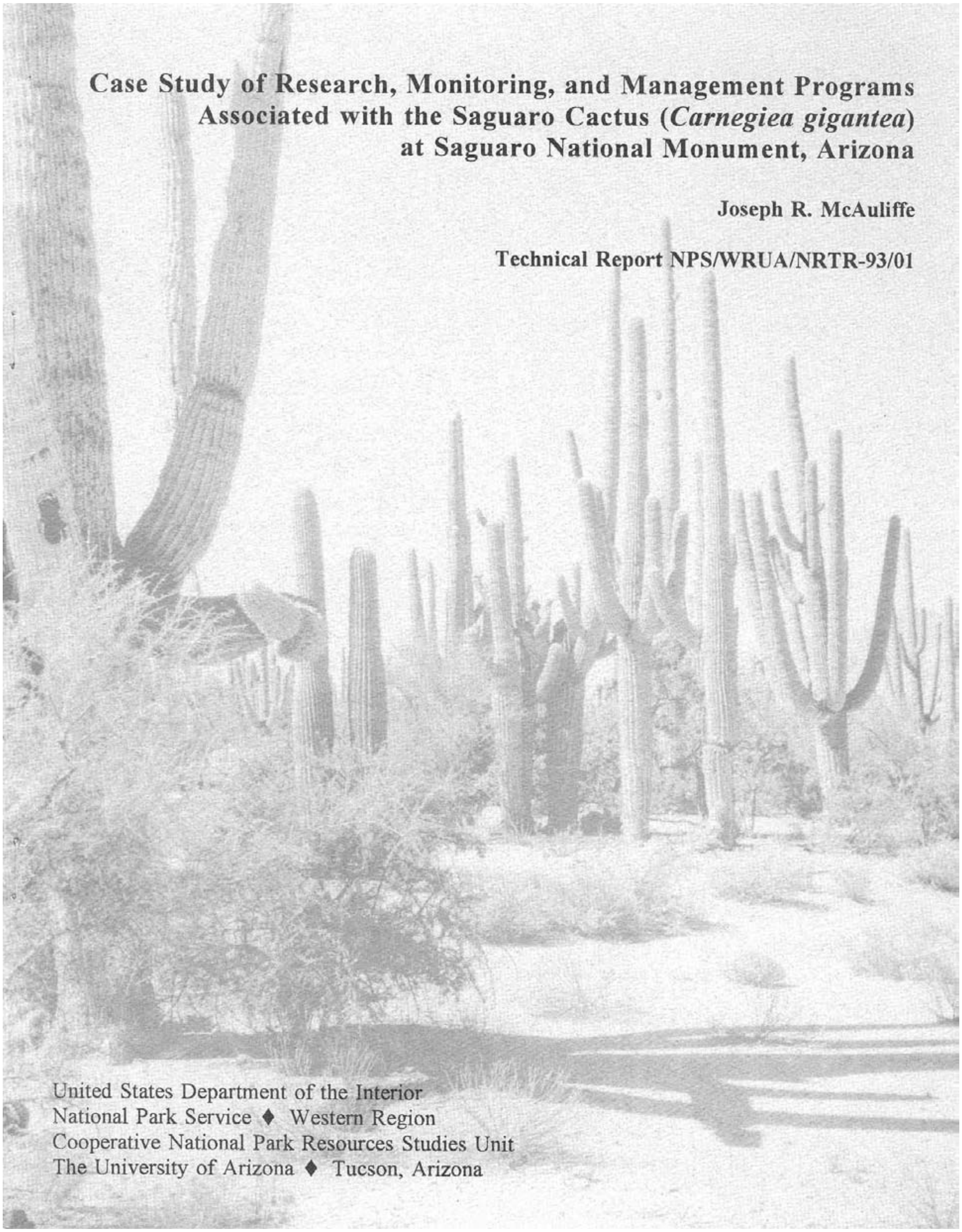

Case Study of Research, Monitoring, and Management Programs Associated with the Saguaro Cactus (*Carnegiea gigantea*) at Saguaro National Monument, Arizona

Joseph R. McAuliffe

Technical Report NPS/WRUA/NRTR-93/01

United States Department of the Interior
National Park Service ♦ Western Region
Cooperative National Park Resources Studies Unit
The University of Arizona ♦ Tucson, Arizona

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The University of Arizona, Tucson

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ABSTRACT

Saguaro National Monument (SAGU) near Tucson, Arizona, was established in 1933 to protect what was at that time one of the most awe-inspiring stands of saguaros *(Carnegiea gigantea)* to be found anywhere in the Sonoran Desert. However, subsequent decline of that particular saguaro population has spawned many research and monitoring efforts over the last 50 years in an attempt to understand the factors responsible for the local population decline. As a consequence of the research attention focused on the saguaro, this plant species has become one of the most intensively studied, non-agricultural plants of the world. However, despite this research attention, it is ironic that factors that affect saguaro populations are extremely misunderstood on the part of some scientists, National Park Service (NPS) personnel, and the public in general. Many of these misunderstandings originally arose from investigations of the 1940s through 1960s that were narrowly focused on plant pathology and did not consider the breadth of ecological factors that affect saguaro populations. A considerable amount of ecologically oriented research conducted in the last few decades has helped clear up some of the widespread interpretive errors resulting from the era of plant pathology investigations. Unfortunately, a recent flurry of research activity focusing on possible links between atmospheric pollution and saguaro population decline has contributed to an additional layer of confusion and misunderstanding regarding the ecology of the saguaro. The conclusions of many scientific investigations, even when in error, have greatly affected the way in which SAGU has been managed by NPS and perceived by the public. National Park Service must do much more to clear up many of the misconceptions that resulted from some types of research supported by NPS at SAGU. This will require strengthening the capability to conduct research within the NPS system and devoting more attention to the identification and review of research priorities and proposals.

INTRODUCTION

In comparison to the vegetation of most of temperate North America, the southwestern deserts contain highly unusual plants adapted in form and function to the extremes of arid environments. So striking are some of these plants that three national monuments-Saguaro, Organ Pipe Cactus, and Joshua Tree-are named for them. In each case, it is a single species that gives unique character to the desert landscape within the monument. Of all the remarkable plants of the desert Southwest, the giant cactus, or saguaro *(Carnegiea gigantea),* stands out in the minds of many Americans as an icon representing the novelty and grandeur of the desert realm.

Saguaro National Monument (SAGU) was established in 1933 on the east side of Tucson, Arizona, to protect what was then one of the most awe-inspiring stands of saguaros to be found anywhere in the Sonoran Desert. Yet today, little more than a half century later, the giant, many-branched saguaros have all but disappeared from the original "cactus forest" of the 1930s (Fig. 1). Since the primary mission of National Park Service (NPS) at SAGU is to protect the distinctive cactus species for which the monument was named, the saguaro has understandably been the subject of considerable concern and research at SAGU since the late 1930s. The purpose of this report is to (1) trace the development of various research and monitoring efforts involving the saguaro at SAGU, (2) evaluate the rationale for these investigations, and (3) examine some of the impacts of these research efforts on management decisions and public perceptions regarding the ecological status of this extraordinary plant.

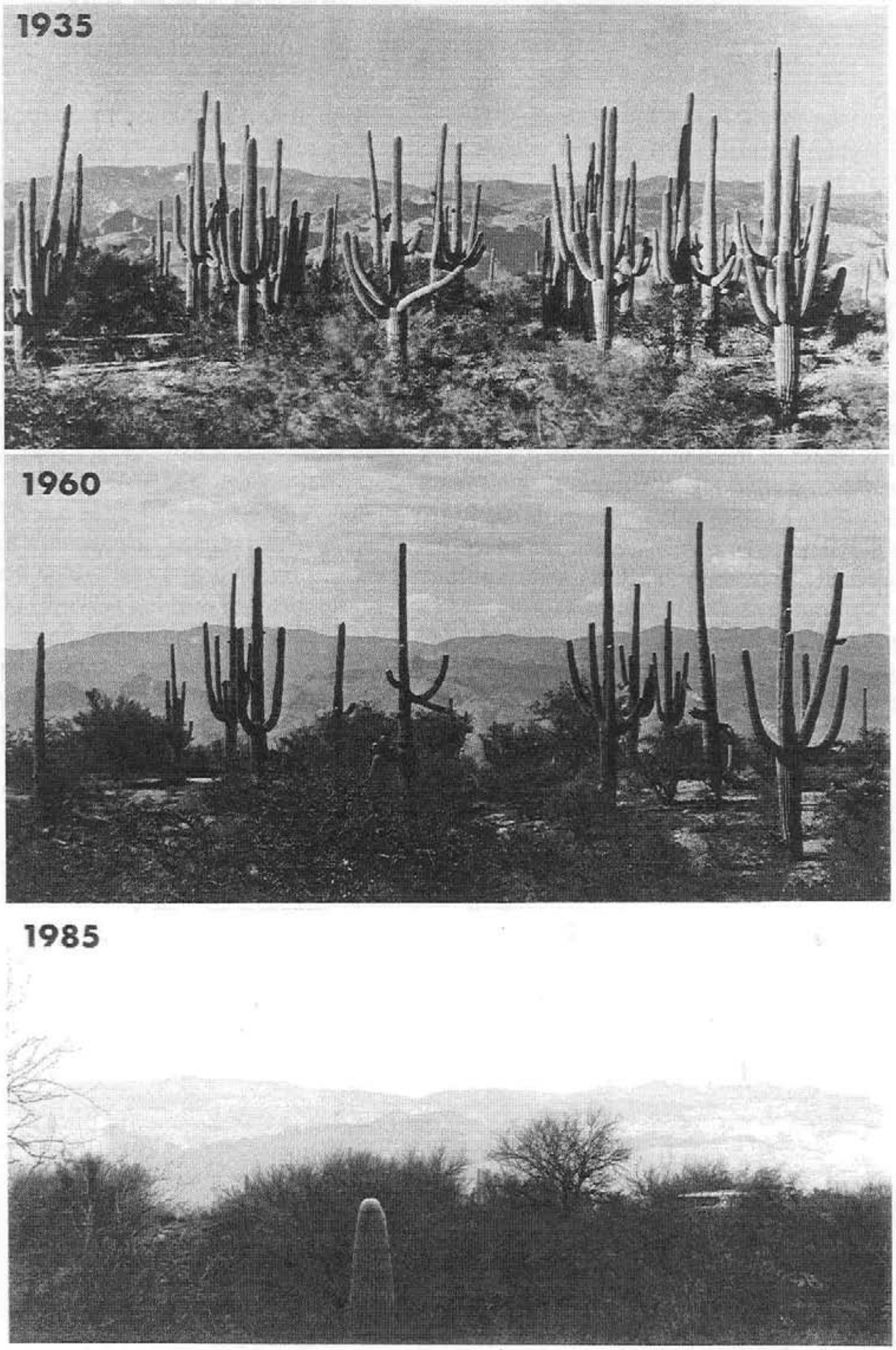

Figure 1. Matched landscape photos from 1935, 1960, and 1985: Rincon Mountain District, Saguaro National Monument, Arizona. H. Shantz took the 1935 photo; 1960 and 1985 photos were by R. M. Turner.

THE ENVIRONMENTAL SETTING AND ESTABLISHMENT OF THE MONUMENT

The saguaro is limited in distribution to the Sonoran Desert of Arizona and adjacent Sonora, Mexico (Fig. 2). Very small, natural populations of saguaros are also found at two localities bordering the Colorado River in southern California. The eastern and northern limits to the distribution of the saguaro nearly coincide with the limits of the Sonoran Desert. With higher elevations, lower minimum temperatures, and greater precipitation to the east and north, desertscrub vegetation gives way to desert grassland, interior chaparral, or evergreen woodlands (Brown 1982). The westward distribution of the saguaro is limited by the scarcity and greater unpredictability of summer precipitation received in the lower elevations of the Sonoran Desert along the Colorado River. The 340-km (210-mi) distance between Tucson and Yuma, Arizona, involves an elevational drop from 760 m (2,495 ft) to 50 m (165 ft) above sea level and a decline in average annual precipitation from approximately 280 mm (11 in.) to less than 70 mm (3 in.). To the south in southern Sonora, Mexico, the saguaro disappears as Sonoran desertscrub vegetation gives way to Sinaloan deciduous thorn forest (Steenbergh and Lowe 1977; Brown 1982).

Populations of saguaros achieve their greatest densities not in the hottest, driest parts of the Sonoran Desert, but rather in environments generally receiving more than 200 mm (8 in.) precipitation per year split between summer and winter seasons. This zone in Arizona includes a belt-like margin on the eastern and northern limits of the Sonoran Desert originally referred to as the Arizona Upland by Shreve (1951) (see also Turner and Brown 1982). Saguaro National Monument is located near the eastern limit of the Sonoran Desert within this band of relatively lush vegetation. The monument contains two districts geographically separated by a distance of 40 km (25 mi) with the intervening area largely covered by the city of Tucson (Fig. 2, inset). The eastern portion of the monument, or Rincon Mountain District (RMD), contains most of the Rincon Mountains and the lowland areas below the western flank of the Rincons. The other half of the monument, the Tucson Mountain District (TMD), includes the northern two-thirds of the Tucson Mountains and the western slopes, foothills, and bajadas of that range.

Rincon Mountain District contains the area designated as the original monument in 1933. It ranges in elevation from approximately 820-2,640 m (2,690-8,665 ft). Sonoran desertscrub environments and associated saguaros are limited to the lowermost part of this considerable elevational gradient. Only about 20% of the land area of RMD contains desertscrub vegetation. With the cooler temperatures and greater precipitation of higher elevations, desertscrub vegetation gives way to desert grassland, oak and pine-oak woodlands, and finally forests of ponderosa pine and fir in the highest elevations. The upper elevational margin of the distribution of the saguaro cuts through the western part of the district at about 1,280 m (4,200 ft).

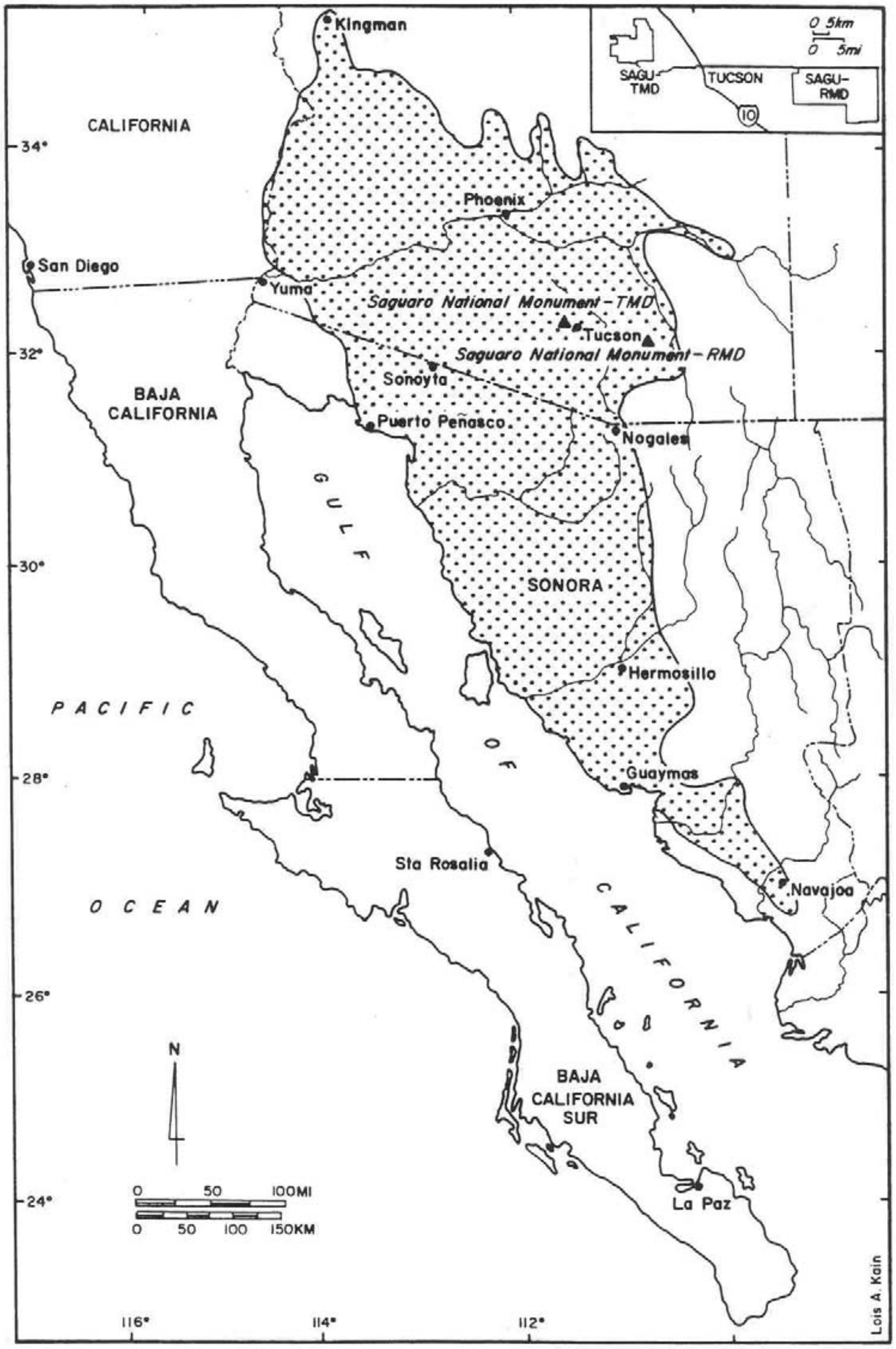

Figure 2. Map of Sonoran Desert and location of Saguaro National Monument. Inset: detail of separately managed districts in the monument.

In contrast, TMD has a much more restricted elevational range (approximately 670-1,428 m [2,200-4,690 ft]). Rather than being located on the margin of the Sonoran Desert, TMD is surrounded on all sides by Sonoran desertscrub. Nearly 90% of the land area of this part of the monument is classified as Sonoran desertscrub (Shelton 1985). The remaining small area of slightly higher elevation supports plant species characteristic of desert grasslands. Tucson Mountain District was added to SAGU in 1961. With the decline of the saguaro forest at RMD, TMD now contains the most impressive stands of saguaros.

Land to both east and west sides of the city of Tucson was originally considered as possible locations for establishment of the national monument. Roger Toll, superintendent of Yellowstone National Park, was responsible in the 1930s for evaluating various areas in the Southwest for possible acquisition by NPS for new national parks and monuments. Toll (1932) recommended to the NPS director that three species of desert plants--the saguaro, the organ pipe cactus, and the Joshua tree-were sufficiently spectacular to warrant creation of national monuments. In terms of the saguaro, Toll gave highest recommendation to an area east of Tucson at the base of the Rincon Mountains. The area contained a spectacular stand of giant, many-branched saguaros in approximately ten sections (25.6 km^2 [6,325 a]) of land held by private owners and by The University of Arizona (UA) in the "University Cactus Forest" (Shantz n.d.). However, Toll warned that if the estimated $75,000 required to purchase these lands could not be secured, the area "must be dropped from consideration as a national monument." Toll gave secondary recommendation to an area of about 80.9 km^2 (20,000 a) on the west side of the Tucson Mountains. This area was in public domain and was leased by Pima County as a recreation area and preserve. Pima County officials were willing to allow establishment of a national monument at the site, provided the county would not bear the expense of development. Although the stand of saguaros found there was quite dense, the Tucson Mountain location was considered second in merit because, Toll explained, the Tucson Mountain site contained "a large proportion of young and unbranched plants, so that it does not present as spectacular an appearance as does the University of Arizona tract east of Tucson."

Despite the land ownership problems Toll (1932) warned of, lobbying efforts of influential Tucson citizens pushed the choice of the Rincon Mountain area as the location for the monument. Homer Shantz, a prominent botanist and range ecologist, assumed the presidency of UA in 1929 and quickly became a leading advocate for preservation of the spectacular stand of saguaros contained within the University Cactus Forest. A realistic fear that the lands would be developed led individuals such as Shantz and Tucson newspaper editor Frank H. Hitchcock to press for establishment of a monument that included both privately and publicly held lands (Clemensen 1987). In February 1933, a year after Toll's original inspection of the area, Hitchcock expressed concern that the government was moving too slowly in creation of a monument. National Park Service director Horace Albright responded with the message that the Department of the Interior would not at that time recommend establishment of a monument that included the area of the University Cactus Forest, because of the land ownership issue. Albright thought government control of the area was a prerequisite for the creation of a monument. Hitchcock disagreed, thinking that a monument should be proclaimed that included parts of Coronado National Forest in the Rincon Mountains and private lands that contained the impressive University Cactus Forest. He believed that land ownership issues could later be resolved.

Consequently, Hitchcock immediately took matters in his own hands. Together with UA president Shantz, Hitchcock convinced Coronado National Forest supervisor Fred Winn of the need for a monument that included lands of the national forest. Hitchcock, Shantz, and Winn then drafted provisions for proclamation of a monument that specified US Forest Service (USFS) administration of the monument and continued grazing in order to placate USFS concerns and ranching interests (Clemensen 1987). With his influence in the Republican Party, Hitchcock traveled to Washington, DC, and presented the draft of the proclamation to the Secretary of Agriculture. The Secretary accepted the proposal, and on his recommendation President Herbert Hoover signed the proclamation establishing SAGU on 1 March 1933, only three days before F. D. Roosevelt took office. The land ownership problem, though, was not resolved for another 25 years, and during this time considerable damage to the University Cactus Forest area undoubtedly occurred.

Tucson Mountain District was created in 1961 as a response to local concerns that more than 28.3 km' (7,000 a) of public land leased by Pima County and used as a recreation area would be opened by the Department of the Interior for expanded mining activities. Consequently, President J. F. Kennedy transferred part of the Tucson Mountain holdings to SAGU by presidential proclamation (Clemensen 1987).

LAND USE BEFORE ESTABLISHMENT OF THE MONUMENT

Individual saguaros may live for two centuries. The forest of giant, many-branched saguaros that was present at the base of the Rincon Mountains in the 1930s represented reproduction that had occurred long in the past. In addition, the rarity of younger saguaros within the University Cactus Forest at the time the monument was founded (Fig. 1) suggests environmental changes in the half-century preceding 1933 that greatly affected the establishment of young saguaros. A comprehensive understanding of the saguaro population decline that began about 1940 requires a knowledge of the types of impacts that had been occurring for at least a half century prior to 1933. Since concern about this population decline has been the major impetus behind much of the saguaro research conducted during the last 50 years, a knowledge of this historical context is necessary for an understanding and evaluation of various research efforts. Likewise, an understanding of these historical impacts and their potential long-term consequences is a prerequisite for planning relevant research programs in the future.

In 1929, Shantz, having only recently taken the post of president of UA, addressed the UA Board of Regents concerning the issue of preservation of the University Cactus Forest:

> Nowhere in the world is there so fine a. stand of the giant sahuaro (*Carnegiea gigantea*) *as* in the area included in the University Cactus Forest... To allow this area to pass to private ownership ... would not only be a calamity to Arizona but to the nation and to science as well. Unfortunately, the area has already been homesteaded, but the vegetation still remains in its *virgin state* [emphasis mine].

Such a claim for a relatively undisturbed environment by Shantz was born out of either a lack of awareness of land use in the area or his zealous promotion-of the saguaro forest. In 1929, the dense stand of giant, many-branched saguaros of the University Cactus Forest was singularly impressive, yet after more than 50 years of considerable impacts from ranching and heavy woodcutting activities, the vegetation of the bajada below Tanque Verde Ridge was far from being in a "virgin state."

Ranching in southern Arizona did not expand until a truce was reached with the Apaches in 1872. Ranching activities in the late 1800s were concentrated in areas with perennial water, such as those near the base of the Rincons where snowmelt from higher elevations contributed to perennial flows of streams. Considerable settlement along Tanque Verde and Rincon creeks below the west and southwest slopes of the Rincon Mountains led to heavy grazing pressure on adjacent public domain lands, including what would become the University Cactus Forest and SAGU. An 1893 map of Pima County showed 36 ranches and two schools located along these two creeks. Three additional ranches were located at higher elevations in the Rincons (Gile 1967; Clemensen 1987). By 1880, an estimated 1,000 cattle from three principal ranches along Tanque Verde Creek grazed on public domain in and around the University Cactus Forest area (Clemensen 1987). By 1890, the number of cattle grazing in all of southern Arizona was five times the number present only 10 years earlier. This increase continued until the catastrophic drought of 1892-1893, during which 50-75% of cattle in southern Arizona died. To this day, the vegetation of the bajada areas of RMD bears the mark of heavy grazing pressures exerted from the late 1800s through the middle of this century. In the saguaro forest area, the composition of the vegetation resembles neither typical Sonoran desertscrub nor desert grassland. Instead, shrub species, such as burroweed (*Isocoma tenuisecta*), that typically increase as a response to severe disturbances (e.g., extreme grazing pressure) form a dominant part of the understory vegetation.

The west side of the Tucson Mountains differed greatly from RMD in terms of land use and escaped heavy grazing impacts. This side of the Tucson Mountains is without perennial surface water, and, consequently, farming and large ranching operations were naturally excluded during the same time when heavy impacts were exerted in the Rincon Mountains. Because of its unsuitability for extensive livestock operations, a system of granting grazing permits was never established for the public lands to the west side of the Tucson Mountains. Not until the late 1920s did homesteading begin to occur in this area to any great extent, and in response to local concerns for protecting the area, the US government withdrew 117.3 km^2 (28,988 a) from further homesteading and mining claims. This withdrawn land was leased to Pima County in 1929 for development of a recreation area and preserve (Clemensen 1987).

Livestock grazing was not the only, and perhaps not even the most serious long-term impact on the environment at the base 9f the Rincon Mountains in the decades surrounding 1900. Some of the photographs of the University Cactus Forest area taken in the 1930s portray vistas with an anomalous lack of typical Sonoran Desert trees, such as paloverdes (*Cercidium* spp.) and mesquites (*Prosopis* spp.) (compare 1935 vs. 1985 in Fig. 1). This lack may be explained by the several decades of heavy woodcutting that occurred in the area before establishment of the monument. Mesquite was the fuel of choice for Tucson, and a map drawn in 1883 indicates "Thick mesquite timber" along Tanque Verde Creek immediately north of the present monument boundary. Surveyors working in the area that would become RMD noted numerous roads used by woodcutters in the 1890s. By 1905 fuelwood became scarce in the immediate vicinity of Tucson, and reportedly every tree with a trunk diameter of more than 17.8 cm (7 in.) had been cut within a radius of 16 km (10 mi) of town (Clemensen 1987). Woodcutting within the University Cactus Forest would continue even after the 1933 establishment of the monument boundaries (see following section on early administrative problems).

In addition to fuel cut for domestic consumption, the use of fuelwood for local lime manufacture may have caused the loss of many trees from upland desert locations within the saguaro forest. From the 1890s to the 1920s, growth of the city of Tucson created a large demand for lime for use in construction (Clemensen 1987). Lime was often produced locally by firing limestone in small kilns made of adobe (Clemensen 1987). Individual beehive shaped kilns were several meters in diameter and height. Remains of several kilns are located within the saguaro forest area of RMD. The preferred wood for firing the lime kilns was green paloverde (*Cercidium* sp.), but green mesquite (*Prosopis* sp.) was also used. The production of a single batch of lime in a kiln of this type reportedly required the continuous burning of 36 to 54 m^3 (10-15 cords) of stacked wood during a period of four days and four nights (Clemensen 1987). The large blue paloverde (*Cercidium floridum*) and velvet mesquite (*Prosopis velutina*) found principally along ephemeral waterways might individually yield up to 5 m^3 (1.4 cords) of stacked cordwood. However, the considerably smaller foothills paloverde (*Cercidium microphyllum*) *would* probably not yield more than 2 m^3 (0.6 cords) of stacked wood per tree. Consequently, it is likely that individual firings of limestone used perhaps 10 to more than 20 trees. The extent of woodcutting and disappearance of trees was so great that the operation of the kilns in the vicinity of the saguaro forest was ended by court order in 1920, not because of concern for the saguaro forest, but rather because of the outcry of local ranchers. Apparently, the extent of woodcutting and disappearance of trees was so great that ranchers' cattle were deprived of "tree seeds" (probably mesquite fruits), an important forage item (Clemensen 1987).

Any evaluation of the potential causes for the eventual decline of the original stands of saguaros at RMD must consider the environmental impacts that preceded establishment of the monument and the ages of the individual saguaros that were to be "protected." The more than 50 years of heavy use of the saguaro forest area and the maturity of the saguaros set the trajectory of decline in the saguaro population that was to follow for more than a half century after the establishment of the monument. This inevitable population crash (Fig. 1) has been without question one of the dominant themes that has driven management concerns and research approaches at SAGU for more than 50 years.

MANAGEMENT PROBLEMS FOLLOWING ESTABLISHMENT OF THE MONUMENT

Despite formation of the monument in 1933, the most impressive stands of saguaros were only nominally included in the monument; lands containing them were owned by UA and private landholders until the late 1950s. Consequently, during 25 years following the monument's creation, NPS lacked official jurisdiction over the saguaro forest area. This lack of official control resulted in continued heavy use of the saguaro forest by livestock. Failure to resolve the land ownership issue for a quarter century after founding of the monument perpetuated and perhaps even worsened environmental conditions. During this time, the private owners and UA proprietors imposed far looser controls on grazing within the University Cactus Forest than those imposed on adjacent lands administered by the federal government. Within the limited area of the University Cactus Forest, 100 or more cattle were sometimes stocked. The state and UA charged only $.03/a to lease this land for grazing with no restrictions on the number of cattle stocked (Clemensen 1987). Not until 1958 were cattle finally removed from the saguaro forest with the official transfer of land title to NPS. In contrast, TMD had been free of all livestock grazing since 1929.

The lack of official jurisdiction over some of the most sensitive areas of the original national monument also resulted in other blatant abuses. For example, superintendent Egermayer (1940a) reported that considerable woodcutting for fuelwood was occurring within the saguaro forest. He stated that in a 24-hour period "six loads [probably pickup truck loads] of wood are known to have been hauled out through a break in the north boundary fence." These woodcutting activities were limited to the state and private lands included in the monument over which NPS had no official control. Consequently, no trespass action or prosecution was possible. Egermayer reported that without legal recourse, all he could do with woodcutters he apprehended was to "run a bluff' that involved lecturing the woodcutters, making them scatter the wood gathered, and then sending them on their way.

An even more startling portrayal of the lack of authority of NPS over the university and privately held sections of the monument involved a case in which crews employed by Columbia Pictures Corporation cut and removed entire, large saguaros from the saguaro forest for use as props in movie sets (Egermayer 1940b). Similarly, no legal action could be taken directly by NPS, so the trespass was reported to UA, owner of the land.

As originally predicted by Roger Toll and NPS director Albright, the failure to settle land ownership questions before establishment of the monument resulted in considerable administrative problems and inability to protect resources within the monument. This ownership problem persisted for more than two decades after establishment of the monument (Clemensen 1987). The continuation of livestock grazing, woodcutting, and other impacts within the saguaro forest area no doubt inflicted additional damage on natural populations, including the saguaro.

PRINCIPAL LINES OF RESEARCH AND MONITORING

The combination of an extremely dense, but aged, population of saguaros together with the depression of new seedling establishment for more than a half century set up a situation in which decline of the saguaro forest in RMD was inevitable. Fluctuations in the size of any population are due to the tandem effects of mortality and recruitment, but the research that commanded the most attention early in the history of the monument did not include both sides of the demographic ledger. Instead, early management and research concentrated on preserving the saguaro forest and were primarily focused on death of the giant members of the population. Some mortality occurred at a rapid pace in the early 1940s. Naturally, the potential demise of such a magnificent stand was met with much concern and even great alarm by a succession of superintendents, resource managers, and scientists. This alarm has driven many of the investigations and management decisions, even to the present day in SAGU.

Three successive lines of investigation have attempted to answer questions regarding the cause(s) of saguaro population fluctuations, and in the case of the population in RMD, the reasons for the catastrophic decline. The first, initiated in 1940 but continuing through the late 1960s, concentrated on causes of death of old individuals and centered around plant pathology and disease control. The second line of research was more ecological and comprehensive in scope and involved basic research on factors contributing to both mortality and recruitment. These investigations began primarily in the 1960s and still continue. The third line of investigation has developed only within the last decade, is related to federal air quality legislation, and concentrates on potential links between man-induced atmospheric alteration and saguaro vigor, mortality, and reproduction. Case histories of each research area follow.

SAGUARO DISEASE INVESTIGATIONS

Despite the continued impacts inflicted by livestock and woodcutting in the first few decades after the establishment of the monument, the extensive forest of giant cacti seemed to be, at least superficially, a healthy population. However, in 1939 and 1940, UA plant pathologist James G. Brown reported the existence of an unidentified bacterial disease that was afflicting the saguaros of the saguaro forest and other parts of southern Arizona. Survey plots within SAGU examined by Brown indicated that up to 20% of the giant cactus plants were infected. The supposed causative agent, a bacterium (*Erwinea carnegieana),* was described (Lightle et al. 1942). The disease was reported to exist over a wide area ranging 322 km (200 mi) north to south, and 402 km (250 mi) west from the Tucson area. The earliest reports, both in the scientific and popular press (e.g., Gill 1942) fueled a hysteria that the saguaro stands of the Sonoran Desert, especially the saguaro forest of SAGU could potentially succumb to the ravages of this disease.

From the earliest reports, the blackening necrosis that was ravaging the saguaro population at SAGU was referred to as a pathogenic disease. This disease hypothesis, in an era of chestnut blight, dutch elm disease, and white pine blister rust, was uncritically accepted, and personnel of the US Department of Agriculture (USDA) Bureau of Plant Industry (BPI) began immediately with "disease suppression experiments" in SAGU. The principal goal of the experiment was to determine if spread of the disease could be checked by removing affected plants that were the possible source of inoculation of healthy plants (Gill 1942). This was a war-like stand against yet another catastrophic "enemy."

An entire section of land (2.59 km^2 [640 a]) within the saguaro forest at SAGU was selected for the experiment. One half (1.30 km^2 [320 a]) was a "treatment" area in which all diseased plants were removed. The downed material was disinfected at three- to four-day intervals with paradichlorobenzene dissolved in kerosene and buried in large trenches. The remains of any additional dried remains of dead saguaros were burned in order to destroy any remaining viable pathogenic organisms. The treated 1.30 km^2 (320 a) was compared with the adjacent untreated 1.30 km^2 (320 a) in which no disease-control measures were taken (Gill and Lightle 1942).

Considering that the entire saguaro forest area is contained within about 8-10 sections (20.7225.9 km^2 [5,120-6,400 a]) of land, this scale of experimental manipulation demonstrates the degree of concern that NPS personnel must have had to allow such a large-scale manipulation to take place within the boundary of the monument. But then again, the area that included the experiment was not under official NPS jurisdiction, which may account for the rapidity with which personnel from USDA acted. The direct environmental impacts of this experiment within the area of study were undoubtedly large. The operation required three months in the winter of 1941-1942, during which 313 affected saguaros were removed along with 12 healthy individuals that were injured in the process of removing affected individuals. Felling of saguaros was achieved by cutting the main roots and pulling down the giant plants with cables attached to vehicles. Downed saguaros were cut up into small sections and transported by dump truck to four large trenches dug by bulldozers. An estimated volume of 765 m^3 (1,000 yd) of earth was excavated at the site in the construction of these trenches. Every three to four days the saguaro stem sections accumulated, in the trenches were fumigated by dousing them with a solution of 9,072 g (20 lb) of paradichlorobenzene dissolved in 208 litres (55 gal) of kerosene. The trenches were then covered with soil. Steenbergh and Lowe (1983) documented the history of this project more completely with their inclusion of copies of original proposals and reports for the disease control studies. Gill (1942) provided a photodocumentary of the disease control efforts.

Ten thousand dollars were provided in 1941 by the federal government for this disease control experiment (Bardsley 1957). Although small by today's research grant standards, this amount was considered major funding 50 years ago, especially considering that it came on the dawn of US involvement in World War II.

Subsequent monitoring of this experiment showed no marked differences between the treated and untreated areas in the development of further cases of the "disease." Investigators from BPI (Gill and Lightle 1946; Grill 1951) reported this finding but, nevertheless, claimed that the experiments may have held the disease in check to some extent. The repeated assertion of the possible benefit of these experiments without data to back up such statements demonstrates the mind-set of uncritical acceptance of the disease hypotheses under which the plant pathologists were working.

Despite the general support of NPS for the cactus disease investigations, in 1944 NPS biologist W. B. McDougal of Santa Fe questioned the massive disease control experiment. References of the "disease" going back to 1889 had been reported to McDougal, and after inspecting the site, he noted that the disease seemed only to affect the older saguaros. He believed that although a thinning of the saguaro stand might occur, the stand would eventually regenerate and that NPS should observe a policy of allowing such natural phenomena to proceed without interference (Clemensen 1987).

Although disease control measures on the scale of the BPI operation of the 1940s were never again attempted, research on various aspects of the bacterial necrosis disease of saguaros held a high profile for at least 20 years. Various antibiotic treatments either applied superficially or injected internally into saguaros were investigated as potential cures for the bacterial rot (Boyle 1949, Bardsley 1957). A moth whose larva tunnels in live cactus tissue was identified as the principal vector of the disease (Boyle 1949), and measures for controlling this vector with pesticide applications were suggested (Bardsley 1957; Clemensen 1987). Alcorn and May (1962) extrapolated the losses from the disease into the future and predicted extinction of the saguaro forest before the turn of the century.

Yet despite the extended period over which the conclusions derived from disease-related investigations held primary influence, the hypothesis that a disease was the cause of the observed catastrophic mortality of saguaros in SAGU and other Arizona locations was eventually rejected. The University of Arizona ecologist Charles H. Lowe concluded that catastrophic freezes cause considerable mortality in saguaros at the northern and eastern margins of their range and that the subsequent but sometimes delayed bacterial decomposition of freeze-killed tissues was mistakenly diagnosed as a "disease" (Steenbergh and Lowe 1976, 1977, 1985).

ECOLOGICAL INVESTIGATIONS 1960-1991

Even to those investigators in the 1940s and 1950s who waved the banner of science in their quest for a "cure" for the saguaro "disease," the decline of the once spectacular saguaro forest involved more than simply the death of old members of the population. The loss of old saguaros was not compensated by a commensurate level of establishment of young cacti. The rarity of most smaller age classes indicated that establishment had been meager for several decades. Understanding this problem would require a far different research orientation than the narrowly focused plant pathology investigations that had dominated earlier research and management concerns about the saguaro.

From the late 1950s to the present, the contributions of ecologists including C. H. Lowe, R. M. Turner, and NPS research scientist W. F. Steenbergh would dramatically alter the way the "saguaro problem" would be investigated and interpreted. These and other ecologists would point out the complexity of multiple factors potentially affecting reproduction, establishment, and mortality of saguaros in attempts to understand the trajectory of population decline in the original saguaro forest. In this section, I distinguish six major lines of ecological investigations: (1) the consequences of catastrophic freezes, (2) requirements for seedling establishment, (3) impacts of livestock grazing, (4) climate (especially precipitation) variability, (5) permanent plot studies of demographic patterns, and (6) pollination and seed dispersal.

Consequences of Catastrophic Freezes

In 1911, Forrest Shreve, the unrivalled and perceptive pioneer of Sonoran Desert plant ecology (Bowers 1988), published a short paper entitled "The influence of low temperatures on the distribution of the giant cactus." In that paper Shreve argued that the greatest number of consecutive hours of sub-freezing temperatures was the most important factor controlling the northward and upper elevation distributional limits of the saguaro. He pointed out that in passing either from lower to higher latitudes or from lower to higher elevations, the number of consecutive hours of freezing gradually increases until the location is reached where days without a mid-day thaw would be first encountered. At such a geographic location there would be a climatic discontinuity from an environmental condition characterized by 22 hours or less of below-freezing temperatures to one with more than 36 to 42 hours of continuous frost. Shreve pointed out that the rather abrupt end to the occurrence of saguaros at about 1,280 m (4,200 ft) elevation near Tucson is best explained by this environmental discontinuity involving the number of consecutive hours of sub-freezing temperatures.

Using salt-'and ice-cooled freezers and other simple equipment available to him, Shreve (1911) demonstrated that saguaros subjected to -3°C (26.6°F) to -11°C (12.2°F) for time periods greater than 29 hours were all killed, yet saguaros subjected to similar freezing regimes of only 6-15 hours experienced no mortality. Furthermore, he observed that within two weeks after the experiment began, the cacti subjected to the longer freezing regime had begun to show a blackening of their tissues. After four weeks, one individual subjected to only -3^{0}C (26.6°F) for a 46-hour period had become black and soft throughout its lower half. None of the damaged individuals exhibited any sign of recovery during the subsequent month.

The findings of Shreve (1911), so important to understanding the ecology of the saguaro at the northern and upper elevational margins of its distribution (such as the case of RMD), went unnoticed for nearly a half century-until C. H. Lowe would explain the catastrophic loss of cacti in SAGU and other marginal sites as a consequence of periodic, prolonged freezing events.

Lowe's studies indicated that prolonged catastrophic freezes not only kill juvenile saguaros of the size originally studied by Shreve (1911) but also kill the taller, older members of the population. His documentation of the consequences of the 11-13 January 1962 freeze on saguaro mortality in the Santa Catalina Mountains convincingly demonstrated the impact of freezing on large saguaros. During this period, sub-freezing temperatures continued after the first night, through the second day, and into the second night. Small cacti were reported frozen during the first night, but because of the greater heat retention by massive stems of larger individuals, many of the larger plants did not succumb to freezing until the second night (Niering et al. 1963). Following this extreme freezing event, Lowe demonstrated that mortality of saguaros increased with elevation on the slopes of the Santa Catalina Mountains immediately northwest of SAGU. For saguaros greater than 3.5 m (11.5 ft) in height, mortality was 10% at 900-1,050 m (2,954-3,446 ft), 22% at 1,050-1,200 m (3,446-3,939 ft), and 30% at elevations exceeding 1,200 m (3,939 ft). Mortality was as high as 70% in some exposed, upper elevations (Niering et al. 1963). These data, coupled with the photographic documentation of the extent of mortality and necrotic decay of giant cacti within months following the freeze, provided convincing evidence of the importance of such catastrophic events at the distributional margin of this cold-sensitive plant species. In the 1962 catastrophic freeze, some cacti began to fail immediately, but other moribund individuals did not completely decay until several years later. Steenbergh and Lowe (1976) recorded similar effects at RMD following the severe freeze of 1971.

The heavy impact of catastrophic freezes on mortality of adult saguaros in the Tucson area has also been recorded by other botanists. Three days of severe cold were experienced in December 1978 in southern Arizona, and some desert areas in the Tucson vicinity experienced lows of -7.2°C (19°F) to -8.9°C (16°F) (Coate et al. 1979). This cold episode followed an unusually warm, wet fall, and considerable freeze damage to saguaros was reported in the Tucson Mountains on the grounds of the Arizona-Sonora Desert Museum (M. Dimmitt, pers. com., 1992). Within the 8- to 12-ha (19.8- to 29.7-a) grounds of native desert vegetation at the museum, freeze damage was immediately observed in saguaros following the cold period. However, many plants stricken during this extreme event remained standing but became necrotic in years immediately following the freeze. Personnel at the museum have attributed the loss of approximately 200 adult saguaros from these limited grounds to the effects of the 1978 freeze. In the first five years following the freeze, saguaros exceeding 3 m (9.8 ft) in height were succumbing to necrosis at a rate of 25 to 35 individuals per year on the museum grounds. Numbers of cacti subsequently succumbing to necrosis and decay declined to less than 3-4 individuals per year between 1983 and 1991. The "cactus disease investigations" of the 1940s (Gill 1951) recorded a similar pattern after the catastrophic freeze in 1937.

Steenbergh and Lowe (1976, 1977, 1983) argued that the bacterial necrosis first observed in 1939 and through the early 1940s was the direct consequence of the 1937 freeze event during which temperatures dropped lower than they had for more than 20 years. They concluded that the "saguaro necrosis disease" was an extremely mistaken interpretation. Instead, this condition was neither a disease nor cause of death, but rather the consequence of mortality due to freeze damage followed by natural (and often delayed) bacterial decay of moribund plants.

The investigations by Lowe and his students on the importance of extended freezing temperatures to the ecology of the saguaro included far more than mere descriptions of catastrophic mortality following unusual cold. Lowe (1959) and Soule and Lowe (1970) experimentally investigated the degree to which supercooling occurs within saguaros before ice formation occurs and the degree to which varying osmotic concentrations depress the freezing point of saguaro tissues. These investigations of freezing point depression in saguaros are important to understand the seemingly unpredictable manner in which cold spells can affect saguaros. The ability of saguaros to withstand subfreezing temperatures is related to the state of hydrature of individual plants. Recent studies have shown that saguaros in somewhat water-stressed condition with higher osmotic concentrations are more resistant to freezing than extremely well-hydrated plants (Helbsing 1989; Helbsing and Fischer 1992). A field demonstration of the heightened susceptibility to freeze damage and mortality in well hydrated plants is the extremely high mortality that followed the December 1978 freeze at the Arizona-Sonora Desert Museum. As pointed out, this episode of freezing was preceded by an unusually warm and wet period that left saguaros in a relatively well-hydrated condition.

Steenbergh and Lowe (1969, 1976) also reported on experiments with transplanted juvenile saguaros in which survivorship was monitored through winter seasons following periods of cold.

These studies demonstrated the link between colder minimum temperatures and greater mortality. They showed lower average survival in the colder temperatures of RMD than those of TMD. Within RMD, juvenile saguaros on northern exposures had significantly lower survival than juveniles on southern exposures where minimum temperatures were 1.7-2.2°C (3.0-4.0°F) higher. Similarly, survival of juvenile saguaros was enhanced when cacti were located in the slightly warmer nighttime microhabitats found beneath the canopies of small trees that served as "nurse plants."

In further analyses of the effects of the severe freezes of 1962 and 1971, Steenbergh and Lowe (1976) showed that these natural environmental catastrophes at the margin of the range of the saguaro selectively killed the smallest and the largest plants. Greatest vulnerability to lethal freeze damage occurs during the first four years of life and then declines progressively with growth and increase in stem volume. However, after reaching maturity, an increasing stern surface-volume ratio occurs with increasing age that leads to a corresponding greater susceptibility to freeze damage and death. During the catastrophic 1962 and 1971 freezes, plants less than 0.45 m (1.5 ft) in height suffered 15.4% mortality. Saguaros of intermediate height (0.46-3.8 m [1.5-12.5 ft]) had considerably lower mortality (2.0%), while mortality rose considerably (12%) in saguaros exceeding 3.8 m (12.5 ft) in height.

Recently, a few researchers (Evans et al. 1992b; Stolte 1992) have claimed that freezing cannot be the only or even the most important answer to the saguaro decline at SAGU. They have argued that the 1913 freeze was the most severe recorded this century in southern Arizona (see chronology of extreme freezes in Steenbergh and Lowe 1983, p. 143) yet the many saguaros present in the University Cactus Forest in the early 1930s obviously survived this extreme episode. However, Steenbergh and Lowe (1976) estimated the demographic structure of the 1913 population based on height data reported in 1942 (Gill and Lightle 1942). These analyses demonstrate that the most numerous size class present in 1942 (the 3.9-5.6 m [12.8-18.4 ft] height class, containing approximately 33% of all saguaros tabulated that year) would have been contained entirely within a size class less than 3.7 m (12.1 ft) but greater than 0.55 m (1.8 ft) in height in 1913. This size class was demonstrated by Steenbergh and Lowe (1976) as more resistant to freezing than either extremely small juveniles and seedlings or older adults.

On the basis of their experimental work with seedling and juvenile survival, Steenbergh and Lowe (1976) attributed the lack of smaller size classes reported by Gill and Lightle (1942) to an unusual record of extreme freezes at the turn of the century. They argued that the greater susceptibility of seedlings and very small juveniles to frost-kill would have eliminated most seedlings that had become established during this period, thus contributing to the lack of juvenile cacti in 1942. Although their experiments indicate that freezing events experienced around the turn of the century undoubtedly affected seeding survival, the degree to which other impacts such as woodcutting or grazing, either independently or synergistically, affected survival is unknown.

The contributions of C. H. Lowe, his students, and colleagues regarding the importance of extreme events of freezing temperatures to survival of seedling and juvenile saguaros, mortality of adults, and saguaro distributions provided NPS with a framework for management and realistic interpretation based not on the uncritical acceptance of a hypothesis, but rather on.

careful observation, measurement, and experimentation. Curiously though, this more critical, ecological perspective; may have been achieved far sooner had those involved with the saguaro "disease" investigations been aware of the seminal work of Shreve (1911).

Other Requirements for Seedling Establishment

The Importance of Nurse Plants. Steenbergh and Lowe (1976) showed that the slightly higher temperatures beneath paloverde tree canopies during cold periods significantly increased survival rates of saguaro seedlings and juveniles in the marginal populations of RMD. Nobel (1980) further demonstrated that nurse plant canopies provide young saguaros warmer nighttime microenvironments during winter in the northern part of the Sonoran Desert.

Research conducted by other individuals at SAGU demonstrated that in addition to ameliorating low temperature extremes, the shade produced by nurse plant canopies protects young saguaros from upper, lethal temperature extremes of the hot summer months. Midsummer temperatures of exposed soil surfaces in the Sonoran Desert can exceed 70°C (158°F), but shaded areas are considerably cooler (Shreve 1931; Despain 1974). Experiments on the grounds of RMD by Turner et al. (1966) showed complete mortality of saguaro seedlings in exposed microhabitats during summer months, even when water was abundant. Only the seedlings provided with partial shade survived. Related research conducted elsewhere on the saguaro and other columnar cacti (Despain 1974; Jordan and Nobel 1979) similarly shows the necessity of partially shaded microenvironments for survival of young succulents. Seedling and juvenile saguaros are extremely susceptible to high temperatures near the soil surface, because as stem succulents they store most of their tissue water directly above the soil surface and at the same time are unable to use transpirational cooling during the day because of their crassulacean acid metabolism (CAM) photosynthetic pathway.

The generally greater abundance of young saguaros beneath canopies of nurse plants had been noted long before these experimental studies (Shreve 1951; Wilder and Wilder 1939). However, the work of Turner et al. (1966) demonstrated the absolute requirement of such cover for survival of young plants. Whereas non-living objects, such as rocks, provide adequate cover for young plants in some habitats (e.g., the rocky slopes supporting saguaro populations at the base of the Rincon Mountains), reproduction in non-rocky habitats, such as the saguaro forest area, is almost entirely limited to such cover. Recognizing this ecological limitation, Turner et al. (1966) concluded that at SAGU, "Saguaro stands that are chronically lacking in re-establishment will not recover until the nurse plant cover is restored."

As pointed out earlier, some photographs taken in the early 1930s show an especially dense stand of saguaros in the original saguaro forest area of SAGU. Yet these same photos show an anomalous lack of tree canopies. The extensive woodcutting and livestock grazing from the late 1800s through the early part of this century undoubtedly resulted in loss of much potential recruitment of saguaros through the elimination of necessary nurse plant cover. However, the relative contributions of these two impacts compared to the role of freezes in limiting recruitment is impossible to accurately evaluate. These impacts, though, are undoubtedly linked. Any factor that tends to reduce nurse plant cover will eventually result in increased losses of juvenile saguaros to other factors such as freeze-kill or heat stress.

Impacts of Livestock Grazing

Concerns over possible impacts of cattle at SAGU extend back to the initial decade after establishment of RMD (Egermayer 1940a). The 1947 master plan for SAGU (cited in Clemensen 1987) pointed out an overgrazing problem but offered no solutions, primarily because of the land ownership problem that was not resolved until several decades after formation of the monument. National Park Service recognized that the only way to control livestock impacts would be to control the land through ownership. Recognition of this issue is perhaps the main factor that led to the final acquisition of the saguaro forest area in 1958. Despite the repeated concerns expressed by superintendents of SAGU and other NPS personnel on the effects of livestock on the saguaro population, especially reproduction and survival of young cacti, this topic received very little early study at SAGU other than range condition reports tallied by USFS personnel (Clemensen 1987). The lack of any serious scientific investigation of this problem by NPS is a manifestation of the complete dismantling of the Research and Education Division of NPS in the late 1930s and early 1940s. For nearly two decades following that time, NPS had essentially no capacity to respond to many pressing research needs (Chase 1986, p. 239).

Limited studies of livestock impacts at SAGU have been conducted by researchers from outside NPS. Niering et al. (1963) and Niering and Whittaker (1965) convincingly painted a hypothetical scenario of direct impacts of cattle (trampling and consumption of young saguaros) as well as a complex chain of cause and effect where changes in vegetation caused by grazing resulted in population expansion of rodents such as woodrats (*Neotoma albigula*). The decline of saguaros was attributed in part to consumption of young cacti by these rodents. Although logically deduced, this hypothetical scenario of Niering et al. (1963) and Niering and Whittaker (1965) regarding the various types of livestock impacts at SAGU has never been adequately tested. One attempt to assess the impacts of both domestic cattle and rodents was the construction of three 15.24-m^2 (50-ft) fenced, rodent-proof exclosures in RMD by R. M. Turner and S. Alcorn of UA (R. M. Turner, pers. com., 1992). These exclosures were monitored only twice in the 1960s and 1970s, but information on differences between vegetation within and outside the exclosures has never been published. Furthermore, it is unlikely that differences in saguaro recruitment due to grazing or rodent impacts, should they exist, could be detected in so few exclosures of such relatively small size.

An opportunity to assess impacts of livestock grazing on saguaro reproduction at RMD presented itself as a fence-line contrast dividing an area that had been free of livestock since 1958 and an adjacent tract on which grazing had been permitted until 1978 (Abouhaidar 1988, 19592). In this study, age structure of the saguaro populations on different sides of the fence was significantly related to grazing history. The more recently grazed portion contained a population with a lesser representation of younger saguaros between 11 and 20 years of age and indicated a depression of establishment associated with more recent grazing.

Livestock grazing, especially at the stocking rates that existed on the ranches at the base of Tanque Verde Ridge before the turn of the century, undoubtedly had great impacts on saguaros. Unfortunately, as we move further from that time and even from the more recent date when grazing was completely eliminated from SAGU, it becomes increasingly difficult to decipher the relative amount of damage inflicted by livestock operations in comparison to other "natural" or human-caused impacts. In a sense, a large window of opportunity to learn much about the hypothesized direct and indirect impacts of cattle grazing on saguaros in RMD has passed as we move away from the period during which grazing was allowed.

Climate (Precipitation) Variability

Steenbergh and Lowe (1976) demonstrated the role of extreme freezes as events that tend to structure saguaro populations by causing selective mortality of younger and older plants. Another climatic extreme, extended drought conditions, has been hypothesized to contribute to demographic patterns exhibited by saguaro populations throughout the Sonoran Desert region (Turner 1990). Turner's conclusions arise in part from his detailed study of the vegetation on the inaccessible floor of a 1.6-km- (1-rni-) wide crater in Sonora, Mexico. Because of the difficulty in accessing the crater, the vegetation on the floor has been fully protected from domestic stock grazing and from woodcutting. In addition, the site is located in a hotter part of the Sonoran Desert, where killing freezes are unlikely. Turner determined the relationship between height and age of saguaros from studies of growth during a three-decade period. With this information, Turner could estimate the age and year of establishment of each saguaro. These data indicated a surge of recruitment in the late 1800s followed by lower levels of recruitment after 1900. Turner (1990) suggested the late 1800s spate of saguaro establishment may have been due to summer rainy periods that were unusually moist before the turn of the century compared to subsequent decades. In the 30-year period from 1868-1898, July to August precipitation at Tucson, Arizona, exceeded 180 mm (7 in.) 11 times (180 mm [7 in.] precipitation = 1.75 times the long-term average). This arbitrary threshold was exceeded only 7 times during the 90-year period from 1898 to 1988. Turner furthermore suggested that the apparently more favorable summer moisture conditions of the mid-late 1800s throughout the northern part of the Sonoran Desert could be one of the major contributors to a surge in saguaro reproduction that is recorded in the demographic structure of nine other populations he has monitored in southern Arizona including the two districts of SAGU [see Long-term Saguaro Monitoring Plots by Turner].

Many of the saguaros that contributed to the original saguaro forest in RMD became established in the latter half of the 19th century (Hastings 1961). However, immediately following this period, many types of impacts potentially harmful to saguaro reproduction (heavy woodcutting, grazing, and cold episodes especially lethal to seedlings) were synchronous with the period of lessened summer precipitation identified by Turner that began at the turn of the century. Consequently, it is difficult, if not impossible to decipher the relative contributions of each of these potential factors to variation in past saguaro reproduction at RMD. It is likely that all the factors discussed above contributed in some way to declines in reproduction.

Long-term Saguaro Monitoring Plots

In addition to using saguaro growth and demographic data to study episodes of establishment that occurred long ago, Turner has systematically collected data on more recent establishment from a set of long-term monitoring plots. These data can be used to more precisely pinpoint the relationship between specific patterns of establishment and associated environmental factors.

Between 1959 and 1962, R. M. Turner and J. R. Hastings of UA set up a regional network of 10 plots for the study of climatic effects on saguaro populations in Arizona and adjacent Sonora, Mexico. Most of these plots are 2.5 ha (6.2 a.) in size. The RMD and TMD of SAGU each contain one of these plots. The plots have been monitored at intervals averaging about 10 years in which data on mortality, growth, and recruitment have been recorded. One of the important findings of these plot studies is a marked increase of new recruitment that has occurred during the past 20 years within the area of the original saguaro forest at RMD. Most of these young saguaros are less than 0.5 m (1.6 ft) tall. This abundance of young cacti represents a "phenomenal population surge" and has the potential for becoming a new saguaro forest in the next century (Turner 1992). This concrete documentation of new recruitment counters statements, such as the one by Gladney et al. (1992) that the saguaro decline is continuing at RMD.

The detailed study of recruitment patterns in monitoring plots can shed additional light on factors limiting establishment. Embedded within the 20-year-long surge of recent establishment in the plot studied by Turner in RMD is a single anomalous year, 1976, of extremely low recruitment. A drought in this year was one of the most severe experienced between 1900 and 1986 (Goldberg and Turner, 1986), and Turner (1992) suggested this drought contributed to the brief period in which recruitment was essentially lacking.

In addition to the 2 plots established and monitored by Turner within SAGU, a set of 45, 4-ha (9.9-a) monitoring plots have recently been established in both management units of SAGU (Duriscoe and Graban 1992). These plots represent a considerable monitoring effort, and the data collected from them over time will provide extremely valuable information about saguaro recruitment and mortality throughout the monument. These plots were set up as part of research conducted by the Air Quality Division (AQD) of NPS and are discussed in more detail in the section Air Quality Division Investigations.

Pollination and Seed Dispersal

The possibility that inadequate pollination of saguaro flowers may have contributed to a decline in saguaro establishment at RMD received considerable attention around 1960 and again within the last several years. Alcorn et al. (1959, 1961) and McGregor et al. (1962) demonstrated that setting of fruit and production of viable seeds in saguaros required crosspollination. The morphology of flowers and the large quantities of nectar produced indicated pollination was accomplished by nectivorous animals.

Although observations of visits by pollinator insects to saguaro flowers had been recorded by some earlier botanists, Alcorn et al. (1961) and McGregor et al. (1962) conducted experiments to determine the relative importance of various pollinators to fruit setting and seed production in saguaros. Individual saguaro flowers typically open at night and close the following afternoon. Times during which pollination occurred were determined by covering the receptive stigmas and styles of flowers at various times with sheaths made of soda straws. These sheaths prevented pollination during the period in which they were in place. The studies were conducted on six different dates in 1959 and 1960 and indicated that between 2.9% and 36.4% (average = 11.4%) of flowers exposed only to nighttime pollinators set fruit. Between 44.4% and 85.7% (average = 55.8%) of flowers exposed to both nighttime and daytime pollinators set fruit. Although these studies showed daytime pollinators were responsible for the majority of fruit set, the occurrence of substantial pollination during the hours of night indicated that nectar-feeding bats could be important pollinators.

Subsequent experiments conducted within a screened enclosure containing saguaros examined the potential pollinating effectiveness of honey bees (*Apis mellifera*), white-winged doves (*Zenadia asiatica*), and lesser long-nosed bats (*Leptonycteris curasoae*) [referred to as *L. nivalis* in Alcorn et al. (1961) and McGregor et al. (1962)]. The three sets of animals were introduced into the enclosure during separate periods. Flowers that were open for potential pollination during each period. were tagged and monitored for fruit set and seed viability. Results of these trials showed that each of the potential pollinators visited flowers, and the three animal species were about equally effective as cross-pollinators of saguaros. Percentages of flowers that set fruit attributable to the visitations of bees, doves, and bats were 52%, 45%, and 62%, respectively. Fruit set in uncaged plants in the area was 54%, and controlled cross-pollination by hand resulted in fruit set in 71% of flowers treated. The mode of pollination (bee, dove, bat, or hand-pollination) had no significant effect on viability of seeds (80.2% to 91.9% germinability). From these data, the authors concluded that lack of pollination and production of seed was not a limiting factor in saguaro reproduction.

Renewed concern for potential inadequate pollination of saguaros came after the demise of a maternity colony of lesser long-nosed bats that originally occupied part of Colossal Cave, approximately 18 km (11.2 mi) SSE of the saguaro forest area of RMD. This maternity colony may have at one time contained as many as 5,000 individuals (Cockrum and Petryszyn 1991). Colossal Cave was opened to commercial tours in the early 1920s, and since that time many unsuccessful attempts were made to drive the bats from the cave. The maternity colony persisted until an exhaust fan system was installed in 1961 to eliminate bat odors from the cave.

The elimination of this maternity colony from Colossal Cave, coupled with a reported general decrease in populations of this bat species in southern Arizona, led to the listing of the bat as an endangered species by US Fish and Wildlife Service (FWS) in 1988. An additional factor contributing to the endangered species listing was the role of this bat as a pollinator of agaves, saguaros, and organ pipe cacti. The official justification for listing the bat as an endangered species stated that these plants may be affected by loss of the bat, and "there is concern for the future of the entire southwestern desert ecosystem" (Shull 1988).

One FWS spokesperson at the time went so far as to state that the bats are the major pollinators of saguaros (Hernandez and Erickson 1988). Concern for the long-term viability of saguaro populations was also expressed by NPS personnel. Superintendent W. Paleck recognized that other pollinators of saguaros existed, but, given the information surrounding the endangered species listing of the bat, he commented that if the bats were eliminated, a dramatic decline in the saguaro population would be anticipated (Hernandez and Erickson . 1988). The newspaper article by Hernandez and Erickson (1988) on the day of endangered species listing presented the situation of the "tiny rare bat largely responsible for Tucson's unique saguaro landscape."

The rationale for listing of the lesser long-nosed bat as an endangered species has recently been seriously challenged on the basis of more complete and accurate documentation of the status of bat populations (Cockrum and Petryszyn 1991). Regardless of the bat's actual population status, five lines of evidence indicate that the long-term viability of saguaro populations throughout Arizona, and SAGU in particular, are not dependent on the presence of the bat as expressed in the rationale for the endangered species listing:

1. The only data available on the relative importance of saguaro pollination by bats prior to the elimination of the maternity colony in Colossal Cave are those of Alcorn et al. (1961) and McGregor et al. (196:2). These data collected at SAGU and well within the foraging flight range of Colossal Cave indicate that bats were minor pollinators of saguaros in comparison to daytime pollinators, which included a variety of bee and bird species.

2. Additional studies in the Tucson area, including SAGU, have shown that honey bees from ubiquitous feral colonies are effective pollinators of saguaros (Schmidt et al. 1992; Buchman 1992). These studies add to the previous findings of Alcorn et al. (1961) and McGregor et al. (1962) regarding the important role now played by honey bees.

3. Additional experimental studies in Sonora, Mexico, indicate that the production of viable seed in two species of columnar cacti (the cardon [*Pachycereus pringlei*] and the organ ;- pipe cactus [*Stenocereus thurberi*]) *is* limited by the abundance of bats available for pollination. However, seed set in saguaros at this site was not limited when bats were „ experimentally excluded, because birds were major pollinators (Fleming 1992).

4. Large parts of the distributional range of the saguaro lie well outside the area where nectar-feeding bats have been recorded (Cockrum and Petryszyn 1991). This demonstrates that the absence of bats as pollinators does not prevent saguaros from reproducing.

5. The tremendous amount of recent saguaro establishment documented by Turner (1992) in the saguaro forest area of RMD has occurred after the demise of the giant maternity colony of Colossal Cave. Turner's data show an almost total lack of saguaro reproduction throughout the 1950s when the breeding colony of Colossal Cave was active. This indicates that conditions affecting survival of seedlings and young plants were the principal factors responsible for the lack of reproduction in the past and that establishment of new saguaros has not declined with the demise of the bat colony.

Research on dispersal of saguaro seeds has also been conducted at SAGU. Olin et al. (1989) demonstrated that white-winged doves are important seed dispersers. Transport of fruits and seeds to nests to feed young results in the inadvertent deposition of seeds on the soil surfaces beneath trees. This pattern of dispersal was cited as one factor contributing to the common association of saguaros with nurse tree canopies.

Recent investigations on both sides of the US-Mexico border in the vicinity of Organ Pipe Cactus National Monument indicate possible roles played by lesser long-nosed bats in fruit consumption and seed dispersal of both saguaros and organ pipe cacti (Petryszyn 1992; Peachey and Bethard 1992). Viable cactus seeds are defecated by the bats both in roosting caves and during flight. Although seeds deposited in caves are lost, Peachey and Bethard (1992) attributed the anomalous and disjunct occurrence of an organ pipe cactus population near the mouth of a major roosting cave to the accumulation of defecated seeds along the flight path leading to the cave.

As these studies indicate, the dispersal ecology of seeds of columnar cacti, including the saguaro, can hold considerable surprises and deserves far more study. However, for the saguaros at SAGU, there is presently no evidence to indicate that reproduction is limited by seed dispersal.

AIR QUALITY DIVISION INVESTIGATIONS

A considerable amount of recent research involving the saguaro has been influenced by federal requirements regarding air pollution and its potential impacts. An understanding of these federal requirements is helpful in understanding the rationale behind much of this research at SAGU.

The Clean Air Act and Development of Monitoring Programs

In the original Clean Air Act of the early 1970s, Congress concentrated on pollution in urban and industrial areas. Amendments to this act in 1977 included the protection of "refuges" of air or "airsheds" above large areas of federal wildlands. These Class I Airsheds include every national park exceeding 2,428 ha (6,000 a) and all wilderness areas greater than 2,024 ha (5,000 a) that existed prior to 7 August 1977 (Air Quality Division 1984). A Class I Airshed need not have "pristine" air. Rather, it is an area designated where no further significant deterioration in air quality will be allowed. For example, SAGU, especially RMD, is a designated Class I Airshed that borders the city limits of Tucson. Officially, Tucson is designated a "non-attainment" area for carbon monoxide levels. Tucson is also close to exceeding standards for ozone and particulates. Despite this juxtaposition of Class I Airshed and the city of Tucson, federal law requires that air quality and Air Quality-Related Values within Class I airsheds be protected from further deterioration. Direct air quality measures include levels of gaseous pollutants (e.g., ozone, carbon monoxide, sulfur dioxide, and nitrogen dioxide). Air quality-related values (AQRVs) include the soils, surface water, biota, cultural and historic resources of an area and visibility within the designated airshed. For example, one AQRV that has received considerable attention throughout the United States is plant health as affected by ozone pollution (Karnosky et al. 1992).

The US Environmental Protection Agency (EPA) is responsible for regulatory enforcement of the Clean Air Act and its amendments. The EPA works with state and local agencies to develop programs to protect local air quality. Within the Department of the Interior, this responsibility lies with the assistant secretary for fish, wildlife, and parks. In NPS, jurisdiction is passed from the assistant secretary through the NPS director to the Air Quality Division (AQD).

Air Quality Division, located in Denver, was created to deal with the considerable requirements placed upon NPS by the federal clean air regulations. This division is responsible for providing all the necessary planning, policy, and legal expertise, as well as research and monitoring that enable NPS to satisfy mandated requirements under the Clean Air Act. Air Quality Division contains three branches: (1) Policy, Planning, and Permit Review Branch, (2) Research Branch, and (3) Monitoring and Data Analysis Branch. The Research Branch is responsible for investigations that support the Policy, Planning, and Permit Review activities of AQD and investigations aimed at protecting air quality-related values such as visibility and the biota of parks. The Monitoring and Data Analysis Branch is responsible for direct monitoring of gaseous and particulate pollutants and acid deposition.

Local federal land managers (a superintendent in the case of *a* national park or monument) are required to take steps to prevent further deterioration of airshed under their jurisdiction. To accomplish this requirement, a superintendent needs to know the baseline pollution level and its impact on AQRVs within the park. In order to understand air quality issues, the superintendent must work with AQD. Further help is provided to the local superintendent when any point source of additional pollution is proposed in the area (e.g., a coal-fired generating plant). . Applications for permits to construct and operate such additional point sources must be obtained from the appropriate state. These applications are sent to the NPS Regional Office or directly to AQD for review and not to the individual parks. The parks do not do the reviews because they generally do not have the expertise to do so.

Research Concerns of AQD at SAGU

Initial investigations of possible air quality impacts on the biota of SAGU concentrated on effects of ozone on ponderosa pines (*Pinus ponderosa*) of higher elevations in the Rincon Mountains. Within monument boundaries, nighttime ozone levels slightly higher than those of adjacent Tucson were recorded as early as 1982. Suspected ozone-related damage to ponderosa pines in the Rincon Mountains was recorded in 1985 (Hall 1991). From 1982-1986, considerable effort and funding was directed toward monitoring suspected ozone damage to ponderosa pines and direct monitoring of atmospheric pollutants. Ozone sensitivity of yellow pines (ponderosa pine and Jeffrey pine [*P. jeffreyi*]) had been previously demonstrated, and AQD studies in California national parks demonstrated significant ozone impacts in the early 1980s. The subsequent effort at SAGU was part of examinations of wider regions to investigate the national extent of the problem (M. Scruggs, pers. com., 1992).

The saguaro was not included in AQD investigations until approximately 1985. At that time, the SAGU superintendent and the resource management specialist discussed the long-occurring decline of saguaros in RMD with the AQD Research Branch. The monument staff was concerned that there might be ozone effects on saguaros and that ozone damage could be a potential contributor to the saguaro population decline (R. L. Hall, K. Stolte, pers. com., 1992). Initially, it was believed by AQD staff that cacti in general are resistant to elevated ozone levels, and the explanation was accepted that the decline of the saguaro forest in RMD was due to its location at the upper elevational limits of the species and greater impacts of catastrophic freezes in this locale as proposed by Steenbergh and Lowe (1976, 1977, 1983).

Actual involvement of AQD with saguaro-related research began with reconnaissance and comparison of saguaro populations in the San Pedro Valley in the vicinity of San Manuel, Arizona, 40 km (25 mi) NE of RMD. Although deleterious impacts on saguaros were evident near the San Manuel smelter, "green, fat saguaros" were observed in areas more distant from the smelter, contrasting greatly with the slightly to much browned, thin main stems of saguaros that were typical of RMD (K. Stolte, R. Hall, pers. com., 1992). This reconnaissance led to a belief that the condition of the saguaros in RMD was an "accelerated aging process" of the type that ozone could potentially produce and to the hypothesis that severe epidermal browning and decline of the saguaro forest at SAGU could be a localized phenomenon, possibly related to greater air pollution in areas near Tucson. These concerns and hypotheses eventually led to several areas of investigation of possible air quality impacts on saguaros with funding for these projects starting in 1987. These studies included (1) investigations of the epidermal browning phenomenon and its cause(s), (2) potential effects of acid precipitation, (3) biomonitoring garden studies, and (4) a planned study on impacts of nitrogen enrichment. Discussion and evaluation of each of these areas of investigation follow.

Studies on Epidermal Browning. Epidermal browning is a brown discoloration of the normally green epidermis that originates at the areoles near the base of the saguaro stem (Air Quality Division 1991; Fig. 3.). This condition is typically associated with the loss of spines and may in some cases completely cover lower parts of the stem. Epidermal browning was perceived to be related to the population decline at RMD (AQD 1991) . Four principal lines of investigation were formulated by AQD to investigate the phenomenon:

1. Establishment and collection of baseline data from a network of monitoring plots in both management districts of SAGU;

2. Morphological, histological, and histochemical characteristics of browned vs. normal cacti and investigation of possible causes;

3. Studies of elemental characteristics of soils and saguaro tissues; and

4. Ecophysiological studies of normal vs. affected cacti.

Each of these areas of investigation involving epidermal browning are detailed below.

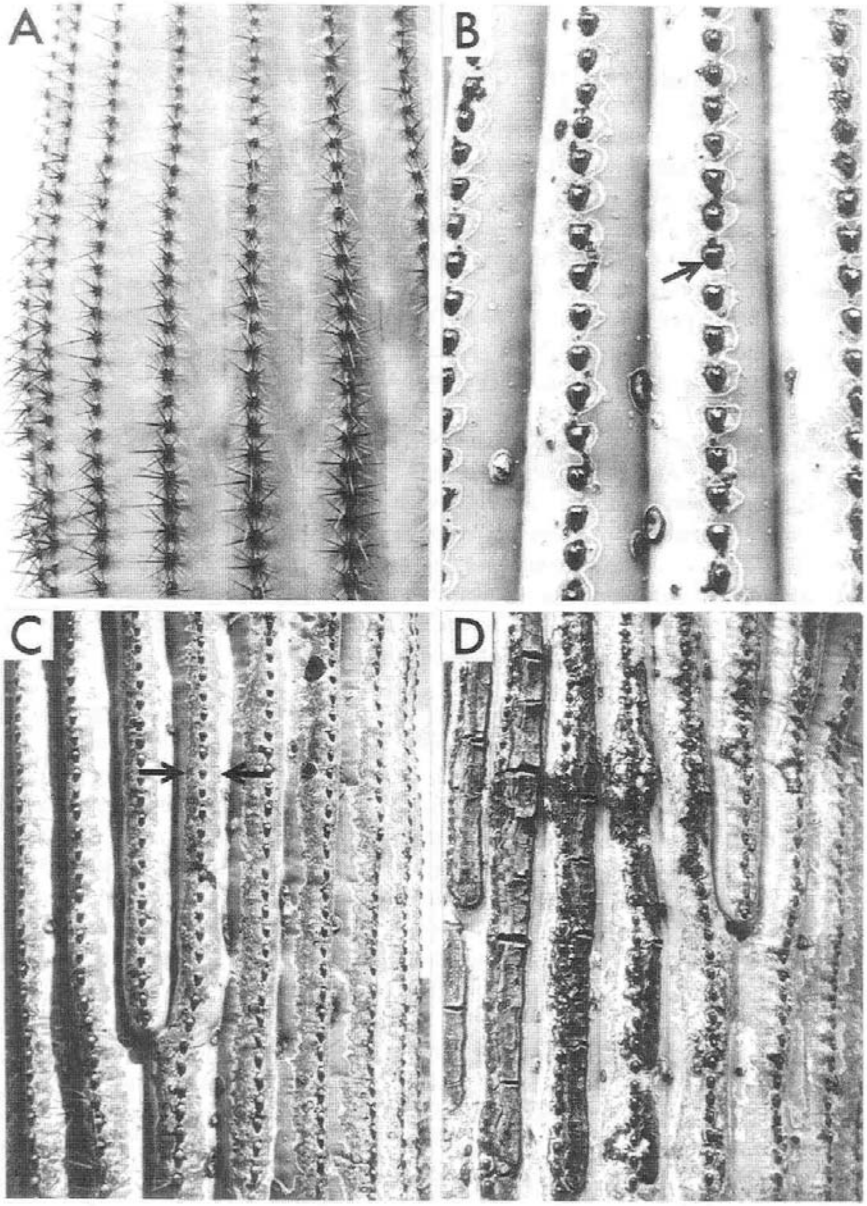

Figure 3. Epidermal browning on saguaros. A. Spine-covered epidermis of a saguaro showing no epidermal browning. B. Slight manifestation of epidermal browning characterized by discolored epidermis encircling areoles from which spines have been lost. Arrow indicates a single, black-colored areole. C. More extensive epidermal browning characterized by discoloration of entire ridges. Discolored zone on one ridge indicated between arrows. Troughs of epidermal pleats are not discolored. D. Cactus showing recent epidermal browning together with dark, lignified bark (material with cracked appearance). Areas covered with bark probably indicate healing response to previous episodes of epidermal browning.

Long-term Saguaro Trend Plots. In 1988 to 1989, 45, 4-ha (9.9-a) plots-each 200 X 200 m (656 X 656 ft~-were randomly located and established at SAGU. Twenty-five of these plots are located at RMD, and the remainder are located at TMD (Duriscoe and Graban 1992). All saguaros 10 cm (3.9 in.) or taller were tallied in each plot, and 30 randomly chosen individuals at least 2 m (6.6 ft) tall were selected for detailed measurements. A variety of data was collected on characteristics exhibited by each of these saguaros. In addition, data were recorded on attributes of the physical environment and vegetation composition in the immediate vicinity of each saguaro. Each of these saguaros was photographed and marked with an aluminum tag attached to a steel stake for location and identification in the future. Within each plot, a smaller (100 m^2 [1,075 ft^2]) "subplot" was established, and within each of these subplots all perennial plants were identified and mapped.

Baseline data collected by Duriscoe and Graban (1992) indicated two principal patterns of epidermal browning: (1) browning is a height- or age-related phenomenon, and (2) the south-facing surfaces of cactus stems exhibited more browning than north-facing surfaces. Levels of epidermal browning ranging from complete absence of browning to high levels were recorded in both RMD and TMD. Whereas two plots at RMD exhibited the highest "browning indexes" recorded in the study, four plots in which saguaros exhibited little or no browning were also located in RMD. Three of these four plots were located next to major washes; the significance of this association will be discussed later.

The extent of browning in individual saguaros was also correlated with presence of other associated perennial plants. Saguaros associated with mesquites exhibited significantly lower browning indexes than saguaros not associated with mesquites. Saguaros growing in association with foothill paloverdes had significantly greater amounts of browning than those not associated with paloverdes, as well as greater amounts of. browning than that exhibited by saguaros associated with mesquites. Since mesquites are primarily limited to areas along major washes (runoff-collection areas) in SAGU and paloverdes are the dominant tree on the considerably drier slopes and runoff-producing areas of mountainsides and bajadas, these data further indicate an association between epidermal browning and either water status of soils and/or growth rates.

Duriscoe and Graban (1992) also documented a strong negative correlation between spine retention and the severity of browning but were careful to point out that this relationship provided no evidence that browning caused spine loss. Since spine retention and browning both vary with height, they pointed out that decreased spine retention may be a normal part of the aging process. Indeed, for saguaros in the area around Tucson, spines are produced only at the growing apex and are not replaced with new tissue during the life of the plant. Therefore, spines present near the base of an extremely old saguaro considerably exceed a century in age and might be expected to show much weathering and even loss.

To summarize, Duriscoe and Graban concluded that epidermal browning is a widespread condition, occurring in both management districts of SAGU. Browning is found principally on the southern exposures of saguaro stems, but large cacti can be found in both TMD and RMD that show no evidence of browning. Considering the great variability in the expression of the browning condition, they suggested some "plant-specific factor," such as age or growth rates, must be involved.

In addition to the data collected on epidermal browning, the information obtained on age structure, condition, and vegetational compositions in each of the 45 plots represents an unparalleled effort serving as a foundation for long-term population studies. The importance of the preservation of this complete set of records and photographs for future study is discussed in Conclusion and Recommendations.

Morphological. Histological, and Histochemical Studies. In studies conducted at SAGU, the findings of Evans et al. (1992a) corroborated the findings of Duriscoe and Graban (1992) that epidermal browning and spine loss in saguaros was greater on southern exposures than on northern exposures of stems. Portions of cacti facing 120-220° S exhibited greater amounts of browning than more northerly aspects within single cacti. The accordion-like external pleats of the epidermis can be divided into the protruding rib and the depressed trough. Within individual cacti exhibiting considerable epidermal browning, the extent of browning in trough areas of southern exposures was about six times greater than troughs facing the north. Additional work reported by Evans et al. (1992b) described morphological changes associated with epidermal browning in the epicuticular waxes, the obscuring of stomata, and discoloration of the internal parenchyma. On the basis of these histological studies, Evans et al. (1991) and Evans (1992a) suggested that sheeting of epicuticular wax is a precursor to stomatal dysfunction. Death of chloroplasts and the development of internal discoloration and epidermal browning was linked to this obscuring of stomata.

Although the initial work of Evans concentrated on histological descriptions of epidermal browning, by 1990 he had begun work attempting to establish a causal link between epidermal browning and solar ultraviolet radiation. Evans observed epidermal browning in saguaros in sites throughout the Sonoran Desert in both Arizona and Sonora, Mexico, and concluded that because of its widespread occurrence, the phenomenon could not be attributed to a local pollution problem as originally suggested by Ken Stolte of AQD. In addition, research conducted by Evans in the Southern Hemisphere (Argentina and Chile) indicated similar types of epidermal discoloration of various cactus species on the northern or equatorial exposures in that hemisphere (L. Evans, pers. com., 1992).

Evans further examined 241 saguaros recorded in archived photographs dating to 1903 that were taken in the vicinity of RMD. Evans et al. (1992a, c) concluded from these that epidermal browning of saguaros has increased at a rate of 4-5% per decade between 1903 to 1987.

However, this conclusion is questionable. According to the statistics presented in Evans et al. (1992a, c), the correlation between the occurrence of epidermal browning and the passage of time is actually extremely weak. Only 5-7% of the purported increase in epidermal browning can be explained by the passage of time between 1903 and 1987 (as estimated by r^2, the coefficient of determination). In other words, 93-95% of the variation in the observed occurrence of epidermal browning is related to factors other than the passage of time. The conclusions of Evans et al. (1992a, c) are further called into question because the claim for a linear increase in epidermal browning over time appears to simply be a consequence of the inappropriate use of linear regression to analyze data consisting only of binomial scores (0,1) representing the presence or absence of characteristics of epidermal browning.

On the basis of the conclusion that a gradual increase in epidermal browning has been taking place over the last several decades, Evans continued to attempt to establish a link with increases in ultraviolet radiation caused by stratospheric ozone depletion. In a letter justifying this research to the superintendent of SAGU, Evans (1992b) stated "the UV-B hypothesis should not be rejected, and based on other data, is the only viable hypothesis relating to epidermal browning of saguaros and other columnar cacti in the Americas." In July 1991, Evans began a pilot "experiment" in RMD that involved the irradiation of two large saguaros with an electric ultraviolet light fixture (Evans 1991). This experiment was funded by SAGU and halted after one year because of design weaknesses and the failure to consider alternate hypotheses.

Alternative Explanations of Epidermal Browning: Impacts of infrared wavelengths and, more specifically, heat loading of tissues in excess of lethal temperature limits, is a factor that may contribute to epidermal browning in saguaros.

The localized pattern of discoloration associated with initial stages of epidermal browning strongly suggests a connection to excessive (but localized) heat loading. The lightest forms of epidermal browning appear as discolored zones several millimeters wide completely encircling areoles on the south sides of stems from which spines have been lost in the lowermost, oldest parts of the stem (Fig. 3B). These denuded areoles are 5-7 mm (0.2-0.3 in.) across and are black in color. The lower albedo associated with this localized black coloration undoubtedly results in the absorbance of more incoming solar radiation and localized, higher (and possibly lethal) tissue temperatures. A rise above the lethal limit could cause local tissue damage or death that leads to the browning condition. Healing after such an injury would likely result in the formation of ligniferous "bark" at the site of the original damage (Fig. 3D; Steelink et al. 1967; Gibson and Nobel 1986).

The typical rarity or absence of the epidermal browning condition in well-hydrated saguaros along washes compared to the greater degree of browning in saguaros of immediately adjacent, drier microhabitats (see Duriscoe and Graban [1992], Fig. 6) is far more plausibly explained by the effects of varying hydrature on heat dissipation and cumulative heat loading than it is by a consequence of UV-B radiation.

Elemental Analyses of Soils and Saguaro Tissue. The reportedly greater local incidence of epidermal browning in RMD led AQD biologist K. Stolte to initially believe that local pollution, perhaps emissions from copper smelters, or even the turn-of-the-century lime kilns at the base of Tanque Verde Ridge, may have led to local soil contamination that contributed to reduced vigor of saguaros. Contracted studies of elemental content of soils were conducted from 1978 to 1990 by E. S. Gladney and R. W. Ferenbaugh of Los Alamos National Laboratories. Additional analyses of saguaro tissues for heavy metal content were conducted by K. Lajtha of Boston University.

The work of Gladney (1991) and Gladney et al. (1992) involved analytical assessments of elemental concentrations from 825 soil samples within RMD and sites near the San Manuel copper smelter approximately 40 km (25 mi) NE of SAGU. The concentration of 13 elements was determined for tissues of 4 saguaros sampled in 1988. Elemental analyses from samples taken in 1990 from 60 additional saguaros had not been performed as of September 1992 (E. S. Gladney, pers. com., 1992).

The soil samples were analyzed for up to 46 different elemental constituents including common contaminants associated with ore processing such as tin, indium, and zinc. In addition to these common elements, concentrations of a multitude of rare-earth elements including dysposium, europium, lanthanum, lutetium, neodymium, samarium, terbium, and ytterbium were determined. The purpose for inclusion of this diverse array of unusual, rare elements was the identification of "elemental profiles" of soils and tissues that might indicate enrichment (due to pollution) beyond the normal, average elemental abundances in the earth's crust.

Analyses indicated that concentrations of all the rare-earth elements listed above were "within normal ranges." A few elements, such as indium (commonly associated with zinc ores), tin, and zinc, were significantly enriched in soils near the San Manuel smelter. No conclusive pattern of elemental enrichment of soils in the monument due to pollution could be detected other than slightly elevated levels of tin (Gladney et al. 1992). Although these detailed elemental analyses of soils generated tremendous amounts of information, they have yielded little more in terms of meaningful or important results beyond a demonstration of an expected enrichment of soils near the San Manuel Smelter with a few metallic elements commonly associated with mining and smelting operations. No connection can be made between these results and saguaro condition at SAGU.

Of the four saguaros from which tissue samples were analyzed for concentrations of 13 elements, only manganese showed any possible trends (Gladney et al. 1992). One of the four saguaros sampled exhibited considerable epidermal browning, and tissues from this cactus exhibited slightly higher manganese concentrations than tissues from the three healthy saguaros. Although Gladney et al. (1992) commented that these data were not sufficient to implicate manganese as a causal agent of epidermal browning, they stated that manganese toxicity could potentially cause severe chlorosis in plants and was "worthy of further investigation."

However, the finding of slightly elevated manganese levels in epidermally browned tissues is not surprising considering the normal location and function of this element in plant cells. Chloroplasts (specifically the Photosystem II component) contain one or more proteins with bound manganese called manganese proteins (Salisbury and Ross 1978). Manganese proteins form part of the thylakoid membrane, and Mn^{2+} is thought to play an important part in photosynthesis. The destruction or damage of chloroplast structures during the process of epidermal browning may easily result in the slight accumulation of manganese with respect to tissue volume or weight, given the considerable shrinkage of saguaro stems that typically occurs during the process of browning. This is an alternate hypothesis that must be considered before concluding that even ubiquitous, elevated manganese levels in damaged saguaros are due to abnormal environmental manganese concentrations.

Additional studies of elemental concentrations of saguaro tissues by Lajtha were limited to lead and cadmium, heavy metals known to inhibit plant physiological function, root growth, nutrient uptake, or soil nutrient cycling. The concentrations of these two metals were extremely low within the saguaros examined and were well within the range of concentrations seen in plants considered to be free of trace metal contamination (Lajtha and Kolberg 1992).

Ecophysiological Studies. Studies by Lajtha and Kolberg (1992) concentrated on carbon dioxide uptake as a function of condition of saguaros in RMD. The study was conducted during the summer rainy seasons (August) of 1990 and 1991. In the year of record-breaking quantities of summer precipitation (1990), tissues on the south sides of healthy saguaros had higher maximum rates of CO_2 uptake and remained active longer than healthy tissues on the north sides of the same cacti. The reverse was true for saguaros with more than 20% of the south sides of stems covered by epidermal browning. In epidermally browned saguaros, $C0_2$ uptake was lower on south sides than on the north. In the dry summer of 1991 (one of the driest on record) $C0_2$ uptake was significantly lower than in 1990, and many plants, both with and without epidermal browning, experienced daytime respiration losses exceeding nighttime $C0_2$ accumulation. In this drier year, $C0_2$ uptake was only marginally related to degree of browning and was primarily controlled by the drought conditions. Further studies of water relations and gas exchange of this sort combined with tissue temperature measurements are needed for testing the hypothesized cause-and-effect relationships of epidermal browning, water status, and potential heat loading discussed previously.

Other AQD investigations. In addition to the various investigations of (1) epidermal browning discussed above, other studies formulated by AQD dealt with (2) potential effects of acid precipitation, (3) biomonitoring garden studies and (4) a planned nitrogen enrichment study.

Effects of Acid Precipitation. High sulfur emissions from copper smelters and electricity generating plants contribute to acidified precipitation. Of greatest concern in southern Arizona were emissions from copper smelters near San Manuel 40 km (25 mi) NE of SAGU and the so-called "Gray Triangle" (Shields 1985) consisting of the Douglas, Arizona, smelter and two additional, large smelters located in adjacent Sonora, Mexico. An analysis of regional wet deposition has shown a positive correlation between sulfate in precipitation and quantities of sulfur dioxide emitted from regional smelters (Oppenheimer et al. 1985, 1986). Experiments were conducted to examine the effects of simulated acid rain on saguaro seedlings and germination of saguaro seeds (Temple 1990). Although germination of saguaro seeds at pH 3.5 (30.5% germination) was slightly less than at pH 4.5, 5.5, and 6.5 (germination percentages = 40.0%, 44.0%, and 41.5%, respectively), the lower germination at pH 3.5 was not significantly different.

The authors observed no adverse effects of simulated acidic precipitation on seedling growth and concluded that the highly alkaline nature of desert soils apparently buffered the effects of acid precipitation but stated that potential long-term impacts of acid precipitation are not known.

These experiments were conducted in 1988 without knowledge of the degree to which precipitation received at SAGU was actually acidified. Records of pH of 47 individual precipitation events between July 1989 to February 1992 ranged from 4.22 to 7.25 (Mean = 5.46) (Arizona National Atmospheric Deposition Program [NADP] data at Saguaro National Monument), putting average precipitation pH at the monument well within the "natural" range of pH 4.8-6.0 (Baron 1991). It is unlikely that this range of pH of precipitation at SAGU has any effect on saguaro establishment or desert vegetation, in general.

Biomonitoring Garden Studies. In 1989, AQD biologist K. Stolte drew up plans for establishment of a biomonitoring garden near the gaseous pollution monitoring station in RMD. The stated purpose of the garden was to co-locate known or suspected "bioindicator" species with the gaseous pollution monitoring station in order to increase knowledge about the sensitivity of native plant species to pollution (Danisiewicz 1992).

The fenced and irrigated biomonitoring garden measures 26 m X 13 m (85.3 ft X 42.7 ft) and contains 18 separate plots. Thirteen perennial plant species have been selected for inclusion in the garden either because of suspected sensitivity to pollution, their wide distribution, or their biological significance to the monument. These species range from those typical of low desert elevations (the saguaro, barrel cactus [*Ferocactus wislizenii*], brittlebush [*Encelia farinosa*]) to those of higher or more mesic habitats in the Rincon Mountains (Arizona sycamore [*Platanus wrightii*], squaw bush [*Rhus trilobata*]). The garden has required continual maintenance since its establishment (weeding, watering system maintenance, pruning: an estimated 51 person-hours per month). Although the garden was set up in 1989 to provide specimens for histological examinations, no protocols were established for the collection and preservation of plant tissues with suspected damage. Samples were apparently collected once during 1990 by Stolte and L. Evans. Guidelines for monitoring observations were developed with SAGU staff input, in 1990. Recommended procedures included inspection of the plants every two weeks between the months of April and October, since highest ozone measurements had been previously recorded during the summer season. These inspections were done in 1991 and 1992. Summer documentation in 1990 was limited to casual observations by the biological technician, and no records of plant condition are known to exist for the summer of 1989.

Approximately 80-100 juvenile saguaros ranging up to 10 cm (3.9 in.) in height are included in the garden. Possible damage attributable to air pollution effects has not been observed in any of these plants. The only potentially relevant damage observed to date has been a slight stippling on squaw bush leaves of 6 of 11 plants recorded in August 1990 and a similar stippling on squaw bush leaves of 11 of 14 plants in summer 1991. On the basis of fumigation studies and other biomonitoring garden results at Joshua Tree National Monument, it was concluded by Stolte that the stippled squaw bush leaves were indicative of ozone damage. The 1990 biomonitoring garden observations led to a survey of natural populations of squaw bush in west-facing. canyons at higher elevations in the Rincon Mountains. One large stand contained approximately 25 squaw bush plants, but only one of them exhibited any stippling similar to that observed in the garden. Further field surveys in 1991 and examination of the same 25 plants revealed no visual signs of damage to leaf surfaces.

<u>Evaluation of the Biomonitoring Effort.</u> Data sheets with information on condition of plants in the biomonitoring garden are filed at SAGU. Air Quality Division has requested summarized reports, yet monument personnel really do not have the expertise necessary for conducting the analysis required in such reports. Information or instructions necessary for such analyses have not been provided to the monument by AQD. As a consequence, the biomonitoring effort included considerable data collection, but could hardly be considered a viable monitoring

program since information was simply filed without meaningful analysis of the possible relationship between suspected ozone damage to plants and actual ozone levels measured at the site.

The biomonitoring garden required considerable investment in materials and effort in its establishment, maintenance, and information gathering. However, this effort yielded little, if any, return in terms of conclusive results regarding the effects of gaseous pollutants on various plants of the monument and was stopped on the basis of a review conducted in the fall of 1992.

Planned Nitrogen Enrichment Studies. Sites near urban areas typically show elevated levels of nitrogen oxides as atmospheric pollutants due to emissions from automobiles and power plants (Baron 1991). Stolte (1991) speculated that an additional nitrogen input (e.g., from nitrogen of air pollution origin in precipitation) can alter phenological cycles and delay winter dormancy, consequently upsetting "natural balances" in terms of species compositions. Some of these speculations were based on Tilman's (1987) findings that nitrogen levels were an important determinant of competitive outcomes and successional sequences in abandoned agricultural fields in Minnesota. Due to these concerns regarding potential effects of nitrogen enrichment, a research plan was developed to evaluate the effects of nitrogen fertilization on growth, competition, and survivorship of Sonoran Desert annuals and grasses and the winter hardening process of saguaros. The research was to be carried out in RMD and executed and maintained by SAGU personnel. The experimental design for the saguaro experiments called for 15, 1-m^2 (3.3-ft^z) plots, each containing 20 saguaro seedlings. The research plan called for three treatment blocks, each block containing five treatments of varying nitrogen enrichment levels: no N addition (ambient soil level), and 1.5X, 2X, 3X and 4X ambient soil N levels. Experiments with annuals included a similar design carried out in greenhouse trays with various combinations of ephemeral grasses and broad-leafed plants subjected to low, medium, and high N levels. Changes in species biomass, height, and relative abundances of the various species were to be recorded throughout the plant life cycle.

The experimental plots were installed at RMD by monument staff in November-December 1990. However, because new personnel at AQD raised questions regarding the rationale of the experiments, the project was halted in August 1991 and finally stopped altogether after formal review in fall of 1992.

<u>Evaluation of the Nitrogen Enrichment Study</u> The most serious shortcoming of this experimental plan was the lack of any data collected at SAGU to indicate whether significant deposition (dry or wet) of nitrogen from pollution sources is great enough even to be of potential concern. Although the pH of precipitation received at RMD headquarters is measured following each precipitation event, SAGU is not part of the NADP monitoring network (Baron 1991). Consequently, there are no data regarding nitrogen content of either precipitation or dry-deposited materials at SAGU.

The Process of Formulation and Review of Research Programs Originating within the Denver Air Quality Division. Between 1986 and 1992 more than $120,000 was provided by AQD to fund various projects involving the saguaro at SAGU. The previous descriptions and reviews of these projects show that many of the research efforts failed to provide useful information regarding either specifics of air pollution effects or aspects of the ecology of the saguaro. These failings in some cases are attributable to lack of rigor in terms of scientific approaches by individual investigators. However, the success of any research and monitoring program begins with the procedures by which (1) research questions and priorities are identified; and (2) proposals that address those issues are requested, reviewed, and awarded. These two areas are the responsibility of the Air Quality Division and are considered in the following paragraphs.

Determination of Research Priorities by AQD. The goal of research implemented at national parks and monuments by AQD is to provide managers of those parks with information that will help them with resource management problems, specifically questions regarding responsibilities of managers under the Clean Air Act. Ideally, these problem areas would be indicated by either the park management staff or as a cooperative effort between park and AQD personnel. However, this ideal was not achieved with plans for research programs at SAGU.

Research priorities and plans concerning biological resources at SAGU were drawn up almost unilaterally by a single individual within AQD between the mid-1980s and August 1991. Although the administration of SAGU definitely showed interest and cooperation in developing and implementing these programs (see Hall 1991), the research questions, priorities, and methodological approaches were determined primarily by this one individual who also had many other responsibilities and often did not have the time to be effective in any one of them. One member of the SAGU staff commented that during the later part of AQD efforts at SAGU, there had too frequently been little or no notification of who would be conducting research or what would be happening concerning the implementation of various projects. As a consequence of the overextended responsibility for planning and implementing projects assumed by AQD and the lack of meaningful involvement of SAGU staff in the planning and implementation of research priorities, much of the work lacked a meaningful and effective connection to resource management concerns.

AQD Procedures for Request. Review, and Funding of Research Proposals. 'Inadequate procedures for the request and review of research proposals was a major factor that contributed to the poor quality of some of the work supported by AQD in SAGU.

One problem experienced by AQD that limited the manner of funding is a requirement of the NPS procurement system for scientific research proposals. The reason for going after big, non-specific umbrella contracts from 1982-1987 is that all contracts from AQD in Denver were submitted through the main NPS office in Washington, DC, for final approval. The AQD office simply does not consider requests of less than $100,000. As a consequence, AQD was forced to seek ways of getting big funding packages pushed through NPS administrative channels in order to get even small projects funded.

This funding procedure received a poor evaluation by an outside review panel, and, consequently, in 1988 AQD turned to different funding procedures involving the other branches of NPS, scientists from academic institutions, and inter-agency agreements between other federal agencies such as USFS and EPA. In the case of saguaro-related research at SAGU, a Request for Quotes was sent to six potential researchers identified by AQD staff. In the case of work eventually conducted by Lajtha and Evans, quotes from these two investigators were the only ones received in response to the separate requests for ecophysiological and histological studies.

The criterion for awarding a contract to a potential investigator was exclusively on the basis of the lowest bid. All that was required for a potential investigator to be awarded a contract was receipt by AQD of a three-page form listing simply the amount requested and administrative information. No abstract of the proposed work or statement of the kind of research to be done, methods, and so forth were a part of the initial quotes upon which funding decisions were made. Work plans submitted by the investigator were required only after the awards were made and usually contained no more information than that on the original Request for Quotes. This process by which awards for research were made was clearly inadequate. Research funded in this manner by AQD has been treated as little more than a business "product" with questions and approaches already stipulated and lacking any emphasis on creativity and innovation on the part of the contracted investigator in development of the scientific "product."

The poor quality of some investigations conducted at SAGU was the direct consequence of a lack of any rigorous review procedures of the qualifications of researchers and their proposals for research, and adequate staff time to communicate properly with SAGU staff and researchers. Little follow-up was done to make sure that reports were in on time, reviewed and shared within NPS. In August 1991, personnel changes in the AQD Research Branch brought about a second review of procedures and set in motion a change toward improving the responsibilities of formulation and review of the air quality research program.

IMPACTS OF RESEARCH ON MANAGEMENT DECISIONS AND PUBLIC PERCEPTIONS

Conclusions reached by researchers regarding the status of the saguaro have greatly affected the way in which SAGU has been managed by NPS and perceived by the public. Some of these consequences of research efforts, both helpful and deleterious, dating to the era of saguaro "disease" investigations of the 1940s, are discussed below.

IMPACTS OF INVESTIGATIONS ON "BACTERIAL NECROSIS"

The uncritical acceptance and rapid promotion of the hypothesis of a disease that was responsible for widespread mortality and potential extinction of saguaro populations literally placed a strangle hold on NPS policy and management from 1940 through the mid-1960s. The manner in which the saguaro disease investigations were reported in the popular press at the time only tightened the hold these investigations had on management concerns. Magazine articles and pictorial essays showing plant pathologists, at work in disease control experiments (Gill 1942) and administering antibiotics to stricken saguaros under the title "Will Science Save the Saguaros?" (Bardsley 1957) together with references to the rampaging effects of "epidemics of bacterial necrosis" and "cactus cancer" (Robinson 1966), the emotional depiction of the saguaro "fighting against ... an insidious disease-carrying insect" (Bardsley 1957) and the frightening question "Will King Cactus Lose His Throne?" (Ingle 1964) all contributed to a hysteria that understandably would affect management concerning the saguaro by the NPS system. A genuine concern that saguaros would be irrecoverably lost from RMD led to a variety of management proposals that fortunately were not all implemented.

Convinced that the saguaro population of the original monument was doomed by the necrosis disease and frustrated by the continuing land ownership problem, the regional NPS director recommended the abolishment of SAGU in 1945 (Clemensen 1987). Fortunately, though, the national director did not accept that proposal and instructed that solutions to ownership problems and livestock grazing be pursued more vigorously. The possibility of abandonment of SAGU (RMD) continued, though, through the mid-1960s and had a detrimental effect on effective planning for the monument. Because of its uncertain future, SAGU typically had one of the lowest priorities with respect to funding and resources provided to western park areas (W. Paleck, pers. com., 1992).

Measures other than abandonment were proposed and sometimes seriously considered as management solutions to the problem of the saguaro decline. In 1946, the principal pathologist of BPI (the agency responsible for the saguaro disease investigations) offered to spray the saguaros of the monument with DDT by airplane at six-week intervals in order to kill the moth suspected of spreading the bacterial disease (Clemensen 1987). The pathologist acknowledged that such spraying would eliminate all insects but that if the majestic saguaros of the monument were indeed valued above all else, then the spraying of DDT would allow them to survive for many more years. The long-term consequences of DDT, including biomagnification of the pesticide in food chains, were not known at that time. Considering the long-lasting impact that this proposed pesticide application would have had, it is fortunate the USDA offer was declined by NPS.

Another misguided management strategy that arose in this era was a plan for "reforestation" of the declining saguaro forest through a massive effort of transplanting juvenile saguaros. Although this approach was strongly questioned by NPS personnel (see Steenbergh and Lowe 1983, Appendix 1), a lath house was constructed at the monument and saguaros were propagated for this purpose in the late 1950s. This facility provided seedlings and juvenile cacti for the experiments of Turner et al. (1966). However, the "reforestation" program was never implemented because of destruction of the lath house by a fire in the 1960s (R. M. Turner, pers. com., 1992).

Concern about the decline of the saguaro population in the monument led to initial considerations in the 1940s to acquire land administered by Pima County in the Tucson Mountains as part of the monument. However, this interest was dropped; the reason for the eventual inclusion of TMD was not due to the saguaro decline in the original monument, but rather, public outcry over the possibility of Tucson Mountain lands being opened up to largescale mining operations in the early 1960s (Clemensen 1987).

Ode of the most detrimental impacts of the era of cactus disease investigations has been the fostering of incorrect notions on the part of the general public regarding the biology and ecology of the saguaro. The sensational reporting in magazines and newspapers of the day did much to fan the flames of a mistaken hysteria that has yet to be extinguished.

To summarize, the failings of the cactus disease investigations that spanned more than two decades have been the source of much confusion on the part of the public and ill-conceived management solutions on the part of NPS and other federal agencies. Steenbergh (1970) stated the situation rather bluntly: "The public has enjoyed the company of the National Park Service on their journey down this emotional primrose path as, at times, we proposed and supported desperate non-solutions to the non-problems derived from the non-valid interpretations of ecological non-sense."

IMPACTS OF SOME ECOLOGICAL RESEARCH, 1960-1991

One of the most important roles of the ecologically-oriented investigations has been to clear up the widespread misconceptions borne out of the previous era of cactus "disease" investigations. Yet, even though Steenbergh and Lowe (1977) declared a "requiem" for the "ecologically unsupportable myth" of the bacterial necrosis disease, this myth certainly has not died in the minds of many. To this day, many people still believe the saguaro is afflicted by some mysterious, lethal malady and, as a consequence, is declining steadily toward extinction. This confusion is not limited to the residents of Arizona. Reporters from national magazines and newspapers in phone interviews still express these misconceptions. National Park Service must do much more to clear up these sorts of misconceptions that resulted from research sanctioned by NPS at SAGU.

Another important role that research findings, such as those of Steenbergh and Lowe (1976, 1977, 1983), Turner et al. (1966), and Turner (1992), can play is to serve as a foundation for other studies in building a greater scientific understanding of processes affecting saguaro populations. Unfortunately, though, some recent research supported by NPS has either disregarded or ignored the valuable foundation that these ecological investigations provide. As a consequence, some of these investigations have taken misguided trajectories, because researchers have ignored or failed to understand what knowledge has been accumulated. For example, Evans et al. (1992b) claimed that "Little systematic research has been done to determine the cause(s) of the saguaro decline." The failure to recognize and understand the significance of the observations, measurements, and experiments recorded in several hundred pages of technical papers and monographs (Steenbergh and Lowe 1969, 1976, 1977, 1983) and publication of the misleading statement above by Evans et al. (1992b) is indefensible and professionally irresponsible considering the impacts such statements can potentially have on NPS plans and policy.

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Despite the impacts inflicted on SAGU before and even decades after its establishment, this national monument unquestionably deserves protection afforded by monument status. The range of biotic communities present over the elevational gradient of RMD is unique. The Tucson Basin is one of the few places where one can find Sonoran desertscrub communities with stands of saguaros so close to forests of pine and fir in the adjacent mountains. Most of these special Sonoran Desert habitats that were also originally present at the base of the nearby Santa Catalina Mountains are privately owned, and many have been either destroyed or irreparably altered by the urban development of Tucson. Rincon Mountain District remains as a preserve not only of a saguaro forest, but of the spectacular transition from hot, dry desert to the dense forests of cooler and moister mountain slopes.

The close proximity of a city exceeding a half million inhabitants and housing developments on the monument boundary are likely to result in an increasing number of perceived and actual environmental threats to SAGU in the future. For protection of this special monument, it is necessary that programs for ecological monitoring be well-planned and carefully implemented. It is important to realize that despite the past impacts on SAGU, irreparable ecological damage has not generally occurred. One of the most striking demonstrations of this recovery is the recent surge in establishment of saguaros in an area where it was once feared saguaros would disappear forever. The abundant, young saguaros, most of which today are no more that waist-high, hold the realistic promise of forming a grand saguaro forest of the future. Our monitoring efforts from this point of time onward can provide the tremendous opportunity for studying the process of environmental recovery as well as real potential threats to that recovery. However, considerable improvement must be made in the administration of these scientific endeavors by NPS.

Recommendations for improving research and monitoring efforts at SAGU focus on three areas: (1) strengthening the research capacity within NPS, (2) the process of identification and review of research priorities, and (3) the importance of long-term monitoring records.

STRENGTHENING THE CAPABILITY TO CONDUCT RESEARCH WITHIN THE NPS SYSTEM

The lack of research staff either located within or closely associated with park areas has required that park managers either rely on outside investigators or other NPS divisions. The research priorities and agenda of these other entities may differ greatly from the types of priorities that exist within a park or monument. Divisions, such as AQD, with narrowly focused research and monitoring missions cannot be expected to provide managers of national parks and monuments with information on the multitude of resource management and environmental issues with which they are continually confronted.

As of 1989, NPS had only about 75 scientists for its 354 units, and research comprised only about 2% of the entire NPS operating budget, compared to approximately 10% in other federal land management agencies with similar responsibilities (Simon 1989). The problem of inadequate research staffing and expertise is especially great for small parks, such as SAGU where it is unreasonable to expect that personnel stationed at an individual park area can fulfill a variety of different specialized research needs. The requirement for scientists with various types of expertise can be served, in part, by research staff within Cooperative Park Studies Units (CPSUs). However, the CPSU/UA is responsible for a geographic area that includes 11 parks and monuments, has been chronically understaffed (three scientists) and has suffered from a lack of administrative direction concerning its relationships to parks and its responsibilities in terms of providing research and basic information for park management needs. The southern Arizona CPSU, despite its location in Tucson, has had little involvement with research conducted on saguaros at SAGU during the last half decade. Clearly, the CPSUs must be strengthened, and their responsibilities more clearly identified in order for them to contribute in more meaningful ways to pressing research and monitoring concerns.

Even with a strengthened CPSU working in concert with local administrators and resource managers of SAGU, there will be many research problems that require expertise drawn from outside LAPS. Establishment of fruitful liaisons with recognized local, regional, and national experts is a responsibility that must be shared by local park managers and scientists of the CPSU. These liaisons must form an important link for consultation and guidance regarding the formulation, implementation, and review of various research programs.

IDENTIFICATION AND REVIEW OF RESEARCH PRIORITIES

Many AQD projects conducted at.SAGU were conceived and designed by a single individual within AQD; these ideas became priorities that were implemented with minimal review. Considering the potential implications of research investigations to park managers, local park officials must be more fully involved in the evaluation of research priorities. In addition to local park officials, this review process requires involvement of local NPS scientists and qualified experts from outside NPS.

The considerable demands placed on personnel by the needs of research and monitoring projects should be realized in any future discussion of needs and setting of priorities by staff of SAGU. Park managers must take the lead in identifying potentially important research areas through greater cooperation with a strengthened local NPS research unit and non-NPS scientists. A greater use of local "think-tanks" organized by park managers that include NPS and other scientists could provide valuable guidance in the pursuit of various research goals. A greater amount of involvement of the scientific community in matters ranging from initial evaluations of research concerns to more widespread and open notification of requests for research proposals would contribute greatly to the credibility and quality of NPS research efforts.

DISPOSITION OF LONG-TERM ECOLOGICAL MONITORING RECORDS

Recent monitoring efforts at SAGU have involved the collection of considerable baseline data that must be preserved and made available to researchers and managers in the future. For example, the complete set of original data on each of the 45 saguaro trend plots established by

Duriscoe and Graban (1992) will become increasingly valuable 25, 50, and 100 years from now as saguaros in those plots mature and age. The summaries of these data published in internal reports or formal publications will not serve the needs of scientists in the future, who will require the complete set of data in order to examine the future of individual plants within plots. However, the care and management of this valuable original data by NPS has been inadequate.

Without more care given to the preservation of valuable monitoring records such as these, considerable future research opportunity will be lost along with the expense and effort involved. Preservation of these records must involve both long-term archiving and storage of multiple copies in locations and on media that are accessible to scientists. Wherever studies are initiated, complete copies of all data obtained in any project involving saguaros must be on file at SAGU. Storage of data should include working paper copies and perhaps other easily retrieved media such as microfilm for archival storage. Additional archival copies should be stored in regional NPS repositories such as the one at the NPS Western Archeological and Conservation Center in Tucson.

Data records may be commonly submitted by investigators on machine-readable media such as microcomputer diskettes. However, it is important that such information be immediately transferred to acid-free paper copy and other media for archival storage. The rapidity with which existing computer technology becomes obsolete has made it impossible to retrieve some records stored solely on computers a mere three decades ago. This serious problem has been experienced with records of the US Census Bureau (Cobb 1986) and some of the earliest LANDSAT imagery data stored in the 1960s on antiquated computer tapes for which machines no longer exist that could retrieve the stored information. The original data collected from the saguaro trend plots at SAGU will have considerable value 50 and 100 years from now. If the pace at which computer technology has developed over the last 30 years is any indication, information stored today only on microcomputer diskettes may be difficult or impossible to retrieve 50 years from now.

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