June 11	0	441.2	+0.4	462.7	+0.6	451.95
June 18	0	441.3	+0.1	463.4	+0.7	452.35
June 25	0	441.1	−0.2	463.2	−0.2	452.15
July 2	6	440.7	−0.4	463.0	−0.2	451.85
July 8	7	441.5	+0.8	463.7	+0.7	452.60
July 16	2	441.0	−0.5	463.4	−0.3	452.20
July 23	31	442.1	+1.1	464.2	+0.8	453.15
July 30	19	443.8	+1.7	465.9	+1.7	454.85
Aug. 6	26	445.9	+2.1	467.7	+1.8	456.80
Aug. 13	10	446.9	+1.0	469.1	+1.4	458.00
Aug. 20	9	447.6	+0.7	469.7	+0.6	458.65
Aug. 27	10	448.4	+0.8	470.8	+1.1	459.60
Sept. 3	0	449.0	+0.6	470.9	+0.1	459.95
Sept. 10	65	451.4	+2.4	474.0	+3.1	462.70
Sept. 17	7	451.6	+0.2	474.2	+0.2	462.90
Sept. 24	0	451.7	+0.1	473.9	−0.3	462.80
Oct. 1	0	451.7	0.0	473.8	−0.1	462.75
Oct. 15	5	451.8	+0.1	473.8	0.0	462.80
Oct. 30	0	451.3	−0.5	474.2	+0.4	462.75
Dec. 1	0	451.7	+0.4	473.8	−0.4	462.75
1971						
Jan. 3	18	451.9	+0.2	474.0	+0.2	462.95
Feb. 4	0	451.7	−0.2	473.9	−0.1	462.80
Mar. 11	25	452.0	+0.3	474.0	+0.1	463.00
Apr. 2	0	451.6	−0.4	473.5	−0.5	462.55

[a] Cumulative since preceding date.
[b] Cumulative, 1 Dec. 1969-12 Jan. 1970.

growth rates occurring along a gradient of increasing summer precipitation from *west to east* (Table 2-1) as reported by Steenbergh and Lowe (1977).

The greatest differential in these saguaro stem growth rates occurs in young plants. The young saguaro has a shallow, poorly developed root system that extends only a few centimeters below the soil surface, where the greatest and most rapid loss of soil moisture occurs (Fig. 2-22). Thus, the young saguaro is subject to longer and more frequent periods of low plant-available moisture (and interrupted growth) than the more deeply rooted larger plants with roots extending into a zone of stabler moisture conditions.

It should be emphasized that all of these growth data and the age estimates we present are for one topographic habitat type, "flat" (nonrocky) bajada habitats. These values are not adjusted for differences in growth rates that undoubtedly occur between "rock" habitats with shallow, rocky soils, and "flat" habitats with deeper, relatively fine-textured soils. Neither are these values adjusted for differences in growth expected for north-facing and south-facing slopes.

Freeze-caused depression of growth rates of both young and adult saguaros partially offsets the advantage of more favorable moisture conditions at Saguaro National Monument (east) and elsewhere along the cold-limited northeastern boundary of the species' distribution (Steenbergh and Lowe 1977). However, the effects of such injury (Table 2-16; Figs. 2-15 to 2-20) are not fully expressed in the growth curves shown in Figs. 2-2, 2-3, and 2-5. Data on freeze-damaged moribund plants and plants with actively growth-inhibiting, freeze-caused injury to their apical meristem were not included in the determination of growth curves for healthy saguaros provided here.

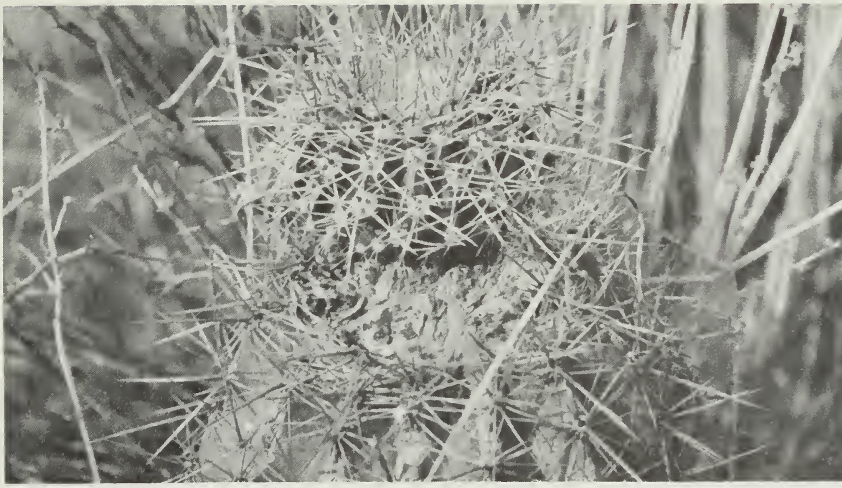

Fig. 2-15a. Regeneration by apical branching of a freeze-damaged juvenile saguaro (ht 22.5 cm) at Saguaro National Monument (west).

The ball-shaped upper stem (apical branch) of this plant is new growth produced following destruction of the original apex by freezing in January 1971. Such deforming injury increases the plant's vulnerability to subsequent freeze injury. The black coloration of the regenerated tip is the result of a second freeze that occurred in December 1975—the apical branch is dead. Photographed 25 Mar. 1975.

Fig. 2-15b. After four years, the same juvenile saguaro shown in Fig. 2-15a has grown to a height of 25.4 cm. The dead apical branch that appears in the 1975 photograph is seen on the left. The new apical branch (right) represents growth since 1975.

Stem height has increased 3.9 cm from the original 1971 height (21.5 cm), approximately 14% of normal 8-year growth (28.5 cm, Table 2-11) for a plant of this size growing in this habitat. Photographed 23 Mar. 1979.

Fig. 2-16. Freeze-caused apical branching of an adult saguaro at Saguaro National Monument (east). Fruits are borne only on the uppermost portion of stems and branches. Apical rebranching of the damaged crown restores the plant's ability to produce fruits on the central stem. Photographed 31 Jan. 1979.

Fig. 2-17a. Developing cristate crown on a young adult saguaro (height approximately 3 m). This relatively rare form apparently results from freeze-caused or other mechanical injury to the apical meristem. It is likely that development of the cristate crown on this individual was induced by injury resulting from freeze-damage during and since January 1962. Photographed 19 Nov. 1971.

Fig. 2-17b. Adult saguaro with fully developed cristate crown at Saguaro National Monument (east). Bilateral growth from the linearly aligned apical meristem results in the development of a comblike crest. Photographed 30 June 1969.

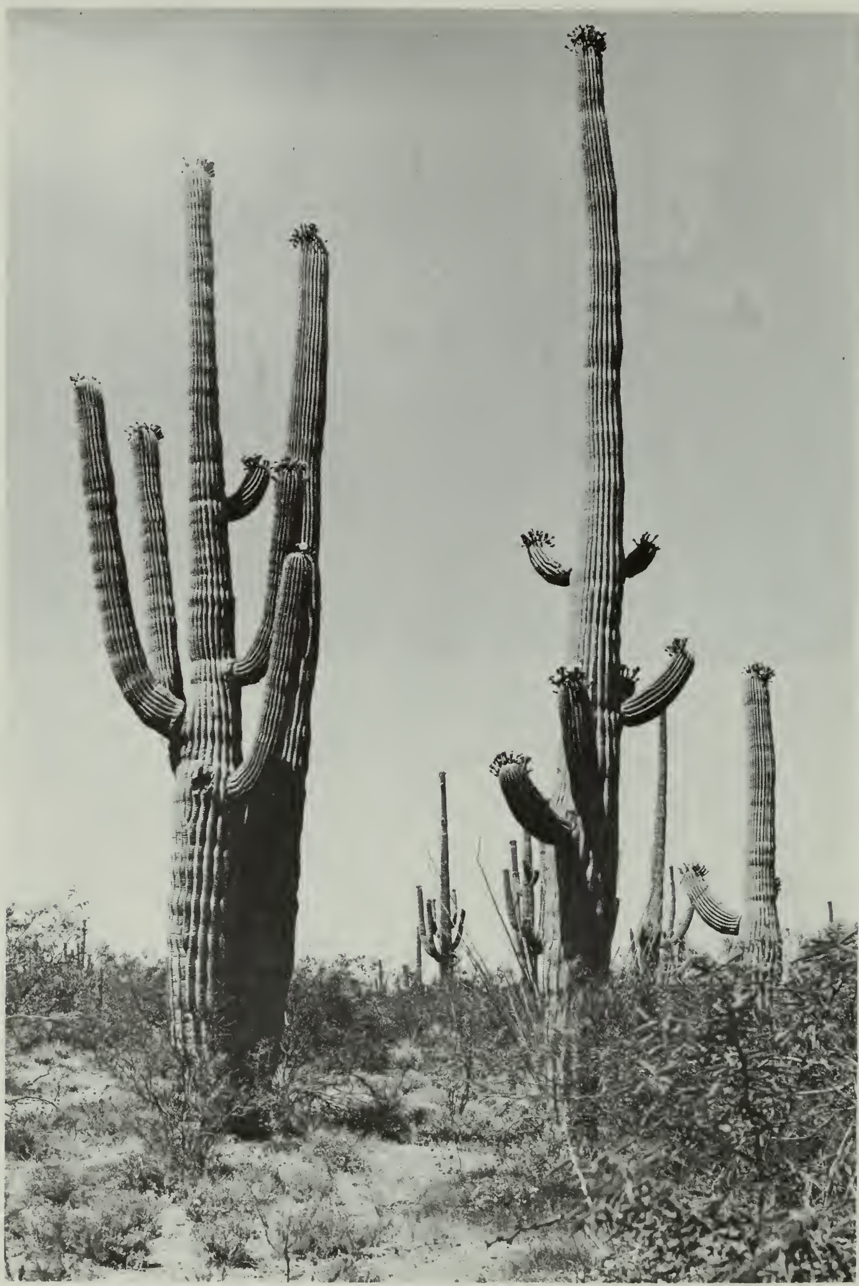

Fig. 2-18a. Nineteen forty-one photograph of saguaros at Saguaro National Monument (east, flats). Note the abnormally slender trunk and branches on the tallest saguaro (right). High surface-volume ratio increases vulnerability to freeze-caused injury. Compare with Fig. 2-18b, a photograph of the same site taken 28 years later. Photographed 12 June 1941 by Paul C. Lightle.

Fig. 2-18b. Drooping branches on the saguaro in the foreground are the result of freeze-caused injuries which occurred between 1941 and 1969. Drooping arms occur with loss of turgor which results from desiccation of freeze-damaged tissues at the base of branches. Dry rot pockets visible on the stems are further evidence of freeze-caused damage to soft tissues. Of the three foreground plants—all moribund in 1969—only the saguaro on the right was still standing in 1979. Photographed 27 May 1969.

Fig. 2-19a. Vigorous adult saguaro (height 1117.1 cm) at Cactus Forest, Saguaro National Monument (east). Compare the hemispherical crown and stout form of upper stem and branches with the adjacent moribund saguaros shown in Fig. 2-19b. For this healthy saguaro, the 1-year stem height growth (April 1975 to March 1976) was 6.7 cm. Photographed 25 Mar. 1976.

Fig. 2-19b. Freeze-damaged saguaros (foreground) showing characteristically attenuated crowns and slender, radially compressed (flaccid) stems and branches—the plants are moribund. The healthy plant visible in the center background is the same individual shown in Fig. 2-19a. One-year stem height growth (April 1975 to March 1976) of the larger of the two saguaros in the foreground (center, ht 1034.3 cm) was 3.0 cm, less than 1/2 that of the healthy saguaro growing in the same environment. Photographed 24 Mar. 1976.

TABLE 2-16. 1-year stem height growth of healthy (normal, $N = 11$) and non-vigorous (flaccid stems, $N = 7$) adult saguaros at Saguaro National Monument (east), 1975-1976 (see text). Graphed in Fig. 2-21.

No.	Normal		Flaccid	
	Height (cm)	Growth (cm)	Height (cm)	Growth (cm)
1	732.0	10.6	703.8	3.2
2	744.6	5.4	826.3	2.8
3	789.5	7.3	877.3	3.4
4	865.9	8.3	1,006.2	2.3
5	900.5	5.4	1,034.3	3.0
6	986.6	5.4	1,133.8	3.4
7	1,051.6	7.5	1,139.2	4.0
8	1,110.4	6.7		
9	1,193.5	8.4		
10	1,193.5	8.4		
11	1,276.2	7.0		
Total	10,844.3	80.4	6,720.9	22.1
Mean	985.85	7.31	960.13	3.16
S.E.	± 58.25	± 0.48	± 61.78	± 0.20

Fig. 2-20a. Initial response of adult saguaros to the freeze of January 1971. Five months after the freeze, a 3-meter branch (stub on left) has broken from the larger (7-meter ht) plant. Blackened, withered (dead) tissues are present on ball-like branches of the smaller saguaro in the foreground. The abnormally small number of fruits on both individuals is a further result of freeze-damage. Photographed 23 June 1971.

Fig. 2-20b. Eight years after the 1971 freeze, both saguaros shown in Fig. 2-20a are still standing. Injuries to the smaller saguaro have healed. The larger plant—with still-green tissues on the upper stem—is dead. All soft tissues (pith and cortex) of the lower stem have decomposed and fallen from the dead supporting woody ribs (secondary xylem). As much as 9 years or more can elapse between the date of lethal freeze-damage and the final collapse of the dead plant. Photographed 27 Feb. 1979.

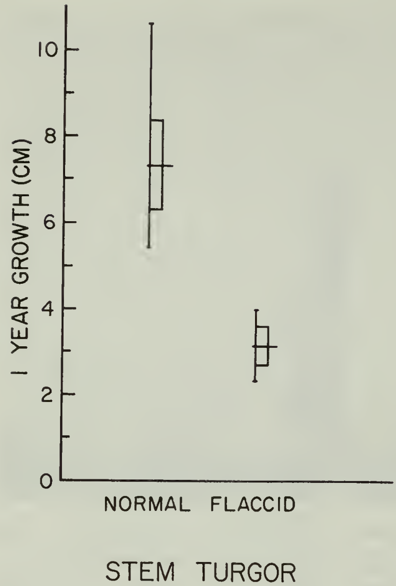

Fig. 2-21. Comparison of apical growth of healthy (normal, $N = 11$) and non-vigorous (flaccid stem, $N = 7$) adult saguaros at Saguaro National Monument (east). Mean, range, and 95% confidence interval of 1-year apical growth increments, 1975-1976. Data in Table 2-16.

The difference in growth rates is highly significant ($p<0.001$). The mean yearly stem height growth of healthy saguaros is approximately double that of non-vigorous plants growing in the same environment—the flaccid plants are moribund.

Freeze-damaged moribund adult saguaros, growing at reduced rates, can survive up to 9 years or more after lethal injury (Steenbergh and Lowe 1977; Fig. 2-20). Thus, such individuals may be older, by several years, than healthy plants of the same height. Accordingly, age-height relationships for *healthy* adult saguaros (shown in Tables 2-10, 2-11, and 2-13, and Fig. 2-4) are conservative estimates for these populations. Furthermore, mean age-height relationships for large saguaros in any population will depend upon the proportion of moribund individuals present at any given time.

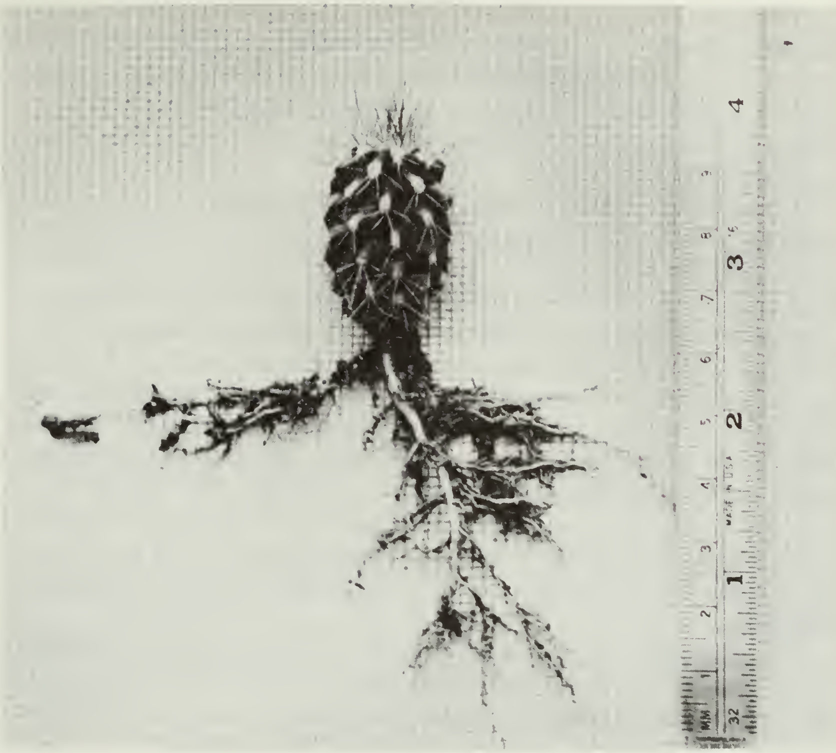

Fig. 2-22. Root system of a 4-year-old saguaro, total stem height 32 mm. The stout tap root is 50 mm in length. Shallow, wide-spreading lateral roots allow rapid uptake of water from light summer rains. Because its root system extends only a few centimeters below the soil surface, the young saguaro is subject to longer and more frequent periods of drought than more deeply rooted older plants. Photographed 26 June 1979.

Previous Reports on Saguaro Age-Height Relationships

Age estimates for saguaros at Saguaro National Monument (east) provided here (Table 2-10; Fig. 2-4) are reasonably consistent with Shreve's (1910) earlier estimates of age-height relationships for saguaros growing in the Tucson area (Table 2-17). However, as shown in Table 2-17 and Fig. 2-23, values for age and growth rates of saguaros provided by our investigations differ markedly from those reported by Hastings (1961) and Hastings and Alcorn (1961). Our values indicate slower growth (and greater age) to approximately 380 cm in height, and, for larger plants, faster growth (and lesser age) than the estimates given by Hastings and Alcorn. Discrepancies between the two estimates for saguaros growing in the same locality and habitat are attributed to important differences in data bases used as described below.

Hastings (1961), using Alcorn's field data, reported no on-site growth data for saguaros ". . . . under two feet in height . . . ." Our growth data base for young saguaros reported here includes 114 on-site measurements (Table 2-2; Appendix II) for plants in this size range (0-61 cm), thus providing a basis for accurate estimates of growth and age during the critically important early years of life.

Comparison of growth rates reported by Hastings and Alcorn with values given in Table 2-10 (graphed in Fig. 2-23) shows discrepancies in growth rates for adult saguaros ranging upward to a maximum difference of 2.5 cm per year for 500-cm plants. Depressed growth rates and short remaining life expectancy are characteristic of moribund saguaros (Table 2-16; Fig. 2-21). The methods reported by Hastings and Alcorn indicate that no attempt was made to exclude from their growth sample such unhealthy individuals, abundant in that population (see Alcorn and May 1962). Their report, in fact, states that many saguaros in their original sample died during the course of that investigation. The lower growth rates (Fig. 2-23) and greater age (Table 2-17) for large saguaros reported by Hastings and Alcorn are attributed to the inclusion in their growth sample of a relatively large proportion of such slow-growing moribund individuals.

The growth curve shown in Fig. 2-2 is based on data for *healthy* plants; data on moribund individuals were not included in the analysis. The values given in Table 2-10, therefore, provide correct age-height relationships for healthy saguaros growing in this environment.

Apparent discrepancies between the growth rates and age estimates for juvenile saguaros at Saguaro National Monument (east) provided here, and the earlier estimates for that locality reported by Steenbergh and Lowe (1977),[1] result from important differences in the data bases used. That report (1977) provides values for *aggregate* stem height (i.e., aboveground stem plus the buried lower portion of the stem) as measured from the *root crown*. Heights given in this report are for *aboveground* stem height, measured from *mean groundlevel*. Some differences are further attributable to the substantially enlarged data base (N = 250 observations obtained over a 9-year period) for generating values reported here. Thus the values shown in Table 2-10 and graphed in Fig. 2-4 provide a more useful and accurate estimate of growth and age for young saguaros growing at Saguaro National Monument (east).

[1]The manuscript for the 1977 report was submitted to the National Park Service for publication in 1974; latest field data referred to in that report were obtained in 1974.

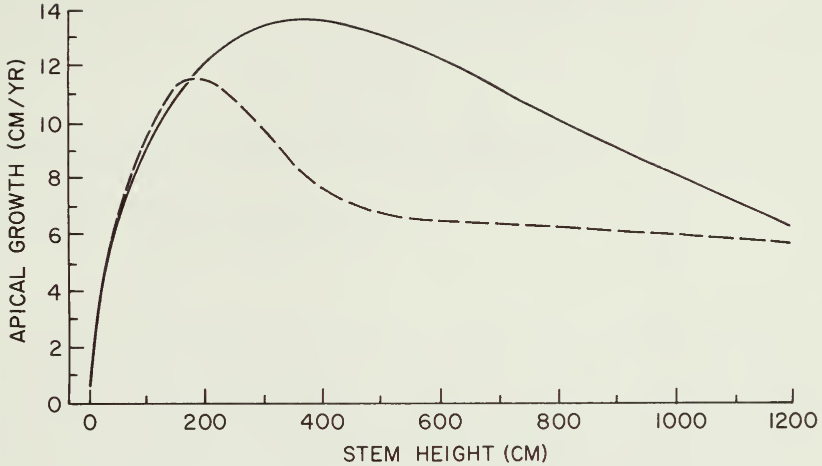

Fig. 2-23. Comparison of two estimates of saguaro growth (1-year apical growth on stem height, arithmetic coordinates) in the same locality and habitat at Saguaro National Monument (east). Dashed line represents values reported by Hastings and Alcorn (1961, Fig. 6). The solid line represents growth data on healthy saguaros in Table 2-10.

Lower growth rates for large saguaros reported by Hastings and Alcorn are attributed to the inclusion in their growth sample of a large proportion of slow-growing, moribund individuals.

TABLE 2-17. Comparison of saguaro age-height relationships as reported by Shreve (1910; Col. A), Hastings and Alcorn (1961; Col. B), and this investigation (Col. C).

Age	Stem height (cm)		
(yrs)	(A)	(B)	(C)
1.0	—	—	0.35
2.0	—	—	0.51
3.0	—	—	0.73
4.0	—	—	1.04
5.0	—	—	1.49
6.0	—	—	2.1
7.0	—	—	2.9
8.0	10	—	4.0
9.0	—	15	5.3
12.5	20	—	12.7
13.0	—	30	14.2
18.0	—	61	34.5
19.1	40	—	40.4
21.0	—	91	51.9
24.0	—	122	73.3
27.0	—	152	98.6
27.3	80	—	101.3
30.0	—	183	127.5
30.3	100	—	130.6
32.0	—	213	148.6
35.0	—	244	182.6
38.0	—	274	219.0
40.5	200	—	250.6
41.0	—	305	257.3
47.5	300	—	344.0
48.0	—	366	350.5
54.0	400	—	431.5
56.0	—	427	458.2
60.0	500	—	510.8
64.0	—	488	561.9
74.0	—	549	681.8
83.0	—	610	779.8
107.0	—	762	999.4
131.0	—	914	1,172.3
157.0	—	1,067	1,323.6
170.0	—	—	1,388.8

3
Population Structure and Dynamics

Surveys of saguaro populations in permanent study plots at Saguaro and Organ Pipe Cactus national monuments, initiated in 1941 and supplemented by establishment of additional plots and follow-up surveys, provide long-term data on these populations. Differences in density, and size and age structures of these populations provide useful insights into the natural dynamics of the saguaro in characteristic habitats and environments in this northern portion of the species' range—Arizona and northern Sonora, Mexico (see Figs. 3-1 to 3-3).

It should be noted that the smaller saguaros in these populations were not detectable by the methods employed in these surveys. Saguaros, during the first few years of life, are so small and inconspicuous that they can be found only by intensive hands-and-knees search. With few exceptions, saguaros of less than 10 cm in height were not observed or recorded in these surveys. It is highly probable that large numbers of plants in this size range were missed and, therefore, that the actual frequency of saguaros in the smallest size-classes is, in some instances considerably greater than these data indicate.

Thirty-four Years of Change, 1941-1975

Data on saguaro populations at Saguaro National Monument (east) and Organ Pipe Cactus National Monument, obtained in both locations in 1941, provide a basis for evaluating subsequent changes in plant numbers and size-class structure in these two populations. Data on all saguaros present in 5-acre (2 ha) plots ($N = 5$) at Saguaro National Monument (east), and three 0.9-acre (0.36 ha) plots at Organ Pipe Cactus National Monument were recorded in 1941 in conjunction with United States Department of Agriculture cactus disease investigations[1] (Table 3-1; Gill and Lightle 1942). Gill and Lightle (1946) also provide 1941 height-class

[1]Appendix I.

data on all living saguaros in a 1-mi^2 (2.59-km^2) plot (Sect. 17, flat habitat, N = 12,898) at Saguaro National Monument (east). The smaller plots were resurveyed in 1975, providing a 34-year record of changes in these populations.

Comparison of saguaro densities in these plots in 1941 and 1975 (Table 3-2; Fig. 3-4) shows a decrease in saguaro numbers at all sites. However, the decrease in density at Saguaro National Monument (east, 51.1%) was more than twice that at Organ Pipe Cactus National Monument (21.8%), with the greatest decreases occurring in the nonrocky rolling hill and bajada habitats (flats) at Saguaro National Monument (east).

Fig. 3-1a. The Cactus Forest, Saguaro National Monument (east) in 1941. Approximately one-half of the plants in the population were then over 70 years old. High mortality which occurred in this population after 1940 was a delayed response to lethal injuries resulting from the deep-freezes of January 1937 and February 1939 (see Turnage and Hinckley 1938; Gill and Lightle 1942, 1946; Mielke 1944; Gill 1951). Compare with Fig. 3-1b. Photographed 22 Oct. 1941.

Fig. 3-1b. All of the large saguaros seen in Fig. 3-1a are dead in this photograph of the same scene taken 38 years later. The population has been decimated by a series of catastrophic freezes (see Steenbergh and Lowe 1977). However, regeneration of the population is now occurring with establishment of thousands of young saguaros (not shown) beneath tree crowns. Woody skeletons of dead saguaros (foreground) can remain for as long as 30 years or more after the death of the plant. Photographed 27 Feb. 1979.

Comparison of 34-year changes in the height-class structure of the Saguaro and Organ Pipe Cactus national monuments populations in nonrocky habitats (Figs. 3-5 and 3-6; Tables 3-3 and 3-4) shows important differences in the distribution of size-classes in these two populations.

At Organ Pipe Cactus National Monument there were *decreases* in the smallest (Classes I and II, ht$<$396.2 cm) and largest (Class V, ht$>$761.7 cm) size-classes and an *increase* in the number of intermediate size plants (Table 3-4; Fig. 3-6). The 1975 population contained only two new (Class I) individuals; 38 of the 40 individuals present in the 1975 Class I group were present in 1941. In the Saguaro National Monument (east) population, there were *increases* in the smallest (Class I) and largest (Class V) size-classes and *decreases* in the intermediate classes (Table 3-3; Fig. 3-5). The 14.6% increase in Class I plants resulted from recruitment. In 1975 all of the 16 plants in this class were new individuals established after 1941.

A downward trend in the Organ Pipe Cactus National Monument population is evidenced by the low recruitment rate and a decrease in the

TABLE 3-1. Location, elevation, slope exposure, and topographic habitat of saguaro cactus study plots at Saguaro and Organ Pipe Cactus national monuments. Plots in each series are arranged in order of increasing elevation.

Location	Plot no.	Size (ha)	Elevation m	Elevation ft	Slope exp.	Topographic habitat
Sag. N. Mon. (east)	41A[a]	2.0	856	2,810	North	Bajada (Cactus Forest "flats")
"	41B[a]	2.0	869	2,850	North	" " "
"	41F[a]	2.0	878	2,880	North	" " "
"	41D[a]	2.0	902	2,960	North	Rolling hill
"	41C[a]	2.0	951	3,120	West	Rocky footslope
"	75M	2.0	991	3,250	South	Rocky footslope
Sag. N. Mon. (west)	75J	2.0	693	2,275	West	Lower bajada
"	75G	2.0	716	2,350	West	Mid-bajada
"	75L	2.0	792	2,600	West	Upper bajada
"	75H	2.0	914	3,000	South	Rocky footslope
"	75K	2.0	960	3,150	North	Rocky footslope
OPC N. Mon.	4105	0.36	439	1,440	East	Rolling hill
"	4103	0.36	575	1,885	West	Mid-bajada
"	4104	0.36	671	2,200	West	Upper bajada
"	7711[b]	2.00	600	1,970	West	Lower bajada
"	7712[b]	2.00	658	2,160	West	Mid-bajada
"	7713[b]	2.00	683	2,240	West	Upper bajada

[a] Plots established in 1941 by Gill and Lightle (see text).
[b] Established in 1977, Alamo Canyon.

number of Class I plants. At Saguaro National Monument (east), on the other hand, higher recruitment and the increase in the number of Class I plants indicate a reversal in the downward trend of this population, and, in the period since 1941, the population has entered a growth phase. Recruitment rates, however, are not adequate at either location to soon return these populations to the relatively high densities that characterized them during and before 1941.

Fig. 3-2a. Saguaro population on lower flank of Tanque Verde Ridge, Saguaro National Monument in 1941. The population includes a large proportion of young, small- and intermediate-sized, plants growing on rock outcrops. Jumping cholla *(Opuntia bigelovi)* growing on these same outcrops is indicative of a winter-warm microenvironment. Compare with Fig. 3-2b. Photographed 12 Sept. 1941.

Height-class Structure

Six additional 2-ha plots established in the two sections of Saguaro National Monument in 1971 and 1975 were surveyed in 1975 to obtain supplemental comparative data on saguaro population structure in differing topographic habitats in the two (east and west) sections of the monument (Table 3-1). Distribution by 2.5-m height-classes of these data and 1975 data from the 1941 plots established at Saguaro National Monument (east) and Organ Pipe Cactus National Monument by Gill and Lightle (1942; Table 3-1) are shown in Tables 3-5 and 3-6.

Fig. 3-2b. After 38 years, saguaro population density has decreased by approximately 29%. However, the population still includes substantial numbers of small- and intermediate-sized plants. Highest mortality has occurred in the immediate vicinity of washes (foreground) which are areas of cold-air drainage. Photographed 27 Feb. 1979.

TABLE 3-2. Summary of 34-year change in saguaro density in study plots at Organ Pipe Cactus National Monument and Saguaro National Monument (east), 1941-1975.

N is number of plants per plot, "Density" is number of plants per ha, and "Change" is the 34-year decrease in density (%). Graphed in Fig. 3-4.

Plot no.	1941 *N*	1941 Density	1975 *N*	1975 Density	Change (%)
		Organ Pipe Cactus National Monument			
4105	69	189.44	50	137.28	−27.54
4103	21	57.66	12	32.95	−42.86
4104	52	142.76	49	134.53	− 5.77
Total	142[a]	129.96	111	101.59	−21.83
		Saguaro National Monument (east)			
41A	209	104.50	64	32.00	−69.38
41B	187	93.50	40	20.00	−78.61
41F	60	30.00	25	12.50	−58.33
41D	106	53.00	44	22.00	−58.49
41C	291	145.50	244	122.00	−16.15
Total	853	85.30	417	41.70	−51.11

[a] Includes plants missed in 1941 that were recorded in subsequent surveys.

TABLE 3-3. Thirty-four-year change in saguaro population height-class structure at Saguaro National Monument (east) 1941-1975: 1941 data for Section 17 (640 acres, 259 ha) from Gill and Lightle (1946); 1975 data from plots 41A and 41B (2 ha ea.) located within the 1941 survey area.

N is number of plants per plot, "Density" is number of plants per ha, and "Change" is 34-year increase or decrease in density (%). Data graphed in Fig. 3-5.

Class	Height		1941			1975			Change
	ft[a]	cm	*N*	Density	%	*N*	Density	%	%
I	0.00 – 6.99	0.0 – 213.1	903	3.49	7.0	16	4.00	15.38	+14.61
II	7.00 – 12.99	213.4 – 395.9	1,651	6.37	12.8	5	1.25	4.81	−80.38
III	13.00 – 18.99	396.2 – 578.8	4,127	15.93	32.0	12	3.00	11.54	−81.77
IV	19.00 – 24.99	579.1 – 761.7	3,521	13.59	27.3	25	6.25	24.04	−54.01
V	25.00 +	762.0 +	2,683	10.36	20.8	45	11.25	43.27	+ 8.59
Unclassified (broken stems)			13	0.05	0.1	1	0.25	0.96	+ 0.80
Total			12,898	49.80		104	26.00		−47.79

[a] Class intervals as originally reported by Gill and Lightle (1942).

Fig. 3-3a. Overview of lower bajada habitat at Saguaro National Monument (west) in 1941. Although this saguaro population does not include some small individuals, it is dominated by intermediate- and large-size adult plants. Saguaro density decreases to zero at the center of the valley in the distance. Compare with Fig. 3-3b. Photographed 18 July 1941.

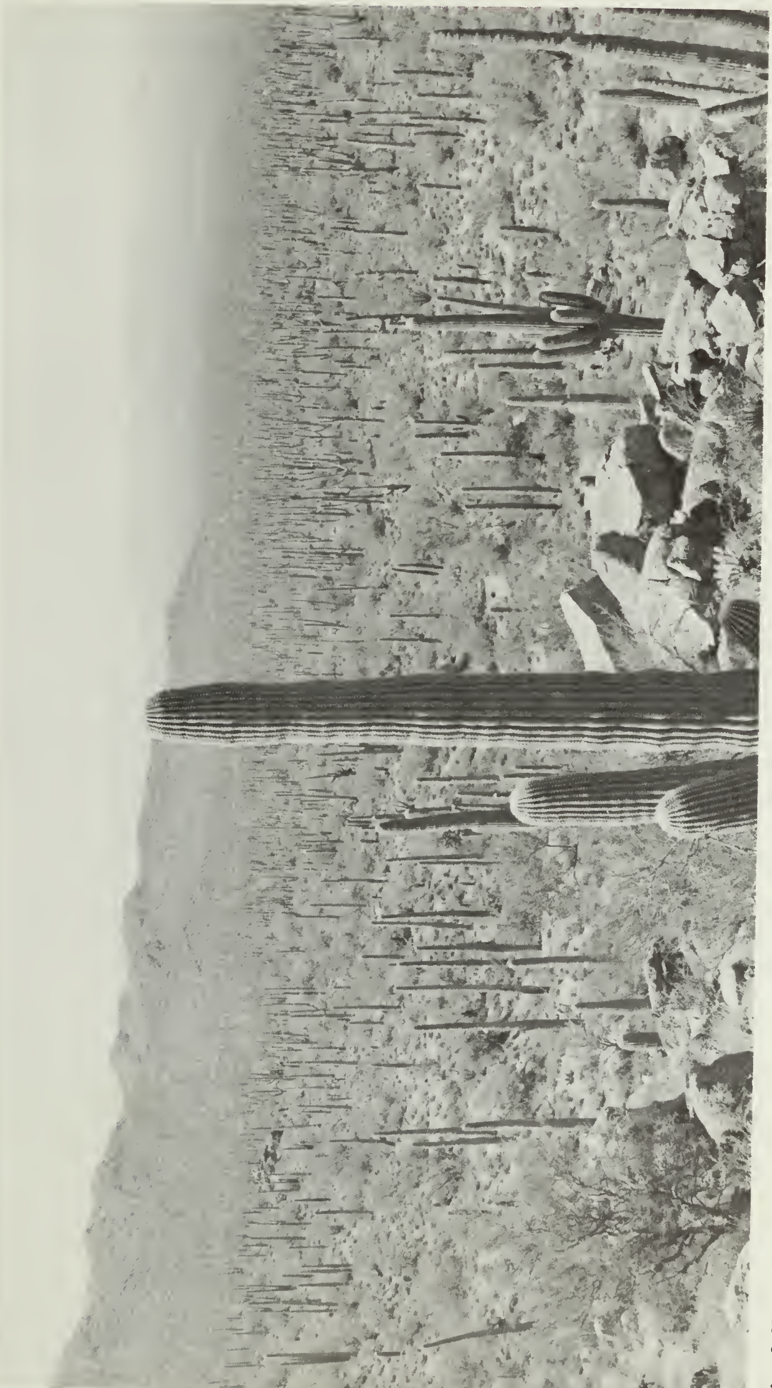

Fig. 3-3b. Thirty-eight years later, a decrease in overall saguaro population density is evident. Numbers of large- and intermediate-sized saguaros have declined. Smaller plants, fewer in number, are not numerous enough to maintain the population at its present level. Photographed 23 Mar. 1979.

TABLE 3-4. Thirty-four-year change in saguaro population height structure at Organ Pipe Cactus National Monument, 1941-1975. Pooled data for three 0.9 acre (0.364 ha) plots (Nos. 4103, 4104, and 4105).

N is number of plants per plot, "Density" is number of plants per ha, and "Change" is 34-year increase or decrease in density (%). Data graphed in Fig. 3-6.

Class	Height		1941			1975			Change
	ft[a]	cm	*N*	Density	%	*N*	Density	%	%
I	0.00 – 6.99	0.0 – 213.1	73[b]	66.81	51.41	40	36.61	36.04	−45.21
II	7.00 – 12.99	213.4 – 395.9	22	20.13	15.49	21	19.22	18.29	− 0.05
III	13.00 – 18.99	396.2 – 578.8	15	13.73	10.56	16	14.64	14.41	+ 6.25
IV	19.00 – 24.99	579.1 – 761.7	13	11.89	9.15	20	18.30	18.02	+35.00
V	25.00 +	762.0 +	19	17.39	13.38	14	12.81	12.61	−26.32
Total			142	129.95		111	101.58		−21.83

[a]Class intervals as originally reported by Gill and Lightle (1942).

[b] Includes 15 plants missed in 1941 that were recorded in subsequent surveys.

TABLE 3-5. Height-class distribution (1975) of saguaros in 2-ha plots (N = 6) at Saguaro National Monument (east); number (N) and density (Den.) per ha. Data graphed in Fig. 3-7a.

Class	Height (m)	Plot numbers											
		41A		41B		41F		41D		41C		75M	
		N	Den.	N	Den.	N	Den.	N	Den.	N	Den.	N	Den.
1	0.00-2.49	7	3.5	10	5.0	0	0.0	7	3.5	127	63.5	115	57.5
2	2.50-4.99	9	4.5	0	0.0	4	2.0	5	2.5	63	31.5	67	33.5
3	5.00-7.49	16	8.0	11	5.5	9	4.5	11	5.5	48	24.0	29	14.5
4	7.50-9.99	23	11.5	18	9.0	10	5.0	17	8.5	5	2.5	12	6.0
5	10.00-12.49	8	4.0	1	0.5	1	0.5	3	1.5	0	0.0	1	0.5
Unclassified[a]		1	0.5	0	0.0	1	0.5	1	0.5	1	0.5	2	1.0
Total		64	32.0	40	20.0	25	12.6	44	22.0	244	122.0	226	113.0

[a] Broken stems.

TABLE 3-6. Height-class distribution (1975) of saguaros in 2-ha plots (N = 5) at Saguaro National Monument (west) and three 0.36-ha plots (Nos. 4103-4105, pooled data) at Organ Pipe Cactus National Monument (OPC); number (N) and density (Den.) per ha. Data graphed in Fig. 3-7b.

Class	Height (m)	Plot numbers											
		75J		75G		75L		75H		75K		OPC	
		N	Den.	N	Den.	N	Den.	N	Den.	N	Den.	N	Den.
1	0.00-2.49	12	6.0	43	21.5	99	49.5	220	110.0	20	10.0	48	44.04
2	2.50-4.99	24	12.0	38	19.0	52	26.0	67	33.5	23	11.5	25	22.94
3	5.00-7.49	29	14.5	39	19.5	35	17.5	21	10.5	41	20.5	24	22.02
4	7.50-9.99	22	11.0	36	13.0	33	16.5	11	5.5	18	9.0	11	10.09
5	10.00-12.49	6	3.0	3	1.5	1	0.5	1	0.5	1	0.5	3	2.75
Unclassified[a]		1	0.5	6	3.0	0	0.0	2	1.0	1	0.5	0	0.00
Total		94	47.0	165	82.5	220	110.0	322	161.0	104	52.0	111	101.83

[a] Broken stems.

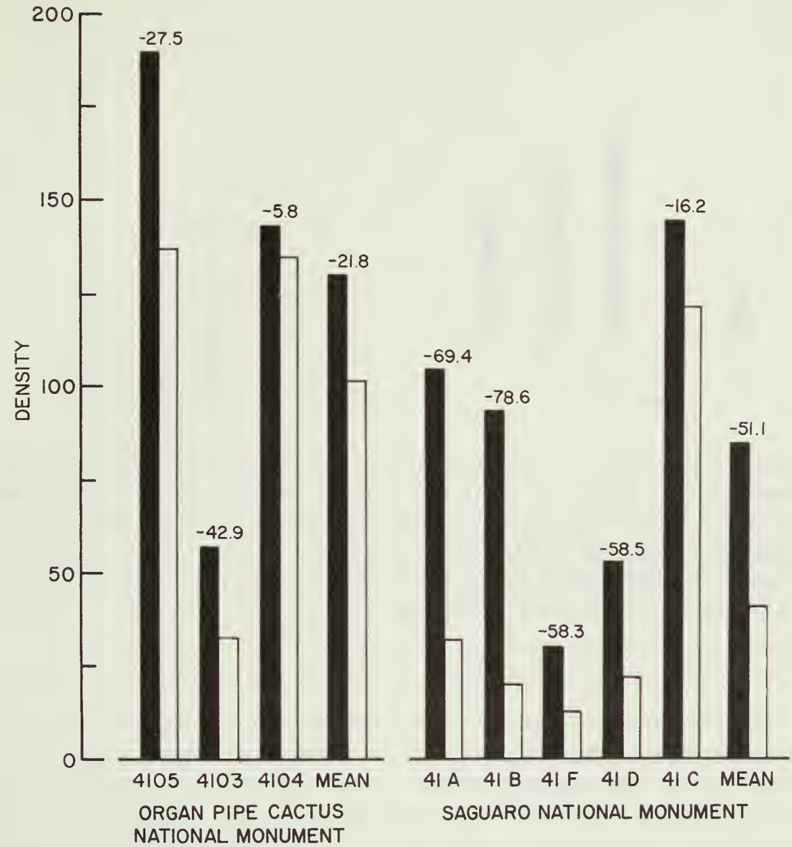

Fig. 3-4. Thirty-four-year change in saguaro density (plants per ha) in population study plots at Organ Pipe Cactus National Monument (left) and Saguaro National Monument (east, right) 1941 (shaded bars) to 1975 (open bars). Numbers above bars are percent change in density. Data in Tables 3-1 and 3-2.

Density decreased in all plots at both locations. The mean decrease in density at Saguaro National Monument was approximately twice that at Organ Pipe Cactus National Monument.

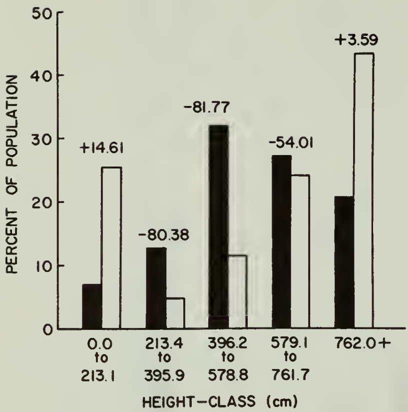

Fig. 3-5. Thirty-four-year change in saguaro population height-class structure at Saguaro National Monument (east), 1941 (shaded bars, Section 17) to 1975 (open bars; plots 41A, 41B). Numbers above bars are percent change in density for each height-class. Data in Table 3-3.

In this population, there was an *increase* in the smallest and largest size-classes and a decrease in intermediate size-classes.

The histogram of density on height-class for the Saguaro National Monument (east) plots (Fig. 3-7a) shows a marked difference in the size-class structure of populations in rocky and nonrocky habitats. In nonrocky habitats, the population is characterized by a predominance of plants in the three largest size-classes (ht>5 m). In the rocky habitats, however, the size-class structure is reversed, characterized by progressively lower plant densities in successively larger height-classes.

The nature of the relationship is clearly expressed by the data for Saguaro National Monument (west) where four plots (75J-75H) were established along a gradient of increasingly rocky habitat that occurs from low to high elevations (Tables 3-1 and 3-6). As shown in Fig. 3-7b, the size-class structure of the population shifts along the gradient of increasingly rocky habitat from a predominance of large (old) plants in a *non-rocky* habitat at low elevations (plot 75J) to a predominance of small (juvenile and young adult) plants in the higher elevation *rocky* habitat (plot 75H).

Comparison of the histogram of density on height (Fig. 3-7b) for the north slope plot (75K) with plot 75J (flats) shows a closely similar size-class structure in these topographically dissimilar habitats. Height-class distribution of the Organ Pipe Cactus National Monument data (rolling hill and bajada habitats, plots 4103-4105 pooled data) compares closely with that of the upper bajada (plot 75L) at Saguaro National Monument (west).

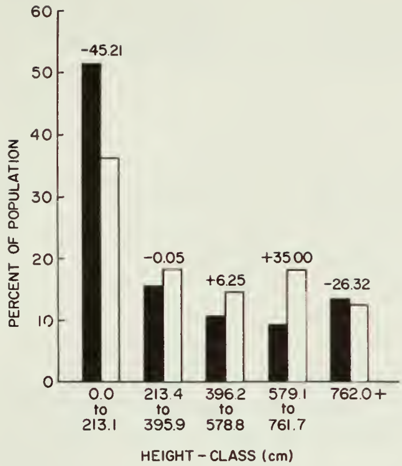

Fig. 3-6. Thirty-four-year change in saguaro population height-class structure (pooled data, plots 4103, 4104, 4105) at Organ Pipe Cactus National Monument, 1941 (shaded bars) to 1975 (open bars). Numbers above bars are percent change in density for each height-class. Data in Table 3-4.

In this population there was a *decrease* in the smallest (youngest) and largest (oldest) size-classes, and an *increase* in intermediate size-classes. Compare with Fig. 3-5.

Proportional distribution by reproductive size-class (juvenile and adult) of saguaros in the 11 Saguaro National Monument plots is shown in Table 3-7. Regression of these data (Fig. 3-8) shows that the ratio of juvenile (nonreproductive) to adult (reproductive) plants increases with total saguaro density. This relationship further reflects the relative suitability of differing topographic habitats. The greatest numbers of juvenile saguaros occur in high density populations growing on rocky south-facing slopes, which provide winter-warm microenvironments most favorable for saguaro establishment and survival. The lowest overall population densities and the smallest number of juvenile saguaros occur on winter-cold north-facing slopes and valley-bottom habitats.

Age Structure

Height-age relationships for saguaros in Tables 2-10, 2-11, and 2-13 provide a basis for comparison of population age structure in different environments and habitats as shown in Tables 3-8 and 3-9. Histograms of distribution by 20-year age-classes (Fig. 3-9) reveal important differences in age structure and provide insights into past and probable future dynamics of these populations.

TABLE 3-7. Number, density (plants per ha), and percent distribution of juvenile (nonreproductive) and adult (reproductive) saguaros in 2-ha study plots ($N = 11$) at Saguaro National Monument (1975). Data graphed in Fig. 3-8.

Plot no.	*N*	Density	Reproductive class					
			Adults (2.5 m+)			Juveniles (0-2.49 m)		
			N	Density	%	*N*	Density	%
				East Monument				
41A	64	32.0	57	28.5	89.06	7	3.5	10.94
41B	40	20.0	30	15.0	75.00	10	5.0	25.00
41F	25	12.5	25	12.5	100.00	0	0.0	0.00
41D	44	22.0	37[a]	18.5	84.09	7	3.5	15.91
41C	244	122.0	117[a]	58.5	47.95	127	63.5	52.05
75M	226	113	111[a]	55.5	49.12	115	57.5	50.88
				West Monument				
75J	94	47.0	82[a]	41.0	87.23	12	6.0	12.77
71G	165	82.5	122[a]	61.0	73.94	43	21.5	26.06
75L	220	110.0	121	60.5	55.00	99	49.5	45.00
75H	322	161.0	102[a]	51.0	31.68	220	110.0	68.32
75K	104	52.0	84[a]	42.0	80.77	20	10.0	19.23

[a] Includes unclassified broken stems.

Fig. 3-7a. Height-class distribution (density per ha) of saguaros in 2-ha plots at Saguaro National Monument (east), 1975. Height-classes are: (1) 0-2.49 m, (2) 2.5-4.99 m, (3) 5.0-7.49 m, (4) 7.5-9.99 m, and (5) 10.0-12.49 m. Data in Tables 3-1 and 3-5.

Obvious differences in the size-class structure of the populations growing in nonrocky (flat) habitat and rocky habitat (south-facing slopes) clearly indicate the greater long-term suitability of the rocky, south-facing slope habitat.

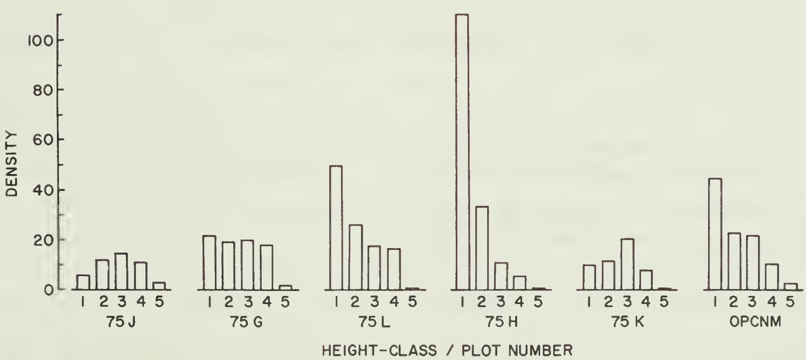

Fig. 3-7b. Comparison of height-class distribution (density per ha) of saguaros in 2-ha plots at Saguaro National Monument (west; Plot 75K, north-facing slope; Plots 71J, 71G, 75L, and 75H) and Organ Pipe Cactus National Monument (three 0.36-ha plots, pooled data), 1975. Height-classes as given in Fig. 3-7a. See data in Tables 3-1 and 3-6.

Plots 71J-75H, arranged in order of increasing elevation, clearly show the gradient of changing population size-class structure which ocurs with increasing rockiness of the habitat. Population structure shifts from a predominance of large (old) saguaros in nonrocky (low elevation) habitats to a predominance of small (juvenile and young adult) plants in the rocky habitat (higher elevations).

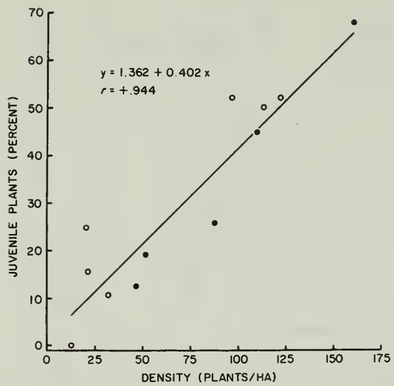

Fig. 3-8. Regression of juvenile saguaros (percent of population) on population density at Saguaro National Monument east (open circles) and west (solid circles). Regression of juvenile plants (%) on density (total number of plants per ha) in 2-ha plots (N = 11). Data in Tables 3-1 and 3-7.

The proportion of nonreproductive saguaros (juvenile, height 0-250 cm) in these populations increases with total population density. This relationship reflects the higher suitability of the rocky, south-facing slope habitats which provide winter-warm environments favorable for saguaro establishment and survival.

Saguaro populations in both the east and west sections of Saguaro National Monument exhibit generally similar patterns of age distribution (Fig. 3-9a). However, with two minor exceptions, the east monument population exhibits lower densities in all age-classes in both rocky and flat habitats. Lower saguaro survival and establishment at the east monument are attributable to greater freeze-caused mortality that occurs in the colder winter environment at this near-eastern limit of the species' distribution (see Steenbergh and Lowe 1976, 1977).

Populations in the "flats" (nonrocky habitats) in both sections of Saguaro National Monument (Fig. 3-9a; Table 3-8) show a grossly unbalanced age structure dominated by large numbers of old plants (age greater than 60 years) most of which became established prior to 1895. The paucity of plants in the younger age-classes absolutely ensures that, regardless of any future increase in recruitment rates, the decline in numbers of large (old) plants in these populations must continue into the middle of the next century. Thus, the period of large-scale fluctuations in these populations spans the entire lifetime of a saguaro generation.

Populations in the rock habitats, however, are characterized by a high proportion of individuals in the youngest age-classes (age less than 60 years) with progressively smaller numbers of plants in successively older age-classes. The favorable balance of young-to-old plants in these rock

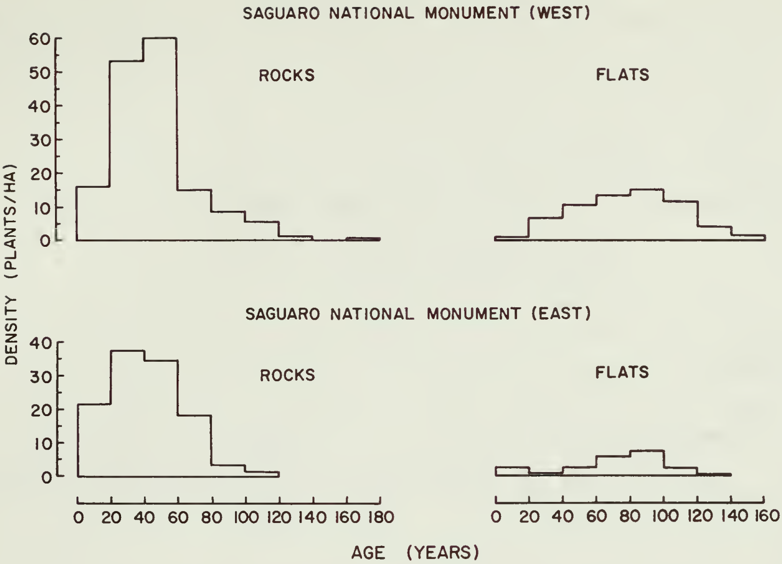

Fig. 3-9a. Distribution by 20-year age-classes of saguaros in rocky and flat (nonrocky) habitats at Saguaro National Monument. Data in Tables 3-1 and 3-8.

The balance of young to old plants in rocky habitats indicates that these relatively stable populations have been less subject to the long-scale perturbations that are characteristic of populations in the marginal flat (nonrocky) habitats. Age structure in the nonrock habitats ensures that the decline in numbers of large, old saguaros there will continue into the middle of the next century.

habitats indicates that these are comparatively stable populations that have maintained themselves over a long period of time without the large-scale perturbations characteristic of populations in the marginally flat (nonrocky) habitats. Further, the relatively well-balanced age structure in rock habitats indicates that, barring a major reduction in recruitment rates, these populations will continue to maintain themselves at, or near, present levels.

The age structure for two population samples at Organ Pipe Cactus National Monument is shown in Table 3-9. The 1975 data (N = 111) were obtained from the three original 0.36-ha (0.9-acre) plots established in 1941. The larger and more representative 1978 sample (N = 321) is from a series of three 2-ha plots located on the lower, middle, and upper bajada at Alamo Canyon (Table 3-1).

This population, like the Saguaro National Monument (east) flats populations, is dominated by large numbers of plants in the over 60-year age-classes established prior to 1915. The population is in a state of slow decline, with a low recruitment rate and insufficient numbers of plants in

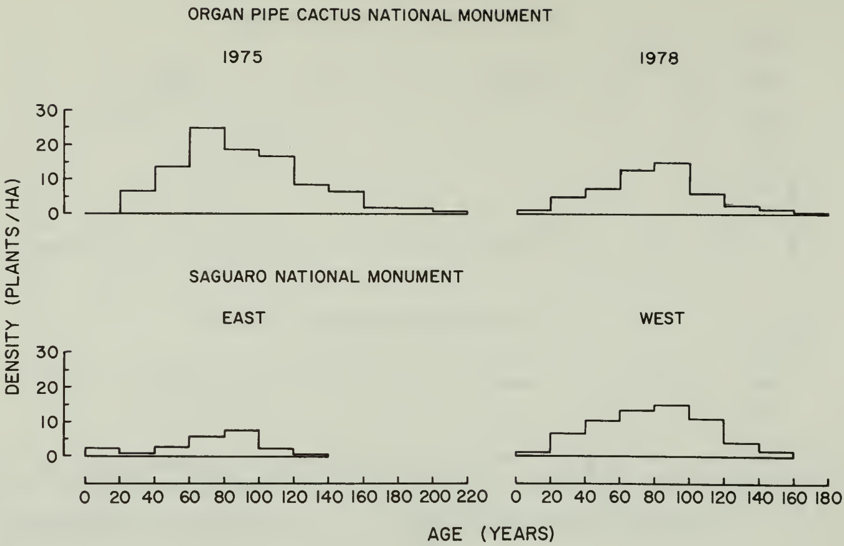

Fig. 3-9b. Comparison of saguaro population age structure at Organ Pipe Cactus National Monument (1975 data from plots 4103, 4104, and 4105; 1978 data from plots 7711, 7712, and 7713) and Saguaro National Monument, flats. Data in Tables 3-8 and 3-9.

The age structure of the saguaro population at Organ Pipe Cactus National Monument (1978 data) is nearly identical to that of the Saguaro National Monument (west) flats population. All of these populations are responding in a similar manner to the critical stresses of recurring catastrophic freezes.

the under 60-year age-classes to maintain the population at its present level.

Comparison of the data for Organ Pipe Cactus National Monument with the Saguaro National Monument (west) flats data (Fig. 3-9b) shows a close similarity in the age structure of these two populations. The Alamo Canyon (1978) sample is, in fact, nearly identical in density as well as age structure with the west monument flats sample. These data indicate that the Organ Pipe Cactus National Monument population is responding in like manner to the same—but less intense—critical environmental stresses, i.e., *catastrophic freezes,* affecting populations at Saguaro National Monument.

Population Stability

Slope exposure, microclimate, and age structure

Even greater than the differences in saguaro population density and age structure that occur between similar topographic habitats in dissimilar climatic environments are those that are found between populations inhabiting different slope exposures, growing under the same general climate in the same locality. These differences—which are the expression of importantly different, limiting microclimates—are most strongly evidenced on opposed rocky south-facing and north-facing slopes. Not only do such local saguaro populations growing on adjacent north-facing and south-facing slopes differ significantly in density and age structure, but also in the upper elevational limits of their occurrence.

The age-size class distribution as well as the densities of saguaros are so distinctly *different on south-facing and north-facing slopes*—throughout the entire geographic range of the species—that only a glance at the age pyramids shown in Fig. 3-10 is necessary to appreciate this large and highly significant difference in population density and age structure (Table 3-10). While most saguaro populations differ in some degree from *theoretical stable age distribution,* the usually greater departure on the colder north-facing slope is obvious. For those who are more comfortable with a quantitative measure, an index of departure from stable age distribution (I_d) associated with the two populations illustrated in Fig. 3-10 is $I_d = 0.191$ on the south-facing slope and $I_d = 0.272$ on the north-facing slope.[1]

Stable age distribution

The idea of *stable age distribution* is an important concept in population ecology. It is assumed that populations that reproduce themselves in relatively steady environments attain relatively steady age distributions. Stable age distributions, therefore, are expected to exhibit pyramidal form (the stable age pyramid) in which the proportions of individuals in each age group or class (each step level in the pyramid) remain more or less constant over long periods of time, generation after generation. The population age pyramid may become larger or smaller as a whole, but remains a positive pyramid of progressively smaller as well as older age-classes from bottom to top. This, basically, is the theory.[2]

For long-lived plant species, what constitutes a "steady" ("constant," "stable") environment? How do we recognize one when we are in one? Within parts of the tropics (equable climate) the answer can be obvious. For terrestrial plant populations at mid-latitudes (nonequable climate), it is not.

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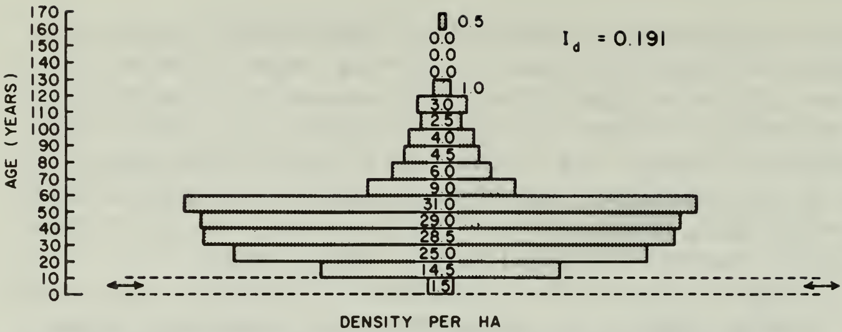
[1]I_d is given by: $I_d = (N_i - N_{i-1}) / \overset{m}{\underset{i=1}{S}} N_i$

[2]Surprisingly little information on the subject is available for perennial plant populations; see Harper and White (1974) and Harper's (1977) recent populations biology of plants. Where the subject is discussed in ecology texts, the explanations and examples are centered on animal population theory and practice (e.g., MacArthur and Connell 1966; Odum 1971; Wilson and Bossert 1971; Krebs 1972; Pianka 1978).



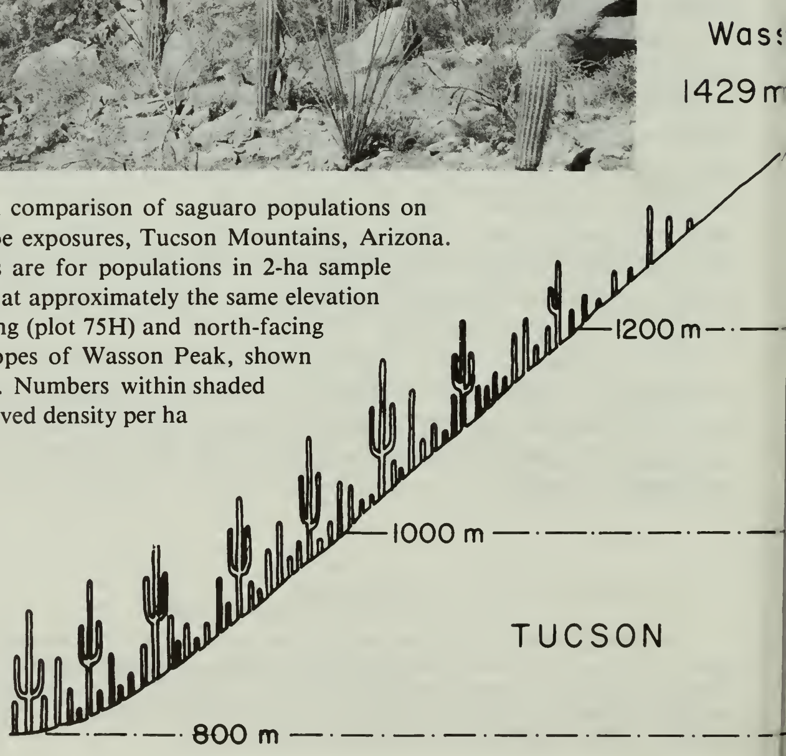
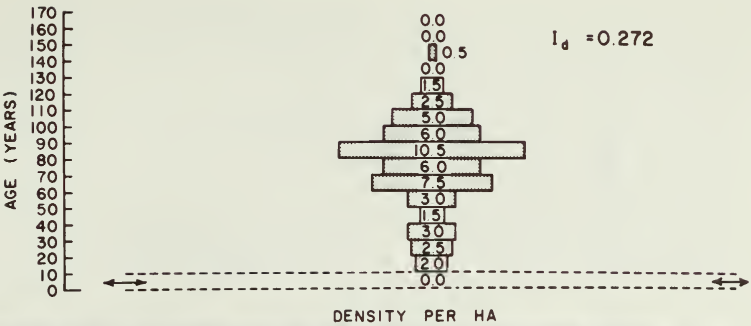


Fig. 3-10. A comparison of saguaro populations on opposing slope exposures, Tucson Mountains, Arizona. Age pyramids are for populations in 2-ha sample plots situated at approximately the same elevation on south-facing (plot 75H) and north-facing (plot 75K) slopes of Wasson Peak, shown schematically. Numbers within shaded bars are observed density per ha



based on 2-ha field samples. Highly significant differences in population density and age structure shown by the age pyramids are readily apparent in the photographs of the two sites. See discussion in text; data in Tables 3-1 and 3-10.

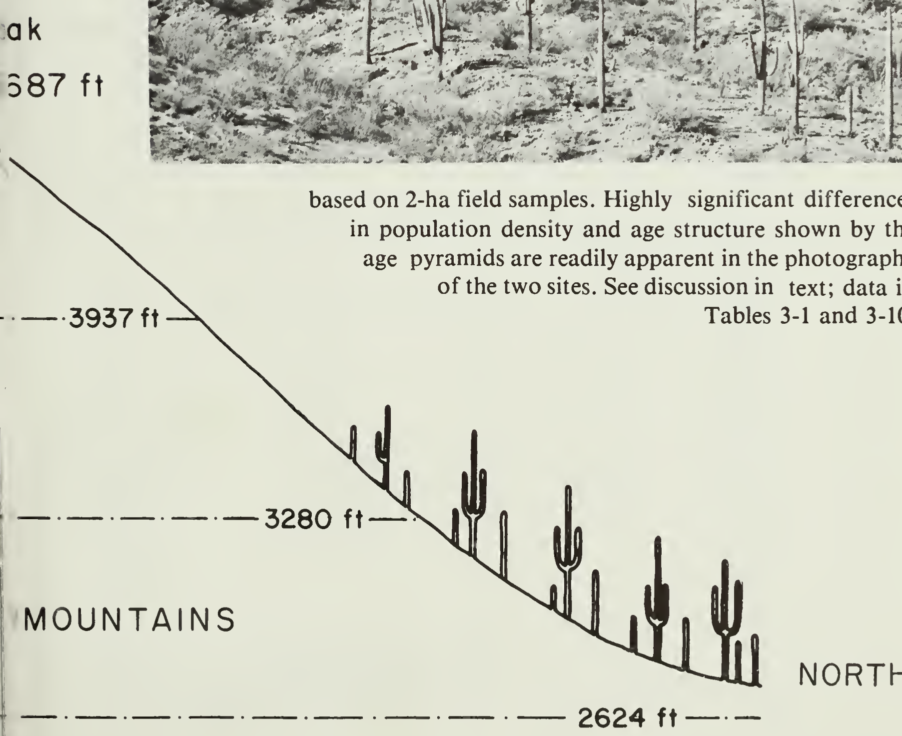


TABLE 3-8. Distribution by 20-year age-classes of saguaros in flat and rock habitat at Saguaro National Monument; number (*N*) and density (Den.) per ha. Age data from Tables 2-10 and 2-11. Graphed in Fig. 3-9a.

Age-class (yrs)	East Monument					West Monument				
	Height (m)	Flats[a]		Rocks[b]		Height (m)	Flats[c]		Rocks[d]	
		N	Den.	*N*	Den.		*N*	Den.	*N*	Den.
0-19.9	0.00-0.45	14	2.33	87	21.75	0.00-0.21	4	1.00	32	16.00
20-39.9	0.46-2.43	3	0.50	150	37.50	0.22-1.22	26	6.50	107	53.50
40-59.9	2.44-5.10	15	2.50	138	34.50	1.23-3.18	41	10.25	120	60.00
60-79.9	5.11-7.47	35	5.83	73	18.25	3.19-5.44	53	13.25	30	15.00
80-99.9	7.48-9.40	45	7.50	13	3.25	5.45-7.40	59	14.75	17	8.50
100-119.9	9.41-10.97	14	2.33	6	1.50	7.41-8.98	47	11.75	11	5.50
120-139.9	10.98-12.27	2	0.33	0	0.00	8.99-10.25	16	4.00	2	1.00
140-159.9		0	0.00	0	0.00	10.26-11.30	6	1.50	0	0.00
160-179.9		0	0.00	0	0.00	11.31-12.20	0	0.00	1	0.50
Unclassified[e]		2	0.17	3	0.75		7	1.75	2	1.00
Total		129	21.50	470	117.50		259	64.75	322	161.00

[a] Plots 41A, 41B, 41F (6 ha).
[b] Plots 41C, 75M (4 ha).
[c] Plots 71G, 75J (4 ha).
[d] Plot 75H (2 ha).
[e] Broken stems.

Compared to the human lifetime, the saguaro is a long-lived species. Individuals begin reproducing at 35-65 years of age, reproduce most of their remaining lives, and may live to 200 years. In many such cases that involve perennial plant populations, the long-period environment itself may be more difficult to measure and assess accurately (or at all) than is a species population living in it, e.g., a long-lived plant species reproducing in that environment. The long-range "stability" of the local environment on the scale of centuries may best be judged, or only possibly be judged, by the nature and degree of long-range stability recorded in the local population structure of such a long-lived species.[3]

[3]In a more limited sense this is an objective in obtaining tree-ring (age and moisture) information in dendrochronology. Ideal plant population structure information would include data from growth-ring analysis.

TABLE 3-9. Distribution by 20-year age-classes of saguaros at Organ Pipe Cactus National Monument; number (*N*) and density (Den.) per ha. Age data from Table 2-13. Graphed in Fig. 3-9b.

Age-class	Height	1975[a]		1978[b]	
(yrs)	(m)	*N*	Den.	*N*	Den.
0-19.9	0.00-0.10	0	0.00	4	0.67
20-39.9	0.11-0.54	7	6.41	30	5.00
40-59.9	0.55-1.37	15	13.73	47	7.83
60-79.9	1.38-2.95	30	27.46	78	13.00
80-99.9	2.96-4.88	20	18.30	89	14.83
100-119.9	4.89-6.61	18	16.47	34	5.67
120-139.9	6.62-8.10	9	8.24	19	3.17
140-159.9	8.11-9.39	7	6.41	8	1.33
160-179.9	9.40-10.52	2	1.83	2	0.33
180-199.9	10.53-11.53	2	1.83	0	0.00
200-219.9	11.54-12.46	1	0.92	0	0.00
Unclassified[c]		0	0.00	10	1.67
Total		111	101.58	321	53.50

[a] Plots 4103, 4104, 4105 (1.09 ha).
[b] Plots 7711, 7712, 7713 (6 ha).
[c] Broken stems.

TABLE 3-10. Distribution by *10-year* age-classes of saguaros in 2-ha plots on north-facing (plot 75K) and south-facing (plot 75H) slopes, Wasson Peak, Saguaro National Monument (west). Age data from Table 2-11. Density given is number of individual saguaros per hectare. Graphed in Fig. 3-10.

Age-class (yrs)	Height (cm)	Slope exposure			
		South-f (75H)		North-f (75K)	
		Number (*N*)	Density (*N*/ha)	Number (*N*)	Density (*N*/ha)
0-9.9	0.00-3.94	3	1.5	0	0.0
10-19.9	3.95-21.76	29	14.5	4	2.0
20-29.9	21.77-59.66	50	25.0	5	2.5
30-39.9	59.67-122.53	57	28.5	6	3.0
40-49.9	122.54-211.22	58	29.0	3	1.5
50-59.9	211.23-318.79	62	31.0	6	3.0
60-69.9	318.80-433.33	18	9.0	15	7.5
70-79.9	433.34-544.77	12	6.0	12	6.0
80-89.9	544.78-647.78	9	4.5	21	10.5
90-99.9	647.79-740.75	8	4.0	12	6.0
100-109.9	740.76-823.98	5	2.5	10	5.0
110-119.9	823.99-898.51	6	3.0	5	2.5
120-129.9	898.52-965.49	2	1.0	3	1.5
130-139.9	965.50-1,026.01	0	0.0	0	0.0
140-149.9	1,026.02-1,081.02	0	0.0	1	0.5
150-159.9	1,081.03-1,131.31	0	0.0	0	0.0
160-169.9	1,131.32-1,177.53	1	0.5	0	0.0
170-179.9	1,177.54-1,220.24	0	0.0	0	0.0
Unclassified[a]		2	1.0	1	0.5
Total		322	161.0	104	52.0

[a] Broken stems.

4
Survivorship, Mortality, and Ontogeny

Age and mortality data for the Saguaro National Monument (east) population provide a basis for evaluation of saguaro survivorship per unit area and permit the generation of life expectancy tables for this population. These data, which span a period of 37 years from 1941 to 1978, further provide information on the changing relationships of biotic and abiotic factors and saguaro survival associated with progressive age-related ontogenetic changes that occur with the growth and development of this long-lived plant species.

Known-age Seedlings and Juveniles

Field observations from 25 February 1965 to 29 November 1978 (N = 38) on 85 naturally growing saguaros germinated at Saguaro National Monument (east) during the summer of 1964 (see Steenbergh and Lowe 1969) were used to determine survivorship for saguaros during the first 14 years of life (Table 4-1). Graphic analysis and least-squares regressions of the data in Table 4-1 were used to generate smoothed survival values shown in Table 4-2 and the 14-year survivorship curve graphed in Fig. 4-1.

Values for the first-year segment of the smoothed curve were calculated by semilogarithmic regression of survivors (Y) on age (X) in days from 30 June 1964 (Table 4-1, observations 1-17; Table 4-3, equation 1). The predicted initial cohort ($\hat{Y}$) for 15 July 1964 (X = 15 days) is 1560.5 seedlings (Table 4-2).

Preliminary values for the second segment of the smoothed curve (years 2-14) were generated by semilogarithmic regression of survivors (Y) on reciprocal transform ($1/X$) of age in days from 30 June 1964 (Table 4-1, observations 18-38). The curve is described by equation 2 in Table 4-3. The 14-year intercept ($\hat{Y}$ = 3.059) of this preliminary curve was then adjusted to correspond with actual survival to 15 July 1978 (observed N = 3, Table 4-1). The adjusted curve is described by equation 3 (Table 4-3), used to generate adjusted 2 to 14-year survival values shown in Table 4-2 and graphed in Fig. 4-1.

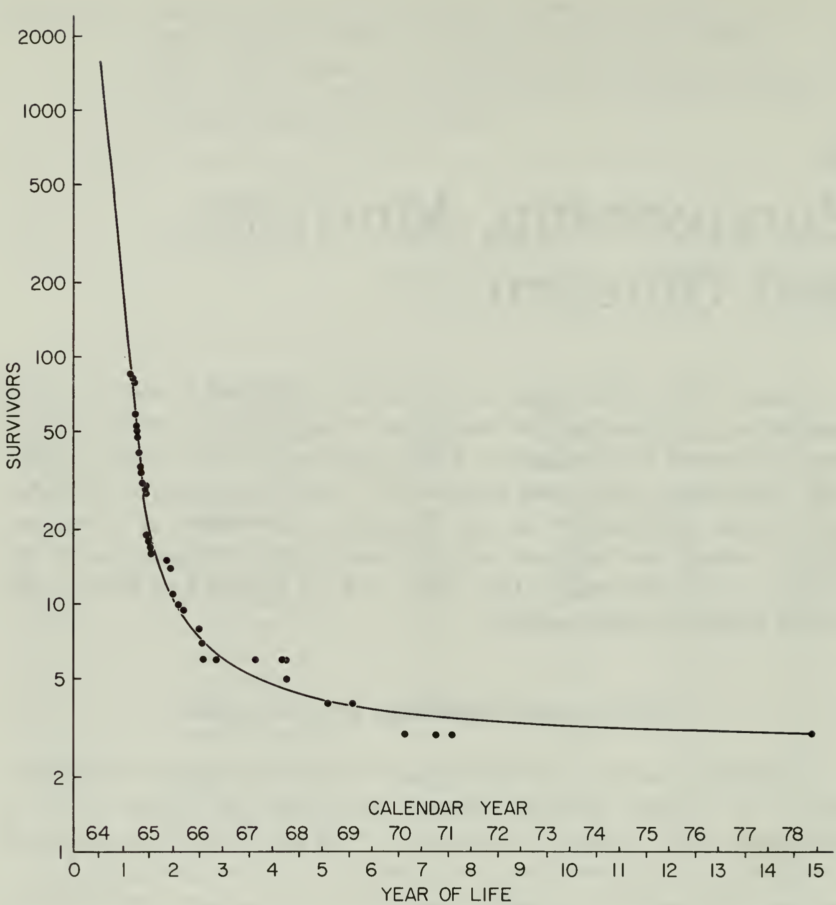


Fig. 4-1. Smoothed semilogarithmic curve of saguaro survival, age 1-14 years (1964-1978) at Saguaro National Monument (east), seedling class of 1964, survivors on age. Observed survival data (circles) in Table 4-1. Regression equations and adjusted ($\hat{Y}$) survival values in Tables 4-2 and 4-3.

TABLE 4-1. Survival of wild saguaro seedlings (class of 1964 N = 85) at Saguaro National Monument (east), 25 February 1965 to 29 November 1978. Graphed in Figs. 4-1, 4-3, and 4-4.

	Date	Days from June 30, 1964	Survivors (N)
		Year 1	
1.	Feb. 25, 1965	240	85
2.	Mar. 11, 1965	254	83
3.	Mar. 18, 1965	261	81
4.	Mar. 25, 1965	268	78
5.	Apr. 1, 1965	275	59
6.	Apr. 8, 1965	282	52
7.	Apr. 15, 1965	289	51
8.	Apr. 22, 1965	296	47
9.	Apr. 29, 1965	303	41
10.	May 6, 1965	310	36
11.	May 13, 1965	317	34
12.	May 27, 1965	331	31
13.	June 3, 1965	338	30
14.	June 10, 1965	345	29
15.	June 17, 1965	352	28
16.	June 14, 1965	359	19
17.	July 1, 1965	366	18
		Year 2	
18.	July 15, 1965	380	17
19.	July 29, 1965	394	16
20.	Nov. 17, 1965	505	15
21.	Dec. 17, 1965	535	14
22.	Jan. 2, 1966	551	11
23.	Feb. 5, 1966	585	10
24.	Mar. 19, 1966	627	9
25.	July 9, 1966	739	8

TABLE 4-1—*continued*

	Date	Days from June 30, 1964	Survivors (N)
		Years 3-6	
26.	July 30, 1966	760	7
27.	Aug. 6, 1966	767	6
28.	Nov. 13, 1966	866	6
29.	Aug. 27, 1967	1,153	6
30.	Mar. 6, 1968	1,345	6
31.	Apr. 3, 1968	1,373	6
32.	Apr. 10, 1968	1,380	5
33.	Feb. 5, 1969	1,681	4
34.	Aug. 6, 1969	1,863	4
		Years 7-13	
35.	Aug. 30, 1970	2,252	3
36.	Apr. 8, 1971	2,473	3
37.	Aug. 3, 1971	2,590	3
38.	Nov. 29, 1978	5,265	3

TABLE 4-2. Survival of known-age saguaros aged 0-14 years (seedling class of 1964) at Saguaro National Monument (east). Observed survivors graphed in Figs. 4-1, 4-3, and 4-4.

Year	Age (yrs)	Survivors: Observed	Survivors: Adjusted
1964-65	0-1	—	1,560.50
1965-66	1-2	17	20.26
1966-67	2-3	8	7.38
1967-68	3-4	6	5.22
1968-69	4-5	5	4.38
1969-70	5-6	4	3.94
1970-71	6-7	3	3.68
1971-72	7-8	3	3.50
1972-73	8-9	3	3.36
1973-74	9-10	3	3.27
1974-75	10-11	3	3.19
1975-76	11-12	3	3.13
1976-77	12-13	3	3.08
1977-78	13-14	3	3.04
1978-79	14-15	3	3.00

TABLE 4-3. Regression equations for survival of known-age saguaros age 0-14 years at Saguaro National Monument (east) class of 1964; survivors (Y) on days from 30 June 1964. Data in Table 4-1; equations 1 and 3 graphed in Fig. 4-1.

	Years	N	Equation	r
1.	0-1	85	$\log Y = 3.27436 - 0.00541\ X$	0.981
2.	2-14.4	21	$\log Y = 0.41988 + 336.96191/X$	0.964
3.	2-14.0	2	$\log Y = 0.41073 + 340.43734/X$	—

Thirty-four Year Survivorship, 1941-1975

Survival data for saguaros growing in flat and rolling hill habitats at Saguaro National Monument (east) were used to estimate survivorship per unit area and age-specific life expectancy for saguaros aged 14 years and over. Four 2-ha (5 acre) plots (plots 41A, 41B, 41D, and 41F; Table 3-1) established in 1941 (Gill and Lightle 1942) were resurveyed in 1975 providing a 34-year record of survival and cumulative mortality in this population.

A total of 562 saguaros was present in these plots in May 1941 (Gill and Lightle 1942). The total number living in 1975 was 173 plants. Of this total, 21 were plants germinated after the 1941 survey (age less than 34 years), and 10 additional plants were of such small size in 1941 (estimated 1941 height 0.35 to <11.4 cm, age 1 to <12 years) that it is highly probable they were missed in the original survey. These 31 plants living in 1975, not reported for the 1941 survey, are therefore not included in calculations of survivorship. Thus, the 1975 sample includes 142 survivors from the original sample of 562 measured saguaros aged 12 years and over for the 34-year period from 1941-1975 (Table 4-4).

Height-age data given in Table 2-10 are used to determine saguaro age estimates for the analysis. All height-age relationships given follow the "birthday rule," i.e., plants of less than full-year age are assigned to the previous year-class.

The reports of Gill and Lightle (Appendix I) include summary data (density per plot) for living saguaros present in the four 2-ha plots (41A, 41B, 41D, and 41F) in 1941 (Gill and Lightle 1942). Their reports do not, however, include information on initial height-class composition for this particular sample.[1] The 1941 height-class composition for these plots (N

[1]The authors have been unable to determine the disposition, by the entrusted holder, of the original field data which include individual saguaro height measurements recorded during these surveys. Our requests to the holder to obtain copies of existing field data in his possession, from the 1941 surveys conducted by the U.S.D.A., have been refused.

= 562) shown in Table 4-4 (cols. 6 and 7), therefore, is the best available estimate of original height-class composition based on the 1941 height-class distribution (percent of N) of a larger sample (259 ha, N = 12,898 saguaros) of the same population (Section 17, Saguaro National Monument—east) as reported by Gill and Lightle (1946, Table 2). The 1975 height-class distribution shown in Table 4-4 is based on data from our field measurements described in Chapter 3.

Determinations of essential survivorship and age-specific mortality values from these data necessitate a series of preliminary data transformations, extrapolations, and computations that go beyond those usually required to derive values suitable for the construction of a life table. Our employment of such data to obtain useful survivorship and mortality values for a long-lived species represents, in part, a new approach to the difficult problem of constructing life tables for long-lived plant species. For these reasons, we include here the detailed procedures used to derive survivorship values appearing in Tables 4-4, 4-5, and 4-6, and graphed in Fig. 4-2.

The 34-year survival rate (1941-1975) for each of the 1941 height-classes (I_b-V) was used to determine age-specific survivorship by the following steps:

1. Mean ages for height-classes in 1975 shown in Table 4-4 (col. 10) were calculated for each class, using ages obtained by conversion of individual plant height to age as given in Table 2-10. Data on individual height measurements from the original 1941 survey were not available for calculation of mean ages for 1941 height classes. Therefore, the 1975 mean-age less 34 years—the elapsed time interval between surveys—is used as the best estimate of 1941 mean age for each class (Table 4-4, col. 5).

2. Individual age-class limits and year intervals for calculating survivorship (Table 4-5, cols. 2, 3, and 4) are defined by the differences between the mean ages of consecutively older age-classes shown in Table 4-4 (cols. 5 and 10). It should be noted that the intervals for classes II-V (Table 4-5, col. 4), based on differences between these means, are, therefore, less than the timespan of the data; i.e., the 34-year timespan of the data overlaps the shorter span of the class age-interval (Table 4-5, cols. 2 and 3) for each of these four classes.

3. To eliminate the data overlap a proportional estimate of survival for nonoverlapping age ranges (Table 4-5, cols. 2 and 3) was calculated by semilogarithmic regression of log density (Y) on age (X) for an initial cohort of 100 individuals in each of Classes II-V based on the 34-year survival (= %) to 1975 shown in Table 4-4, col. 13. From Table 4-4, values used for calculation of the regression equation for each class are X_1 = col. 5, Y_1 = 100, X_2 = col. 10, and Y_2 = col. 13:

X	Y
(1) 1941 age	1941 density (= 100)
(2) 1975 age	1975 density (= % survival)

TABLE 4-4. Summary of age structure and 34-year survival (1941-1975) of saguaros (N = 562) in four 2-ha plots (41A, 41B, 41D, and 41F) at Saguaro National Monument (east). Height classes (col. 2) as defined by Gill and Lightle (1942). See text.

	1941						1975					
Class	Height		Age		N	% of	Height	Age		N	% of	% Surv.
	ft	cm	years	mean		Total[1]	(cm)	years	mean		Total	(34 yr)
1	2	3	4	5	6	7	8	9	10	11	12	13
I_b	0.37-699	11.4-213.3	12.0-37.9	27.50	39[2]	7.0	323.5-658.7	46-71.9	61.50	37[2]	25.35	92.31
II	7.00-12.99	213.4-396.1	38.0-51.9	45.50	72	12.8	658.8-810.3	72-85.9	79.50	46	32.39	63.89
III	13.00-18.99	396.2-579.0	52.0-59.9	58.22	180	32.0	810.4-940.8	86-99.9	92.22	37	26.06	20.56
IV	19.00-24.99	579.1-761.9	66.0-81.9	73.29	153	27.3	940.9-1068.7	100-115.9	107.29	17	11.97	11.11
V	24.00 +	762.0 +	82.0 +	90.75	118[3]	20.9	1068.8-1165.5	116-129.9	124.75	6[4]	4.23	5.08
Total					562	100.0				142	100.00	24.27

[1] Gill and Lightle (1946), Table 2
[2] Class Ia plants (N = 31), missed in 1941 survey, excluded
[3] Includes 1 unclassified plant (broken stem)
[4] Includes 2 unclassified plants (broken stem)

TABLE 4-5. Summary of saguaro survivorship (N = 562) in four 2-ha plots (41A, 41B, 41D, and 41F) at Saguaro National Monument (east). Class-age estimates based on age and growth rates in Table 2-10. Survivorship per ha graphed in Fig. 4-2. See text.

Class	Age means (yrs)		Interval (yrs)	Survival (%)	Survivorship		
					$X_o = 100$	8 ha	1 ha
1	2[a]	3[b]	4	5	6	7	8
X_o	(27.50)				100.00	182.15	22.77
I_b	27.50- 61.50		34.00	92.31	92.31	168.14	21.02
II	61.51- 79.50		17.99	78.88	72.82	132.64	16.58
III	79.51- 92.22		12.71	55.33	40.29	73.39	9.17
IV	92.23-107.29		15.06	37.76	15.21	27.71	3.46
V	107.30-124.75		17.45	21.65	3.29	6.00	0.75

[a] Age based on estimated mean height of class at beginning of interval.
[b] Age based on mean height of class at end of interval (1975 measurements, Table 4-4).

4. Regression equations calculated in step 3 were used to predict proportional initial survival values ($\hat{Y}$) for each of the nonoverlapping age-classes (II-V) shown in Table 4-5:

X = age at beginning of interval (col. 2)
$\hat{Y}$ = survival at beginning of interval

5. The 1975 survival (from Table 4-5, col. 13) for each class divided by $\hat{Y}$ from step 4—the calculated initial survival for each class—multiplied by 100 gives the adjusted survival percentage (Table 4-5, col. 5) for each nonoverlapping age-class:

$$\text{Adjusted survival \%} = \frac{\text{1975 survival (100)}}{\text{Initial survival}}$$

6. The adjusted survival percentages calculated in step 5 were used to determine the 97-year survivorship of an initial cohort of 100 individuals, from mean age 27.5 years (X_o, Table 4-5, col. 6). Survivorship was obtained by multiplying the number of survivors in each successive age-class by the survival percentage (Table 4-5, col. 5) of the next older class.

7. Proportional values for survivorship per unit area, shown in Table 4-5, cols. 7 and 8, were obtained by application of a conversion factor to the values generated in step 6 (Table 4-5, col. 6). The actual number of Class V survivors was 6 (Table 4-4, col. 11). This divided by the Class V survivorship (Table 4-5, col. 6, = 3.29) is:

$$k = \frac{6}{3.29} = 1.82$$

Each of the survivorship values in Table 4-5, col. 6, multiplied by this constant, gives class survivorship (Table 4-5, col. 7) for the 8-ha sample area.

8. Survivorship per ha (Table 4-5, col. 8, = density per ha) was obtained by dividing survivorship per 8 ha (Table 4-5, col. 7) by 8 (total plot area).

Saguaro Life Table and Survivorship Curve

The adjusted survivorship values for known-age seedling and young juvenile saguaros (Table 4-2) and values based on the above 34-year survival data for saguaros aged 12 years and over from the 1941 plots were used to generate the saguaro life table (Table 4-6) and the life survivorship curve shown in Fig. 4-2. Equivalent survivorship values for these two samples from the same population were obtained by transformation of 0-14-year adjusted survivorship values (1964 seedling cohort) to density per ha survivorship as follows:

1. By equation 3, Table 4-7, the predicted density per ha ($\hat{Y}$) of the 1941 sample at age 14 years (X) is 23.504.

2. This value divided by the actual survival of the 1964 seedling class to age 14 (N = 3; Table 4-1) is:

$$k = \frac{23.504}{3} = 7.835$$

3. Multiplied by this constant (7.835), the adjusted 0-14-year survivorship values shown in Table 4-2 are transformed to density per ha survivorship (l_x per ha) shown in Table 4-6.

An overall reduction in annual mortality associated with increase in age and size (growth) is evident in the year-to-year survival of saguaros during the seedling (first year) and juvenile stages of growth (Tables 4-2, 4-6; Fig. 4-1). The graphs of observed survival for the seedling class of 1964 (Table 4-1; Figs. 4-3 and 4-4), however, show important fundamental patterns of age-specific and seasonal mortality that are masked by the smoothed survivorship curves and life table data (Figs. 4-1 and 4-2; Table 4-6).

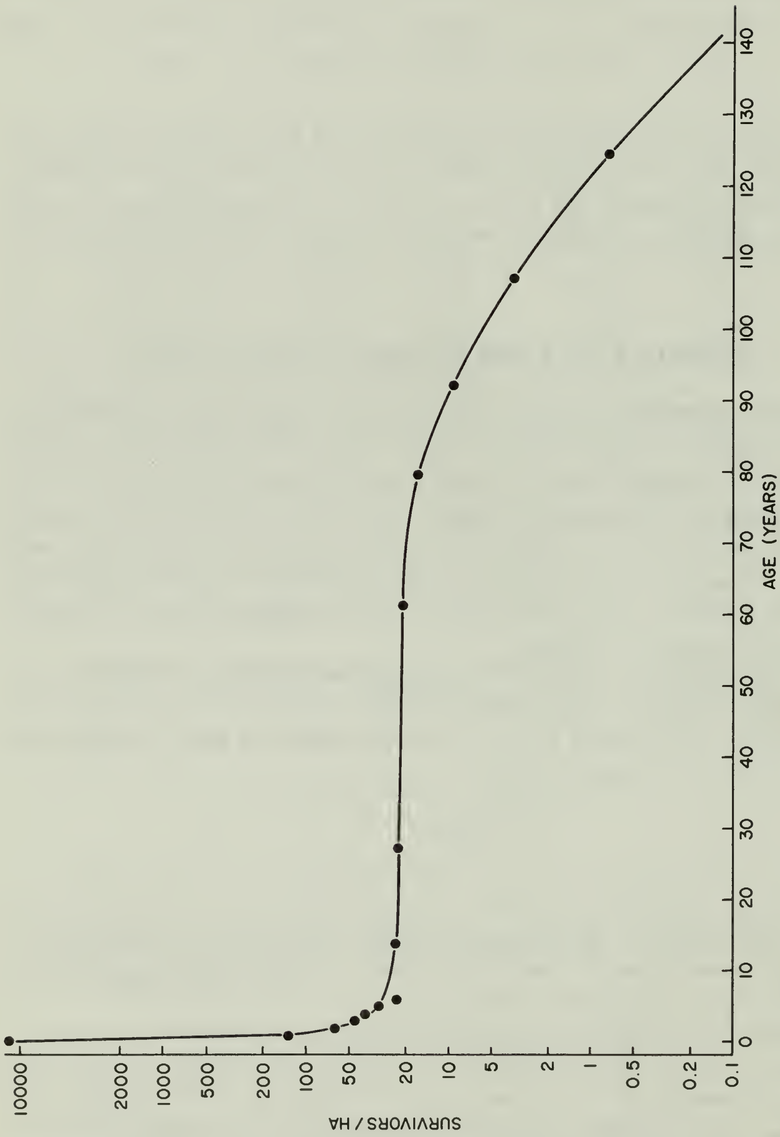


Fig. 4-2. Life survivorship curve, 0-141 years, on semilogarithmic coordinates, Saguaro National Monument (east), survivors on age. Regression equations in Table 4-7. Survival data in Tables 4-1, 4-2, 4-4, and 4-5. Life table data in Table 4-6.

TABLE 4-6. Life table for saguaros at Saguaro National Monument (east). Survival data in Tables 4-1, 4-2, 4-4, and 4-5. Survivorship (den/ha) graphed in Fig. 4-2.

Standard demographic notation used is: x = age in years; l_x = number of individuals surviving at the beginning of the age interval; d_x = number of deaths during the age interval; q_x = mortality rate; L_x = the mean number of plants alive between age x *and* $x + 1$; T_x = the sum of the mean number of plants alive (L_x) in year-classes $x - x_n$ used to calculate e_x, *expectation of life* ($e_x = T_x / l_x$). $k = 8.17909$, the constant used to calculate values for the hypothetical cohort, 100,000 individuals.

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
0-1	12,226.3	100,000	98,702	98,702.0	50,649.0	68,218.0	.68
1-2	158.7	1,298	825	63,559.3	885.5	17,569.0	13.54
2-3	57.8	473	139	29,386.9	403.5	16,683.5	35.27
3-4	40.9	334	53	15,868.3	307.5	16,280.0	48.74
4-5	34.3	281	28	9,964.4	267.0	15,972.5	56.84
5-6	30.9	253	18	7,114.6	244.0	15,705.5	62.08
6-7	28.8	235	11	4,680.9	229.5	15,461.5	65.79
7-8	27.4	224	9	4,017.9	219.5	15,232.0	68.00
8-9	26.3	215	6	2,790.7	212.0	15,012.5	69.83
9-10	25.6	209	5	2,392.3	206.5	14,800.5	70.82
10-11	25.0	204	4	1,960.8	202.0	14,594.0	71.54
11-12	24.5	200	3	1,500.0	198.5	14,392.0	71.96
12-13	24.1	197	2	1,015.2	196.0	14,193.5	72.05
13-14	23.8	195	3	1,538.5	193.5	13,997.5	71.78
14-15	23.5	192	0	0.0	192.0	13,804.0	71.90
15-16	23.4	192	1	520.8	191.5	13,612.0	70.90
16-17	23.4	191	0	0.0	191.0	13,420.5	70.26
17-18	23.3	191	1	523.6	190.5	13,229.5	69.26
18-19	23.3	190	0	0.0	190.0	13,039.0	68.63
19-20	23.2	190	0	0.0	190.0	12,849.0	67.63

TABLE 4-6—*continued*

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
20-21	23.2	190	1	526.3	189.5	12,659.0	66.63
21-22	23.1	189	0	0.0	189.0	12,469.5	65.98
22-23	23.1	189	1	529.1	188.5	12,280.5	64.98
23-24	23.0	188	0	0.0	188.0	12,092.0	64.32
24-25	23.0	188	1	531.9	187.5	11,904.0	63.32
25-26	22.9	187	0	0.0	187.0	11,716.5	62.66
26-27	22.8	187	1	534.8	186.5	11,529.5	61.66
27-28	22.8	186	0	0.0	186.0	11,343.0	60.98
28-29	22.7	186	0	0.0	186.0	11,157.0	59.98
29-30	22.7	186	1	537.6	185.5	10,971.0	58.98
30-31	22.6	185	0	0.0	185.0	10,785.5	58.30
31-32	22.6	185	1	540.5	184.5	10,600.5	57.30
32-33	22.5	184	0	0.0	184.0	10,416.0	56.61
33-34	22.5	184	1	543.5	183.5	10,232.0	55.61
34-35	22.4	183	0	0.0	183.0	10,048.5	54.91
35-36	22.4	183	0	0.0	183.0	9,865.5	53.91
36-37	22.3	183	1	546.4	182.5	9,682.5	52.91
37-38	22.3	182	0	0.0	182.0	9,500.0	52.20
38-39	22.2	182	1	549.5	181.5	9,318.0	51.20
39-40	22.2	181	0	0.0	181.0	9,136.5	50.48
40-41	22.1	181	1	552.5	180.5	8,955.5	49.48
41-42	22.1	180	0	0.0	180.0	8,775.0	48.75
42-43	22.0	180	0	0.0	180.0	8,595.0	47.75
43-44	22.0	180	1	555.6	179.5	8,415.0	46.75
44-45	21.9	179	0	0.0	179.0	8,235.5	46.01
45-46	21.8	179	1	558.7	178.5	8,056.5	45.01
46-47	21.8	178	0	0.0	178.0	7,878.0	44.26

TABLE 4-6—*continued*

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
47-48	21.7	178	1	561.8	177.5	7,700.0	43.26
48-49	21.7	177	0	0.0	177.0	7,522.5	42.50
49-50	21.6	177	0	0.0	177.0	7,345.5	41.50
50-51	21.6	177	1	565.0	176.5	7,168.5	40.50
51-52	21.5	176	0	0.0	176.0	6,992.0	39.73
52-53	21.5	176	1	568.2	175.5	6,816.0	38.73
53-54	21.4	175	0	0.0	175.0	6,640.5	37.95
54-55	21.4	175	0	0.0	175.0	6,465.5	36.95
55-56	21.3	175	1	571.4	174.5	6,290.5	35.95
56-57	21.3	174	0	0.0	174.0	6,116.0	35.15
57-58	21.2	174	1	574.7	173.5	5,942.0	34.15
58-59	21.2	173	0	0.0	173.0	5,768.5	33.34
59-60	21.1	173	0	0.0	173.0	5,595.5	32.34
60-61	21.1	173	1	578.0	172.5	5,422.5	31.34
61-62	21.0	172	1	581.4	171.5	5,250.0	30.52
62-63	20.9	171	2	1,169.6	170.0	5,078.5	29.70
63-64	20.7	169	1	591.7	168.5	4,908.5	29.04
64-65	20.5	168	2	1,190.5	167.0	4,740.0	28.21
65-66	20.3	166	2	1,204.8	165.0	4,573.0	27.55
66-67	20.1	164	2	1,219.5	163.0	4,408.0	26.88
67-68	19.8	162	2	1,234.6	161.0	4,245.0	26.20
68-69	19.6	160	2	1,250.0	159.0	4,084.0	25.53
69-70	19.4	158	2	1,265.8	157.0	3,925.0	24.84
70-71	19.1	156	2	1,282.1	155.0	3,768.0	24.15
71-72	18.9	154	2	1,298.7	153.0	3,613.0	23.46
72-73	18.6	152	2	1,315.8	151.0	3,460.0	22.76
73-74	18.3	150	2	1,333.3	149.0	3,309.0	22.06

TABLE 4-6—*continued*

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
74-75	18.1	148	2	1,351.4	147.0	3,160.0	21.35
75-76	17.8	146	2	1,369.9	145.0	3,013.0	20.64
76-77	17.5	144	3	2,083.3	142.5	2,868.0	19.92
77-78	17.3	141	2	1,418.4	140.0	2,725.5	19.33
78-79	17.0	139	2	1,438.8	138.0	2,585.5	18.60
79-80	16.7	137	4	2,919.7	135.0	2,447.5	17.86
80-81	16.2	133	5	3,759.4	130.5	2,312.5	17.39
81-82	15.6	128	5	3,906.3	125.5	2,182.0	17.05
82-83	15.0	123	5	4,065.0	120.5	2,056.5	16.72
83-84	14.4	118	5	4,237.3	115.5	1,936.0	16.41
84-85	13.8	113	5	4,424.8	110.5	1,820.5	16.11
85-86	13.2	108	5	4,629.6	105.5	1,710.0	15.83
86-87	12.6	103	5	4,854.4	100.5	1,604.5	15.58
87-88	12.0	98	4	4,081.6	96.0	1,504.0	15.35
88-89	11.5	94	5	5,319.1	91.5	1,408.0	14.98
89-90	10.9	89	4	4,494.4	87.0	1,316.5	14.79
90-91	10.4	85	5	5,882.4	82.5	1,229.5	14.46
91-92	9.8	80	4	5,000.0	78.0	1,147.0	14.34
92-93	9.3	76	4	5,263.2	74.0	1,069.0	14.07
93-94	8.8	72	4	5,555.6	70.0	995.0	13.82
94-95	8.3	68	4	5,882.4	66.0	925.0	13.60
95-96	7.9	64	3	4,687.5	62.5	859.0	13.42
96-97	7.4	61	4	6,557.4	59.0	796.5	13.06
97-98	7.0	57	3	5,263.2	55.5	737.5	12.94
98-99	6.6	54	4	7,407.4	52.0	682.0	12.63
99-100	6.2	50	3	6,000.0	48.5	630.0	12.60

TABLE 4-6—*continued*

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
100-101	5.8	47	3	6,383.0	45.5	581.5	12.37
101-102	5.4	44	3	6,818.2	42.5	536.0	12.18
102-103	5.0	41	2	4,878.0	40.0	493.5	12.04
103-104	4.7	39	3	7,692.3	37.5	453.5	11.63
104-105	4.4	36	3	8,333.3	34.5	416.0	11.56
105-106	4.1	33	2	6,060.6	32.0	381.5	11.56
106-107	3.8	31	2	6,451.6	30.0	349.5	11.27
107-108	3.5	29	2	6,896.6	28.0	319.5	11.02
108-109	3.3	27	2	7,407.4	26.0	291.5	10.80
109-110	3.0	25	2	8,000.0	24.0	265.5	10.62
110-111	2.8	23	2	8,695.7	22.0	241.5	10.50
111-112	2.6	21	2	9,523.8	20.0	219.5	10.45
112-113	2.4	19	1	5,263.2	18.5	199.5	10.50
113-114	2.2	18	1	5,555.6	17.5	181.0	10.06
114-115	2.0	17	2	11,764.7	16.0	163.5	9.62
115-116	1.9	15	1	6,666.7	14.5	147.5	9.83
116-117	1.7	14	1	7,142.9	13.5	133.0	9.50
117-118	1.6	13	1	7,692.3	12.5	119.5	9.19
118-119	1.4	12	1	8,333.3	11.5	107.0	8.92
119-120	1.3	11	1	9,090.9	10.5	95.5	8.68
120-121	1.2	10	1	10,000.0	9.5	85.0	8.50
121-122	1.1	9	1	11,111.1	8.5	75.5	8.39
122-123	1.0	8	1	12,500.0	7.5	67.0	8.38
123-124	0.9	7	0	0.0	7.0	59.5	8.50
124-125	0.8	7	1	14,285.7	6.5	52.5	7.50
125-126	0.7	6	1	16,666.7	5.5	46.0	7.67

TABLE 4-6—*continued*

x	l_x per ha	kl_x	kd_x	kq_x	kL_x	kT_x	e_x
126-127	0.7	5	0	0.0	5.0	40.5	8.10
127-128	0.6	5	1	20,000.0	4.5	35.5	7.10
128-129	0.5	4	0	0.0	4.0	31.0	7.75
129-130	0.5	4	0	0.0	4.0	27.0	6.75
130-131	0.4	4	1	25,000.0	3.5	23.0	5.75
131-132	0.4	3	0	0.0	3.0	19.5	6.50
132-133	0.4	3	0	0.0	3.0	16.5	5.50
133-134	0.3	3	1	33,333.3	2.5	13.5	4.50
134-135	0.3	2	0	0.0	2.0	11.0	5.50
135-136	0.3	2	0	0.0	2.0	9.0	4.50
136-137	0.2	2	0	0.0	2.0	7.0	3.50
137-138	0.2	2	1	50,000.0	1.5	5.0	2.50
138-139	0.2	1	0	0.0	1.0	3.5	3.50
139-140	0.2	1	0	0.0	1.0	2.5	2.50
140-141	0.1	1	0	0.0	1.0	1.5	1.50
141-142	0.1	1	1	100,000.0	0.5	0.5	0.50

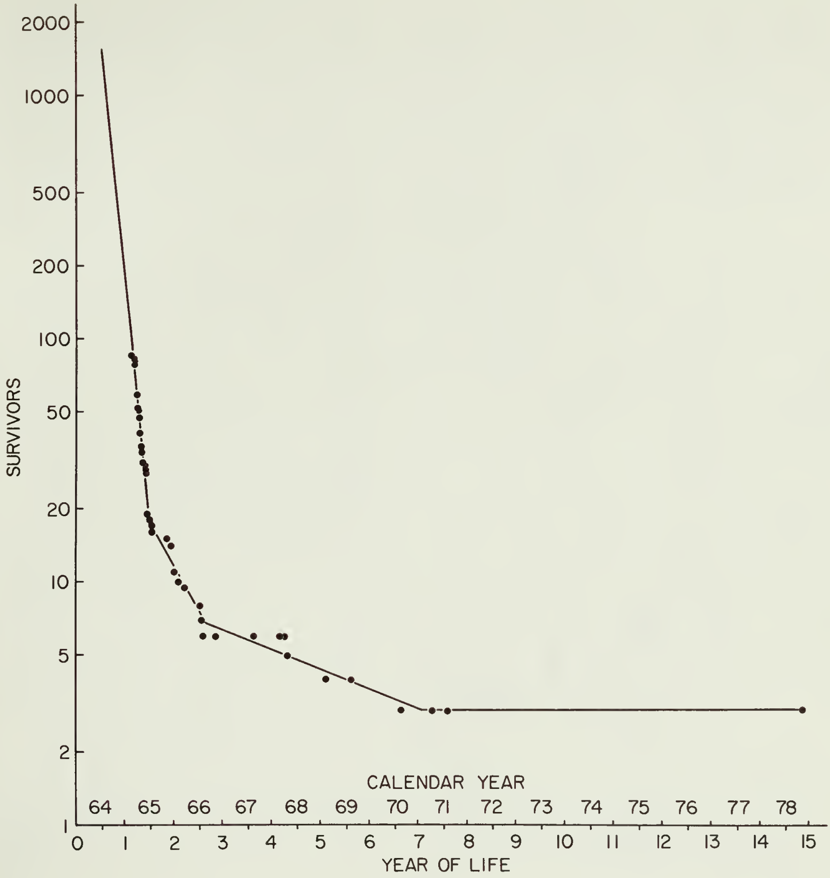


Fig. 4-3. Segmented curve, semilogarithmic regressions of saguaro survival (seedling class of 1964) on age at Saguaro National Monument (east), 1964-1978. Regression equations in Table 4-8. Observed survival data (circles) in Table 4-1.

Changing responses to environmental factors with growth and age are evidenced by abrupt reductions in the slope of successive curve segments. There is no mortality during the 7th through 14th year of life.

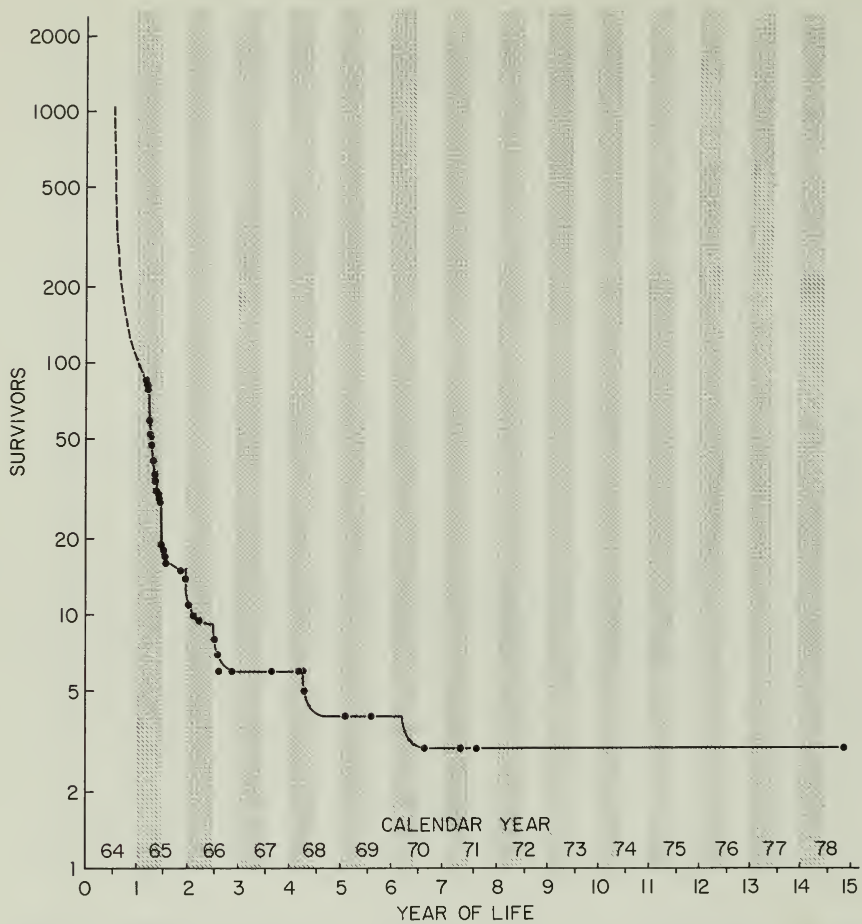


Fig. 4-4. Seasonal survival-mortality on semilogarithmic coordinates of saguaro survival (seedling class of 1964) at Saguaro National Monument (east). Shaded intervals, January-June; unshaded intervals, July-December. Survival data (circles) in Table 4-1.

The series of successively dampened curves is a result of increasing differential summer and winter mortality with age and increasing size of the plant. Dampening oscillations represent a transition from relatively intensive biseasonal biotic- and abiotic- caused mortality during the first 3 years of life to primarily density-independent, climatically caused (freeze-caused) mortality in subsequent years.

Short-term changing responses of seedling and young juvenile saguaros to seasonally operative limiting factors with growth and age is shown by oscillations in the curve of observed survival shown in Fig. 4-4 (Table 4-1). The oscillations express a clearly defined and predictable pattern of seasonal (summer-fall and winter-spring) mortality. The series of progressively dampened curves is a result of increasing differential rates of summer and winter mortality with age and increased size of the plant—the ratio of summer/winter mortality decreases with age. The dampening oscillations (and increasing life expectancy) represent a shift from density-dependent, biseasonal mortality (biotic factors) and density-independent mortality (abiotic factors) during earliest years of life to primarily density-independent, winter-kill mortality during later years.

The saguaro survivorship curve for the Saguaro National Monument (east) population shown in Fig. 4-5a illustrates the special case for northern populations of a subtropical species growing in a *warm-temperate* climatic environment, i.e., populations subject to natural selection by recurring catastrophic freezes. The curve is an expression of the changing role of biotic and abiotic factors with growth and the relationships of saguaro size and stem geometry to saguaro mortality and survival.

The steeply descending initial curve, which characterizes survivorship during the seedling and early juvenile stages of life, flattens with the start of the adult (reproductive) stage of life. Low rates of annual mortality expressed by the relatively flat mid-section of the curve are a measure of the adaptive significance of the saguaro stem geometry that occurs in the 0.5-3.8-m range of saguaro height. Maximum resistance to freeze-caused injury is directly related to the thermodynamically favorable stem form that is associated with this period of growth (Lowe 1966).

Natural selection for freeze resistance in the adult population is expressed by relatively rapid changes in annual mortality rates, life expectancy, and the sigmoid form of the survivorship curve after the 60th year of life. The annual mortality rate sharply increases during the 60th-85th years of life (5.1-8.0 m in height) as a result of the selective removal, by freezing, of cold-intolerant individuals from the population. Differential survival of the more freeze-resistant individuals is expressed by progressively reduced annual mortality rates and the decreasing slope of the survivorship curve after the 85th year of life (Table 4-6; Fig. 4-2).

Figure 4-5b presents the model for saguaro survivorship in *tropical-temperate* environments—the relatively frost-free southernmost portions of the species distribution. In winter-warm environments, the annual rate of adult saguaro mortality increases *gradually* with growth and age of the plant. Thus, in the absence of catastrophic freezes the sigmoid undulation in the adult survivorship curve characteristic of northern populations (Fig. 4-5a) does not occur. Rather, there is, with increasing age, a gradual transition in form from Deevey's (1947) Type III ("positively skew rectangular") curve for seedling and juvenile saguaro survivorship to a Type I ("negatively skew rectangular") survivorship curve for the adult saguaros.

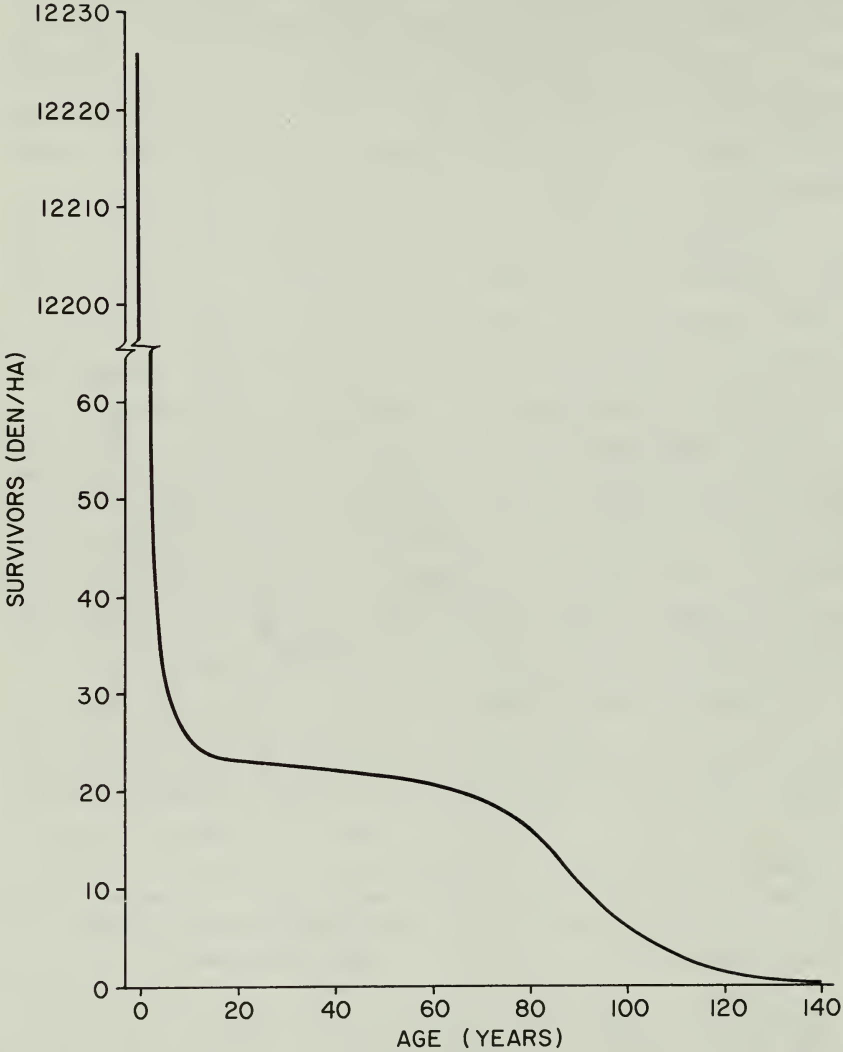


Fig. 4-5a. Saguaro life survivorship curve for populations at Saguaro National Monument (east) on arithmetic coordinates. Data in Table 4-6.

The curve for this population growing in a warm-temperate (winter-cold) environment illustrates the special case for survival in a subtropical species population subject to natural selection for freeze resistance. The sigmoid undulation in the curve beginning at approximately 60 years (5.1 m in ht) occurs with sharply increasing annual mortality rates—a result of selective removal, by freezing, of cold-intolerant individuals from the population.

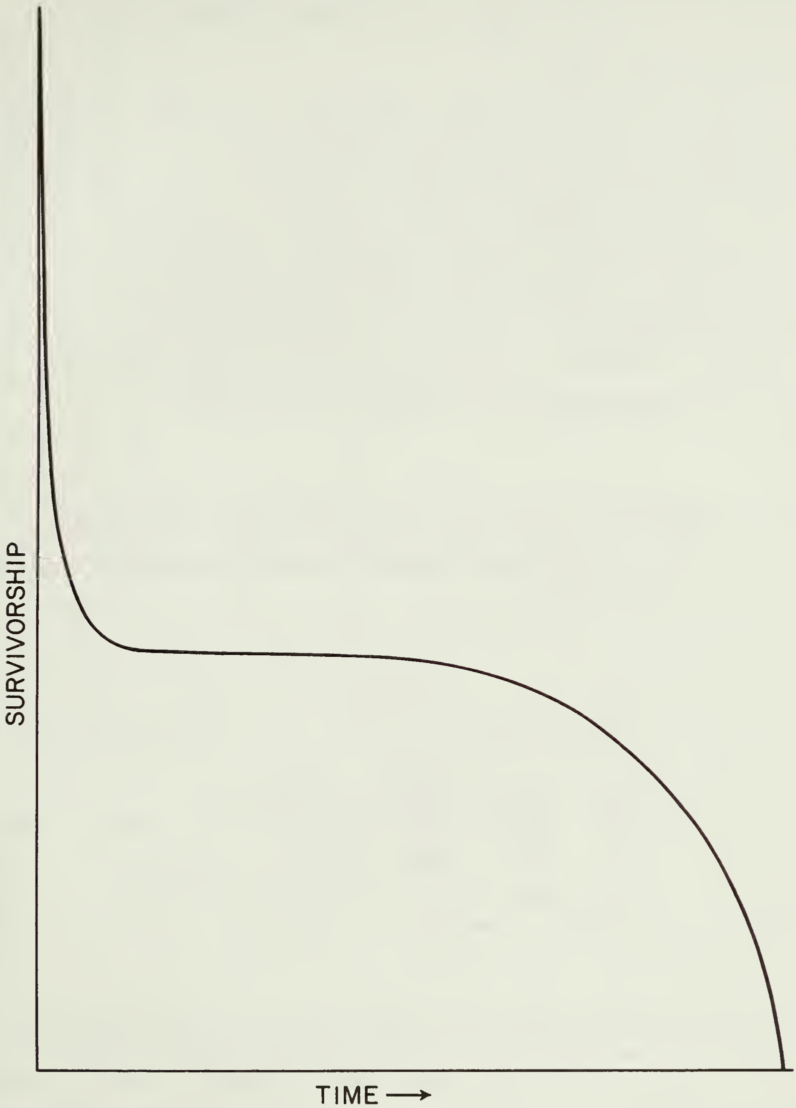


Fig. 4-5b. General model of the saguaro survivorship curve for populations growing in tropical-temperate environments. In the absence of recurring catastrophic freezes, natural attrition by other climatic factors gradually increases with growth and age of the adult plant. Thus, midsized adult saguaros in these southern populations have (1) lower annual mortality rates and (2) longer life expectancies than individuals of the same size growing in colder northern (warm-temperate) environments. Compare with Figure 4-5a.

Age, Ontogeny, and Vulnerability

Ontogenetic change with age

A series of physical changes and relationships that accompany distinct stages of saguaro development from germination to full maturity significantly relate to differential rates of survival that occur with increasing age. These are changes in stem form, surface architecture, aboveground/underground stem-height ratio, spine characteristics, and the physical character of the stem apex. Significant age-associated changes in these structural characteristics that relate to changes in survival rates are described here (See Tables 4-1, 4-6, 4-7, and 4-8; Figs. 4-2, 4-3, and 4-5). The changes described do not, of course, occur abruptly but, rather, as gradual transitions during the continuing growth process.

TABLE 4-7. Regression equations for smoothed survivorship curve graphed in Fig. 4-2. Age (X) on density per ha (Y). Age 0-14 (equations 1 and 2): X = age in days from June 30; age 15-141 (equations 3-5): X = age in years.

	Age (yrs)	Equation
1.	0-1	$\log Y = 4.16840 - 0.00541\,X$
2.	2-14	$\log Y = 1.30476 + 340.43734/X$
3.	15-61	$\log Y = 1.38543 - 0.00102\,X$
4.	62-79	$\log Y = 1.23255 + 0.00702\,X - 0.00009\,X^2$
5.	80-141	$\log Y = 0.63031 + 0.03104\,X - 0.00029\,X^2$

TABLE 4-8. Regression equations for survival of known-age saguaros age 0-14 years at Saguaro National Monument (east); log survivors (Y) on days (X) from June 30, 1964. Data in Table 4-1. Graphed in Fig. 4-3.

	Years	Age (yrs)	N	Equation	r
1.	1964-65	0-1	17	$\log Y = 3.27436 - 0.00541\,X$	0.981
2.	1965-66	1-2	8	$\log Y = 1.61353 - 0.00099\,X$	0.942
3.	1966-70	2-6	10	$\log Y = 1.00313 - 0.00022\,X$	0.921
4.	1970-78	7-14	4	$\log Y = 0.47712 - 0.00000\,X$	1.000

Earlier in this report we described *size-related* changes in growth rates associated with changes in stem form and phenological events. *Age-related* changes described in this section are specifically applicable to the Saguaro National Monument (east) population from which the survivorship data were drawn (Tables 4-1, 4-4, and 4-6). The ages at which these events occur are *size-dependent.* Thus, the *size* at which the described development occurs remains relatively constant in Arizona populations examined during this investigation. The *age* at which development occurs, however, varies from one growth environment to another and will depend in each case upon the growth rate in the specific environment of the population in question. Furthermore, it must be noted that even within the population described there exists considerable individual variation in the structural characteristics and the age at which they occur.

Distinctive ontogenetic growth-form stages are illustrated in Figure 4-6. Descriptive terminology used here is synonymous with and equivalent to terms we have previously used to identify these forms.[2]

The saguaro at germination is a more or less globular mass of succulent tissue—the *bulbous seedling* form (Fig. 4-6a). The first fine, hairlike spines develop within a few days, followed by the growth in pairs of small tubercles, each bearing a cluster of short (2-3 mm) soft spines. The *total* stem of the 1-year-old saguaro (aboveground height 0.35 cm) is egg-shaped (ovoid). Approximately 40% of the total stem height projects above the soil surface; the remaining 60% of the stem is situated *in* the ground (underground stem). The hemispherical aboveground portion of the stem has 8-16 well-defined tubercles—the *tuberculate juvenile* form, Fig. 4-6a—each bearing a single cluster of approximately six 0.5 cm, stiff, hairlike spines growing from a small mass of short, feltlike hairs surrounding the areole at the tip of each tubercle.

The young saguarro continues to retain the egg-shaped *total* stem form through the second and succeeding years to approximately 8 years of age. At age 2 years (aboveground height 0.51 cm), the aboveground portion of the stem increases to approximately 50% of the total stem height and is slightly spherical in form. The number of tubercles increases to approximately 24 during the second year. Spines are bristlelike, approximately 7-8 mm in length.

At the end of the third year of growth (aboveground height 0.73 cm) the aboveground portion of the stem increases to approximately 60% of total stem height and assumes the nearly spherical form which it retains through the seventh year of life. The tapered spines are slightly thicker and stiffer, with maximum spine lengths of approximately 10-12 mm at the apex.

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[2] *Tuberculate juvenile* = "globose juvenile"; *clubform juvenile* = "club" = "columnar juvenile"; *bowlingpin adult* = "wine-bottle" = "bowling-pin"; *branched adult* = "mature adult."

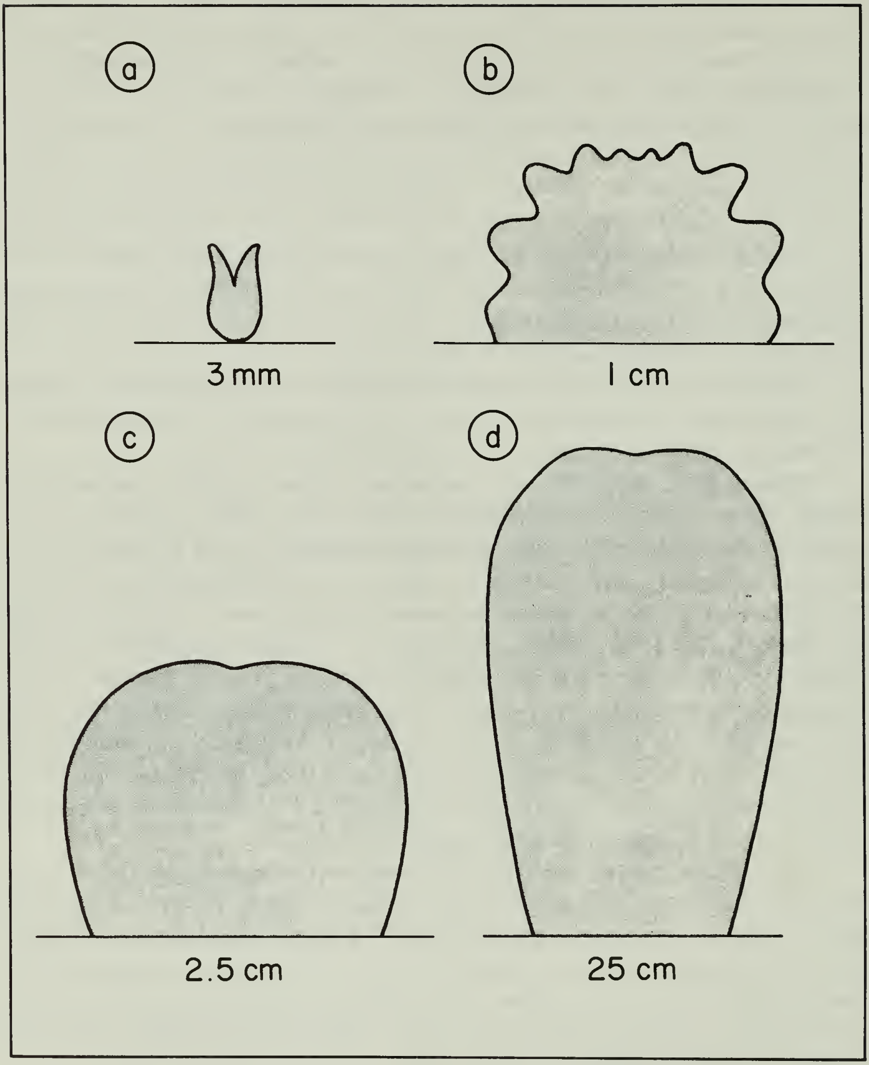

Fig. 4-6a. Ontogeny of saguaro stem geometry—seedling and juvenile stages: (a) *Bulbous Seedling.* The seedling at germination and directly afterward is a bulbous mass of succulent tissue. (b) *Tuberculate Juvenile.* The tuberculate, or hemispherical form of the young juvenile. Approximately 40-60% of the stem is situated *in* the ground. (c) *Spherical Juvenile.* The spherical form of the early-ribbed juvenile, with tubercles vertically aligned to form 10-13 ribs (flutes). Number of ribs remains constant with growth to approximately 18 cm in height. (d) *Clubform Juvenile.* The club form of older juveniles and subadults. Additional ribs originate at the apex with further height growth and expanding girth of the upper stem.

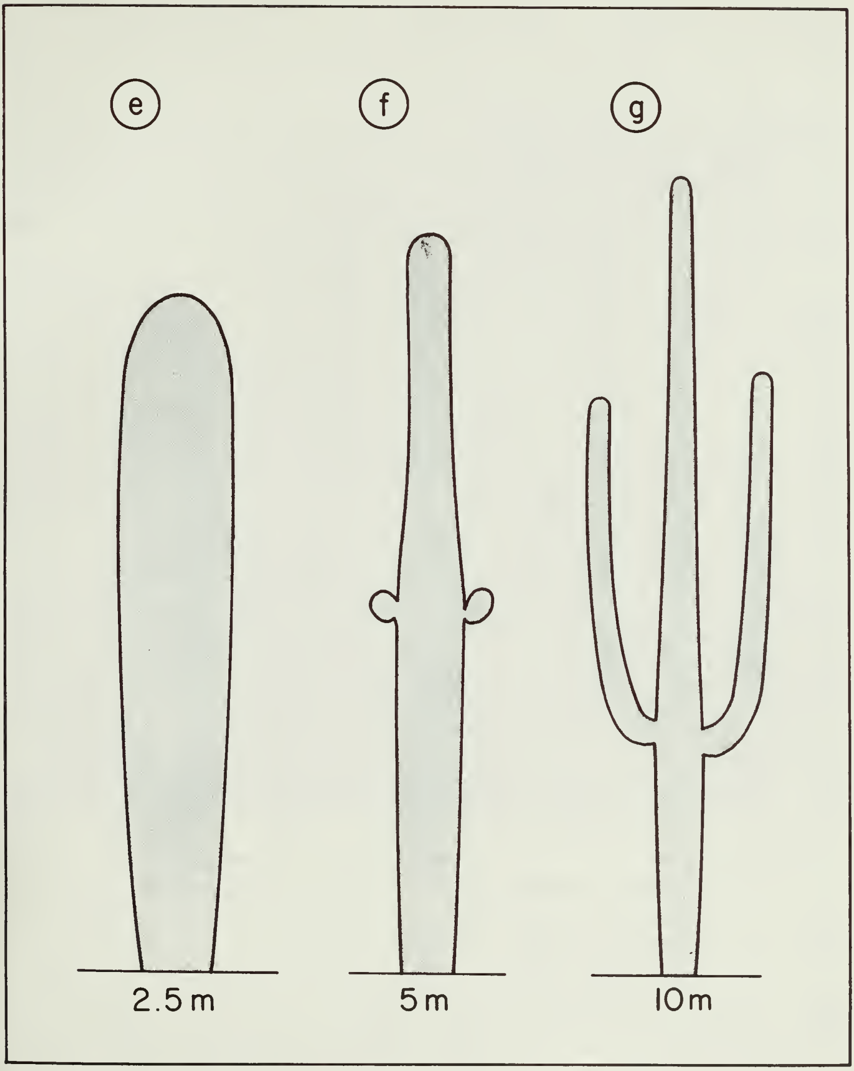

Fig. 4-6b. Ontogeny of saguaro stem geometry—adult stages: (e) *Clubform Adult.* The club form of the young adult at age of first reproductive growth. Stem form usually becomes increasingly ellipsoidal with further height growth. (f) *Bowlingpin Adult.* The common "bowling-pin" form of the prebranching adult. Branches (arms) originate from areoles on the central stem (trunk) at a height of 350-450 cm; this is 100-200 cm below the apex and is the point of maximum stem girth and maximum number of ribs. (g) *Branched Adult* form. Upper-stem diameter continues to decrease with height growth above the point of branching; the number of ribs remains constant.

Rib development (fluting) of the stem occurs abruptly at approximately age 7 years (aboveground height 2.92 cm). At this age, the spherical aboveground portion of the stem—*spherical juvenile form,* Fig. 4-6a—constitutes approximately 80% of the total stem height. During the sixth or seventh year, tubercles become vertically aligned to form 10-13 well-defined ribs (flutes) with areoles on the rib margins bearing slender, needlelike spines approximately 1.5 cm in length near the apex. At this age, the plant has developed well-defined lateral roots which may extend 10 cm or more outward from the base of the plant.

The stem becomes increasingly elongated (columnar; increasing height-diameter ratio) during the 8th through 14th years of life. Elongation of the stem continues through the remainder of the juvenile stage of development—the *clubform juvenile,* Fig. 4-6a. At age 14 (aboveground height 17.4 cm) approximately 85% of the stem is aboveground (underground stem = ca 2-3 cm). The initial number of ribs is 10-13—no additional ribs are added during the 8th through 14th years. At age 14, the plant bears relatively stout apical spines up to 3 cm long surrounding a small mat of dense feltlike hairs at the apex (Fig. 4-7a).

Age 37 (height 206.7 cm) marks the beginning of transition from the *clubform juvenile* stage (Fig. 4-6a) to the *clubform adult* and *bowlingpin adult* forms (Fig. 4-6b) of the unbranched young adult saguaro. At this age, approximately 98% of the stem height is above ground—in an undisturbed situation, we estimate that approximately 10 cm of the stem is situated belowground. In the usual field situation, however, highly variable underground stem depth results from normal long-term soil erosion or deposition at the particular site. Additional ribs develop with expanding girth of the upper stem after age 14. At age 37, ribs on the upper stem have increased to 15-20 in number. Central spines increase in length and diameter, attaining lengths up to 8 cm. Crowded apical spines and woolly hairs surrounding the areoles form a dense protective mat over the slightly depressed apex of the stem (Fig. 4-7b).

A distinctive change in form occurs with growth between ages 37-51 years. At age 51 years (aboveground height 391.1 cm), the plant has attained the *bowlingpin adult* form (Fig. 4-6b) that normally precedes initiation of branch growth. Development of additional ribs continues at a reduced rate, resulting in a usual total of 17-20 upper-stem ribs at this age. The cross-sectional geometry of the individual ribs shifts during this stage of development from the triangular cross-section of juvenile plant ribs to a hyperbolic cross-section—the margins of upper-stem ribs are rounded rather than angular. A marked change in spine character also occurs during this period of growth. Central spines become gradually reduced in length and diameter, with the result that the spines on the upper stem are relatively short (1-3 cm), slender, and needlelike. With this change in spine character the feltlike mass of woolly hairs surrounding each areole increases. This results in a dense, thick, feltlike mat which protectively blankets the apical meristem situated within the depressed apex of the stem.

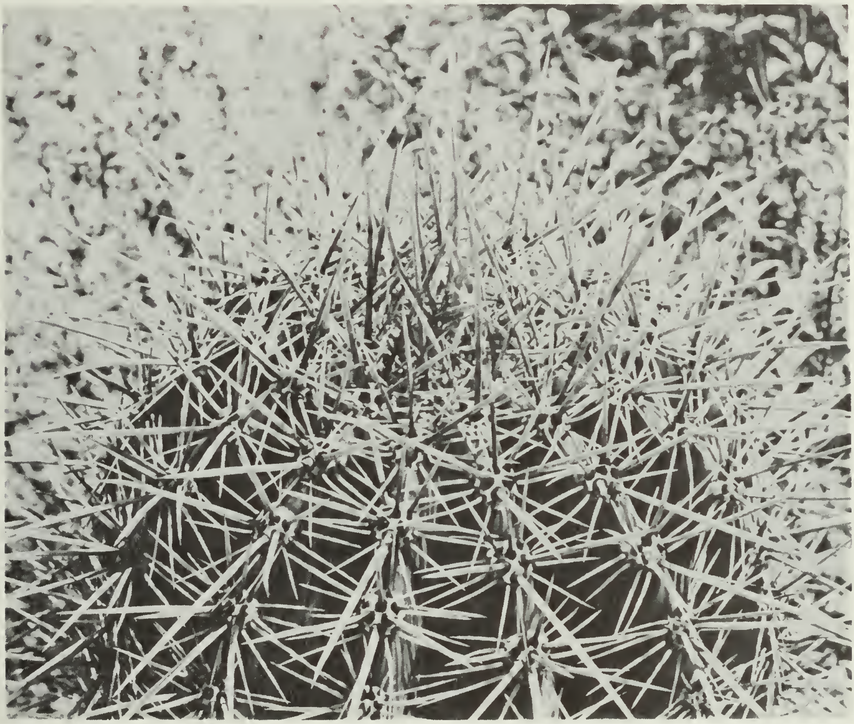

Fig. 4-7a. Apical spines on a juvenile saguaro, 115 cm height. The dense crown of stout spines shades the growing tip of the young plant reducing water loss and provides an effective barrier to potentially destructive mammals. Short woolly hairs (hidden beneath the spines) cover the apex, further reducing moisture loss and protecting the plant against insect invasion. Most important, however, the dense crown of spines together with the woolly hairs that surround the growing tip of the plant function as an efficient thermal barrier which protects the delicate apex against freezing. Photographed 18 May 1979.

At age 65 years (height 561.8 cm), the saguaro normally bears one or more short branches (Fig. 4-6b). These usually originate from areoles 100-200 cm below the growing tip at a height of 350-450 cm on the central stem (trunk), the point of maximum stem girth. At this age, the plant has developed the maximum number of central-stem ribs that will be produced during its lifetime, usually 18-22. Ribs of the central stem remain constant throughout the remaining life of the plant. Spine characteristics and physiognomy of the apex are as previously described and remain so throughout the remaining lifespan of the plant.

Fig. 4-7b. The crowns of adult saguaro stems and branches bear short slender spines and a thick mat of feltlike hairs that grow from the areoles. This insulating blanket of feltlike hairs effectively reduces nocturnal reradiation at the crown where greatest nocturnal heat loss occurs. Thus, the feltlike hairs not only provide protection against freezing for the vulnerable growing tip, but also for developing reproductive structures which are borne at the areoles on the uppermost portion of stems and branches. Photographed 26 June 1979.

At age 85 years (height 758.8 cm), the saguaro has attained the ultimate *branched adult* form (Fig. 4-6b). Curved branches with tips usually 100 cm or more below the tip of the central stem closely resemble the morphology and physiognomy of the upper central stem. Upper-stem diameter decreases with upward growth of the central stem and mature branches, i.e., upper stem and branches gradually taper towards the tips.

Age, size, and mortality factors

Shreve (1920) observed, "The sanguaro appears to suffer from very few diseases and natural enemies, the greatest decimation in its numbers being occasioned by mechanical agencies." Our observations on saguaro mortality over a period of three decades fully support this conclusion with respect to *adult* saguaros. Additional factors, however, play a major role in limiting the establishment and survival of the saguaro through the first years of life.

Saguaro deaths result from a variety of biotic and abiotic causes. The relative importance of individual factors varies with season, habitat differences, size, and stem form. Furthermore, the role and importance of specific factors change with the development and growth of the plant, i.e., vulnerability to specific factors is size (age) related. It is the cumulative effect of this change in vulnerability to specific factors with time that determines the ultimate form of the saguaro survivorship curves shown in Fig. 4-5.

The life expectancy of the young saguaro increases rapidly with age. Most saguaro deaths occur during the first year of life—the establishment period. During this prejuvenile stage of development, the tiny, succulent, weakly rooted seedlings are subject to a broad variety of destructive agents (Steenbergh and Lowe 1969, 1976, 1977). Biotic factors attain their greatest importance during the summer and fall months immediately following germination. During this period a major proportion of the current-year seedling crop is consumed by insects and rodents or uprooted by foraging birds, rodents, and other mammals. Climatic factors—erosion, drought, and winter freezing—are additional major causes of first-year saguaro mortality.

Transition from the seedling to the juvenile stage of development which occurs with the start of the second year of life is accompanied by a marked reduction in mortality. The importance of density-dependent factors—which account for the major proportion of seedling (first-year) deaths—decreases sharply during the second year of life and continues to diminish thereafter as the young plant successively outgrows the individual consumptive capacity of insect and rodent predators (Steenbergh and Lowe 1969, 1977). Drought and erosion are also eliminated as important post-establishment causes of mortality with root growth and increased water storage capacity of the stem that develop during the second year of life. With the decrease in vulnerability to death from these other factors, freezing assumes principal importance. In northern populations of the species, freezing is the primary cause of death of young saguaros that survive earlier exposure to predators and destructive climatic events.

Susceptibility of young saguaros—seedlings and juveniles—to freeze-caused death decreases with age-related changes in size and form of the plant (Lowe 1966; Steenbergh and Lowe 1976). Greatest vulnerability to freezing occurs during the first 4 years of life and declines progressively thereafter with further increase in stem volume. Freezing impact is reduced to its lowest level on older juvenile and unbranched adult saguaros in the 0.5-3.8-m height range. High resistance to freezing of plants within this size-range is associated with the thermodynamically favorable physical characteristics specifically related to stem geometry that occurs during this stage of growth (Lowe 1966). Deaths from biotic and other climatic factors are rare within this size group. Thus the highest survival rates occur within this period of the saguaro lifespan.

Natural deaths of larger adult saguaros, with few exceptions, result from the action of climatic factors, namely freezing, lightning, wind,[2] and fire (Figs. 4-8 to 4-10; Shreve 1920; Hemenway 1934; Lowe 1966; Steenbergh 1970, 1972; Steenbergh and Lowe 1976, 1977).

Vulnerability to death from freezing, lightning, and wind increases with size and age of adult plants. Freezing, however, is the *primary* cause of adult saguaro deaths in the northern portion of the species' range. The increasing surface-volume ratio of the stem that occurs with continued growth and age of the adult plant results in progressively greater vulnerability to freeze-caused injury and death (Lowe 1966; Steenbergh and Lowe 1976).

Few adult saguaro deaths result from action by biotic agents. The large size and natural defense mechanisms of the healthy adult saguaro effectively minimize lethal injuries resulting from biotic factors. A relatively insignificant number of adult saguaro deaths occur as the indirect result of consumption of soft tissues by native mammals—woodrats, jackrabbits, and bighorn sheep—particularly in the most arid western portions of the species range (Simmons 1969; Fig. 4-11). Such damage rarely kills the plant outright, but rather, structurally weakens the plant thereby increasing its vulnerability to destruction by freezing or wind breakage.

Nesting holes drilled in healthy saguaros by woodpeckers are rapidly sealed off completely by *callus tissue* formation and do not kill or seriously injure the plant. Such natural injuries structurally weaken the saguaro stem to a minor degree. Woodpecker holes, especially the larger, re-excavated ones, increase the probability of wind breakage and, most importantly, alter the stem's thermal characteristics. Such nest-hole excavations increase vulnerability of the plant to freezing that is initiated at tree-hole sites. Occasional decapitation is the characteristic result of such secondary injury (Fig. 2-13). However, the direct impact of woodpeckers on saguaro populations is relatively minor. Old giants that are 100-150 years or older may have 40-50 woodpecker holes.

Invasion of soft tissues by tunneling insects, primarily larvae of the noctuid moth, *Cactobrosis fernaldialis* (Hulst), occurs in both healthy and moribund saguaros. These invasions cause no major damage to *healthy* adult and large juvenile saguaros; the tunnels are rapidly sealed off by the formation of callus tissue (Fig. 4-12). Moribund individuals—deficient in this critically important capacity—are subject to a higher frequency of successful invasions by insect larvae. Heavy infestation of larger juvenile and adult saguaros by insects is a subsequent and usual consequence of lethal, freeze-caused injuries.

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[2] "Wind-throw" usually results from loss of root anchorage, which can occur with or without wind, during periods of soil saturation on sites with fine-textured soils.

Neither bacteria nor insects—once believed by some investigators to function interactively as an important cause of adult saguaro deaths[3]—are among the confirmed causes of adult saguaro mortality (Steenbergh 1970; Steenbergh and Lowe 1977).[4] Rather, both are effective agents of tissue breakdown and decomposition which follow damage to living tissues and the disruption of normal physiological functions of the plant by other factors, primarily freezing.

Hemenway (1934:513) observed early on that "Traumatic tissues [wound tissue] in *Carnegiea gigantea* are formed apparently in response to acute wounds made by the plant's natural enemies, birds and insects, and to general surface irritation by weathering." He provides an insightful anatomical comparative analysis of the defensive callus tissue types associated with surface weathering of stems and roots, and those formed at the sites of the excavations into saguaro stems made by animals. Hemenway came to an important conclusion. He tells us correctly and prophetically that

> The success of the cactus in protecting its tender tissues in this way from the effects of acute internal wounds is naturally limited to *injuries which are somewhat localized.* In the case of *general serious injury,* such as, for instance, the result of a bolt of lightning, the cortex and pith tissues ferment so rapidly, especially in hot weather, when the alcoholic stage may be reached within two or three days, *that the plant is apparently unable to develop protective tissue rapidly enough to save itself.* (Italics ours)

Steelink and his associates (1967, 1968) have investigated the chemical processes in saguaro wound-tissue formation that produce the protective callus layer(s) at the site of injury.[5] This highly successful callus-cover defense system evolved through natural selection in pre-Pleistocene time, antedating both Quaternary glaciation and the advent of humans in the New World (Lowe and Steenbergh 1980). It is a marvelously adaptive defense system for the time, place, and its function in the evolution of

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[3]The larva of the noctuid moth, *Cactobrosis fernaldialis,* was described early as a vector of the rot bacterium, *Erwinia carnegieana,* by Boyle (1949). However, Schuyler (1968), using sterile techniques, was unable to confirm that conclusion. Concerning her efforts to recover the bacterium from larvae of this species collected at Saguaro National Monument (east), Schuyler states, "Of 20 larvae found free on the outside of the covered arms, 23 found similarly on uncovered arms, and 146 larvae found on plants (other than the 25 from which flowers were collected), no soft rotting bacteria were recovered."

[4]Our continued observations made on thousands of additional saguaros since the latter report was completed in 1974 further confirm our original observation that no ". . . pathogenic micro-organism is, or ever has been, a significant cause of the death of saguaros . . . ." young or old.

[5]They explain that "When the saguaro cactus is wounded, bacterial infection and necrosis frequently follow, unless a protective callus is formed at the site of injury. This callus is highly ligniferous and contains numerous phenols. The healthy cortical tissue (pulp) is mainly polysaccharide in nature, containing dopamine as the principal phenolic constituent. Dopamine concentrations increase markedly at the site of wounding." (Steelink, Yeung, and Caldwell 1967:1435).

Fig. 4-8a. Freeze-killed saguaro. Freezing is the primary cause of adult saguaro deaths in Arizona and northern Sonora, Mexico. The streams of black fluid are the result of bacterial breakdown of freeze-killed tissues of stem and branch crowns. Massive freeze-caused damage disrupts or disables the saguaro's normal mechanism for walling off damaged tissues, thus allowing the unrestrained spread of decomposition bacteria into seemingly healthy—but effectively dead—adjoining soft tissues of the plant. The resulting spread of bacterial rot into moribund, but still green, tissues has contributed to the erroneous and widespread belief that the condition is caused by a disease. The so-called "bacterial necrosis disease" is a misnomer. *It is not a disease; it is decomposition, a result—not a cause—of saguaro death.* Photographed 23 Mar. 1979.

Fig. 4-8b. Fifteen weeks after lethal injury, dried remains of disintegrated soft tissues cling to the supporting woody framework of a saguaro killed by the freeze of early December 1978. Invasion of moribund tissues by the larvae of tunneling insects hastens the process of bacterial decomposition. Final collapse—and evident death—of freeze-damaged saguaros can occur within a few weeks, or may continue for years after the lethal event, depending upon the severity of the original injury and contributory damage by subsequent freezes. Photographed 23 Mar. 1979.

Fig. 4-9a. Lightning-caused destruction of two adjacent large adult saguaros. The chaotic jumble of broken stems and explosively severed arms surrounding the standing trunk is characteristic. Rapid bacterial decomposition of damaged tissues quickly masks other characteristic evidence of lightning-caused death. Vulnerability to lightning strikes increases with the height (age) of the plant. Photographed 9 Sept. 1969.

Fig. 4-9b. "Wind-thrown" saguaro. Note the shallow root system—the adult saguaro has no taproot. Loss of root anchorage usually occurs, with or without wind, during periods of soil saturation on sites with fine-textured soils. Leaning saguaros such as the individual seen in the background are particularly vulnerable to loss of root anchorage. Photographed 19 Feb. 1968.

Fig. 4-10. Fire-killed saguaros and foothill paloverde trees *(Cercidium microphyllum)* near Phoenix, Arizona. Saguaros of all ages are highly vulnerable to fire-kill. Fire-caused saguaro deaths most commonly occur in mountain habitats at higher elevations with sufficient rainfall to support a more-or-less continuous ground cover of annual and/or perennial grasses. During years with unusually high precipitation, that generates a dense growth of annual grasses and forbs, fires fueled-by the dead, dry plants do occur in more arid habitats. Photographed 18 June 1974.

Fig. 4-11a. Mammal-caused injury to a 5-m tall saguaro, Cabeza Prieta Game Refuge, Arizona. Bighorn sheep and/or jackrabbits in search of moisture have eaten all succulent tissues down to the woody xylem. ''Girdling'' of the stem does not directly cause saguaro death—note the presence of buds and flowers on the stem tip. Such injury does, however, increase the plant's vulnerability to freezing and wind breakage. Photographed 4 May 1971.

Fig. 4-11b. White-throated woodrat *(Neotoma albigula)* damage to a large saguaro, Cabeza Prieta Game Range, Arizona. Mechanical injury by woodrats increases vulnerability to death from freezing and wind. The woodrat is the only mammal capable of surviving on a diet consisting largely of saguaro tissue. Injury to adult saguaros by bighorn sheep, jackrabbits, and woodrats most frequently occurs in the more arid portions of the saguaro's range, but does occur elsewhere, especially during periods of severe drought. Photographed 3 Feb. 1971.

Fig. 4-12a. External callus tissues formed at insect larvae emergence sites on the stem of a healthy adult saguaro. Nearly all adult saguaros bear numerous similar scars resulting from insect invasion. Such scars, however, are rare on juvenile (nonreproductive) plants. Photographed 26 June 1979.

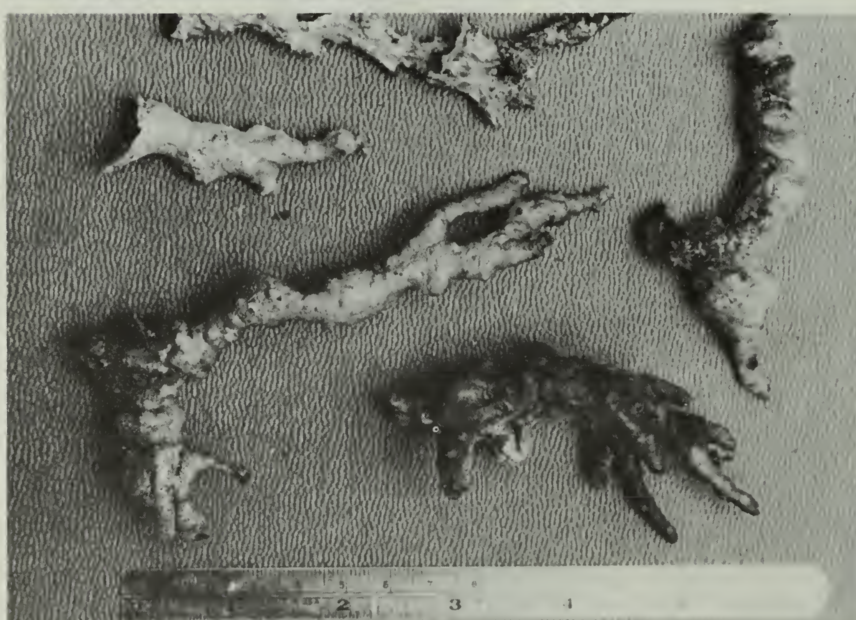

Fig. 4-12b. Insect larvae tunnels walled off by internal callus tissue formation. Damage to healthy saguaros is confined to the immediate area of mechanical injury by rapid formation of callus tissues surrounding the tunnels. In moribund saguaros, however, impairment of the plant's capability to rapidly wall off damaged tissues—resulting from freezing, lightning damage, or other massive mechanical injury—contributes to the growth of decomposition bacteria. Neither insects nor bacteria are a cause of death or significant damage to healthy adult or large juvenile saguaros. Photographed 26 June 1979.

the species, providing genetic fitness in subtropical environments against such high-frequency events as weathering, sandblasting wind actions, and the continual wounding and removal of healthy tissue by native insects, birds, and mammals.

Accordingly, like most other subtropical plants and animals, the individual saguaro's natural body defense mechanisms can be suddenly *overwhelmed* by mechanical actions in catastrophic events such as (1) severe freezing, (2) direct lightning strikes, and (3) massive attack by humans, with axe, machete, machine, and other mechanical devices. The saguaro has not evolved effective defense mechanisms against such outrageous low-frequency environmental insults.

Only one of the three, lightning, was a saguaro killer during the Tertiary evolution of its callus-cover defense system. Lightning is a low-frequency, density-independent lethal event for the saguaro, against which it neither has nor needs special defenses to survive well as a species; we estimate that occasional lightning strikes take out much less than 0.1% of the population per year (see Steenbergh 1972).[6] Accounting for <0.1% mortality per annum, lightning is like wind-throw and other essentially density-independent environmental factors that are effectively limiting on occasional individual plants (or animals) but not on the population or species as a whole.

Our observations on lightning-damaged saguaros (Steenbergh 1972) are entirely consistent with those of Hemenway (1934) as quoted above. Furthermore, our observations and those of others on the massive damage inflicted upon thousands of adult saguaros by the catastrophic freezes of 1962 and 1971 (Niering et al. 1963; Lowe 1964; Steenbergh and Lowe 1976) leave no doubt that freezing also must be included with—and far outranks—lightning as an important cause of such "severe general injury." In both cases the results and the conclusion—that the plant's normal ability to generate protective callus tissue is critically impaired by such massive mechanical damage—are the same.

The saguaro has evolved the ability to survive mechanical injuries, a capability contingent upon its integrity as a whole and functioning organism. Freezing, lightning-damage, or other massive injury—overwhelming mechanical damage—disrupts or disables the plant's normal physiological functions, specifically including the critically important survival mechanism that is the ability to rapidly develop protective callus tissue at sites of mechanical injury. This impairment of the plant's ability to "wall-off" injuries allows the unrestrained spread of decomposition

[6]Values for a single intense storm reported by Steenbergh (1972) are percent lightning-caused saguaro mortality per ha *within the storm path.* Extreme variability is the basic nature of convectional storms in the Sonoran Desert during the monsoons. Accordingly, and in similar degree, the pattern of lightning-caused saguaro mortality occurs as a shifting geographic mosaic, shifting in intensity and in time—on both a seasonal and annual basis—from one segment of the population to another.

bacteria (and insect larvae) into seemingly healthy—still green, but functionally dead—tissues of lethally freeze-damaged saguaros. The resulting progressive bacterial breakdown of this moribund tissue—the so-called "bacterial necrosis disease"—is decomposition, a natural result, not a cause of saguaro death.

5
Overview and Outlook

Viewed within the perspective of an evolutionary time scale, the cacti in general and the saguaro in particular are among the relative newcomers to the plant kingdom. The cold-intolerant saguaro, which has the most northerly distribution (to Lat 35° 6′ N) of any of the columnar cacti, is still actively evolving under the continued powerful selective pressure of recurring critical climatic events—catastrophic freezes—that have been a dominant force in the evolution of the species. Subfreezing temperature and aridity under warm season (and biseasonal) rainfall have been codominant selective forces in molding the gigantic columnar cacti of the American deserts. It is not surprising, therefore, that saguaros in the populations we have examined exhibit broad variations in those characteristics that constitute adaptive strategies appropriate to survival of the species in the climatic extremes characteristic of its present desert distribution in Arizona, extreme southeastern California, and adjacent Sonora, Mexico.

Cenozoic Ecology and Evolution of the Saguaro

Little is known with great certainty on the evolution of the saguaro and other columnar cacti that live today in the Sonoran Desert—the species usually thought of as desert giant cacti. The family (Cactaceae) has a poor fossil record; there are no known materials older than 40,000 radiocarbon years before the present (Van Devender 1973). In spite of a poor fossil record, there is much circumstantial evidence bearing on the problem of origins. The circumstantial evidence is strong for early cactus representation in the Madro-Tertiary Geoflora evolving within and marginal to the Neotropical-Tertiary Geoflora (Chaney, Condit, and Axelrod 1944; Axelrod 1950-1979).

It appears beyond reasonable doubt that the Cactaceae is a tropically derived family. It is not surprising, therefore, that this New World plant group has strong representation in the deserts that border the tropics—the subtropical warm deserts—with relatively little continental representation beyond them. For example, cacti are either poorly represented, greatly reduced to substratum level, or nonexistent in habitats within the cold Great Basin Desert of North America and in similar habitats within its South American analog, the cold Patagonian Desert in southern Argentina.

Regarding species, in the absence of an adequate fossil record, answers to questions on evolutionary history of desert columnar cacti can be given or estimated with fair security on the basis of the circumstantial evidence. Much of that evidence lies in the history of the Madro-Tertiary Geoflora and the evolution of the North American Desert. The following scenario for Cenozoic history of the Cactaceae is consistent with and/or drawn in part from information in Britton and Rose (1920, 1922), Bravo (1937), Chaney, Condit, and Axelrod (1944), Deevey (1949), Axelrod (1950-1979), Shreve (1951), Just (1952), Backeberg (1958), Buxbaum (1958), MacGinite (1959), Dorf (1960), Van der Hammen (1961), Raven (1963), Lowe (1964, 1966), Martin and Mehringer (1965), Felger and Lowe (1967), Hunt (1967), Wolfe and Hopkins (1967), Pascual (1970), Vuilleumier (1971), Wright (1971), Lowe et al. (1973), Solbrig (1973, 1976), Turner (1973), Van Devender (1973), Raven and Axelrod (1975), Steenbergh and Lowe (1976, 1977), Wells (1976), Orians and Solbrig (1977), Gibson and Horak (1978), Van Devender and Spaulding (1979), Lowe and Steenbergh (1980). For reconstruction of Tertiary environment see Axelrod (1950-1979); for Quaternary environment see Wells (1976) and Van Devender and Spaulding (1979).

Cenozoic history of the Cactaceae

Early Tertiary: Paleo-Oligocene time, 67 to 30 mybp[1]
Evolution of the Cactaceae within and marginal to the widespread broad-leaved evergreen Neotropical-Tertiary Geoflora. Evolution of cactus family and subfamily adaptive strategies, during approximately 40 or more million years.

Middle Tertiary: Oligo-Miocene time, 30 to 10 mybp
Evolution of tropical and subtropical cactus groups—involving both northern and southern sides of the tropics—in tropical and subtropical deciduous forest and scrub environments. Evolution and radiation of principal cactus growth-form strategies; establishment of higher categories of modern aspect—the major genera and groups of genera (tribes)—during 20 million years of increasing cooling, dryness, and accelerated evolution of the Madro-Tertiary Geoflora.

Late Tertiary: Mio-Pliocene time 10 to 3 mybp
Widespread expansion of semiarid and arid subtropical scrub of the Madro-Tertiary Geoflora, with derivation of larger columnar cacti out of the subtropical phylads bordering the tropics in North and South America. Speciation of major lower categories—modern species and

[1]Million years before present.

species-groups of extra-tropical cacti—during 5-10 million years of expanding dry climate and increasingly seasonal climatic patterns.

Latest Tertiary: Plio-Pleistocene time, 3 to >1.7 mybp
Continuing evolution of taxa in the arid subtropical scrub and expanding desert environment, essentially finalizing modern desert species as we know them today in North and South American deserts and bordering environments during 1-2 million years of response to increasing orogeny and expanding aridity—with progressive seasonal cooling—in southwestern regions of the continents. Selection for greater stem-mass (thermoregulatory energy conservation) progressing to gigantism in columnar cacti within progressively cooling subtropical scrub and desertscrub environments, producing intercontinental convergent evolution of gigantic adaptive form and function—including convergent thick-pithed ecological equivalent *Carnegiea gigantea* in the North American Sonoran Desert and *Trichocereus terschekii* in the South American Monte.

Quaternary: Pleistocene time, *ca.* 1 to ~ 0 mybp
Mixing of species compositions of biotic communities under strong secular climatic change, with biogeographic shifts of taxa in both elevation and latitude. Glaciation, with glacial periods on the order of 100,000 years duration, and interglacials on the order of 10,000 to 20,000 years. Known fossil materials of cacti—all of which date less than 40,000 radiocarbon years before present—indicate no difference from modern populations of taxa.

Quaternary—Late Pleistocene: Middle and Late Wisconsinan time, 40,000 to 11,000 ybp
Mesophytic pinyon-juniper woodland communities predominant across landscapes presently in the Chihuahuan, Sonoran, and Mohave Deserts, before, during, and after the glacial maximum (22,000-17,000 ybp). Environmental domination by winter climate, however equable, did not provide summer requirements for germination, establishment, and growth of the subtropical columnar cacti within Wisconsinan needle-leaved woodland. *Carnegiea* remained within latitudinally displaced subtropical scrub environments south and below the perimeter of the woodland.

Quaternary—Holocene: Early Holocene time, 11,000 to 8,000 ybp
Xeric juniper woodlands under dominant winter-season precipitation persisted widely and inclusive of Southwest landscapes presently occupied by vegetation established under dominant warm-summer monsoon precipitation. *Carnegiea* remained southward in Sinaloan upland rocky sites, as it does today within such relatively frost-free subtropical communities at the southern edge of its geographic distribution in northern Mexico.

Quaternary—Holocene: Middle and *Late Holocene* time, 8,000 ybp to present
Desertscrub communities of modern aspect formed into the regional biotic communities (biomes) recognizable today under significant summer as

well as winter precipitation. Rapid northward and upward deployment of floral and faunal elements into modern subtropical and warm temperate desertscrub assemblages accelerated by melting of the ice sheets and stronger development of the Azores (Bermuda) High—with increased and expanded summer precipitation—favored by warmer global temperatures. Derivation of communities of modern aspect during late Holocene, following movements of species elements into present positions during both middle and late Holocene. The presence of *Carnegiea* today in ecotone stands with junipers, oaks, and other woodland and chaparral taxa at the edge of the desert results from secondary contact during middle to late Holocene time in the current Holocene interglacial.

Freezing and the historical record—the last 200 years

Catastrophic freezes occur throughout the range of the saguaro and are an integral component of the species environment during the Holocene interglacial we are currently experiencing. Such climatic events are neither "new" nor "unique" and do not in themselves indicate a climatic trend.

We examined conventional climatic data records in an earlier report (Steenbergh and Lowe 1976). Among other kinds of diverse long-period records, the freeze-caused constrictions at the base of the largest (oldest) saguaros provide a most important record of critical freezes dating back to the first half of the 19th century (Steenbergh and Lowe 1977, Fig. 54).

Historical observations further complement the record of such events. Of particular significance are such accounts as recorded on Papago Indian calendar sticks (Tatom 1975):

> *1848*—In this year happened an almost unbelievable thing. Cold weather of unheard-of intensity swooped down on the Papagos and almost snuffed them out. Snow fell to a depth of three feet on the level and as deep as the tops of houses in drifts, and lay on the ground for many weeks. Cattle and horses could not find food under the snow and the People could not find firewood. There was great suffering because the People had always been accustomed to warm winters.
>
> * * *
>
> *1870*—Snow again fell to a remarkable depth. It remained on the ground only two days before melting away.

The historical record of freeze-caused damage to the subtropical citrus and other agricultural crops in Arizona constitutes another important and previously unexamined indicator of the impact of catastrophic freezes on the subtropical saguaro and other cold-sensitive native plant populations in the Sonoran Desert during this century (Table 5-1). It is apparent in our observations over the past three decades in the Sonoran Desert that the severity of damage to saguaros and similarly cold-sensitive native plant species by a given freeze is closely reflected by damage to citrus crops.

TABLE 5-1. Chronology of critical winter freezes and reported crop damage in Arizona. The following climatic briefs are from U.S. Weather Bureau summaries for the period 1895 to 1957. Tucson minimum (min.) temperatures (F°) shown are for the University of Arizona station, 2,423 ft (730 m).

1895—Tucson December min. 14°.

1897—Lowest temperature of the year. Tucson Dec. min. 16°.

1899—January snowfall in Salt River Valley. Crop of orange fruit sustained no serious injuries. Tucson min. 17°.

1901—December Tucson min. 10°.

1902—Principal cause of the light orange crop was cold weather in December 1901 which caused considerable damage to trees.

1904—January Tucson min. 15°.

1905—December temperature greatly deficient. Tucson min. 11°.

1910—Unusually cold January 3-8. Tucson min. 15°.

1911—Tucson January min. 16°.

1913—January freeze most severe in history of the state. Considerable damage to citrus groves in Salt River Valley—orchards killed, set back, fruit frozen. Tucson min. 6°.

1916—December—unusually cold and dry. Tucson min. 15°.

1919—December—coldest month since 1892. Tucson min. 20°

1922—January—unusually cold month, citrus fruit frozen. Tucson min. 17°.

1924—January nights unusually cool, heavy frost but negligible damage to citrus fruits. Tucson min. 24°.

1925—Damaging January frost and freezes in all sections. Tucson min. 18°.

1929—January freeze damage to citrus and cantaloupes in Yuma Valley. Tucson min. 22°.

1931—December—killing frosts, much damage to citrus trees and fruit. Tucson min. 23°.

1932—January—citrus fruits and young trees severely damaged by cold weather. Tucson min. 19°.

1933—February cold wave caused extensive damage to lettuce and citrus crops. Tucson min. 18°.

1934—Slight damage to lettuce and citrus by November-December cold wave. Tucson min. 22°.

1935—Slight January damage to citrus trees in Salt River Valley. Tucson min. 21°.

1937—January—the coldest month on record, 40 to 60 percent of citrus crop frozen. Tucson min. 15°.

1939—Coldest February for all years of record. Lettuce growth retarded and citrus injured by cold. Tucson (UA) min. 25°; 20° at Magnetic Observatory station.

1940—Light January freeze in citrus belt—little damage. Tucson min. 22°.

1942—Slight January frost damage to citrus, Salt River Valley. Tucson min. 26°.

1945—December freeze damage to citrus and winter truck crops. Tucson Min. 19°.

1947—Severe January cold damage to orange crop in Salt River Valley. Tucson min. 22°. Considerable December freeze damage to cabbage and broccoli, slight damage to lettuce. Tucson min. 24.

1949—Damaging freeze on January 4th, 5th, and 6th. Bitter cold all month. Heavy losses to fruits and vegetables in southern portions of the state. Tucson min. 16°. December—heavy frosts, moderate damage to citrus and vegetables. Tucson min. 22°.

1950—January freeze most severe since 1913. Citrus and truck crops severely frozen. Many citrus trees sustained considerable damage. Entire Phoenix area citrus crop damaged. Tucson min. 18°.

1953—December—some injury to citrus due to repeated frosts. Tucson min. 24°.

1956—February—some frost damage to melons; frost protection necessary for citrus and truck vegetables. Tucson min. 24°.

1957—December—narrative weather summaries discontinued.

Hilgeman (1965) in a brief historical review of citrus in Arizona notes that "Severe freezes in '13, '37, '49, '50, '62, and '63 have caused extensive fruit losses . . . ." A more complete record of the effects of freezing on citrus (and other crops) reported in U.S. Weather Bureau summaries (1895-1940, 1940-1957) is summarized in Table 5-1. This weather-integrated record is, in some respects, more revealing of the impact of such climatic events on saguaros—and other cold-sensitive native plant populations—than are temperature values available from official climatic data records.

The degree of freeze-caused damage to cold-responsive citrus and other crop plants represents an *integrated* measure of intensity and duration of the particular freeze as well as the immediate post-freeze (rewarming) thermal environment. The succulence and surface-volume ratio of citrus fruits provide thermal characteristics similar to those of saguaros—especially with respect to small juveniles, even though they often occupy different positions in the thermal profile. The severity of damage to citrus and other cultivated crops produced by each of the climatic events as noted in Table 5-1 is a reliable indicator of the seriousness of the impact of these same critical events on saguaro populations. This is true not only for northern populations of the saguaro, but also—in progressively reduced degree southward—for saguaro populations growing in central and southern Sonora, Mexico.

These diverse records leave no doubt that the saguaro and other associated tropically derived species have, during the last 200 years, been subjected to a series of irregularly occuring, intermittent, catastrophic freezes. Neither the historic record nor the status of existing saguaro populations suggests that these events, in themselves, indicate a climatic trend. Rather, they tell us that freezing continues to operate upon these populations as a powerful selective force. Furthermore, the structure of saguaro populations and the continued presence of saguaros throughout the historic range of the species' geographic and ecologic distribution are the final and conclusive evidence that adaptive evolution of increased natural resistance to freezing is a continuing process appropriate to the survival of the species.

Livestock Grazing

There is little doubt that domestic livestock grazing has contributed indirectly to the decline in saguaro establishment rates observed in these populations. Grazing reduces the number and quality of sites suitable for germination, and, by the removal of protective low-level plant cover and mechanical breakdown of detritus, increases vulnerability of young plants to destruction by freezing and other natural environmental hazards (Niering, Whittaker, and Lowe 1963; Steenbergh and Lowe 1969, 1976, 1977; Steenbergh and Warren 1977).

With the possible exception of the Pinacate Craters in northwestern Sonora, Mexico, there are essentially no saguaro habitats that have not been subjected to some degree of degradation by livestock grazing (Hastings and Turner 1965). That exception aside, it does not appear possible to provide a direct comparative evaluation of saguaro survivorship and population status in grazed and in historically undisturbed habitats. There is, however, no substantive evidence that domestic livestock grazing has resulted in irreversible degradation of saguaro habitats. Neither is there conclusive evidence that grazing has resulted in significant increases in populations of rodents or other animals specifically detrimental to saguaro survival.

For saguaros, the greatest impact of livestock grazing occurs in nonrocky habitats where destruction of protective perennial plant cover most severely limits establishment and survival of young saguaros. Conversely, grazing impact on saguaros is least in rocky habitats where survival of young saguaros is strongly associated with proximity to protective rock outcrops (Steenbergh and Lowe 1969, 1976, 1977).

In view of these facts, it is to be expected that an increase in establishment and survival of young saguaros will occur with the recently accomplished elimination of all domestic livestock grazing from Saguaro and Organ Pipe Cactus national monuments. Furthermore, with the now occurring natural regeneration of other perennial vegetation, it is to be expected that the greatest increase to the current saguaro population base will occur in nonrocky habitats. Strong evidence for such a trend exists in the presence of thousands of young saguaros growing in nonrocky habitats at Saguaro National Monument (east)—young plants established there since the elimination of grazing from the "Cactus Forest" in 1958.

Population Structure and Habitat Selection

Our observations and the observations of others on saguaro populations growing in representative Arizona habitats of the species leave no doubt that important long-term changes have occurred and will continue to occur in these populations. A decline in numbers of saguaros has occurred in each of the three geographic localities examined.

More important, however, are observed differences in population age structure that reflect the relative *suitability* of topographically dissimilar habitats. Populations growing in winter-warm habitats—rocky south-facing slopes—are relatively stable. Populations in less suitable, winter-cold habitats—north-facing slopes and nonrocky, bajada, and "flats" habitats—have insufficient numbers of young plants to maintain existing population age structure. The small number of young saguaros in these populations ensures that the numbers of large, old plants in these habitats must continue to decline for at least 50-80 years regardless of any future change in recruitment rates.

The data on saguaro population structure reported here support our earlier observations on the relationship of freezing temperatures to the absolute limits of occurrence, local distribution, and dynamics of saguaro populations in this portion of the species range (Steenbergh and Lowe 1976, 1977). Generally, the age structure of these populations is characterized by increasing density, and higher ratios of young to old plants occurring on a gradient of increasingly favorable, i.e., warmer, winter microclimate. Within the geographic range of the saguaro species, increase in habitat suitability is associated with differences in slope exposure (north to south) and rockiness of the habitat (nonrock to rock). Except at the extreme upper margin of its ecologic tolerance, habitat suitability increases from low to high elevations with the moderation of winter minimum temperatures associated with thermal inversions that result from cold-air drainage and accumulation in valley bottoms.

The *number* of saguaros in a given habitat is limited by the number of microhabitats suitable for germination and seedling survival. Microhabitat suitability is determined by microtopography and the physical structure of the plant community. During the first years of saguaro life, microhabitat suitability determines the differential selective action by biotic and abiotic factors. Thus, for the individual, during this early period in the selective process, chance alone may override differential fitness. In northern portions of the species' range, catastrophic freezing selectively removes cold-intolerant individuals from the population and, by differential selection on the youngest (smallest) and oldest (largest) members, selectively structures these populations.

Ecological Perspective

Our investigations certainly do *not* indicate that the saguaro is becoming extinct, nor do they suggest that it is "vanishing" from any of its historic habitats that have not been converted to intensive human uses. Rather, there has been, in this century, a decrease in the density of populations growing in marginal habitats and a minor reduction in the absolute distributional limits of some local populations.

The observed fluctuations in Arizona populations of the saguaro are a natural and *expected* response to short-term variations in the critical extremes of the controlling environmental factor—recurring catastrophic freezes. Such freezes are the primary cause of adult saguaro deaths in Arizona and northern Sonora, Mexico and are the primary control on the northern, eastern, and upper elevational limits as well as the structure and dynamics of these populations. Furthermore, over a major portion of this species' distribution, winter cold is an important determinant of saguaro growth rates, as well as quantitative aspects of its reproductive success, and the timing of critical events in its life cycle.

Under the influence of the powerful continued selective pressure of recurring catastrophic freezes, the species must be actively evolving increased natural resistance to freezing. Adaptive evolution is most evidently expressed by natural selection for stem geometry and surface architecture that maximizes resistance to freezing.

The related thermoregulatory significance of saguaro spine ontogeny offers a fertile field for future investigations in this regard. While cactus spines in some temperate species have been under study by us and by others, still largely unexplored are important questions on the structure and function of spines. These include the internal and external structure and function of cactus spines *throughout their ontogeny* in relation to stem-surface geography and position, size, strength, shape, density, and other parameters related to climatic adaptation in tropical and temperate taxa. Most revealing should be analysis of the ontogeny of the spines of clinal populations within taxa and closely related series of taxa outward from the tropics into the cold-margined warm deserts.

The concept of stable age distribution with regard to populations of catastrophically selected plant species such as the saguaro is little more than academic. In the presence of strong mid-latitude climatic variation—expected on an annual and longer term basis—such populations fluctuate in response to critical extremes of the controlling environmental factor(s). Populations of such perennial plant species spend most of their time recovering from the last catastrophic events. Furthermore, in such populations the greatest fluctuations in numbers and age structure occur at the climatically limited margins of the species' distribution, where the extremes of the controlling environmental factor or factors most frequently exceed the ecological tolerance of the plant.

The saguaro has evolved, through natural selection, a set of adaptive strategies required to survive the irregular occurrence of climatic extremes that are a normal characteristic of its environment. The "tragedy" of catastrophic die-offs observed in saguaro populations during this century is a human concept that is derived primarily from our inability to relate these natural, climatically controlled events to the time scale of evolution.

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Appendix I

Reports and related correspondence, USDA Bureau of Plant Industry cactus disease investigations, 1941-1951.

The following series of reports on saguaro investigations by the USDA Bureau of Plant Industry has been assembled from official files of the National Park Service. Our original intent was to publish photo-facsimiles of the original typescript reports. Unfortunately, the poor physical quality of the originals was not adequate to accomplish this. The use of typeset copies to insure readable reproduction has resulted in minor deviations from the original formats. The exact original content—including clerical and other errors—has, however, been maintained.

The original reports are on file at Saguaro National Monument, Tucson, Arizona, and xerox copies are distributed to various institutions and files.

CONTENTS

Richey, C. A.

1941. (April 5) Memorandum.

Acting Superintendent, Saguaro National Monument; request to Custodian, Organ Pipe Cactus National Monument, confirming Tillotson's March 26 memorandum.

Gill, Lake S., and Paul C. Lightle.

1942. (June 20) Cactus disease investigations: An outline of objectives, plans, and accomplishments on Project j-2-8.

Illustrated report on disease surveys and efforts to control bacterial rot of saguaros by sanitation methods on a 320-acre plot at Saguaro National Monument.

Lightle, Paul C.

1942. (June 23) Progress report, Organ Pipe Cactus National Monument, 1942: Bacterial necrosis—survey strips and sample plots.

Results of the June 1941 survey employing sample plots to determine extent of bacterial rot in saguaro and organpipe cactus populations.

Coffman, J. D.

1942. (Sept. 24) Letter.

Acknowledgement of receipt of Lightle's June 24 report, with comment on abundance of reproduction.

Mielke, James L.

1943. (March 19) Progress report for 1943 on bacterial necrosis of cacti, Organ Pipe Cactus National Monument.

Results of February 1943 re-survey of 1941 plots, reporting low mortality to saguaro and organpipe cacti.

Mielke, James L.

1943. (March 19) Letter.

Transmittal of Mielke's March 19 report to Custodian, Organ Pipe Cactus National Monument, suggesting possible relationship between water balance of saguaro and disease incidence.

Mielke, James L.

1944. (April 5) Progress report on bacterial necrosis of cacti, Organ Pipe Cactus National Monument.

Report of general inspection of cacti in the monument and adjacent Mexico. Suggests that a moth may be the vector of the rot bacterium, and that previously unconsidered methods of control may be appropriate.

Mielke, James L.

1944. (July 12) Summary of results of control experiments on saguaro disease, Saguaro National Monument.

Summary of disease control work at the monument. Suggests that human and ecological factors may have played a significant role in bringing about the existing condition of this saguaro population. Failure of inoculation experiments is noted.

Gill, Lake S., and Paul C. Lightle.

1946. (July 30) Analysis of mortality in saguaro cactus: A progress report on the experimental area (Section 17 R16ET14S) established in the Saguaro National Monument in 1941 for the study of bacterial rot.

Summary report on sanitation experiment and analysis of the saguaro population. Notes declining mortality rate and suggests that extremely heavy mortality at start of project may have been result of a temporary set of conditions. Highest mortality rates in oldest size classes is noted.

Gill, Lake S.

1946. (Sept. 4) Memorandum.

Transmittal of report to Custodian, Saguaro National Monument. Notes that the war prevented carrying out of original sanitation experiment design.

Gill, Lake S.

1951. (January 31) Mortality in the giant cactus at Saguaro National Monument 1941-1950.

Analysis of experimental control effort includes important data on population age structure. Suggests that stem rot losses are linked with overmaturity and predicts continued decline of the old Saguaro National Monument stand. Notes that stem rot does not appear to be a disease that threatens to wipe out the saguaro species.

Gill, Lake S.

1951. (February 2) Letter.

Transmittal of copy of January 31 report to Superintendent, Saguaro National Monument.

King, Samuel A.

1951. (February 6) Letter.

Acknowledgement to Gill of receipt of his January 31 report.

Davis, John M.

1951. (November 30) Memorandum.

Comments to Regional Director: doubts advisability of project and requests suggestions and guidance on policy concerning proposed saguaro reforestation project. Questions reported importance of bacterial necrosis as a limiting factor. Suggests that measures to restore degraded habitat are ecologically essential prerequisite for successful regeneration of the saguaro population in the Cactus Forest.

Albuquerque, N.M.
March 21, 1941

MEMORANDUM

Preliminary Pathological Inspection of
Organ Pipe Cactus National Monument

On March 16 a pathological inspection of the Organ Pipe Cactus National Monument was made in company with custodian Supernaugh. The object of the visit was to observe the bacterial necrosis reported on the saguaro, organ pipe, and senita cacti.

The disease on saguaro is apparently much less serious at Organ Pipe than at Saguaro. While it occurs generally throughout the Monument it has not as yet resulted in serious mortality. The old stands along the main north-south road through the Monument are as badly diseased as any which were observed. A small area of about five acres near Red Tanks appeared to have suffered heavy losses in the past but is now nearly free from disease.

In general the organ pipe cactus seemed to be much less healthy than the saguaro. It is affected with a necrosis similar to the condition found in saguaro. Recently killed stems and dead plants were conspicuous in all the stands observed. Many plants also exhibited an unhealthy yellowish color. It is not known whether the yellowing is an early symptom of bacterial necrosis. If it is, then the losses in this species will be decidedly serious.

The senita cacti which were observed, generally showed a diseased condition in their older stems. Young stems were seldom affected and there was no sign that entire plants or groups of plants were being killed. The rot usually originated at or near ground level and girdled the stems at the base. The rot in senita appears to be a natural condition associated with overmaturity.

Dr. J. G. Brown of the University of Arizona has studies in progress which should prove whether or not the organism causing the necrosis of saguaro is also responsible for the decay in the organ pipe and senita. Present indications from this work are that the saguaro organism is attacking the organ pipe cactus but that the rot in senita is due to some other cause. Positive information on this point should be available in a few weeks.

It is planned to make a more complete survey of the Organ Pipe Cactus National Monument and to establish permanent observation plots there in June of this year.

Lake S. Gill
Senior Pathologist
Bureau of Plant Industry

Copies to:
- Chief Forester N.P.S.
- Regional Forester N.P.S.
- Superintendent S.N.
- Custodian O.P.C.N.M.
- Oravatt
- Wagoner

UNITED STATES
DEPARTMENT OF THE INTERIOR
NATIONAL PARK SERVICE
REGION THREE
SANTA FE, NEW MEXICO

March 26, 1941

Memorandum for Superintendent Miller, Southwestern National Monuments:

Enclosed are two copies of a memorandum, entitled "Preliminary Pathological Inspection of Organ Pipe Cactus National Monument", prepared by Senior Forest Pathologist Lake S. Gill, of the Bureau of Plant Industry. It will be appreciated if you will forward one of the copies to Custodian Supernaugh with a copy of this memorandum.

The Regional Forester has read Dr. Gill's report with a great deal of interest and believes that we are extremely fortunate in having Dr. Gill's assistance and advice on this problem at this early stage. It would be extremely desirable if Custodian Supernaugh could make frequent observations and notes on the progress of the disease between now and June, at which time Dr. Gill plans to make a more complete survey of the Organ Pipe Cactus National Monument and to establish permanent observation plots.

N. R. Tillotson
Regional Director

Encl. 2371887.
cc: Cust. Supernaugh, through Supt. Miller.
Chief of Forestry

UNITED STATES
DEPARTMENT OF THE INTERIOR
NATIONAL PARK SERVICE
HEADQUARTERS, SOUTHWESTERN MONUMENTS
COOLIDGE, ARIZONA

April 5, 1941

Memorandum for Custodian Supernaugh,
Organ Pipe Cactus National Monument:

Reference is made to the copy of Regional Director Tillotson's memorandum of March 26 sent you during my absence from the office. Mr. Tillotson states that it would be desirable if you could make frequent observations and notes on the progress of the disease between now and June at which time Dr. Gill plans to make a more complete survey of the Organ Pipe Cactus National Monument and to establish permanent observation plots. This letter is simply to confirm the Regional Director's memorandum and to request your full cooperation.

C. A. Richey
Superintendent

cc: Region III

Cactus Disease Investigations:
An outline of objectives, plans, and accomplishments
on Project j-2-8

Lake S. Gill, Senior Pathologist
and
Paul C. Lightle, Agent

Bureau of Plant Industry
June 20, 1942

Contents

1942	1st Week	2nd Week	3rd Week	4th Week
June		Reconnaissance Tucson Mt. Park	Report	Reconnaissance Tucson Mt. Park
July	Sample Plot Mote Forms		Saguaro Sample Plots	
Aug.		Detailed Survey Tucson Mountain Park (?) 1 Asst.		
Sept.	Permanent Plots—Tucson Mountain Park (?) 1 Asst.			
Oct.	Read Tucson Mt. Park Plots (?)	Stake missed plants on Sec. 17	Saguaro Sample Plots	Recheck Sec. 17
Nov.		Recheck Section 17		
Dec.	Recheck Sec. 17	Additional Sanitation work on Sec. 17 (?)	(3 Laborers)	
1943				
Jan.	Tucson Mt. Park Sample Plots (?)		Saguaro Sample Plots	
Feb.	Suppression Experiment—Tucson Mountain Park (?) (8 Laborers)			
Mar.				
Apr.	Tucson Mt. Park Sample Plots (?)		Saguaro Sample Plots	

PART I
DISEASE SUPPRESSION EXPERIMENTS

A. Objects

1. To determine whether or not losses from bacterial rot can be effectually reduced by sanitation measures.

B. Plan

1. To remove all diseased material from the 320 acres comprising the south half of section 17 (Figs. 1 and 2) in Saguaro National Monument by:
   (a) Burying all badly diseased plants.
   (b) Aseptically removing diseased tissue from lesions which had not reached lethal size.
   (c) Burning all dead and dry plants.
2. To make detailed records of all cacti on the treated area and on the adjoining 320 acres to the north. The data from the north half to serve as a check or means of juding the effectiveness of the sanitation work.
3. To conduct detailed reexaminations on the entire section once a year for the next five years at least in order to compare the subsequent losses from disease on the two halves.

This plan was prepared after a conference at the University of Arizona on September 6, 1941, at which time representatives of the University, the National Park Service, and the Bureau of Plant Industry were present.

C. Accomplishments

Sept. 1941–March 1942

Each living cactus on the section was identified with a numbered wooden stake. The numbers starting with No. 1 in the SW corner of each 10-acre quadrat (Fig. 1) and progressing in north-south strips to the east edge of the quadrat. The staking was begun in September, 1941 and completed in January, 1942; 12,968 living saguaros were thus identified.

The dead dry skeletons on each 10-acre quadrat were counted, (a few were staked) 1,836 being present on the entire section.

Between November, 1941 and January, 1942 notes were taken on each cactus on the south half of the section, and those requiring removal were marked with paint. Marking and note-taking was done a day or two ahead of removal. The notes were kept in surveyor's level books, which were made available to the foreman of the removal crew, who entered the date on which each marked cactus was removed or treated by his crew, and in addition made a record of all cacti accidentally injured in the course of operation. Notes on each cactus showed:

(a) It's height to the nearest 6 ft.
(b) Serious mechanical injuries.
(c) Disease Condition—extent and degree of activity.
(d) Miscellaneous remarks pertinent to the object or operation of the project.

Similar notes were taken on the north half of the section (untreated area) between February 23 and March 17, 1942. Cacti that would have been removed or treated had they been on the south half were so indicated.

Typed copies of the notes have been made and both sets are filed in the Tucson office.

Surgical work of removing actively diseased tissue from cacti standing on the south half was done during February 16 to 20, 1942. Over 50 plants had been indicated for surgical treatment at the time the records were made, but of these only 3 showed active lesions at the time the surgical work was done, the rest having apparently "walled-out" the infection naturally. In some cases the callused lesions were operated upon to provide better drainage.

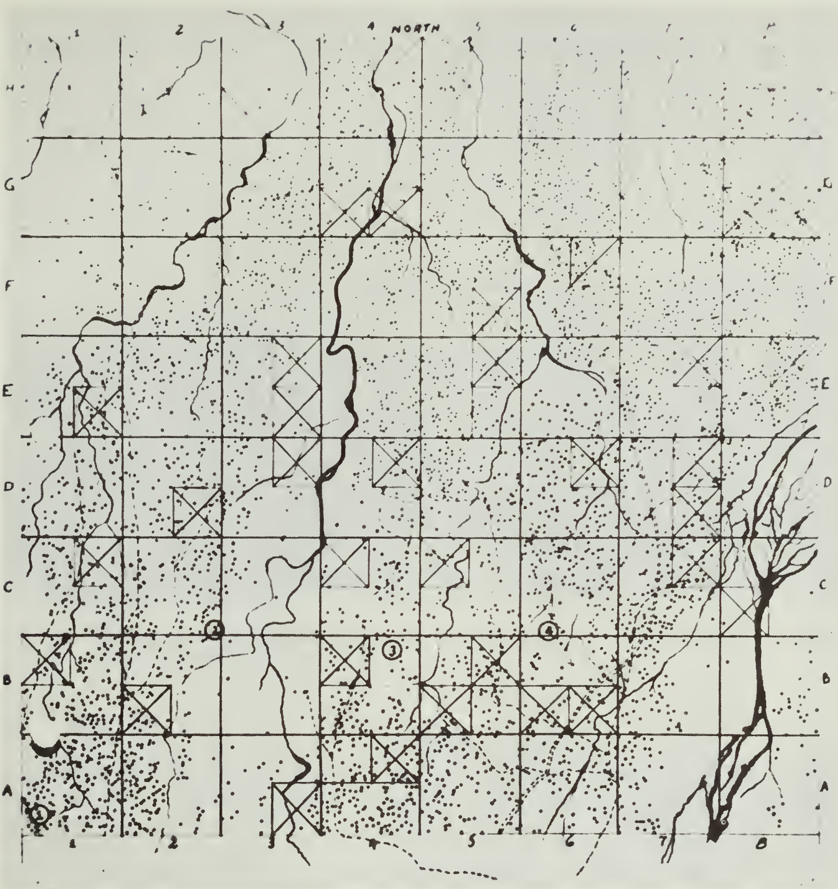


Figure 1. Map of the experimental section at Saguaro National Monument (S17,R16E,T14S) traced from an aerial photograph made at 5000 ft. by courtesy of the U.S. Army Air Corps. Rows A to D incl. were given a sanitation treatment, rows E to H inclusive were not treated.

Legend

- ☒ Random 2½-acre survey plot of April 1941.
- 1 Location of burial pit for sanitation work.
- ● Saguaros visible on air photograph.

Permanent Sample Plots:

A = E 1/2 E5 B = S 1/2 A4

Figure 2. General view of the saguaro forest on the experimental area (Section 17).

Figure 3. One of the unique features of the old stands on Saguaro National Monument is the large number of interesting fasciated specimens.

The sanitation work (Figs. 4, 5, 6) was started in November, 1941, and was completed January 10, 1942. Cacti marked for removal were felled, bucked, loaded on trucks, and dumped into one of four pits which had been previously excavated on the area (see Fig. 1). The cacti in the pits were fumigated and then immediately covered with at least a foot of earth. In a few cases it was possible to amputate diseased arms and leave an apparently disease-free plant. After the removal and burial of all marked cacti, the dry snags or skeletons were gathered up (late December to January 10), piled on the burial pits and burned. At the completion of the work the pits were back-filled and the more evident trails visible from the main roads were obliterated. A more detailed account of the work follows:

Statistics

a. Number of living cacti removed and buried:
   313 diseased; 12 healthy (injured in the operation)
b. Excavation of pits:
   No. of pits—4
   Cubic yards excavated—1,000
   Equipment—65 h. p. bulldozer, 29½ hrs. (rented)
c. Sanitation work:
   Equipment (loaned by National Park Service)
   1—crane truck (2 months)
   2—1½ ton dump trucks (2 months)
   1—1½ ton dump truck (1 month)
d. Labor:
   1 foreman (3 months)
   5 laborers (2 months)
   3 truck drivers (2 months)

Methods

Felling

A belt was adjusted 10-12 ft. above ground on the cactus and attached to a tow line on a truck. Main roots of cactus were cut. The cactus was pulled over by the truck. Undercutting was impossible as a means of directing the fall because of the uneven balance of the plants.

Bucking

The upper ends of the plants were chopped into about 1-foot bolts with broadaxes, but where more than two or three axe strokes would be required to finish a cut, a saw was used. Excessive chopping was discouraged in order to minimize the amount of debris resulting from the operation.

Loading

Short bolts were loaded into dump trucks by hand. Long bolts (up to 5 ft.) from the basal parts of cacti were loaded into dump trucks with the aid of a crane mounted on a truck.

Clean-Up

All debris created in dismembering a cactus was picked up and carried to the pits in the truck. The stake used to identify the cactus was replaced where the plant originally stood. The foreman did not record a cactus as removed until he had inspected its former site. On tiers 1 to 5 inclusive (Fig. 1) the soil around a diseased cactus and also the exposed root bases were sprayed with about a gallon of calcium hypochlorite solution (1% free chlorine). This practice was discontinued on tiers 6, 7, and 8 which received no soil disinfection.

Fumigation

Every three to four days, the cactus sections which accumulated in a pit were fumigated with a solution of 20 lbs. of paradichlorobenzene dissolved in 55 gallons of kerosene. This was poured on the pile at the rate of 1 gallon per cactus, and the pile was immediately covered with tarpaulins to form a fairly air tight cover. After three or four days, the tarpaulins were removed and the cacti were covered with about a foot of soil.

B

A

Figure 4. Sanitation operation: felling. After adjusting a line on the cactus (A) the main roots were cut and the plant was pulled over by a truck (B) where the least damage would occur to surrounding vegetation.

A B C

Figure 5. A portable crane with iron tongs was used to load the heavier butt cuts and stumps (A) and was helpful in removing diseased cacti from group (B) without damaging the healthy members of the group (C).

Figure 6. Diseased cacti were dumped into pits about 9 feet deep. As the sections accumulated they were treated with a solution of paradichlorobenzene in kerosene, covered with canvas tarps for several days, and finally covered with at least a foot of earth. At the close of the operation all dirt was backfilled over the pit.

Disposal of dry snags

After all living diseased plants had been buried, the snags were gathered up in trucks and a tally kept of the number taken from each 10-acre quadrat. They were dumped on Pits No. 1, 3, and 4 (Fig. 1) and burned shortly thereafter.

Final backfilling

On January 21, a bulldozer was rented to backfill all excavated soil into the pits. This required 6½ hours operating time.

Obliteration

After burning the snags, a few man-days were spent in late January obliterating the more obvious truck trails that had been made in the course of the work. In doing this, every effort was made to carry out the suggestion of admninistrative Park Service officials. Thorough obliteration was not attempted. The truck trails will receive occasional use for the next several years in the course of completing the experiment.

Records

About 800 feet of 16 mm. color film were used in a motion picture record of the various activities of the operation. Mr. Marvin E. Frost of Tucson graciously donated his time, equipment and skill to help us obtain this record. In addition, numerous still-photographs in both color and black and white were taken during the work.

The height and condition of each cactus was recorded by a pathologist in surveyor's level books; cacti requiring removal or treatment were also indicated. The books were given to the foreman of the removal crew who entered the date beside the proper number when a cactus was removed or when an arm was amputated. In case a cactus was damaged or had to be removed because of accident incidental to the operation, the foreman also made note of those facts in the book.

D. Results

A comparison of the conditions on the north and south halves of the experimental section respectively is given in Table 1. While the total population on each half is surprisingly similar, the plants less than 19 feet tall on the north half are much more abundant (3,568) than on the south half (2,911), which might explain the difference in the percentages of diseased plants on the two areas.

Table 1 also shows (Column 5) that disease is heaviest in the larger plants.

E. Further Work

1. *Summer, 1942.*

Stake all plants missed in original operation. This will require about two weeks for one man.

2. *Fall, 1942.*

Recheck entire Section 17 and obtain figures comparing disease incidence and mortality on north and south halves respectively. This will require about six weeks for one man in the field.

3. *Fall, 1942.*

Remove or give surgical treatment to infected plants on the south half of the section if this is considered advisable. There is plenty of burial space in hole No. 1 at S. W. corner of the section and some space in hole No. 3. It is estimated that this work will take about two weeks time for one technical man plus the help of some laborers and a team.

4. *Winter, 1942-43.*

Start new suppression experiment on the Tucson Mountain Park if this is considered advisable.

TABLE 1. Comparison of Population and Disease on the North and South Halves of Section 17.

January, 1942

Height Class		Total No. Living Plants	Frequency %	Diseased Living Plants Removed[1] No.	% of Class	% of Total
(1)		(2)	(3)	(4)	(5)	(6)
South Half (treated area)						
0-6′	I	274	4.3	3	1.1	1.0
1′-12′	II	717	11.2	22	3.1	7.0
13′-18′	III	1,920	30.0	64	3.3	20.4
19′-24′	IV	2,061	32.1	105	5.1	33.5
25′ +	V	1,423	22.2	114	8.0	36.4
Unclassified[2]		18	0.3	5	—	1.6
Total		6,413	100.0	313	4.9	100.0
North half (untreated check area)						
0-6′	I	404	6.2	2	.5	.7
7′-12′	II	921	14.0	13	1.4	4.8
13′-18′	III	2,243	34.2	43	1.9	15.9
19′-24′	IV	1,520	23.2	71	4.7	26.2
25′ +	V	1,411	21.5	100	7.1	37.0
Unclassified[2]		56	0.8	42	—	15.5
Total		6,555	100.0	271	4.1	100.0

[1] Plants that would have been removed in N. ½.
[2] Plants mechanically damaged so that height could not be determined.

PART II
SURVEYS

A. Object

April 1941

1. To determine the distribution and spread of the bacterial rot and to estimate losses caused by it.

B. Plan

1. To observe and record the location of the disease wherever observed or reported, in order to determine its general distribution.
2. To estimate the intensity of the disease on the Saguaro and Organ Pipe Cactus National Monuments, in order to evaluate current damage and to establish a starting point from which fluctuations in disease intensity can be detected quantitatively.

C. Accomplishments

1. Records on the general distribution of the disease thus far have been limited to those made incidental to auto and train travel for other purposes. A list of general observations is given below:

(a) Saguaro National Monument—disease heavy at north end becoming less intense southward.
(b) Tucson Mountain Park—disease generally present, heavy in scattered areas especially to the north.
(c) Papago Indian Reservation—disease generally present along Ajo Road.
(d) Organ Pipe Cactus National Monument—disease light but widely distributed.
(e) Picacho Peak—heavy losses from disease.
(f) Casa Grand—extremely heavy losses.
(g) Phoenix and vicinity—heavy losses.
(h) Florence Junction to Globe—disease present.
(i) Tonto National Monument—disease present.
(j) Salome to Congress—disease present in scattered places.
(k) Salome to Buckeye—disease present in scttered places.
(l) Ajo to Gila Bend—disease present in scattered places.
(m) Gila Band to Casa Grande—heavy losses.
(n) Roosevelt Dam to Apache Junction—disease present in scattered places.
(o) Reddington and Vicinity—disease present.

2. *Quantitative Surveys.*

Saguaro National Monument

Between October, 1940 and May, 1941 a section of land (Section 17, R16E, T14S) was gridded into 10-acre blocks, the corners of which were identified with wooden stakes. This work was performed by N.Y.A. engineering students from the University of Arizona under the direction of the Monument Custodian. The section appeared to represent average disease conditions in the older stands and was selected for an intensive survey. For this purpose, four separate drawings of 10 numbers were made from a lot of 64. Each number represented a particular 2½ acre block in a quarter section and each drawing thus applied to a particular quarter section only. The distribution of the forty—2½-acre blocks selected under this procedure is shown in Figure 1. After selecting the sample areas, they were located by pacing and compass, and a tally was made of the healthy and diseased cacti in each. The basic data thus obtained are give in Table 2.

Organ Pipe Cactus National Monument

On this Monument the survey was made in June, 1941 by establishing strips 1000 feet long and 100 feet wide at scattered locations where some disease could be found. A central line was run with a staff compass and steel chain, stakes being set at 200 feet intervals. The width of the strip was obtained by pacing from the center line. Cacti on the strip were tallied according to the height class and condition with respect to disease, the following classifications being used:

Height: I— 6 inches to 3 feet
II— 4 feet to 8 feet
III— 9 feet to 16 feet
IV—17 feet and over

Condition:

	SYMBOL
Healthy	H
Old Dead—(dead over three years)	OD
Recent Dead—(dead less than three years)	RD
Infected—(diseased but living)	I

Following are descriptions of the eight survey strips established in June, 1941.

Plot I
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E-W
Location: West side of Ajo—Sonoyta highway 6.7 + miles from U.S. Customs House at Int. Boundary.
Total number of plants: 23
General topography: flat and rocky.

Plot II
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: N.N.W.—S.S.E.
Location: Dowelling Well Road 1.25 + miles from Customs House, marked by a small stone monument on N. side of road.
Total number of plants: 70
General topography: flat

Plot III
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E—W.
Location: Short distance above Dowelling Well, 2.35 + miles from Customs House.
Total number of plants: 92
General topography: Rolling and rocky.

Plot IV
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E—W
Location: E side of the Ajo-Sonoyta highway 12.6 + miles from the N. boundary of the Monument.
Total number of plants: 39
General topography: flat.

Plot V
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E—W
Location: E. side of the Ajo-Sonoyta highway 10.6 + miles from the N. boundary of the Monument.
Total number of plants: 50
General topography: flat

Plot VI
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E—W (40° S of E)
Location: 200 ′ So. of the N. road to Alamo Canyon 0.1 mi. from the Ajo-Sonoyta road.
Total number of plants: 51
General topography: flat.

Plot VII
Area: 2.3 acres (1000 ′ x 100 ′)
Long axis: E—W
Location: On the W. side of the Ajo-Sonoyta highway, 14.0 + miles from the north boundary of the Monument.
Total Number of plants: 52
General topography: flat.

TABLE 2.

10-Acre Quadrat No.		Quarter of Quadrat	Number of Plants		
			Diseased[2]		
[1] Field	Office		Old	Recent	Healthy
16-17	8H	SE		12	50
	8H	SW		5	77
13-14	5H	NW	7	6	27
45-18	8G	SW	3	1	84
	8G	SE	5	6	64
34-47	6F	NE	1	3	66
48-34	5F	SE	9	8	102
55-35	5E	NE	19	19	211
56-57	7E	NE	4	5	65
57-20	8E	NE	2	7	55
12-13	4H	NE			16
11-12	3H	SW			2
10-11	2H	SW			5
9-10	1H	NW			1
	1H	SW	4	3	7
42-43	4G	SW	11	4	38
	4G	SE		2	7
53-54	3E	NE	2		18
	3E	SE	1	1	6
6-52	1E	SE	4	3	34
61-60	4D	NE	5	2	40
62-61	3D	NE	1	2	9
63-62	2D	SE	7	1	48
4-64	1C	NE	3	9	61
66-67	4C	NW	2	1	25
73-72	4B	NW	8	7	54
75-74	2B	SW	1	4	101
3-75	1B	NW		1	20
77-78	3A	SE		3	15
78-79	4A	NE	6	15	105
59-58	7D	NE	6	12	53
	7D	SE	1	5	39
36-59	6D	NE	5	4	66
67-37	5C	NW	4	2	39
68-69	7C	NE	1	3	54
69-22	8C	SW	2		6
72-33	5B	NE	1	12	62
	5B	SW	1	3	75
38-71	6B	SW	4	3	61
	6B	SE	4	4	50
Total			134	178	1,918
Percent			6.0	8.0	86.0

[1] Numbers on stakes at North corners of quadrat.
[2] Recent - badly diseased plants and dead plants which presumably died within past 2 years.

Plot VIII
Area: 2.3 acres (1000′ x 100′)
Long axis: N—S
Location: In Growler Pass, 500′ on each side of the road.
Total number of plants: 66
General topography: Rough, rocky pass in the hills.
All plots were reexamined during the week ending May 30, 1942.

Basic data from this survey are given in Tables 3 and 4.

Tucson Mt. Park

As this report is being written a preliminary survey of disease conditions on the Tucson Mountain Park is being made.

D. Results

The general survey work indicates that the disease probably exists throughout the range of saguaro in Arizona, although it seems to be serious only in fairly well circumscribed areas. While a more systematic and complete survey of its distribution would be extremely helpful in planning further study of the disease, it is doubtful if such an undertaking would be warranted at this time in view of the scarcity of automotive equipment.

The 100 acre sample on section 17 of the Saguaro National Monument (See Fig. 1) showed that 8% of the 2230 cacti tallied were either badly diseased or had died within the past three years and that an additional 6% had been dead probably longer than three years.

Of the 444 cacti in eight survey plots at Organ Pipe Cactus National Monument approximately 7% have been dead over three years and 2% have been dead less than three years. There is very little active infection at the present time. These percentages, while not extremely low, are of minor importance, since 33.6% of the healthy cacti are 3 feet or less in height and 16.3% are between 4 feet and 8 feet in height. With so much reproduction taking place little importance can be attached to a loss of 7% in older stands. The data from the May, 1942 reexamination have not been analyzed but superficial inspection shows that there has been little or no increase in disease.

E. Further Work

1. *Summer, 1942.*

If considered advisable, a quantitative survey of the disease in the Tucson Mountain Park should be made in July or August. This would be especially advisable if a suppression experiment were planned for that area since the data from the survey will be very helpful in planning the physical requirements of the suppression work. It is estimated that one man could conduct an adequate survey in about three weeks.

2. *April, 1943*

Resurvey the strips on the Organ Pipe National Monument. This should take one man about a week.

TABLE 3. Survey Plots—Organ Pipe Cactus National Monument.

June 1941

Plot No.[1]	Block	Class I[2]	Class II	Class III				Class IV				
		H	H	H	OD	RD	I	H	OD	RD	I	
I	1	2	1	2	1			2	1			
	2	3	2		1			1				
	3	1										
	4	1		2				1				
	5		1		1							
Totals		7	4	4	3			4	1			(23)
II	1	4						2				
	2	1	4	3				4	2		2	
	3	2	1	4				6				
	4	1		6	2			8			1	
	5	5		4	1			6	1			
Totals		13	5	17	3			26	3		3	(70)
III	1	5	6	2	3			9	1			
	2	2	8	2				8	1	2		
	3	4	4 (1-I)	1	2			7	1			
	4	4	2	1				3	1	1		
	5		1	3				7				
Totals		15	22	9	5			34	4	3		(92)
IV	1	4	1	1	1	1		4		1		
	2	1	1	3				1				
	3			1								
	4	1	3	2	1							
	5	7	4		1							
Totals		13	9	7	3	1		5		1		(39)
V	1	6 (1-RD)	3	1		2		1				
	2	7	2									
	3	4	2	1				1				
	4	1	1	1	2							
	5	11 (1-RD)	2 (1-OD)									
Totals		31	11	3	2	2		2				(51)

[1] Plots are 1000′ by 100′ wide and cacti were tallied by blocks 200′ long and 100′ wide.
[2] Cacti were divided into four classes: Class I, cacti from 6″ to 3′, Class II, 4′ to 8′. Class III, 9′ to 16′, and Class IV, 17′ and over. In addition, classes III and IV were subdivided into H-healthy, OD-old dead, RD-recently dead (not over three years), and I-visibly infected.

TABLE 3. Survey Plots—Organ Pipe Cactus National Monument. — *Continued*

June 1941

Plot No.[1]	Block	Height Class										
		Class I[2]	Class II	Class III				Class IV				
		H	H	H	OD	RD	I	H	OD	RD	I	
VI	1	3	1		1			4		1		
	2	7	3	1	1			1				
	3	4	1		2			3	1			
	4	7						2	3			
	5	1	2					2				
Totals		22	7	1	4			12	4	1		(51)
VII	1	1		2	3			2				
	2	8	2	2	1			5	1			
	3	8										
	4	4			2			2				
	5	3	1	2				2		1		
Totals		24	3	6	6			11	1	1		(52)
VIII	1	1		1				4	1		1	
	2	2	2	1	1			7			1	
	3	5		1					1			
	4	11	6 (1-I)	1				7				
	5	5	2	4								
Totals		24	11	8	1			18	2		2	(66)
Grand Total Cacti												(444)

[1] Plots are 1000′ by 100′ wide and cacti were tallied by blocks 200′ long and 100′ wide.
[2] Cacti were divided into four classes: Class I, cacti from 6″ to 3′, Class II, 4′ to 8′. Class III, 9′ to 16′, and Class IV, 17′ and over. In addition, classes III and IV were subdivided into H-healthy, OD-old dead, RD-recently dead (not over three years), and I-visibly infected.

TABLE 4. Survey Plots—Organ Pipe National Monument.

Plot No.	Total Cacti	Class III No. OD	Class III % OD	Class III No. RD	Class III % RD	Class III No. I	Class III % I	Class IV No. OD	Class IV % OD	Class IV No. RD	Class IV % RD	Class IV No. I	Class IV % I
I	23	3	13.0	0	0.0	0	0.0	1	4.3	0	0.0	0	0.0
II	70	3	4.3	0	0.0	0	0.0	3	4.3	0	0.0	3	4.3
III	92	5	5.4	0	0.0	0	0.0	4	4.3	3	3.2	0	0.0
IV	39	3	7.7	1	2.6	0	0.0	0	0.0	1	2.6	0	0.0
V	51	2	4.0	2	4.0	0	0.0	0	0.0	0	0.0	0	0.0
VI	51	4	7.8	0	0.0	0	0.0	4	7.8	1	1.9	0	0.0
VII	52	6	11.5	0	0.0	0	0.0	1	1.9	1	1.9	0	0.0
VIII	66	1	1.5	0	0.0	0	0.0	2	3.0	2	3.0	0	0.0
Totals	444	27	6.1	3	0.7	0	0.0	15	3.4	8	1.4	3	1.1

Of the 444 cacti, 33.6% were in Class I, 16.3% were in Class II, 19.6% were in Class III, and 30.5% were in Class IV. 87.3% of the plants were healthy.
OD—Old Dead (plants dead over three years)
RD—Recently Dead
I—Infected

PART III
PERMANENT SAMPLE PLOT STUDIES

A. Objects

April 1941

1. To learn to recognize incipient stages of the disease.
2. To observe the progress and behavior of lesions.
3. To observe the progress and behavior of disease incidence and mortality in stands.
4. To determine whether or not there are seasonal annual changes in disease incidence or mortality and to determine the meteorological or other causes of such changes.

B. Plan

April 1941

To establish permanent observation plots in the Saguaro and Organ Pipe Cactus National Monuments on which detailed case histories shall be kept on each saguaro or organ pipe cactus present. Thorough reexamination will be made at stated intervals, their frequency depending on the accessibility of the plots and the need as it appears from analysis of previous records.

C. Accomplishments

Saguaro National Monument
Establishment of plots.

During April and May, 1941 six 5-acre plots were established and case histories started on the 979 saguaros thereon. Pertinent information for each plot is given below:

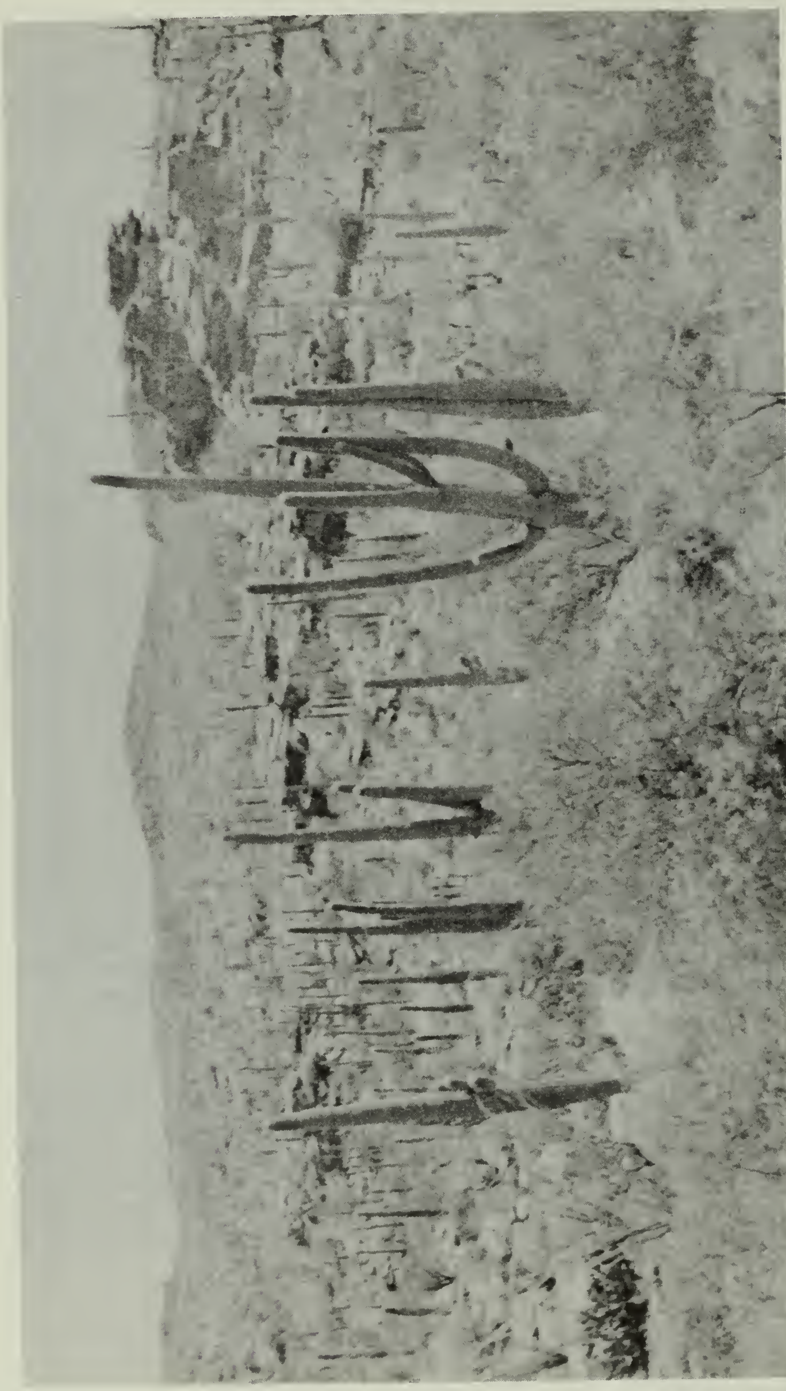


Figure 7. Sample Plot C located on a rocky hillside. All other plots were located in terrain similar to that shown in Figure 2.

Plot A
Area: 5 acres (5x10 chains)
Long axis: N—S
Location: N½ of the SW¼ of the SW¼ of the NE¼ of S.17 T 14 S., R. 16 E.
Total number of saguaros: 209
General topography: flat (Fig. 2)

Plot B
Area: 5 acres (5x10 chains)
Long axis: E—W
Location: S½ of the SE¼ of the SE¼ of the SW¼ of S. 17 T. 14 S., R. 16 E.
Total number of saguaros: 187*
General topography: flat (Fig. 2)
*All badly diseased plants were removed from this plot in the course of the suppression experiment.

Plot C
Area: 5 acres (5x10 chains)
Long axis: E—W
Location: S½ of the SE¼ of the SW¼ of the SW¼ of S. 33, R. 16 E., T. 14 S.
Total number of saguaros: 291
General topography: Lower mountain side having numerous rock outcrops (Fig. 7)

Plot D
Area: 5 acres (5x10 chains)
Long axis: N—S
Location: NE¼ of the SE¼ and the SE¼ of the NE¼ of the SW¼ of the SE¼ of S. 20, R. 16 E., T. 14S.
Total number of saguaros: 106
General topography: Rolling hills.

Plot E
Area: 5 acres (5x10 chains)
Long axis: E—W
Location: N½ of the NE¼ of the SW¼ and the S½ of the SE¼ of NW¼ of the SE¼ of S. 17, R. 16 E., T. 14 S.
Total number of saguaros: 126
General topography: Rolling hills.

Plot F
Area: 5 acres (5x10 chains)
Long axis: E—W
Location: N½ of the SW¼ of the SW¼ of the NW¼ of S. 21, R. 16 E., T. 14 S.
Total number of saguaros: 60
General topography: Flat (Fig. 2)

Examination of Plots.

Formal examinations of the plots were made on the following dates:

Plot A – 5/25/41 – 7/15/41 – 10/21/41 – 1/22/42
Plot B – 5/28/41 – 7/16/41 – 10/22/41 – 1/28/41
Plot C – 4/25/41 – 7/21/41 – 10/24/41 – 1/29/42
Plot D – 5/16/41 – 7/17/41 – 10/23/41 – 1/28/42
Plot E – 5/20/41 – 7/17/41 – 10/23/41 – 1/28/42
Plot F – 5/23/41 – 7/19/41 – 10/21/41 – 1/29/42

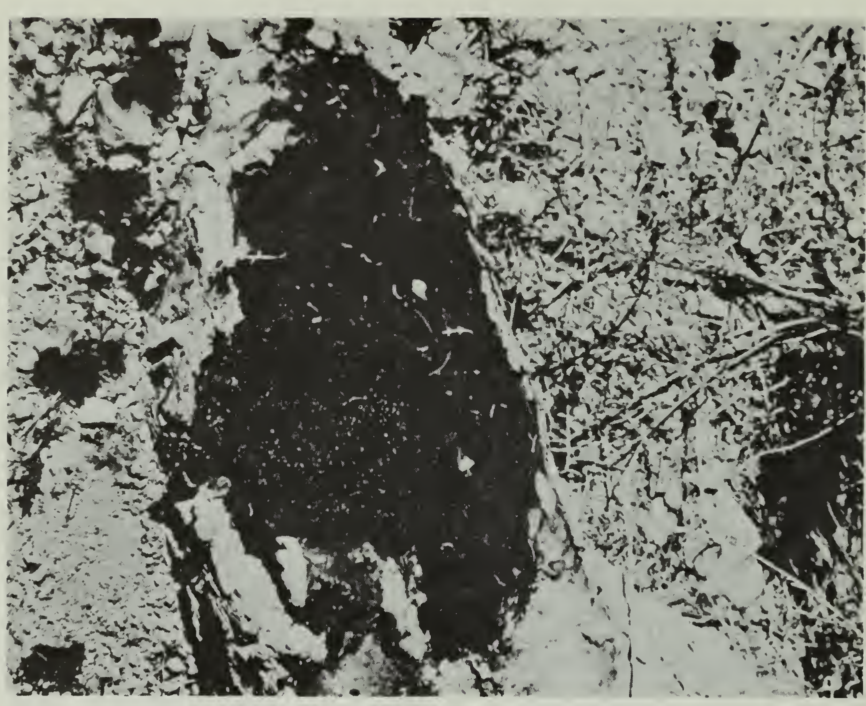


Figure 8. Rot pocket on a main (exposed) root of a large saguaro.

Organ Pipe Cactus National Monument

Establishment of Plots.

Descriptions of the five plots established in June, 1941 are given below. Plots I and II contain only organ pipe cactus whereas plots III, IV, and V apply only to saguaro.

Plot I—Organ pipe cactus, established 6/21/41.
- Area: .9 acres (3x3 chains)
- Location: Cement tanks on the S.W. side of the Big Ajo Mountains.
- Total number of plants: 7
- General topography: flat and rocky.

Plot II—Organ pipe cactus, established 6/21/41.
- Area: .9 acres (3x3 chains)
- Location: At cement tanks, adjacent to plot I on the east.
- Total number of plants: 18
- General topography: flat and rocky.

Plot III—Saguaro; established 6/23/41.
- Area: .9 acres (3x3 chains)
- Location: East side of the Ajo-Sonoyta road 11.4 + miles from the north boundary of the Monument.
- Total number of plants: 20
- General topography: flat.

Plot IV—Saguaro; established 6/24/41.
- Area: .9 acres (3x3 chains)
- Location: On the Alamo Canyon road 3.8 + miles from the Ajo-Sonoyta highway.
- Number of plants: 45
- General topography: flat.

Plot V—Saguaro; established 6/25/41.

Area: .9 acres (3x3 chains)

Location: Above Dowelling Well 2.4 + miles from the Customs House at the International Bdy. on the east slope of the hills. Marked by a small stone monument on W. side of road. Plot is approximately 450′ W. of monument.

Number of plants: 72

General topography: Lower mountain side with numerous rock outcrops.

Reexaminations: A reexamination of all plots was made during the week ending May 30, 1942.

D. Results

Preliminary analyses (Table 5) of the data from five of the Saguaro National Monument plots[1] indicates that the necrotic spots, believed to be incipient stages of the disease, appear in greatest numbers during the summer.

Over 200 new lesions were included in these analyses and about half of these appeared to have become naturally arrested in less than two months. Only about 2 percent of the lesions appeared to be active at the end of the 8-month period covered by the observations (Table 6). Further reexaminations will be essential in order to determine whether this apparently high degree of arrestment is permanent or whether the rot continues to work unseen behind the hard wound tissues of many apparently calloused lesions.

The figures from the Organ Pipe plots (Table 7) tell the same story as the survey of that Region viz., a low percentage of dead plants and very low infection at the present time. The data from the May, 1942 reexamination of these plots have not been analyzed but there was no obvious increase in disease intensity at that time.

PART IV
MISCELLANEOUS

Photographic Records

Since the beginning of the project an attempt has been made to obtain a complete photographic record of the work and the disease. Over 100 photographs are now on file at Tucson.

Repeat photographs showing the progress of the disease by approximately 1-month intervals have been made of the several cacti. Completed series are illustrated in Figures 9 and 10.

Distribution

A map showing the distribution of saguaros, kindly made available by Dr. Forrest Shreve, is shown in Figure 12.

Weather Analyses

Weather Analyses of the Tucson area have been made and are included in this report (Figs. 13, 14, 15 and Tables 8 and 9).

Wound Callus Formation

Samples of saguaro tissue that have been exposed to the weather for different periods have been collected and preserved for future study.

[1] Plot B was not included in the analyses since it was located in the sanitation area and therefore no longer comparable to the others.

TABLE 5. Time of Year Lesions Originate Based on Observations of Sample Plots A, C, D, E, F—Saguaro National Monument.

July 1941 to January 1942

No. and % of Lesions Originating			
May-July	July-Oct.	Oct.-Jan.	Total
127	58	16	201
63.1%	28.9%	8%	100%

TABLE 6. Longevity of Lesions Based on Observations of Sample Plots A, C, D, E, F—Saguaro National Monument

July 1941 to January 1942.

Percent of Lesions Remaining Active		
Less than 2 months	2-5 months	5-8 months
51	34	2

TABLE 7. Sample Plots—Organ Pipe National Monument.

Plot Number	Total Cacti	Dead No.	Dead %	Dying No.	Dying %	Diseased No.	Diseased %
I O.P.	7	0	0.0	0	0.0	1	16.6
II O.P.	18	2	11.1	0	0.0	1	5.5
Totals	25	2	8.0	0	0.0	2	8.0
III S.	20	6	30.0	0	0.0	0	0.0
IV S.	45	0	0.0	0	0.0	1	2.2
V S.	72	6	8.3	0	0.0	0	0.0
Totals	137	12	8.8	0	0.0	1	.7

TABLE 8. Abnormal Temperatures at Tucson, Arizona

From 1938 to 1941.

Jan	'38 - '40 - '41	very warm
Feb	'39	very cold
	'41	very warm
April	'41	very cold
	'39	very warm
May	'40	very warm
June	'41	very cold
Nov	'38	very cold
	'39	very warm
Dec	'39	very warm
	'40	very warm
	'41	(?) cold (no report)

TABLE 9. Weather Conditions at Tucson 1938–1941.

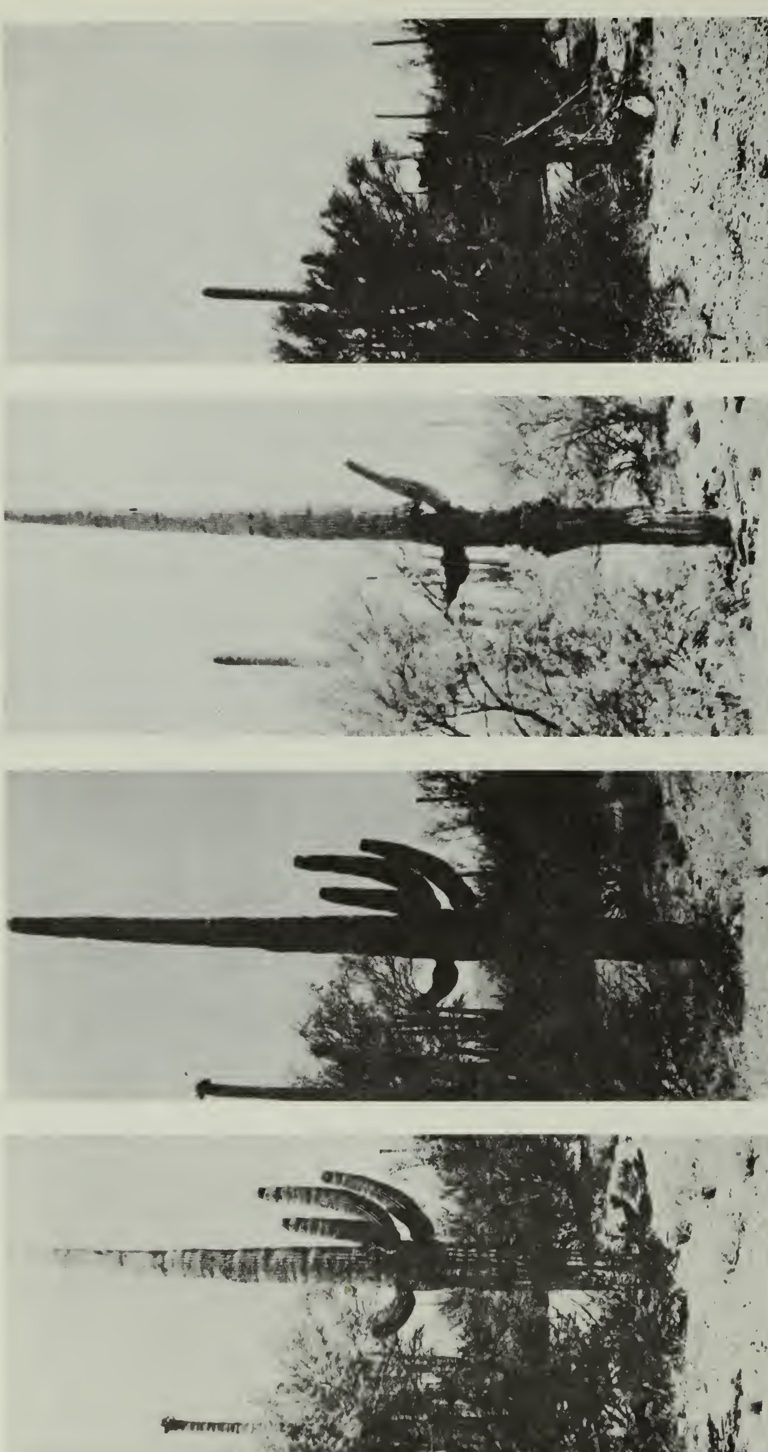
Precipitation: 1938-39 Annual below normal
1940-41 Annual above normal

Summer and fall precipitation

Percent of Normal

Year	April	May	June	April-June	July	Aug.	Sept.	July-Sept.
1938	+104	− 45	+600	+120	−66	+21	− 54	−32
1939	− 83	− 91	−100	− 90	−75	−36	+ 36	−38
1940	− 63	+137	+268	+ 80	−61	+47	+144	+21
1941	+104	+182	−100	+ 60	−35	+72	+27	+17

Normal precipitation
Jan-Mar Moderate
April-June Dry
July-Sept Wet
Oct-Dec Moderate
Annual about 11 inches.



June 12, 1941 July 9, 1941 Aug. 25, 1941 Oct. 22, 1941

Figure 9. Progressive stages of bacterial rot. Cactus No. E5-274. Plot A.

June 12, 1941 July 22, 1941 Aug. 25, 1941 Oct. 22, 1941

Figure 10. Progressive stages of bacterial rot. Cactus No. A4-128. Plot B.

Figure 11. This once fine specimen has probably not been dead more than six months.

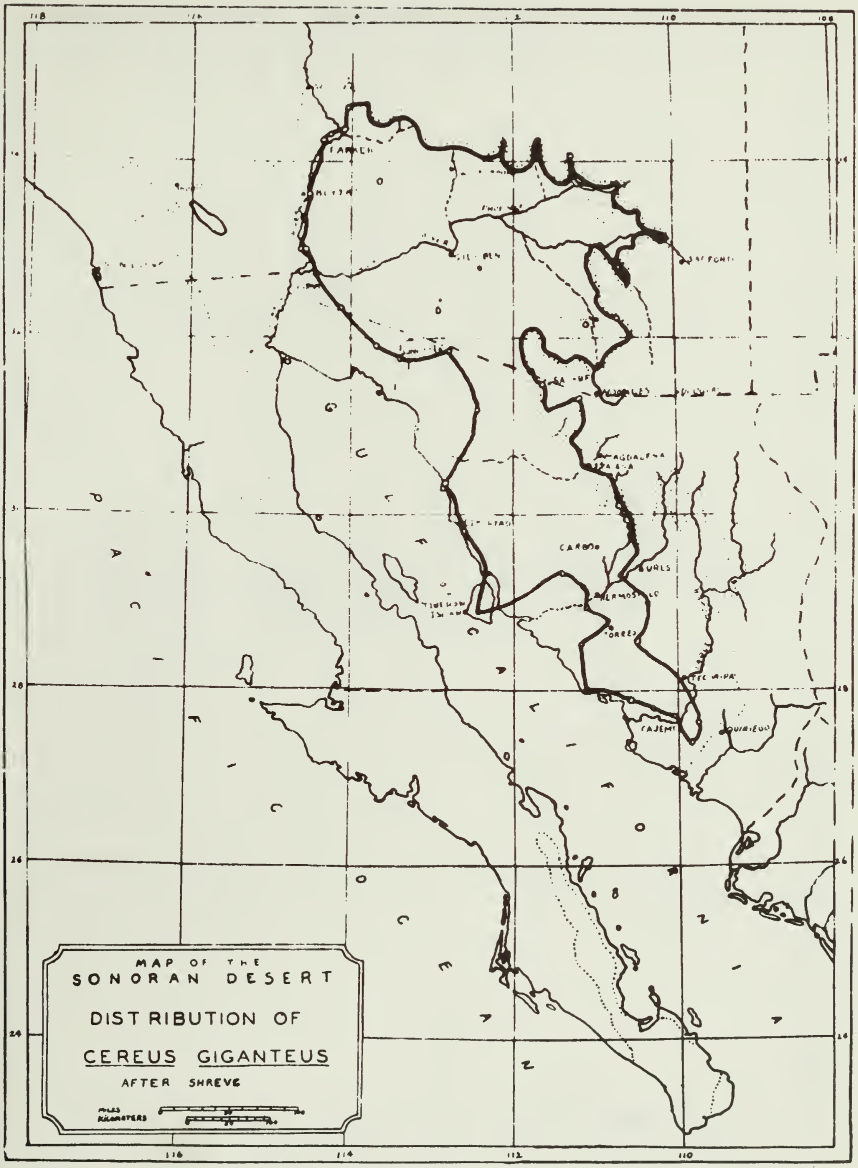


Figure 12. .... Limits of Sonoran Desert
__________ Limits of C. Giganteus

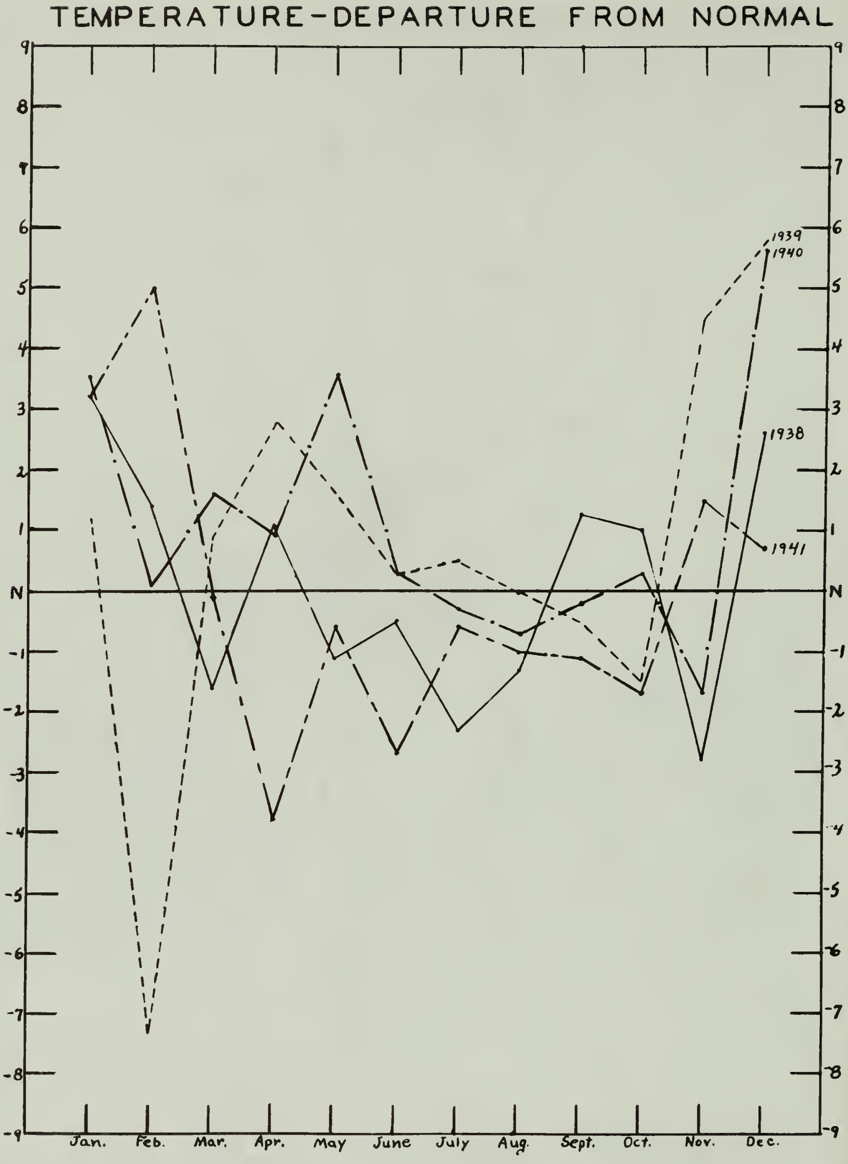


Figure 13. From U.S. Weather Bureau Records, Tucson, Arizona

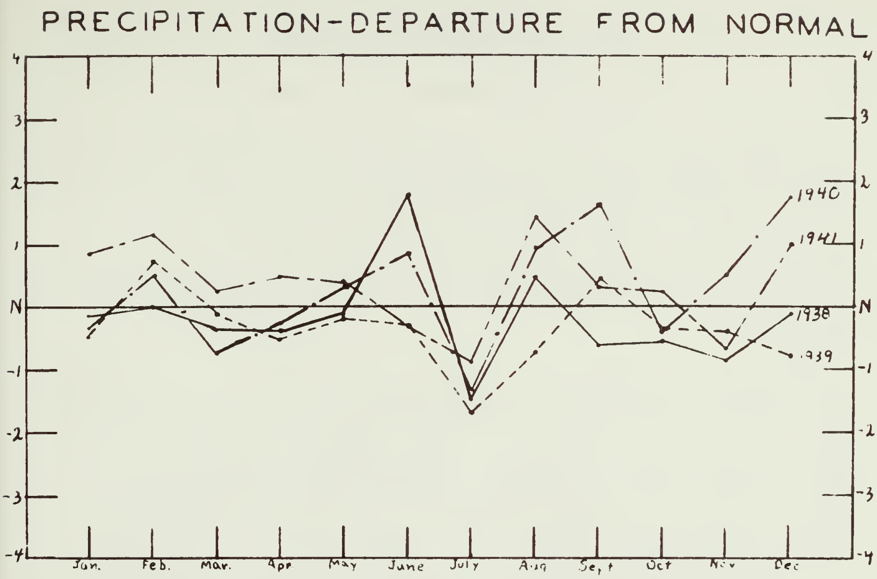


Figure 14. From U.S. Weather Bureau Records, Tucson, Arizona

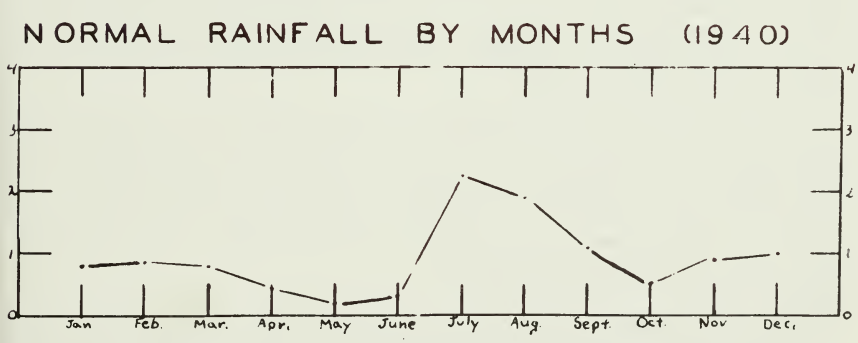


Figure 15. From U.S. Weather Bureau Records, Tucson, Arizona

PROGRESS REPORT
Organ Pipe Cactus National Monument

Bacterial Necrosis-Survey strips and sample plots

Introduction

In June 1941 a survey was made at organ Pipe Cactus National Monument to determine whether the necrosis attacking the giant cactus (and suspected of attacking the organ pipe cactus) was present on that area and, if present, the severity of the infection.

The disease was found to be generally present over the entire area on the saguaros and a similar, if not the same, disease present on the organ pipe cacti.

At that time five permanent sample plots and eight survey plots were established in areas where the disease was observed. The same plots were revisited in May 1942.

Sample plots

Each sample plot consisted of a square 200 feet on a side and having an area of 0.9 acres. Two sample plots were established in pure stands of the organ pipe cactus and three plots in saguaro. The position of every cactus was carefully mapped for each plot and complete notes taken on the condition of each cactus. These notes included the height of the plant, the number of arms or branches, the disease condition (healthy, dead, dying, diseased and if diseased the location, size and state of each lesion), the number and size of any mechanical lesions, and the condition of the roots.

At the time of establishment eight per cent of the organ pipe cacti on the two plots were dead and eight per cent were diseased. The saguaro plots, however, showed 8.8 per cent dead with only 0.7 per cent diseased. The 1942 check showed 12.0 per cent diseased in the case of the organ pipe cactus and 4.4 per cent diseased for the saguaro plots. There were no deaths during the year from June 1941 to May 1942.

Survey Plots

A line of stakes 200 feet apart and 1,000 feet long constituted the survey plots. From this central line of stakes 50 feet were paced off on either side, giving a strip 1,000 feet long by 100 feet wide. A tally of all plants falling within the boundaries of this strip was made by 200 foot blocks. The saguaros were divided into the following four height classes: Class I, cacti from 6 inches to 3 feet; class II, 4 feet to 8 feet; class III, 9 feet to 16 feet; and class IV, over 17 feet. The cacti in classes I and II were considered to be healthy unless specifically designated otherwise, but classes III and IV were divided into four groups: healthy, old dead (over three years), recently dead, and infected.

A total of 443 cacti were present on the survey plots, of which 223 or 50.3 per cent were in class III and IV. Of the 223 plants in these two classes, 12.1 per cent and 6.7 per cent respectively were old dead plants, 1.3 and 2.7 per cent recently dead plants, and 0.0 and 2.2 per cent infected plants. Thus 75 per cent of the plants were entirely healthy. The 1942 check showed that classes III and IV had 12.0 and 10.2 per cent respectively old dead plants, 0.0 and 3.5 per cent recently dead, and 0.0 and 3.5 per cent infected plants. Now, one year later, only 70.8 per cent of the plants are healthy.

Summary

1. All plots studied were located in areas where the disease was observed to be present.
2. Only about 4 per cent of the plants studied are infected at this time.
3. A slight increase in number of plants infected was noted in 1942.
4. About 50 per cent of the plants are less than eight feet in height. With so much reproduction taking place little importance can be attached to a loss of 4 per cent in the more mature plants.

Paul C. Lightle, Agent
Tucson, Arizona
June 23, 1942

UNITED STATES
DEPARTMENT OF THE INTERIOR
NATIONAL PARK SERVICE
WASHINGTON

September 24, 1942

Dr. Lee M. Hutchins,
Division of Forest Pathology,
Bureau of Plant Industry,
U.S. Department of Agriculture,
Washington, D.C.

Dear Dr. Hutchins:

Thank you for your letter of September 16 transmitting copy of the progress report prepared by Paul C. Lightle under date of June 23, 1942 on "Bacterial Necrosis—Survey strips and sample plots, Organ Pipe Cactus National Monument."

This report has been read with interest and we are very glad to note that the 4 per cent loss of mature plants is much more than offset by the abundance of reproduction.

Sincerely yours,

JDC/lmc

J. D. Coffman,
Chief of Forestry.

cc: Regional Director, Region Three,
Supt. Southwestern Monument,
Custodian, Organ Pipe Cactus NM.

PROGRESS REPORT FOR 1943
on
BACTERIAL NECROSIS OF CACTI

Organ Pipe Cactus National Monument

As the result of a survey made in June 1941, on the Organ Pipe Cactus National Monument the necrosis or bacterial rot of the giant (saguaro) cactus and a similar, if not the same disease, of the organ pipe cactus was found to be generally present but not severe over the entire area. Study plots, which were established during the course of this survey, were reexamined in May 1942. The results of the 1941 survey and the data obtained from the reexamination of the plots were summarized in a report by P. C. Lightle dated June 23, 1942. Only a slight increase in number of plants infected was noted in 1942. The slight losses were found to be more than offset by an abundance of young healthy plants. Young plants are rarely attacked, instead the disease is confined almost entirely to the more mature plants.

Most of the plots (some could not be found) were re-examined again in late February 1943. Based on the plot data and observations which were made over a large portion of the Monument, it was evident that the disease is not a serious threat at the present time to either the saguaro or organ pipe cacti. The plot data showed a sharp decline in newly infected plants over that recorded in 1942. Exceptionally few saguaro, organ pipe and senita cacti with active bacterial lesions were seen and evidence of killing of these plants during the past year was practically nil.

The incidence of diseased saguaro on the Organ Pipe Cactus National Monument is much less than on the Saguaro National Monument. On the latter Monument reproduction (young plants) is rare as compared with the former.

According to the Custodian of the Organ Pipe National Monument, no rain of consequence has fallen there in over nine months. This prolonged dry period is reflected in the appearance of the saguaro which are now quite shrunken as a result of depletion of their storage water supply. In comparison the saguaro on the Saguaro National Monument were well filled with water in February. On this Monument last year, following several rain storms in the fall, there occurred a flare up in the disease. As a result of this situation, together with other evidence, the possibility is suggested of a relationship between water balance of the plant and disease incidence.

JAMES L. MIELKE
Associate Pathologist

Albuquerque, N.M.
March 19, 1943

UNITED STATES DEPARTMENT OF AGRICULTURE
BUREAU OF PLANT INDUSTRY
P.O. Box 523
ALBUQUERQUE, N.M.

March 19, 1943

Mr. Bates Wilson, Custodian
Organ Pipe Cactus National Monument
National Park Service
Ajo, Arizona

Dear Mr. Wilson:

Enclosed is a copy of a summary report on the work Dr. Kimmey and I did late in February on the Monument in connection with the bacterial necrosis of saguaro, organ pipe, and senita cacti.

Present indications are that there may be a relationship between the water balance of saguaro and disease incidence. Early in the summer of 1941 there was a severe flare up of the necrosis on the Saguaro National Monument following the occurrence of abundant spring rains. Late last fall on that same Monument, Mr. Richey noted another but less severe flare up following early fall rains. According to what you told me there has not been any rain of consequence on your Monument in over nine months. The saguaro there show the effects of this prolonged dry spell by their shrunken appearance. On the Saguaro Monument they are in comparison now well filled with water. It would be appreciated if you would inform me of any flare up of the disease following rainy periods and the swelling of the saguaro as the result of taking up storage water.

Very truly yours,

Enclosure

JAMES L. MIELKE
Associate Pathologist

PROGRESS REPORT
on
BACTERIAL NECROSIS OF CACTI

Organ Pipe Cactus National Monument

On March 19, 1943, a progress report was made covering plot data collected and observations made late in February of that year on the bacterial necrosis or rot of cacti on the Organ Pipe Cactus National Monument. During mid-February of this year an inspection trip was again made to the Plant Pathologist of the University of Arizona, who is devoting time to studies of the causal organism of the disease. Acknowledgment is made to Monument Custodian R. Supernaugh for his interest in the problem and the time he devotedto the inspection. His assistance as a guide over little-used side roads and trails to stands of organ pipe and senita cacti on the Monument not previously examined is particularly appreciated.

Two days were spent making observations on the Monument and one day in adjacent Mexico where comparisons were obtained on the incidence of disease in saguaro, organ pipe and senita cacti. Owing to the war it has not been possible to establish enough permanent sample plots to be of value for reliable comparative purposes. Consequently only a general inspection was made.

The disease still continues to take a slow toll in saguaro. Losses are confined to the older plants. Nowhere were losses seen that were anywhere near as heavy as they have been on certain areas on the Saguaro National Monument near Tucson. Seedlings and young plants are abundant and occur practically everywhere. The disease was not found in any of these plants. This situation offsets to some extent the losses in the older plants. A comparable situation does not exist on the Saguaro National Monument where exceptionally few young seguaro are found in the older stands. In general, the disease does not at the present time appear to be a serious threat to saguaro on the Organ Pipe Cactus National Monument. Evidence was seen indicating it has been present on the Monument for many years. The disease has been found in saguaro wherever a search has been made for it in the United States and it is known to be widespread in Mexico.

Recent losses in organ pipe cactus and senita did not appear to be as heavy as a few years ago. The organ pipe cactus occurs over a wide altitudinal range on the Monument. Observations showed that this species may be attacked regardless of elevation. Losses have been somewhat heavier on some areas than on others. Many plants attacked by the bacterium are not killed. Instead, a few to many arms may die and than the organism ceases its activity. In general, the killing of a plant seems to be a slow process. A few arms may rot every year or so, but it appears that if this is to continue the plant must be freshly attacked eacy year, i.e., the causal organism of the rot must be re-introduced. The same applies to the senita cactus. There is much yet to be learned about the behavior of this disease in these two plants.

No plants of senita and only two of organ pipe were found with active rot lesions. However, this does not necessarily indicate that the disease has reached such a low ebb in its presence. The evidence so far obtained indicates that the causal organism is most active during the warm months of the year and least active during the winter or cooler months. If possible, a trip should be made to the Monument sometime during the summer to further check on this.

Across the International Boundary in Mexico adjacent to the Monument, losses from disease in organ pipe, senita and seguaro cacti have been heavier than on the Monument. Along the road from Sonoyta to Point Penasco (Rocky Point) on the Gulf of Lower California these three plants are common for about 25 miles. From there on for about 30 miles, or to within about 5 miles of the Gulf, they occur very sparingly and mainly as scattered individuals. Evidence of the disease may be found regardless of stand density. The closer one approaches the Gulf the more desert the country becomes. The few woody shrubs occurring there are very small and practically all of the vegetation is of the herbaceous type. Paloverde, mesquite, catclaw and similar plants found farther inland do not grow there. The Monument actually has rank vegetation in comparison.

All evidence obtained to date indicates that a moth, possibly an undescribed species, is the vector of the bacterium causing the rot of saguaro. The larvae of this insect tunnel around within the plants. It is only in association with the work of this insect that rot pockets have been found to originate.

Laboratory studies of the bacterium associated with the rot of organ pipe and senita cacti have been made by Mrs. Alice M. Boyle, Junior Scientific Aid, Division of Forest Pathology, stationed at Tucson. According to her this organism is not the same as the one causing the rot in saguaro. Additional specimens for her study were collected.

The dissection of some diseased arms of organ pipe and senita cacti, together with other evidence, disclosed that an insect probably also is the vector of the organism causing the rot of these plants. Rot pockets were found associated with the larval tunnels of this insect, which is suspected of being a moth since the character of its attack on these plants is very similar to the moth attack of saguaro. If the insect in question is a moth it would seem probable, however, that it is not the same species as the one found in seguaro because a different bacterium is involved.

Owing to the war it has not been possible to devote much time to the study of this problem. Despite this fact it is felt that progress is being made. Recent findings suggest possible methods of control hitherto not considered.

Division of Forest Pathology
Albuquerque, New Mexico
April 5, 1944

James L. Mielke
Associate Pathologist

SUMMARY OF RESULTS OF CONTROL EXPERIMENTS ON SAGUARO DISEASE,
Saguaro National Monument

By
James L. Mielke, Associate Pathologist

The following report is submitted as a brief summary of control work on the saguaro disease at the Saguaro National Monument. A detailed illustrated report will be prepared after additional data are taken in January and February, 1945.

The experimental plot, Section 17 of the Monument, is a mile square and was established during the winter of 1941-42. On this plot at that time there were approximately 12,750 saguaros. For purposes of identification and reference, a numbered stake was driven in the ground near the base of each plant. Control work has been carried out only on the south half of the plot; the north half has served as a check area for use in evaluation of control results. Each half of the plot contains approximately the same number of saguaros.

In the course of the original control operations, carried out during the winter of 1941-1942, 335 diseased saguaros on the half-section control area were removed and buried, and approximately the same number of diseased plants were left standing on the check area. From that time to January and February, 1944, when a survey was made, a total of 587 additional saguaros have died on the entire section. Of this total, 187 (32%) were on the control area, and 400 (68%) were on the check area where no control has been carried on. In 2 years, therefore, a total of 922 (587 plus 335) saguaros have died on the entire section.

The data obtained to date show that only the older saguaros and those apparently lacking in vigor are killed as a result of attack by the rot. Except of an occasional saguaro that is windthrown, this plant is not known to die from any other cause than the rot, to which it is especially susceptible in old age.

Owing to labor and equipment difficulties, control by the removal and burying of diseased plants was not continued after the first season. Experiments demonstrated that progress of the rot could be stopped by the opening up and draining of lesions and this method of treatment has been followed for parts of the past 2 years. Unfortunately we have been able to carry on the work only at intervals during the winter and spring months so that there has been no opportunity to measure the full effectiveness of the method in reducing losses.

Results of the experimental control work on the disease appear encouraging. This is indicated by the fact that 400 saguaros have died on the check plot and only 187 have died on the control plot.

According to work done at the University of Arizona the rot is caused by a bacterium. Present evidence indicates that a nocturnal moth may be the vector of this organism. The larvas of this moth develop within the saguaro, where they feed on the fresh plant tissues, tunnel indiscriminately, and finally emerge to pupate. It is only in association with the work of the larvas that rot pockets have been found to originate. If wounding from other causes is a factor in initiating the rot, no evidence of it has been found. The moth in question was discovered in Mexico a number of years ago and given a name. This appears to be about the extent of the published information on it. Its like history has not been completely worked out. The bacterium has been isolated from the intestinal tract of all larvas dissected for this purpose. However, it is not yet known if the organism occurs in the egg and all the other stages of development of the moth. Cooperative investigations with the University of Arizona on this phase of the problem are now under way.

In view of the probability that the moth is the principal vector, and in view of the fact that the moth larvas can survive only in fresh tissues, much less significance is now attached to the possibility that rotted saguaros may constitute an important source of inoculum for healthy plants. Consequently, it no longer appears necessary to destroy diseased plants by burial or other means, as was done during the course of the earlier control experiments. Our recent work has demonstrated that in a high percentage of plants, development of the rot can be arrested by merely opening up the lesions and removing most of the rot. The remaining rot then dries in a short time and callous tissue rapidly forms over the wounded area. It is not necessary to sterilize the wound or the treating tools with a disinfectant. Special treating tools have been developed. The present method of treatment is much cheaper than removing and burying diseased plants. Other possible means of control are under consideration.

It is not possible to save all diseased plants by the opening and draining method of control now followed. The point of origin of rot pockets and the intensity of the moth attack are factors which influence the success of the treatment. Also, control by the present method must be carried our practically every month of the year, for the moth larvas may be present in saguaro at all times. Furthermore, a diseased plant that has been successfully treated one year may again develop new infection pockets the following year associated with fresh attacks by the moth larvas.

It is strongly suspected that all these moth larvas carry the bacterium. However, the organism seems to be able to initiate the rot and destroy plants only when the latter are of great age or low in vigor. Saguaros as small as one foot in height have been observed with emergence holes of the moth larvas and all larger plants show evidence of attack to some degree. In general it is the oldest or largest plants that bear the greatest amount of evidence of moth attack. Practically every plant may be attacked to some extent every year. 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.

Many rot pockets dry up and callous out naturally, and as a result about 50 percent of the saguaros that become diseased in a given year do not die. Woodpeckers are an important factor in this callousing out of diseased pockets. Two species of these birds build their nests in saguaro. The larvas of two or more species of drone flies develop within the rot pockets where they feed on the rotting tissues. Very little is known about these insects according to the entomologists at the Unviersity of Arizona, but present evidence indicates that they depend upon the saguaro rot for their existence. A principal food of the two woodpeckers appears to be drone fly larvae. In search of these insects the woodpeckers open up the rot pockets, thus permitting them to dry out and callous formation to take place.

The disease is quite certainly not new or of recent origin on saguaro but rather is of very long standing. This is indicated by its presence practically throughout the range of saguaro, by the evidences in residual saguaro stands, and by some of the early observations on this cactus as well as from other supporting evidence. Its prevalence on the Monument in recent years seems to be due to a combination of favoring conditions which has undoubtedly occurred previously in many other old saguaro stands, of which now only scattered remnants remain.

Saguaro stands that are perpetuating themselves are composed of all-aged plants in about equal representation. The present stand of saguaro on the Monument is composed mainly of large old plants. Over most of the area seedlings and young plants are practically non-existent. Very little reproduction has occurred during the past 60 or 70 years and possibly longer. All evidence indicates that this condition has been brought about by destructive changes by man and domestic animals in the environment in which saguaro once thrived and reproduced itself.

Tucson is one of the oldest towns in the United States. A settlement was established there because of the abundance of wood, water, and also feed for domestic animals; in fact, a swamp and meadow once covered a large area. Now that is all gone, mainly as the result of removal and destruction of the vegetation. As the settlement grew it was necessary to go farther afield for wood. Also, the number of livestock increased and particularly in the 80's and 90's heavy overgrazing occurred everywhere in that general region. Lime kilns, which required much fuel, were in operation at one time on the Monument. Later the area was homesteaded and further woodcutting for fuel, fence posts, and other purposes occurred. The principal tree species utilized were ironwood, catclaw, and mesquite. Paloverde is of practically no value for fuel wood or fence posts, consequently it is the most common tree species on the Monument today. Overgrazing and the accompanying reduction of plant life continued. Today the old giant saguaros are left standing on practically bare soil that is little more than a sand and gravel rain pavement. Rains have washed away most all of the soil humus and the litter and duff. With this gone, together with much of the former vegetation required for protection of the seedlings, the conditions under which saguaro once reproduced itself are practically non-existent over much of the area today. According to Dr. Forrest Shreve—"It is often ten or fifteen years before the seedling becomes large enough to be noticed, and twenty to thirty years before it begins to raise its head above the shrubbery which has sheltered its infancy."

It is quite possible that this reduction in cover, with the accompanying decrease in the humus content of the soil, is contributing to the reduced vigor of the old plants and, in turn, to their reduced capacity to wall off the rot organism before lesions become established. If soil conditions are to be improved and the saguaro is to be given a chance to reproduce, the only practicable method would appear to be by a restoration of ground cover. This cannot take place in the presence of over-grazing or of the large rodent population, particularly of ground squirrels, now on the Monument.

We feel that distinct progress has been made in the understanding of the disease by our studies to date even though their continuity has been interrupted by war conditions. We have demonstrated that the rate of loss of large saguaros on the Monument can be materially reduced by control measures, such as the prompt opening and draining of rot lesions. However, we are not yet in a position to say whether the loss rate in the large plants, which form the chief attraction for the public on the Monument, can be reduced enough to maintain the present character of the Saguaro stands for any considerable number of years. After more is learned of the manner of transmittal of the disease and of the insect with which it seems to be associated, there seems a reasonable probability that some still more effective method of prolonging the life of the present stands may be found.

James L. Mielke
P.O. Box 523
Albuquerque, New Mexico
July 12, 1944.

ANALYSIS OF MORTALITY IN SAGUARO CACTUS

A progress report on the experimental area (Section 17 R16 ET14S) established in the Saguaro National Monument in 1941 for the study of bacterial rot.

By
Lake S. Gill and Paul C. Lightle
July 30, 1946

During the early months of 1946 a compilation of the data relative to mortality on the experimental section was made. This work revealed that slight errors had crept into previous reports, some of which were arithmetical while others resulted from the inclusion of a few dead plants as living ones in the initial tabulation of the data in 1942. The figures presented in this report have been carefully checked and supersede all previous tabulations.

ANALYSIS OF POPULATION

Table 1 shows the number of living plants on the section in 1941 prior to the initiation of the sanitation work on the south half, and also the number living after the last examination in early 1946. Plants that were obviously dead at the outset of the experiment have been excluded. The living plants counted are, therefore, only those which would not have died until 1942 or later.

Table 2 shows the distribution of the living population in 6 foot height classes. The height classifications were made only in 1941 and thus show changes due to mortality alone; they do not take growth into account. Undoubtedly during the five year period some of the plants in the lower height classes at least will have grown into the next higher one. In this connection it is probably significant that in 1941 only 678 plants were recorded in the 0-6 height class whereas annual inspections of the area to date revealed that there should have been at least 902 in 1941. Of the 224 small plants overlooked in the original census of the area, all were obviously over 5 years old when they were discovered but it is unbelievable that they would have been missed had they not increased considerably in size since 1941. Oversights in the other height classes were negligible. If the 224 small plants are considered as incoming population, the losses during the period still exceed the accessions by approximately five times, even disregarding abnormally high mortality that could be attributed to the sanitation operation.

TABLE 1. Living population 1941 and 1946

Year (1)	South half treated (2)	North half untreated (3)	Entire Section (4)
	No. living plants	No. living plants	No. living plants
1941	6358	6540	12898
1946	5618	5989	11607
Loss	740*	551	1291

*Includes living plants removed in sanitation experiment.

TABLE 2. Frequency distribution of living plants in 6-foot height classes 1941-1946 (Percent of plants living in year indicated)

Height Class (Feet) (1)	Treated area (S½) 1941 (2)	Treated area (S½) 1946 (3)	Treated area (S½) Diff (4)	Untreated area (N½) 1941 (5)	Untreated area (N½) 1946 (6)	Untreated area (N½) Diff (7)	Entire Section 1941 (8)	Entire Section 1946 (9)	Entire Section Diff (10)
0-6	5.8	6.4	+.6	8.1	8.7	+.6	7.0	7.6	+.6
7-12	11.3	12.1	+.8	14.2	15.1	+.9	12.8	13.6	+.8
13-18	30.1	31.9	+1.8	33.9	35.6	+1.7	32.0	33.8	+1.8
19-24	32.0	31.5	−0.5	22.7	22.2	−.5	27.3	26.7	−.6
25+	20.7	18.0	−2.7	21.0	18.3	−2.7	20.8	18.2	−2.6
broken	0.1	0.1	0	0.1	0.1	0	0.1	0.1	0
Total	100	100	0	100	100	0	100	100	0

EFFECT OF SANITATION

The next few tables attempt to show the value of the sanitation work as a measure in controlling the disease. Owing to the war the original operation of 1941 was not followed up as planned. There was no attempt to bury or remove diseased material from the area during the subsequent years. During the winter and spring of 1943 all plants that were dead or would surely die in the next few months were felled and chopped into small pieces and left to dry out on the ground. Excision of rot from living plants was continued on the treated half every winter through 1945 but no action was taken on the dead and dying plants after 1943.

Before attempting to compare the mortality on the treated and untreated areas respectively, consideration should be given to the living populations at the outset of the experiment. From Table 1 it can be seen that the untreated half had a slightly higher population, or 50.7% of all plants on the section. In addition, 56.2% of the plants on the untreated area were less than 19 feet high in comparison with 47.2% on the treated area (Table 2, columns 2 and 5). Since, as will be shown later, mortality is markedly higher in plants over 19 feet tall, the preponderance of smaller plants on the untreated area would favor a slightly lower mortality rate if based on total population. In addition, there are other indications that the disease was less intensive on the untreated than on the treated area. One of these is shown in Table 3 where a comparison is made between the plants actually removed on the treated area and those which would have been removed had sanitation been carried out on the untreated area in 1941. The fact that 4.3% of the living plants were removed whereas only 1.9% were marked for removal on the untreated area suggests that the disease was originally nearly twice as severe where sanitation was applied. Another approach indicated the same condition to a lesser degree. It was found that the plants marked for removal on the untreated area died of bacterial rot as shown in Table 4 column 2. These percentages applied to the 273 plants actually removed provide a basis for estimating what the mortality on the treated half might have been if the sanitation work had not been performed. Annual mortality, using both presumptions, is shown in Table 5. These figures suggest that while infection on the treated area appeared to be much heavier than on the untreated one at the outset of the experiment, the difference is much less marked at the end of the 5-year period. Does this, together with the marked drop in mortality on the treated area after 1941 (Table 5, column 7) indicate that the sanitation work was effective? Furthermore, if the diseased material had not actually been removed, would the percentages in column 3 have been higher, and by the same token if the 122 plants (column 8) marked for removal in 1941 had actually been removed and surgical treatment giben to the remaining diseased plants, would the percentages in column 9 have been lower?

PROGRESS OF NECROSIS

Table 4, column 3, was presented in order to illustrate a point relative to the disease that has provoked considerable speculation. From general observations it appeared that certain plants disintegrated quite rapidly after the disease appeared while in others the progress of necrosis seemed to be very slow. The figures tend to substantiate these observations and also to suggest that in the majority of cases the rot progresses rapidly at least after it is manifest from the outside of the plant. Of the 156 plants that died during 1942 only 53 (34%) had showed visible signs of infection at the beginning of the year. Furthermore, of those 53 a fair number had been practically destroyed by rot during 1941. The figures also show the relatively small percent of the annual loss that included plants showing external signs of infection for more than one year.

TABLE 3. Comparison of diseased plants removed on treated half with those marked for removal on untreated half in 1941.

Height Class	Plants Removed or would have been removed			
	Number		Percent of class	
	Treated ½	Untreated ½	Treated ½	Untreated ½
(1)	(2)	(3)	(4)	(5)
0-6	2	1	0.5	0.2
7-12	20	9	2.8	1.0
13-18	52	22	2.7	1.0
19-24	96	35	4.7	2.4
25+	101	55	7.7	4.0
Broken	2	0	28.6	0
Total	273	122	4.3	1.9

TABLE 4. Mortality from bacterial rot of 122 plants marked for removal in 1941.

Year (1)	% of 122 (2)	% of annual loss* (3)
1942	43.5	34
1943	14.7	12
1944	7.4	8
1945	4.1	6
Total	69.7	—
Alive 1946	30.3	—
Check	100	

*Loss from bacterial rot only.

TABLE 5. Comparison of annual mortality from bacterial rot on the treated and untreated halves respectively presuming that sanitation had or had not been performed on each

Year	Without Sanitation				With Sanitation			
	Treated ½		Untreated ½		Treated ½		Untreated ½	
	No.	%	No.	%	No.	%	No.	%
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
1941	—	—	—	—	273	4.29	122	1.86
1942	193	3.04	156	2.38	74	1.16	103	1.58
1943	154	2.42	143	2.19	114	1.79	125	1.91
1944	106	1.67	109	1.67	86	1.35	100	1.53
1945	104	1.64	91	1.39	93	1.46	86	1.32
Total	557	8.76	499	7.85	640	10.07	536	8.43

Note: The figures in columns 2 and 8 were calculated on the basis of presumptions described in the text preceding this table. The actual observed mortality on the two halves is given in columns 4 and 6. Percentages are based on the total number of living plants on each half in 1941 to sanitation work. The apparent increase in *total* mortality with sanitation is due to the fact that 30 percent of the plants marked for removal on the untreated ½ were still alive at the end of the period and it is presumed that a similar condition would have existed among those actually removed.

ANALYSIS OF MORTALITY WITHOUT SANITATION

For the succeeding discussions of uncontrolled mortality the untreated half section (N½ S17) is considered to be a fair example. While it is possible that border effects from the adjoining sanitation area may be present, they could not be detected from inspection of the data at hand.

A test of the border effect was made by comparing populations and mortality from bacterial rot on the entire untreated half-section (320 acres) and on the remaining 240 acres after deducting a border strip ten chains wide adjoining the treated half. The data for this comparison are presented in Table 6. In view of the fact that the elimination of the border strip tended to reduce rather than raise mortality there did not appear to be any logical reason for excluding it in further analyses.

Causes of Mortality

The causes of mortality on the untreated half section are given in Table 7 which shows that from 1941 to 1945 inclusive bacterial rot has been by far the most serious loss factor. The windfall of 1945 actually occurred on January 12, 1946 before the field data on 1945 losses had been taken. It is the only other notable cause of mortality during the 5-year period during which the area has been under observation.

TABLE 6. Comparison of living population and mortality on untreated half of Section 17 including and excluding respectively a border strip 10 chains wide adjoining the treated half.

Height Class (Feet)	Plants living in 1946				Plants died from rot '41-'45 incl.			
	Entire half Section 320 acres		Border strip Excluded 240 acres		Entire half Section 320 acres		Border strip Excluded 240 acres	
	No.	%	No.	%	No.	%	No.	%
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0-6	522	8.7	396	9.1	5	.083	2	.046
7-12	902	15.1	681	15.7	24	.401	16	.368
13-18	2131	35.6	1575	36.2	85	1.419	64	1.473
19-24	1328	22.2	937	21.6	137	2.288	95	2.186
25+	1099	18.3	751	17.3	246	4.108	157	3.613
Broken	7	0.1	6	0.1	2	.033	2	.046
Total	5989	100	4346	100	499	8.332	336	7.731

Note: Percentages based on 1946 living populations for each respective area.

TABLE 7. Frequency of dead plants by cause on untreated half of Section 17 for the period 1941-1945 inclusive. Expressed in percent of plants dying during the period.

Cause	Frequency %
(1)	(2)
Bacterial Rot	90.5
Windfall, 1945	7.1
Windfall other years	2.0
Accidental	0.4
All causes	100

TABLE 8. Frequency percent of dead plants by years, 1941-1945 inclusive.

Year	Treated Area Bacterial Rot	Total Mortality	Untreated Area Bacterial Rot	Total Mortality
(1)	(2) %	(3) %	(4) %	(5) %
1941(*)	42.7	39.5	— —	0.7
1942	11.6	11.5	31.3	29.0
1943	17.8	15.7	28.7	26.1
1944	13.4	12.7	21.8	20.5
1945	14.5	20.6	18.2	23.6
Total	100	100	100	100

(*)Based on plants removed in treatment.

Annual Trend of Mortality

The mortality rate seems to have been dropping steadily since the experiment was begun. This trend is expressed in Table 8 and is also evident in Table 5, columns 5 and 7, and again in Table 9. The departure from the downward trend of total mortality in 1945 is due to the heavy windfall of January 12, 1946. The marked downward trend in loss from bacterial rot suggests that the experiment may have been started at a time when, owing to a temporary set of conditions, mortality from bacterial rot was extremely heavy.

Mortality in Relation to Size

Mortality is directly correlated with size, the larger plants being subject to higher death rates. This trend is shown in Tables 6 and 9. It is interesting that the mortality rate rises sharply in plants over 18 feet high. In 1941 43.7% of the living plants were over 18 feet high.

The reasons for the increase in mortality with size are not fully understood. One possibility is that the larger plants being generally the older ones are in a state of decline and less able to resist the disease. On the other hand recent and as yet unconclusive experiments indicate that the more vigorous plants are more susceptible to the disease once they are attacked. It is possible that the target presented for infection may explain this correlation between mortality and size. Table 10 presents an arbitrary consideration of this possibility, since actual figures on comparative surface area were not available.

Mortality on the Monument

The dense stand of large saguaros which is the outstanding feature of the Monument covers approximately eight square miles. Since the experimental section appears to be a representative sample of the entire stand it is reasonable to assume that the approximate number of living plants in 1941 was 8 × 12898* or 103,184 plants. In order to give a more concrete picture of mortality on the Monument during the period of this study Table 11 has been prepared on the basis of a population of 100,000 plants, assumed to have the size distribution and mortality experience of the untreated half of Section 17. Mortality predictions have not been attempted because the period of observation has been too brief and because of the uncertainty created by the downward trend in annual mortality. When will it level off? Will it rise later? It is also felt that predictions relative to the changes the stand may be expected to undergo in time will require more information on the growth of saguaros than is available at this time.

*From Table 1.

TABLE 9. Mortality in 6-foot height classes on the untreated half Section 17 for the period 1942-1945 inclusive.

Height Class (feet) (1)	Percent of plants in height class dying in 1942 From rot only (2)	1942 From all causes (3)	1943 From rot only (4)	1943 From all causes (5)	1944 From rot only (6)	1944 From all causes (7)	1945 From rot only (8)	1945 From all causes (9)
	%	%	%	%	%	%	%	%
0-6	0.2	0.2	0.2	0.2	0.2	0.2	0.4	0.6
7-12	0.9	0.9	0.8	0.8	0.5	0.5	0.4	0.6
13-18	1.1	1.1	1.2	1.2	1.0	1.0	0.6	0.7
19-24	3.1	3.1	2.5	2.6	1.8	1.8	1.9	2.7
29+	5.6	5.8	5.2	5.2	3.9	4.1	3.2	4.7
All Classes	2.4	2.4	2.2	2.2	1.7	1.7	1.4	2.0

Note: Percentages based on number of living plants in height class in 1941.

TABLE 10. Comparison of Surface area and mortality by height classes.

Height Class	Arbitrary average size		Surface of Individuals		Frequency [1]	Surface in Stand		No. Plants Died 41-45	Relative Mortality
	Height	Diam.	Square	Relative		Square	Relative	Incl.	
Feet	Ft.	Ft.	Ft.			Ft.		[2]	
0-6	3	0.5	4.7	1	522	2453	1	5	1
7-12	9	0.75	21.1	4	902	19,032	8	24	5
13-18	15	1.0	47.0	9	2131	100,157	41	85	17
19-24	21	1.5	98.5	20	1328	130,808	53	137	27
25+	27	2.0	169.0	34	1099	185,731	76	246	49

[1]Table 6 column 2.
[2]Table 6 column 6.

TABLE 11. Mortality in population of 100,000 plants as indicated by data from untreated ½ Section 17. All causes.

Height Class	No. Living in 1941	No. Plants died in: 1942	1943	1944	1945	Period 1942 1945	Relative Loss
Feet:	(2)	(3)	(4)	(5)	(6)	(7)	(8)
0-6	8104	15	15	15	46	91	1
7-12	14,190	122	107	76	92	397	4
13-18	33,945	382	398	336	245	1361	15
19-24	22,630	703	581	413	612	2309	25
25 +	20,993	1223	1088	871	995	4177	46
Broken	138	0	15	15	15	45	—
Total	100,000	2445	2204	1726	2005	8380	—

OFFICE MEMORANDUM

TO : Custodian, Saguaro National Monument, Route 2, Box 544, Tucson, Arizona — DATE: September 4, 1946

FROM : L. S. Gill, Senior Pathologist, Division of Forest Pathology, Albuquerque, N. M.

SUBJECT: Analysis of Mortality in Saguaro Cactus.

Enclosed is a progress report of the subject title which is forwarded for your information and comment.

The primary purpose of the experiment on which the report is based was to determine the effectiveness of sanitation measures for controlling loss from bacterial rot in giant cactus. The war prevented us from carrying out the experiment according to the original design which called for the removal and destruction of diseased plant material for several successive years. It is therefore impossible to determine the true effects of the original sanitation work though there are indications that it may have held the disease in check to some extent. These indications are discussed in the section of the report entitled "Effect of Sanitation."

Since the report was prepared there are even stronger indications that the organism responsible for the rot is capable of killing plants regardless of their vigor once it has been introduced. This point is discussed in the section entitled "Mortality in Relation to Size."

Enc.

Mortality in the Giant Cactus at Saguaro National Monument 1941-1950

By
L. S. Gill, Senior Pathologist,
Division of Forest Pathology, B.P.I.S.&A.E.

In 1941, section 17, T. 14 S., R. 16 E. was set aside in the Saguaro National Monument for study purposes in conjunction with experimental control of a killing disease of the giant cactus or saguaro (*Carnegia gigantea* Britt. and Rose). The study area is in the midst of a spectacular and much visited cactus forest where losses from the disease referred to as bacterial necrosis or stem rot appeared to be unusually high in 1939 and 1940.

At the outset, the experimental section was divided into 64 10-acre squares. Each saguaro within a square was then identified with a numbered stake for the preparation and maintenance of case history records. There were 12,898 saguaros on the section, each of which was examined annually through 1945. Subsequently, it was necessary to confine the annual observations to 1433 plants on a 60-acre random sample and this was continued through 1950. The smaller sample consisted of 6 of the original 10-acre squares so that a record of disease and mortality within the same population is available for a 10-year period.

In 1941, following the cactus census, the south half of the section (320 acres) was given a sanitation treatment. At this time all dead, dying, and badly diseased plants were removed and burned or buried; furthermore, actively decaying tissue was excised from those less severely infected. The north half was left as a check but records were kept of the plants that would have been removed or otherwise treated had sanitation been practiced. The original plan called for annual repetition of the sanitation treatment for several years, and while this was done in a limited way in 1942 and 1943, restrictions caused by the war prevented the experiment from being carried out as planned.

In 1947 statistical analyses of disease losses on the entire section through 1945 indicated that there was no significant difference between the treated and the untreated areas and subsequent observations have given no reason to question that conclusion. That a single sanitation treatment was not effective in reducing losses is not surprising; that the experiment could not be carried out as originally planned is unfortunate.

For the reason just stated, the treated and untreated plots have been combined in making this 10-year analysis. It may therefore be regarded as indicative of natural mortality in the major part of the spectacular saguaro forest that received no treatment whatever.

In obtaining the 60-acre sample used in the 10-year record the 20 10-acre squares bordering each half section were discarded, leaving a block of 12 (2 × 6) in the center of each area for selection. Each square on the south half was then paired with one of similar population and characteristics on the north half. Three pairs were then selected at random. A comparison between the small sample and the population on the entire 640 acres is given in Table 1; the differences in disease losses are well within a normal sampling error and the small sample appears to be representative of the entire section. The greatest discrepancies occur in the 0-6 and 7-12 ft. height classes which together constitute only 20 percent of the population. A much closer relationship was obtained by combining the first three height classes into a 0-18 foot group which, according to Shrove[1], includes mostly immature plants less than 60 years old—the infants and juveniles of a saguaro forest.

In view of the fact that some plants on the treated portion of the area were removed in 1941 before they died from stem rot, the losses for that year are abnormally high. Furthermore, in counting mortality on the untreated portion of the sample all those plants which would have been removed in a sanitation operation were credited as deaths in 1941 and disregarded in subsequent years. All of these have died during the 10-year period 1941-1950. Excluding 1941, there has been no significant trend of mortality with the passing of the years.

---

[1]Shreve, Forrest. The rate of establishment of the giant cactus. Plant World 13: 235-240. Oct. 1940.

Figure 1 gives the mortality from all causes in the 60-acre sample during the past decade. The graphic representations are approximate to the nearest whole plant whereas the figures in the third column are calculated from the basic data. In Table 2 the relative importance of factors affecting mortality are shown. Nearly 95 percent of the deaths were caused by stem rot with wind being a lagging second. Furthermore, most of the wind losses occurred in a single storm during the winter of 1945-46.

From Figure 1 it is clear that mortality increases with the height of plants. Analyses of variance indicate that this relationship is highly significant, being above the 1 percent level. Since height is an expression of age it suggests very strongly that stem rot losses are linked with overmaturity. In any case stem rot does not appear to be a disease that threatens to wipe out the giant cactus as a species. What its ultimate effect will be on the old cactus forest at Saguaro National Monument is quite another problem. There are notable examples where similar forests have degenerated completely within the memory of men living today. The causes are obscure in all cases and the possibility must be recognized that if nature is allowed to take its course, the spectacular groves at Saguaro may in time become sparse and mediocre. While Figure 1 shows a loss of 33.4 percent of the large plants in 10 years it should be remembered that the height classifications have remained unchanged since 1941 and that actually these losses have been offset to some extent by growth of 19-24 foot plants into the higher class, and similarly losses in the medium-sized plants have been countered by ingrowth from the 0-18 foot group. No figures are available showing the extent to which such transition has occurred, but if it is assumed that mortality in the two upper classes has been balanced by growth, then the small class will have been reduced 23 percent in a decade. At that rate it will be practically nonexistent by 1980 after which time the larger classes are bound to degenerate at a fairly rapid rate unless reproduction becomes more abundant than has been the case since these observations were started.

Referring to Table 1 again, the frequency distribution of plants in 6-foot height classes is unusual in that there are relatively few small ones. While such a distribution is abnormal for plant populations as a whole, where one usually encounters a superabundance of young individuals, it could very well be normal for a saguaro forest of the type concerning us here. Tallies in old stands at Tucson Mountain Park and Organ Pipe Cactus National Monument

TABLE 1. Comparison of saguaro population and mortality on 60-acre (1,433 plants) and 640-acre (12,898) samples respectively

Height Class ft.	Percent of Plants living in 1941		Percent Mortality in height class 1941-'45	
	60 A. Sample	640 A. Sample	60 A. Sample	640 A. Sample
0-6	6	7	2.5	7.6
7-12	14	13	2.6	4.0
13-18	32	32	5.1	5.1
0-18	52	52	4.8	5.0
19-24	24	27	11.8	11.8
25 +	24	21	19.8	19.3

TABLE 2. Causes of mortality during the 10-year period 1941-1950 in a 60-acre sample of 1,433 plants

Height Class	Stem Rot percent	Wind percent	Other percent	Total
0-18	96.5	1.8	1.7	100
19-24	93.5	6.5	0	100
25 +	94.5	5.5	0	100
All classes	94.5	5.0	0.5	100

Both showed a dearth of young plants. Within the Saguaro National Monument there are vast acreages well stocked with giant cacti all less than 18 feet high which could very well become the spectacular forests of the future.

Distribution:
Dr. Hutchins (2)
Chief Forester, N.P.S. (1)
Regional Director, N.P.S., Santa Fe (2)
Superintendent, Saguaro National Monument (1)
W. W. Wagener (1)

Prepared at Albuquerque,
New Mexico
January 31, 1951

UNITED STATES DEPARTMENT OF AGRICULTURE
AGRICULTURAL RESEARCH ADMINISTRATION
BUREAU OF PLANT INDUSTRY, SOILS, AND
AGRICULTURAL ENGINEERING
DIVISION OF FOREST PATHOLOGY

P.O. Box 523
Albuquerque, N. Mex.
February 2, 1951

Mr. Samuel A. King, Superintendent
Saguaro National Monument
Route 8, Box 520
Tucson, Arizona

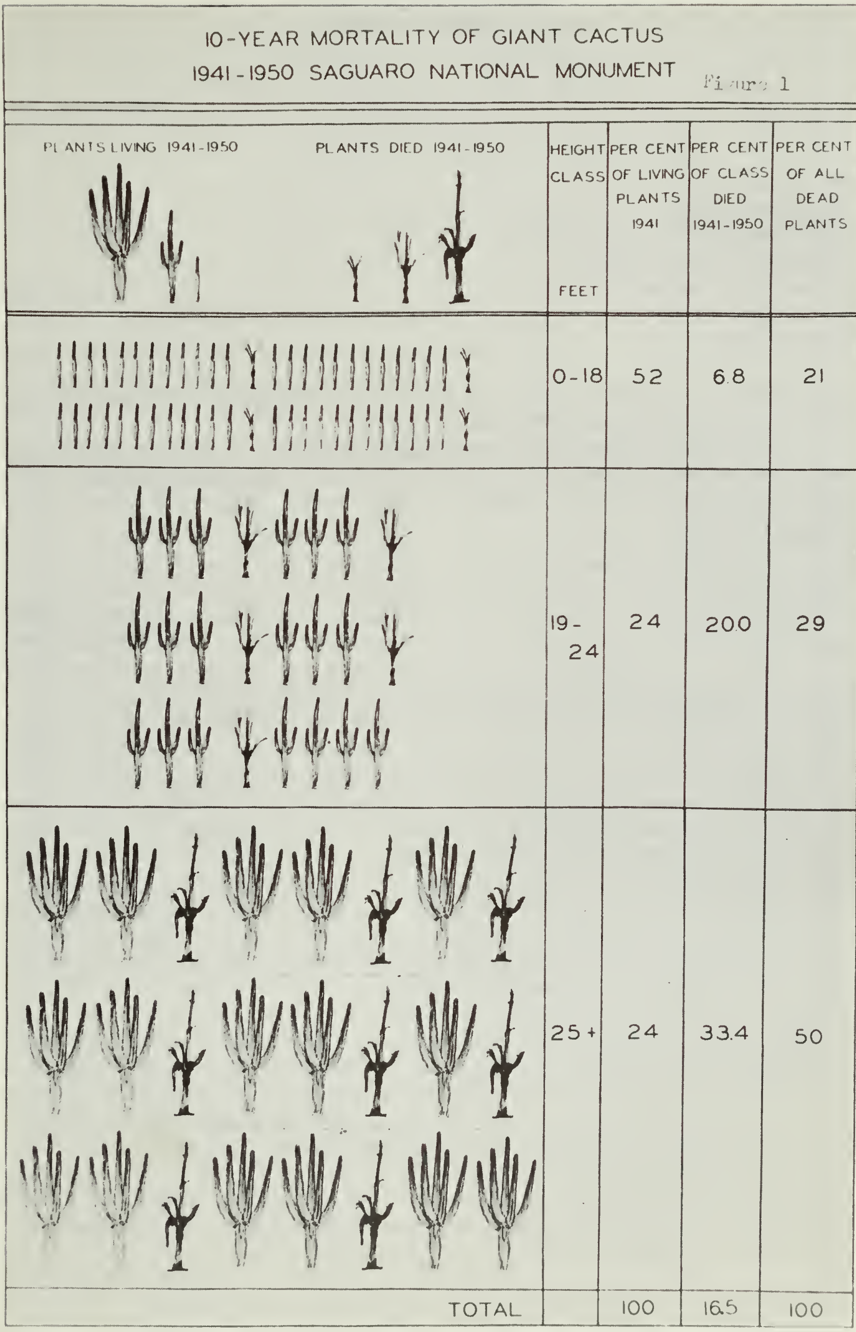
Dear Mr. King:

Enclosed is a report entitled "Mortality in the Giant Cactus at Saguaro National Monument 1941-1950" in which our observations on losses from stem rot and other causes are summarized. I hope you will not find the results too discouraging.

Sincerely,

Lake S. Gill
Senior Pathologist

Enclosure-1



HEIGHT CLASS FEET	PER CENT OF LIVING PLANTS 1941	PER CENT OF CLASS DIED 1941-1950	PER CENT OF ALL DEAD PLANTS
0-18	52	6.8	21
19-24	24	20.0	29
25+	24	33.4	50
TOTAL	100	16.5	100

Figure 1.

Saguaro National Monument
Tucson, Arizona

February 6, 1951

Dr. Lake S. Gill
Senior Pathologist
Agriculture Research Administration
Division of Forest Pathology
Albuquerque, New Mexico

Dear Dr. Gill:

Thank you very much for the copy of the report "Mortality in the Giant Cactus at Saguaro National Monument 1941-1950."

I was surprised to learn that the mortality rate, especially in the mature plants, reached such a high percentage. However, I note with interest that you indicated the possibility of the many younger plants occurring elsewhere on the monument, may become the spectacular forests of the future.

Samuel A. King
Superintendent

UNITED STATES
DEPARTMENT OF THE INTERIOR
NATIONAL PARK SERVICE
SOUTHWESTERN NATIONAL MONUMENTS
BOX 1728
SANTA FE, NEW MEXICO

November 30, 1951

Memorandum

To: Regional Director

From: General Superintendent

Subject: Construction of lath house for germination of saguaro seeds at Saguaro National Monument

I have recently received the attached PCP sheets for the construction of a lath house at Saguaro National Monument. From all reports, it appears that saguaro reproduction in the area known as the Cactus Forest is not sufficient to offset the losses due to disease, old age and vandalism. Mr. Bryan's report, which is attached, offers an interesting possibility for perpetuating the saguaro cactus. However, this matter brings up an important question on policy and I am referring it to your office for suggestions and guidance.

This matter has been given considerable thought in this office and we have serious doubts as to the advisability of initiating such a project. As far as we know, no such reforestation project, if it can be called that in the case of Saguaros, has ever been attempted on the scale that is proposed for Saguaro National Monument. Of course, saguaros have been artificially propagated and cultivated successfully for years, but only on a comparatively small scale in nurseries and botanical gardens. I believe it would be unwise for the National Park Service to undertake such a project in which the results would be so uncertain.

I also wonder if the importance of the bacterial necrosis in the Giant Cactus is not somewhat exaggerated. Certainly there is no doubt that this disease does cause Saguaro mortality, but all living things, plant and animal, are subject to disease which often destroys individuals, but, to my knowledge, has never destroyed an entire species in historical times, at least. I find it difficult to believe that the Saguaro may be extirpated as the result of bacterial necrosis, which some of the reports would seem to indicate. This disease, comparatively speaking, has just recently been discovered and studied, and doubtless has been a factor in cactus mortality for as long as the Giant Cactus has existed in its present form. It most likely was killing cactus 200 years or so ago when the evenly aged stand of Saguaros in the cactus forest germinated and started to grow.

Observations and reports indicate that the stand of Saguaros in the Cactus Forest is on the decline and that bacterial necrosis is one of the major factors responsible for this. However, reproduction is reported to be satisfactory on the upper desert and foothills sections of Saguaro National Monument. It seems likely that the spectacular cactus forest of the future will be located in these sections and will be of sufficient magnitude to warrant National Monument status.

Studies of the giant cactus indicate that we cannot expect uniform reproduction from year to year. Only in exceptional years are all ecologic and climatic factors so favorable as to insure optimum conditions for germination and growth. Such must have been the case about 200 years ago when the present even-aged stand of Saguaros in the Cactus Forest were just starting out. Is it not possible that this rare combination of factors favorable for reproduction might not occur again in the immediate future and thus perpetuate the present cactus forest by natural means?

I am in sympathy with efforts directed toward perpetuating the cactus forest, but I believe this should be done by restoring natural conditions rather than by artificial propagation. One of the chief factors now responsible for lack of Saguaro reproduction is the heavy grazing to which the cactus forest area has been and is subjected. This would doubtless reduce the chances of success of a project of artificial propagation. In years past there was much woodcutting in the area and this has destroyed a large number of the cover plants so necessary for providing protection to young Saguaros. The destruction of cover plants is accompanied by a decrease of humus in the soil and it is quite possible that this is a contributing factor to the reduced vigor of the mature plants and lack of reproduction.

With the situation as it exists today, it is probable that the conditions under which the Saguaro once reproduced itself are practically non-existent over much of the area. I suggest that the answer to the problem lies in directing our efforts along lines which would tend to bring about a return of natural conditions and restore the ecological balance. Until this is done, I am doubtful that any method of propagation, artificial or natural, could be successful.

Perhaps I have gone into this matter in too much detail, but it presents a problem which should be carefully considered. Artificial propagation of the Saguaro may be the only way of perpetuating the plant in the Cactus Forest, but I suggest that our knowledge is not yet sufficient to make such a statement. It is my understanding that Saguaro seedlings could be obtained at nominal cost frcm the Boyce-Thompson Arboretum near Superior, Arizona. If this is true, it might not be necessary to build a lath house in the event it is decided to initiate a project of artificial propagation.

I would be pleased to receive an evaluation of this project with particular regard to its implications relating to Service policy.

John M. Davis
General Superintendent

Attachments 7
Copy to: Superintendent, Saguaro
LPA:oms

Appendix II

APPENDIX II. Above-ground stem height (cm) and subsequent 1-year growth increments (cm, N = 244) of 39 saguaros at Saguaro National Monument (east). Graphed in Fig. 2-2.

No.	Field No.	1969 A.G. Stem Height	1969 Apical Growth	1970 A.G. Stem Height	1970 Apical Growth	1971 A.G. Stem Height	1971 Apical Growth	1972 A.G. Stem Height	1972 Apical Growth
1	G6808	2.70	.40	3.10	.30	3.40	1.60	5.00	3.40
2	G6813	3.10	1.50	4.60	1.20	5.80	3.10	8.90	3.60
3	G6812	3.70	1.30	5.00	.70	5.70	2.50	8.20	3.20
4	G6805	4.60	2.10	6.70	2.10	8.80	4.00	12.80	4.90
5	G6806	5.90	2.70	8.60	2.00	10.60	3.00	13.60	3.70
6	G6807	10.20	3.90	14.10	3.00	17.10	4.80	21.90	6.50
7	G6811	17.60	2.70	20.30	3.60	23.90	3.90	27.80	3.80
8	G6801	17.90	2.10	20.00	3.90	23.90	3.90	27.80	5.80
9	G6814	20.00	3.50	23.50	3.30	26.80	4.50	31.30	6.00
10	G6816	22.30	3.20	25.50	5.00	30.50	4.00	34.50	5.70
11	G6804	23.80	4.00	27.80	4.10	31.90	3.50	35.40	5.80
12	G6802	29.40	3.60	33.00	4.90	37.90	5.00	42.90	6.70
13	G6810	38.30	5.00	43.30	4.90	48.20	4.90	53.10	6.10
14	G6803	59.20	3.30	62.50	5.90	68.40	6.00	74.40	9.60
15	G6809	62.70	9.60	72.30	9.00	81.30	8.20	89.50	10.20
16	G6815	68.80	10.70	79.50	12.00	91.50	9.50	101.00	8.00
17	G6817	92.60	12.30	104.90	13.90	118.80	11.20	130.00	13.00
18	7139							145.70	11.20
19	7133							169.90	18.50
20	7138							174.30	9.70
21	7132							184.30	10.30

APPENDIX II. Above-ground stem height (cm) and subsequent 1-year growth increments (cm, N = 244) of 39 saguaros at Saguaro National Monument (east). Graphed in Fig. 2-2. — *Continued*

		1969		1970		1971		1972	
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth
22	7134							228.60	19.30
23	7140							353.40	19.90
24	7135							395.00	21.50
25	69B	428.30	12.40	440.70	10.90	451.60	14.20	465.80	19.70
26	69D	449.80	11.20	461.00	12.50	473.50	11.60	485.10	19.30
27	7131							491.80	14.00

APPENDIX II. Above-ground stem height (cm) and subsequent 1-year growth increments (cm, N = 244) of 39 saguaros at Saguaro National Monument (east). Graphed in Fig. 2-2. — *Continued*

		1973		1974		1975		1976		1977[1]
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height
1	G6808	8.40	2.30	10.70	.80	11.50	2.00	13.50	5.00	18.50
2	G6813	12.50	3.20	15.70	3.70	19.40	3.20	22.60	3.70	26.30
3	G6812	11.40	3.50	14.90	1.60	16.50	3.50	20.00	3.70	23.70
4	G6805	17.70	4.10	21.80	3.60	25.40	4.30	29.70	4.60	34.30
5	G6806	17.30	4.20	21.50	3.40	24.90	4.30	29.20	4.20	33.40
6	G6807	28.40	6.30	34.70	4.60	39.30	6.60	45.90	6.30	52.20
7	G6811	31.60	3.90	35.50	3.60	39.10	5.10	44.20	6.60	50.80
8	G6801	33.60	7.30	40.90	6.50	47.40	8.40	55.80	10.20	66.00
9	G6814	37.30	7.10	44.40	7.60	52.00	8.90	60.90	9.10	70.00
10	G6816	40.20	7.80	48.00	6.20	54.20	9.90	64.10	10.20	74.30
11	G6804	41.20	7.20	48.40	5.80	54.20	7.30	61.50	5.80	67.30
12	G6802	49.60	7.60	57.20	7.10	64.30	9.00	73.30	11.20	84.50
13	G6810	59.20	5.50	64.70	6.60	71.30	6.80	78.10	7.50	85.60
14	G6803	84.00	10.30	94.30	5.30	99.60	9.90	109.50	10.40	119.90
15	G6809	99.70	8.40	108.10	8.30	116.40	8.80	125.20	10.40	135.60
16	G6815	109.00	3.50	116.50	7.10	123.60	6.30	129.90	6.60	136.50
17	G6817	143.00	12.80	155.80	12.60	168.40	11.70	180.10	14.00	194.10
18	7139	156.90	11.10	168.00	13.80	181.80	13.90	195.70	15.80	211.50
19	7133	188.40	15.20	203.60	13.10	216.70	18.50	235.20	10.20	245.40
20	7138	184.00	10.90	194.90	5.70	200.60	13.40	214.00	9.40	223.40
21	7132	194.60	8.90	203.50	9.00	212.50	12.30	224.80	9.40	234.20
22	7134	247.90	17.20	265.10	14.20	279.30	17.20	296.50	17.20	313.70

APPENDIX II. Above-ground stem height (cm) and subsequent 1-year growth increments (cm, N = 244) of 39 saguaros at Saguaro National Monument (east). Graphed in Fig. 2-2. — *Continued*

		1973		1974		1975		1976		1977[1]
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height
23	7140	373.30	19.90	393.20	14.40	407.60	16.70	424.30	20.00	444.30
24	7135	416.50	19.50	436.00	16.70	452.70	20.30	473.00	18.80	491.80
25	69B	485.50	9.90	495.40	11.20	506.60	11.90	518.50	11.20	529.70
26	69D	504.40	10.30	514.70	16.50	531.20	13.50	544.70	13.30	558.00
27	7131	505.80	10.30	516.10	11.40	527.50	11.50	539.00	11.10	550.10
28	7507					581.00	14.00	595.00	14.30	609.30
29	7502					667.00	7.00	674.00	7.60	681.60
30	7503					732.00	10.60	742.60	13.00	755.60
31	7511					744.60	5.40	750.00	7.30	757.30
32	7505					789.50	7.30	796.80	9.20	806.00
33	7508					865.90	8.30	874.20	5.70	879.90
34	7510					900.50	5.40	905.90	6.70	912.60
35	7517					986.60	5.40	992.00	7.20	999.20
36	7521					1051.60	7.50	1059.10	10.10	1069.20
37	7513					1110.40	6.70	1117.10	9.90	1127.00
38	7518					1193.50	8.40	1201.90	7.60	1209.50
39	7520					1276.20	7.00	1283.20	9.50	1292.70

[1] A.G. stem height

Appendix III

Appendix III. Above-ground stem height (cm) and subsequent 1-year apical growth increments (cm, N = 248) of 41 saguaros at Saguaro National Monument (west). Graphed in Fig. 2-3.

		1969		1970		1971		1972	
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth
1	G6863	8.60	1.60	10.20	1.30	11.50	2.20	13.70	3.20
2	G6837	9.70	1.50	11.20	2.60	13.80	1.30	15.10	4.00
3	G6850	12.50	2.30	14.80	3.40	18.20	2.20	20.40	3.70
4	G6856	13.90	1.90	15.80	2.60	18.40	3.30	21.70	3.70
5	G6854	14.70	2.20	16.90	2.90	19.80	2.60	22.40	4.30
6	G6839	18.50	1.20	19.70	3.00	22.70	2.70	25.40	5.00
7	G6847	19.10	2.80	21.90	4.60	26.50	3.70	30.20	5.10
8	G6849	19.60	2.20	21.80	2.60	24.40	3.60	28.00	5.70
9	G6857	21.30	2.70	24.00	4.20	28.20	2.10	30.30	6.00
10	G6860	28.90	1.80	30.70	3.10	33.80	3.60	37.40	5.60
11	G6858	33.70	2.70	36.40	4.60	41.00	5.20	46.20	4.70
12	G6867	47.20	3.90	51.10	8.50	59.60	5.30	64.90	8.10
13	G6859	51.30	1.50	52.80	5.90	58.70	5.30	64.00	7.80
14	G6853	71.80	8.80	80.60	11.50	92.10	7.10	99.20	12.60
15	G6852	94.40	7.50	101.90	11.60	113.50	8.80	122.30	12.40
16	G6833	95.50	4.40	99.90	8.30	108.20	6.80	115.00	9.00
17	G6841	104.00	4.90	108.90	9.80	118.70	5.00	123.70	8.60
18	7030							135.50	12.10
19	7029							153.50	15.70
20	6868A							181.00	17.40
21	7153							187.20	17.60
22	71-217							190.60	8.60

APPENDIX III. Above-ground stem height (cm) and subsequent 1-year apical growth increments (cm, N = 248) of 41 saguaros at Saguaro National Monument (west). Graphed in Fig. 2-3. — *Continued*

No.	Field No.	1969		1970		1971		1972	
		A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth
23	71-113							246.60	17.00
24	7031							322.90	10.80
25	71-194							346.20	21.80
26	71-181							408.70	9.90
27	71-168							456.40	10.10
28	71-190							482.80	13.90
29	7032							543.60	13.40

APPENDIX III. Above-ground stem height (cm) and subsequent 1-year apical growth increments (cm, N = 248) of 41 saguaros at Saguaro National Monument (west). Graphed in Fig. 2-3. — *Continued*

		1973		1974		1975		1976		1977[1]
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height
1	G6863	16.90	1.20	18.10	3.10	21.20	.80	22.00	2.50	24.50
2	G6837	19.10	2.20	21.30	3.50	24.80	.60	25.40	4.50	29.90
3	G6850	24.10	3.30	27.40	3.70	31.10	1.60	32.70	4.00	36.70
4	G6856	25.40	3.00	28.40	5.20	33.60	2.30	35.90	6.20	42.10
5	G6854	26.70	2.80	29.50	4.30	33.80	3.10	36.90	4.10	41.00
6	G6839	30.40	2.90	33.30	4.40	37.70	3.80	41.50	6.20	47.70
7	G6847	35.80	4.10	39.40	3.70	43.10	2.40	45.50	5.30	50.80
8	G6849	33.70	4.80	38.50	6.50	45.00	3.40	48.40	7.50	55.90
9	G6857	36.30	1.40	37.70	5.30	43.00	1.40	44.40	7.00	51.40
10	G6860	43.00	4.00	47.00	4.10	51.10	.80	51.90	4.90	56.80
11	G6858	50.90	4.20	55.10	4.00	59.10	.90	60.00	4.80	64.80
12	G6867	73.00	5.60	78.60	6.00	84.60	1.10	85.70	6.50	92.20
13	G6859	71.80	6.70	78.50	8.50	87.00	3.00	90.00	11.70	101.70
14	G6853	111.80	11.10	122.90	12.80	135.70	8.30	144.00	16.10	160.10
15	G6852	134.70	9.50	144.20	14.90	159.10	9.10	168.20	16.30	184.50
16	G6833	124.00	6.50	130.50	9.30	139.80	2.20	142.00	9.20	151.20
17	G6841	132.30	6.10	138.40	8.10	146.50	3.10	149.60	6.50	156.10
18	7030	147.60	11.10	158.70	10.30	169.00	3.60	172.60	9.90	182.50
19	7029	169.20	13.10	182.30	11.80	194.10	6.60	200.70	10.10	210.80
20	6868A	198.40	9.80	208.20	11.20	219.40	5.60	225.00	9.30	234.30
21	7153	204.80	13.00	217.80	16.20	234.00	12.30	246.30	17.20	263.50
22	71-217	199.20	6.60	205.80	7.60	213.40	4.40	217.80	10.40	228.20
23	71-113	263.60	14.10	277.70	17.80	295.50	13.70	309.20	16.80	326.00
24	7031	333.70	10.70	344.40	8.90	353.30	11.90	365.20	8.70	373.90

APPENDIX III. Above-ground stem height (cm) and subsequent 1-year apical growth increments (cm, N = 248) of 41 saguaros at Saguaro National Monument (west). Graphed in Fig. 2-3. — *Continued*

		1973		1974		1975		1976		1977[1]
No.	Field No.	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height	Apical Growth	A.G. Stem Height
25	71-194	368.00	8.50	376.50	13.90	390.40	9.60	400.00	15.00	415.00
26	71-181	418.60	6.20	424.80	12.50	437.30	8.00	445.30	10.70	456.00
27	71-168	466.50	9.00	475.50	7.60	483.10	6.00	489.10	14.40	503.50
28	71-190	496.70	12.20	508.90	14.70	523.60	11.30	534.90	10.80	545.70
29	7032	557.00	12.90	569.90	16.80	586.70	12.00	598.70	11.90	610.60
30	71-62					676.10	6.70	682.80	7.50	690.30
31	71-199					716.20	3.70	719.90	8.80	728.70
32	71-175					833.60	5.50	839.10	10.40	849.50
33	71-82					874.20	5.10	879.30	9.60	888.90
34	75-24					982.40	4.50	986.90	6.80	993.70
35	75-23					994.80	4.10	998.90	5.40	1004.30
36	71-116					1001.30	4.10	1005.40	7.10	1012.50
37	75-22					1055.20	3.30	1058.50	4.10	1062.60
38	75-27					1078.30	5.40	1083.70	5.30	1089.00
39	75-26					1087.10	5.80	1092.90	6.60	1099.50
40	75-28					1245.00	5.70	1250.70	9.90	1260.60
41	75-25					1356.40	2.40	1358.80	4.60	1363.40

[1] A.G. stem height

Appendix IV

APPENDIX IV. Above-ground stem height (cm) and 10-year apical growth (cm), 1967-1977, of saguaros (N = 30) at Alamo Canyon, Organ Pipe Cactus National Monument, Arizona. Graphed in Fig. 2-5.

No.	Stem Height		10-Year Growth Increment
	1967	1977	
1	83.8	135.3	51.5
2	101.6	148.9	47.3
3	114.3	187.3	73.0
4	116.8	174.3	57.5
5	129.5	195.1	65.6
6	132.1	200.2	68.1
7	134.6	197.1	62.5
8	157.5	248.3	90.8
9	157.5	230.5	73.0
10	162.5	248.0	85.5
11	165.1	235.7	70.6
12	165.1	228.3	63.2
13	172.7	241.2	68.5
14	210.8	297.3	86.5
15	213.4	314.0	100.6
16	223.5	316.6	93.1
17	259.1	354.0	94.9
18	287.0	427.0	140.0
19	302.3	383.2	80.9
20	345.4	454.1	108.7
21	416.6	518.8	102.2
22	510.5	618.6	108.1
23	528.3	625.8	97.5
24	538.5	612.7	74.2
25	538.5	602.5	64.0
26	660.4	762.0	101.6
27	711.2	770.7	59.5
28	716.3	776.9	60.6
29	718.7	777.5	58.8
30	853.4	939.5	86.1

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