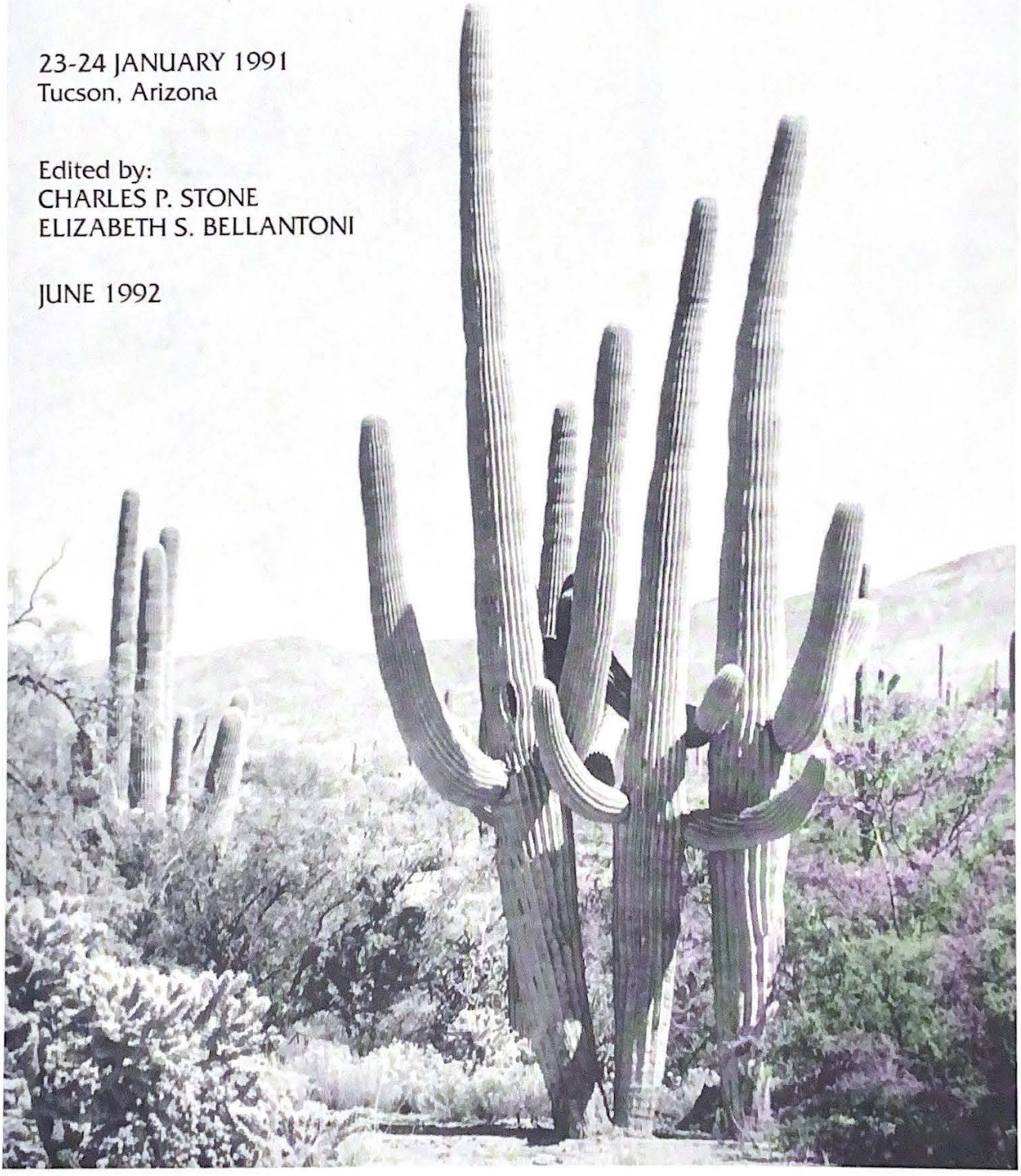
Proceedings of the Symposium on Research in Saguaro National Monument

23-24 JANUARY 1991
Tucson, Arizona

Edited by:
CHARLES P. STONE
ELIZABETH S. BELLANTONI

JUNE 1992



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Foreword

"The outstanding scientific discovery of the twentieth century is not television or radio, but rather the complexity of the land organism. Only those who know the most about it can appreciate how little we know about it."

—Aldo Leopold

The first-ever Symposium on Research in Saguaro National Monument (SNM) could not have taken place without the creativity, dedication and hard work of several people. Dr. Denny Fenn, past Unit Leader of the Cooperative National Park Resources Studies Unit at the University of Arizona (CPSU/UA) and Dr. Robert L. Hall, retired Chief of Resources Management at SNM, were key individuals in initiating and laying out the framework for this event. Dr. Chuck Stone, Acting Unit Leader at the CPSU/UA; Liz Bellantoni, Acting Chief of Science and Resource Management at Saguaro; and Joan Ford who has kept literally dozens of researchers and parks organized and informed in her position at the CPSU/UA, have done a superb job of fleshing out that framework. The financial assistance of our old friends at the Southwest Parks and Monuments Association (SPMA) and our new friends at the Rincon Institute have provided the opportunity to host this symposium and publish the proceedings of this special event.

The idea of a national park system has been called, next to democracy, America's greatest contribution to world culture. That contribution has resulted in preservation of natural and cultural resources for all time, resources that are made available for public enjoyment, inspiration, study, and the renewal of succeeding generations. National parks are our continuing experiment of respect for our past, self-control during the present, and hope for our future. Drawing origins from the romantic movement of the early 19th century, the national park idea has matured into a system of over 354 National Park Service (NPS) areas and has been imitated by dozens of countries throughout the world.

We commemorate the idea and reaffirm our commitment to the experiment yet again as we celebrate the 75th Anniversary of the National Park Service - the agency charged with promoting and perpetuating the national park idea. And I believe that it is particularly appropriate that a research symposium is our "showcase" 75th Anniversary celebration activity at Saguaro National Monument.

Parks have long been recognized as valuable "living laboratories" and used as such by independent researchers working to advance scientific knowledge about our environment. Many of the studies described in this volume were conducted by individuals who received no monetary support from the NPS.

Research to improve or facilitate park management is not new to the NPS, but recognition of its importance to sound decision making, effective resource protection, quality interpretive programs, and sensitive design and construction practices,

increased dramatically with the formal translation of the Leopold Report recommendations into NPS policy in 1968. The importance of research continues to grow at an increasing rate in a rapidly changing world.

In the decade of the 1980s, research activities at SNM progressed with the appearance of what I call "partnership research endeavors". Issues such as air quality and adjacent land use concerns cannot be studied exclusively within the boundaries of the monument and cannot be effectively addressed exclusively within the jurisdiction of the NPS. Partnerships in which several agencies or jurisdictions provide funding or in-kind support either have been, or are currently being, conducted at SNM with SPMA, Pima County, the City of Tucson, The University of Arizona, the Bureau of Reclamation, and the U.S. Forest Service. Several of the projects described in the pages that follow are the products of a partnership approach.

I believe that even more joint venture research endeavors will be forged during the 1990s. We will continue our efforts with Organ Pipe Cactus National Monument to establish a Sonoran Desert Biogeographical Area for the study of global climate change and its potential impacts. We are presently constructing the foundation of a jointly operated Geographic Information System with the Coronado National Forest. And, we will continue to find opportunities for gathering and sharing information with neighbors ranging from Pima County and the City of Tucson to the international scientific and conservation community. That is a promise!

—Bill Paleck

Bill Paleck is the 15th Superintendent of Saguaro National Monument and has served in that capacity since April 1987. Paleck grew up in Tucson, Arizona and began his career with the National Park Service as a seasonal trail laborer in the Rincon Mountains.

The Rincon Institute is pleased to help fund the publication and distribution of the proceedings of the first Symposium on Research in Saguaro National Monument. Widespread dissemination of the findings and results presented at the symposium is essential to inform not only park managers, but also local government officials, conservation advocates, developers, and owners of adjacent land, whose decisions and actions increasingly have a direct impact on the integrity of Saguaro National Monument (SNM). The general public will also benefit from understandings presented here.

The Rincon Institute itself is a new idea, which promises to become an important asset for promoting research, education, and conservation activities necessary to ensure the long-term integrity of SNM. The institute and its affiliated organization — the Sonoran Institute — were created to address a critical challenge facing those who care about the monument, as well as national parks throughout the country. This challenge is to determine what relationships and activities involving park managers, conservation advocates, local governments, and the development community, will protect national park resources and values and ensure that development occurring adjacent to national parks adheres to the highest ecological, social, and financial standards. While consideration of park resources in the planning and design of nearby development is necessary, planning for park resources alone will not adequately ensure the long-term ecological integrity of national parks and other protected areas.

The Rincon Institute was designed to help protect and enhance the resources of SNM over the long-term, through a succession of home owners over several decades. The institute has entered into an innovative agreement with the owners of the Rocking K Ranch, a private holding that shares a five-mile boundary with the monument. This agreement funds the institute through a start-up grant and long-term deed restrictions that will bind all future landowners and developers on the Rocking K Ranch. The restrictions require that nightly hotel room fees, residential and commercial occupancy fees, real estate transfer fees, and monthly homeowner fees be paid to the institute to support a wide range of conservation activities. This long-term funding mechanism demonstrates that the development process can be guided to provide substantial, permanent, dedicated funds for protecting national parks and other protected natural areas.

The Rincon Institute activities include (1) managing natural open space for educational, scientific, conservation, and outdoor recreational values; (2) providing environmental education and research; and (3) providing professional guidance and oversight for the environmentally sensitive development and management of the Rocking K Ranch and the Rincon Valley.

The Sonoran Institute works nationwide, with special emphasis on the Sonoran Desert, to maintain the integrity of national parks and other protected natural areas by encouraging similar special consideration for park values in adjacent land uses.

The concept of earmarking revenues generated by the development process to fund an independent, non-profit conservation and education organization, is an experiment that challenges both the development and the conservation communities. Many developers now realize that stewardship of ecological resources improves market acceptance; however, some fear creating a Trojan horse that will spur anti-development sentiment. Conservation advocates recognize the value of enforceable conservation commitments to fund wildlife habitat protection, environmental education and research, and guidance for environmentally sensitive development; however, some are suspicious that funding the Rincon Institute is merely a clever ploy to gain public support for inappropriate development.

While it is premature to evaluate the ultimate outcome of this experiment, if success is measured by imitation and widespread interest, early signs indicate considerable success. The Sonoran and Rincon Institutes have already assisted proponents of several similar initiatives around the country.

Publication of this volume is one of the Rincon Institute's first undertakings, and a very appropriate one. The institute is pleased to help publish and distribute the proceedings because the integrity of SNM requires local officials, conservation advocates, developers, and landowners to make resource protection and land use decisions that are sensitive to the monument's resources and needs. These decisions require a strong foundation in scientific knowledge.

—Frank Gregg

Frank Gregg, Chairman of the Board of Directors of the Rincon Institute and Sonoran Institute, is on the faculty of the University of Arizona, School of Renewable Natural Resources. He has served as director of the U.S. Bureau of Land Management and Vice-President of The Conservation Foundation.

For more than 50 years, Southwest Parks and Monuments Association (SPMA) has worked in partnership with national parks in the western United States, donating more than $7 million to their interpretive, educational, and scientific research programs. Southwest Parks and Monuments Association's affiliation with Saguaro National Monument (SNM) began in 1943 and over the years our support has enabled the monument staff to offer a wide range of programs and services that visitors to the monument otherwise might not enjoy.

A growing part of our grants program to national parks is dedicated to funding scientific research. Indeed, several of the papers included in this volume resulted from research grants provided by SPMA to the monument. Scientific research is critically underfunded in many of our western national parks. At a time when park resources are experiencing increased impacts as a result of rising visitation, many parks still lack sufficient baseline data on park resources. Without these data, it is difficult for park managers to assess those impacts and make sound management decisions to ensure the preservation of our national park lands.

Saguaro National Monument presents a unique challenge and many opportunities, with its incredible diversity of landscape and natural resources most certainly affected by continuing growth in the Tucson Basin. Wide-ranging, sensitive partnerships must be forged to provide for its stewardship. To that end, Southwest Parks and Monuments Association was pleased to assist in funding the Symposium on Research in Saguaro National Monument and contribute to its publication.

—Tim Priehs

Tim Priehs has been the Executive Director of the Southwest Parks and Monuments Association for 10 years. Prior to his position at SPMA, Priehs published the interpretive newspaper for Grand Canyon National Park.

I.
Biology of the Saguaro and Closely Associated Species

Long-Term Saguaro Population Studies at Saguaro National Monument

Raymond M. Turner

ABSTRACT

All saguaros *(Carnegiea gigantea)* were mapped and their heights measured on two large permanent plots established at Saguaro National Monument in the early 1960s. These plots have been examined on five subsequent dates. All plant deaths and new plants were recorded on the five later visits. By 1989, when the plots were last examined, 80% of the plants first recorded at the Rincon Mountain District (RMD) plot were dead. During the same period, only 26% of the original Tucson Mountain District (TMD) population had succumbed. Striking as these mortality differences may be, of at least equal significance is the difference in recruitment in recent years. At the RMD plot, 136 new plants are now found and 76% of that population comprises young plants encountered since plot establishment. In contrast, at the TMD plot, 19 new plants occur and only 11% of the population includes plants new since plot establishment.

INTRODUCTION

The dense stand of saguaros (*Carnegiea gigantea*) on the flats at the base of Tanque Verde Ridge, the main rationale for the establishment of Saguaro National Monument (SNM) in 1933, has lost most of the saguaros present at that time. This population was composed of mostly old individuals and the losses experienced were the expected attrition in an aging population. What was not expected during the same half century was the persistent failure of new plant establishments, a phenomenon often noted in recent decades (Steenbergh and Lowe 1983). The forces responsible for the population changes are still uncertain, but may be clarified by continued monitoring of existing plots and establishment of new plots at critical sites elsewhere in the Sonoran Desert.

METHODS

In February 1961, a rectangular area 400 x 1000 ft (9.2 a) was permanently marked at the Rincon Mountain District (RMD) in an area of relatively level terrain between the Cactus Forest Loop Drive and Freeman Road. A similar but smaller area, 320 x 640 ft (4.7 a), was established on the west side of the Tucson Mountains near the intersection of Golden Gate and Sandario roads in July 1962. A surveyor's transit was used to place the corners of the plots and to map the location of all saguaros within their boundaries. Saguaro heights were measured either by use of a telescoping 25-ft fiberglass rod or by measurement with a transit. Since their establishment, these permanent plots have been examined five times at approximately six-year intervals. Subsequent visits were made to the RMD plot in March 1965, January 1973, December 1979, March 1983, and January 1989; and to the Tucson Mountain District (TMD) plot in July 1965, July 1973, January 1980, April 1983, and January 1989. At each visit, using the maps as guides, new plant heights were measured and the plots were examined for saguaro losses and additions since the previous visit.

RESULTS

Rincon Mountain District Plot

The saguaro population of 1961 has declined steadily to the present. Of the 210 plants (22.8 plants/a) found that year, only 42 (20%) remained in 1989 (Table 1). No new plants were seen until the visits of 1979, 1983, and 1989 when 13, 12, and 115 plants were located. The last value is perhaps 50% too low because a heavy growth of the grass, *Muhlenbergia porteri*, has developed beneath the desert-tree canopies, hiding the new saguaros, which grow mainly in these microhabitats.

Additional information concerning this group of plants can be obtained by examining the distribution of plant heights (Fig. 1). In 1961, few plants <10 ft tall existed and few existed in the classes from 10-18 ft and in those >30 ft. Height frequencies of the 208 measurable saguaros (strongly leaning plants or those with broken tops are excluded from this table) reached maximum values between 18 and 30 ft, corresponding roughly to ages of 60 to 100 years (Steenbergh and Lowe 1983: Tables 2-10). Thus, the period between 1860 and 1900 appears to be one of robust saguaro establishment, while that from 1900 to 1961, was one of little population augmentation.

At the time of the 1989 examination, the height distribution was strongly skewed toward smaller plants (Fig. 2). As most of the old plants had died, little information remained regarding population composition during the 1860-1900 era. By converting the individual height values to age (Steenbergh and Lowe 1983: Tables 2-10), additional information can be obtained for the timing of new plant establishments. Accordingly, all plants ≤8 ft were grouped by estimated year of establishment (Fig. 3). The histogram shows that during the period from about 1950 to 1988, surviving plants originated mainly between the years of 1962 and 1983. The decrease in numbers of plants assigned to 1976 is noteworthy. The difficulty of finding plants in the field shorter than about 0.1 ft makes the graph segment from about 1983 to 1988 unreliable.

Tucson Mountain District Plot

The 1962 population at this site declined much less abruptly than did its counterpart at the RMD. The 205 plants (43.6 plants/a) first measured in 1962 had decreased to only 152 (74%) by 1989 (Table 2). Comparison of the 1962 and 1988 height-class histograms (Figs. 4 and 5) shows the expected loss of plants in the taller height classes and a moderate recruitment pulse by the relatively large number of plants in the 1-ft class. Interestingly, mortality among the larger plants has not been as great here as at the RMD plot. Mortality differences occurred in spite of initially similar numbers of old plants in the two plots. The height classes from 14 to 29 ft on the 1962 histogram (Fig. 4), singled out because of the higher frequency values they include, represent survivors that became established between about 1850 and 1895 (Steenbergh and Lowe 1983: Tables 2-11). This period of apparent peak establishment is similar to that noted earlier for the RMD plot.

DISCUSSION

Population structure of the two plots at the beginning of this study was similar in that there were relatively many tall (old) plants and there were too few small (young) plants to ensure maintenance of the two populations through time. Although both plots have experienced a greatly increased rate of recruitment in the last decade or so, the new establishments at the RMD plot are far greater than those at the TMD plot. The enhanced establishment at the RMD is probably attributable in part to domestic livestock exclusion, which began there in 1958, and in part to local habitat factors favoring greater seedling establishment there than in the TMD plot, which has been livestock-free since 1929.

Of special note is the large difference in mortality rates among the large plants in the two plots. Although not quantified for this paper, it is clear from comparison of Figures 2 and 5 that mortality since the early 1960s among plants taller than about 17 ft has been far greater at the RMD plot than at the TMD plot. The cause of this mortality difference is unknown but habitat factors with greater impact at the eastern unit than at the western (e.g., catastrophic freezes, air pollution) should be examined. If the greater mortality rate of old saguaros at RMD persists, the disparately large recruitment there may well be nullified by the effects of the greater mortality rate in the maturing population.

What caused the sharp reduction in number of survivors among plants germinating in 1976? Loss from catastrophic freezes is unlikely because the most

severe freezes for the 1951-1988 period occurred in January 1962, January 1971, and December 1978. Drought is strongly implicated as the cause for the one year decline in establishment, as seen by Palmer Drought Severity Index values for Tucson during the period 1900-1980 (Goldberg and Turner 1986). The drought of 1976 was clearly the most severe of that 80-year period.

The presence of large numbers of plants established between 1870 and 1900, at both the SNM plots and at widely scattered localities within the plant's range, suggests that some large-scale force may be shaping these populations. Because of the importance of July-August rainfall to the germination of short-lived saguaro seeds, fluctuations in precipitation for these two months could be a factor in determining saguaro establishment. Indeed, the frequency of large amounts of summer rain was greater during the 1870-1900 period than during the years since (Betancourt 1990). Attempts to understand population dynamics within the monument must clearly encompass studies far beyond national park boundaries.

MANAGEMENT IMPLICATIONS

In recent months, the National Park Service (NPS) has established several permanent saguaro study plots in the monument. The importance of permanently marking these plots and continued monitoring at 5-year intervals is clear. The new plots, in addition to those reported on here, should eventually become part of the same data source to maximize the efficient, consistent treatment and utility of the data. Implementing this plan requires a commitment to long-term research by the NPS.

The time is upon us when the saguaro forest traversed by the Cactus Forest Loop Drive will have no more than a handful of large plants. The forest of giant cacti without cactus giants that was predicted for the year 2000 by Alcorn and May (1962) affords a rich opportunity to teach monument visitors many intriguing lessons about the ecology of our region. The numerous studies conducted at the monument provide an excellent foundation for landscape interpretation by NPS personnel. Challenging indeed is the prospect of turning the once highly acclaimed cactus "forest" into something the public will want to cross the continent or city to see. What is becoming an unphotogenic scrubland can continue as the main attraction for visitors to the RMD, if the phenomenal population surge of new saguaros is emphasized.

ACKNOWLEDGMENTS

As the keeper of records for this long-term study, I am also the project's nominal historian and scribe, and have had the pleasure of giving each participant, living and dead, grateful recognition for valuable contributions to this effort. With many pleasant memories, I have lifted from the archives the following names: Al Macias, Kirk McDonald, Lyle Warner, Doug Warren, and Terry Gustafson. More recent contributors giving freely of their time and talents have been Marshall Moss, Bobbi Simpson, Bud Simons, and Fred Houser. My esteemed colleagues, Jan Bowers and Tony Burgess, require separate recognition for their capable contributions to many aspects of this work. To all of these, my many thanks and the promise that this is just the beginning. Worthy of special but, unhappily, posthumous due is Rod Hastings, who was co-investigator during the early years of the study. My wife, Jeanne, who has assisted in the field, at the computer console, and in ways both subtle and direct, is due more credit than she will probably accept for successful completion of the initial three decades of this study-without-end.

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Table 1. Survivorship of saguaros at Rincon Mountain District plot, Saguaro National Monument.

	Population totals by year first observed					
	1961	1965	1973	1979	1983	1989
1961	210	175	126	88	75	42
1965		0	0	0	0	0
1973			0	0	0	0
1979				13	13	10
1983					12	11
1989						115
Totals	210	175	126	101	100	178

Table 2. Survivorship of saguaros at Tucson Mountain District plot, Saguaro National Monument.

	Population totals by year first observed					
	1962	1965	1973	1980	1983	1989
1962	205	200	183	172	163	152
1965		0	0	0	0	0
1973			2	2	2	2
1980				2	2	2
1983					2	2
1989						13
Totals	205	200	185	176	169	171

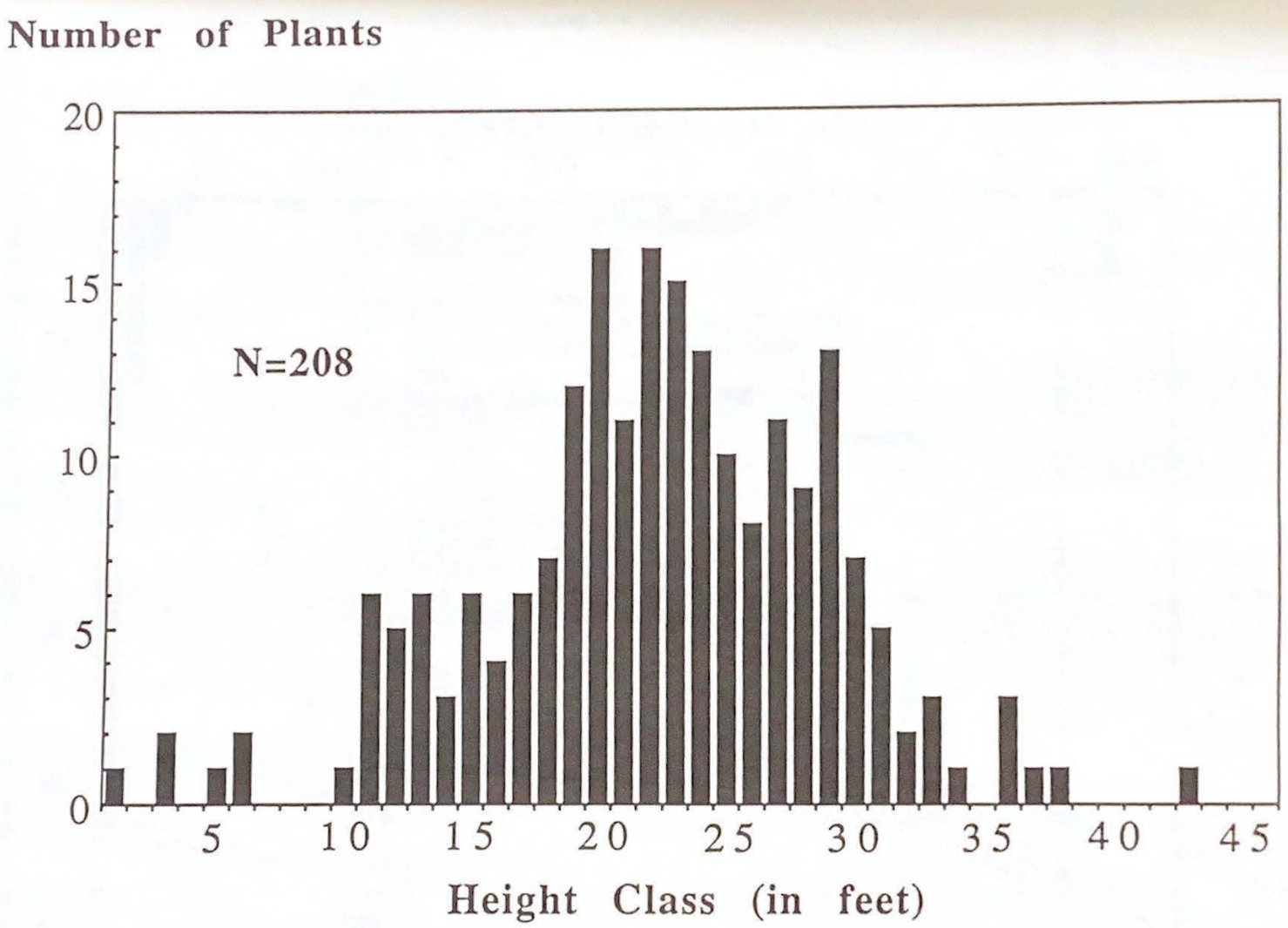


Fig. 1. Height-class frequency of saguaros at end of 1961 growth year, Rincon Mountain District plot, Saguaro National Monument.

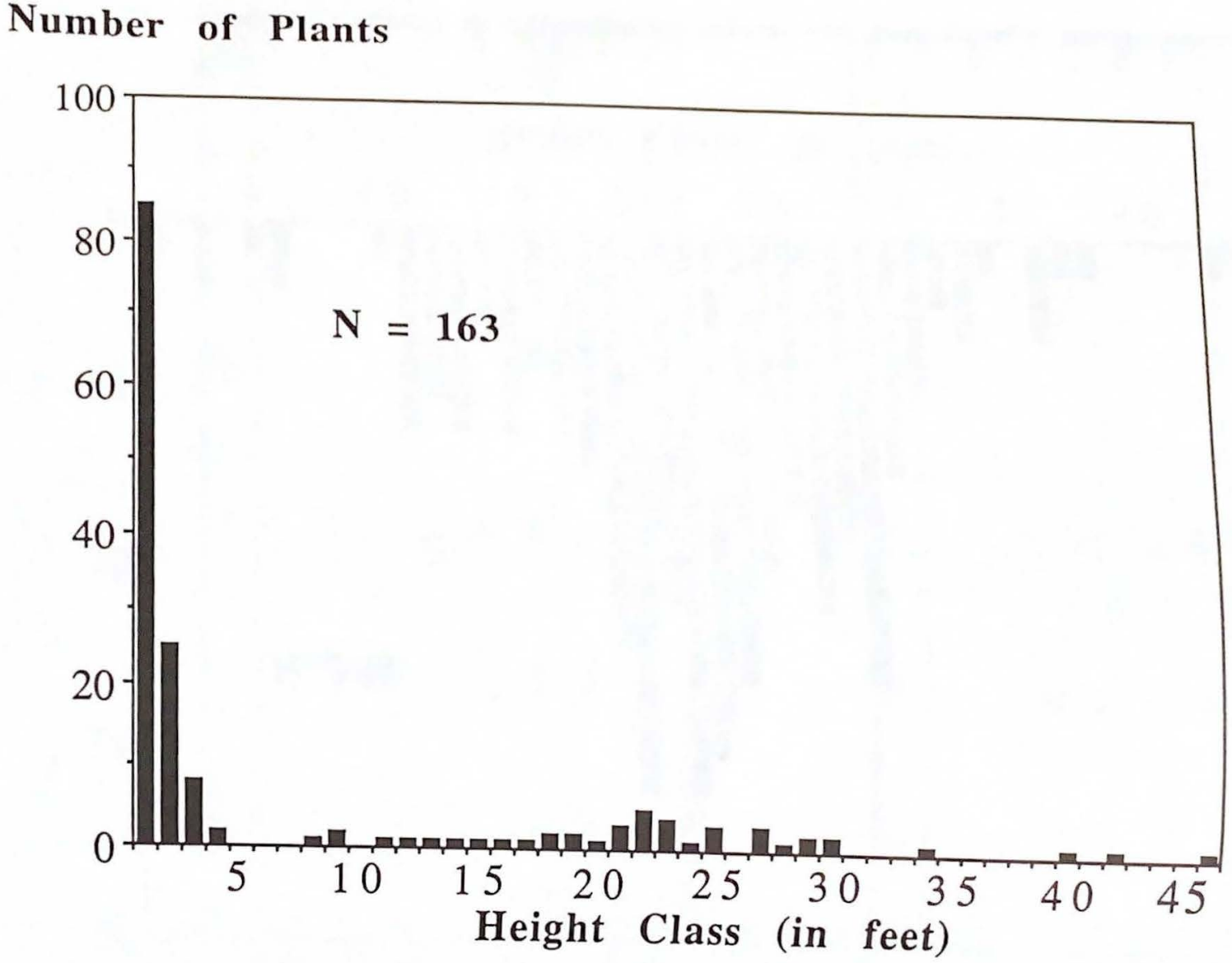


Fig. 2. Height-class frequency of saguaros at end of 1988 growth year, *Rincon Mountain District plot, Saguaro National Monument.*

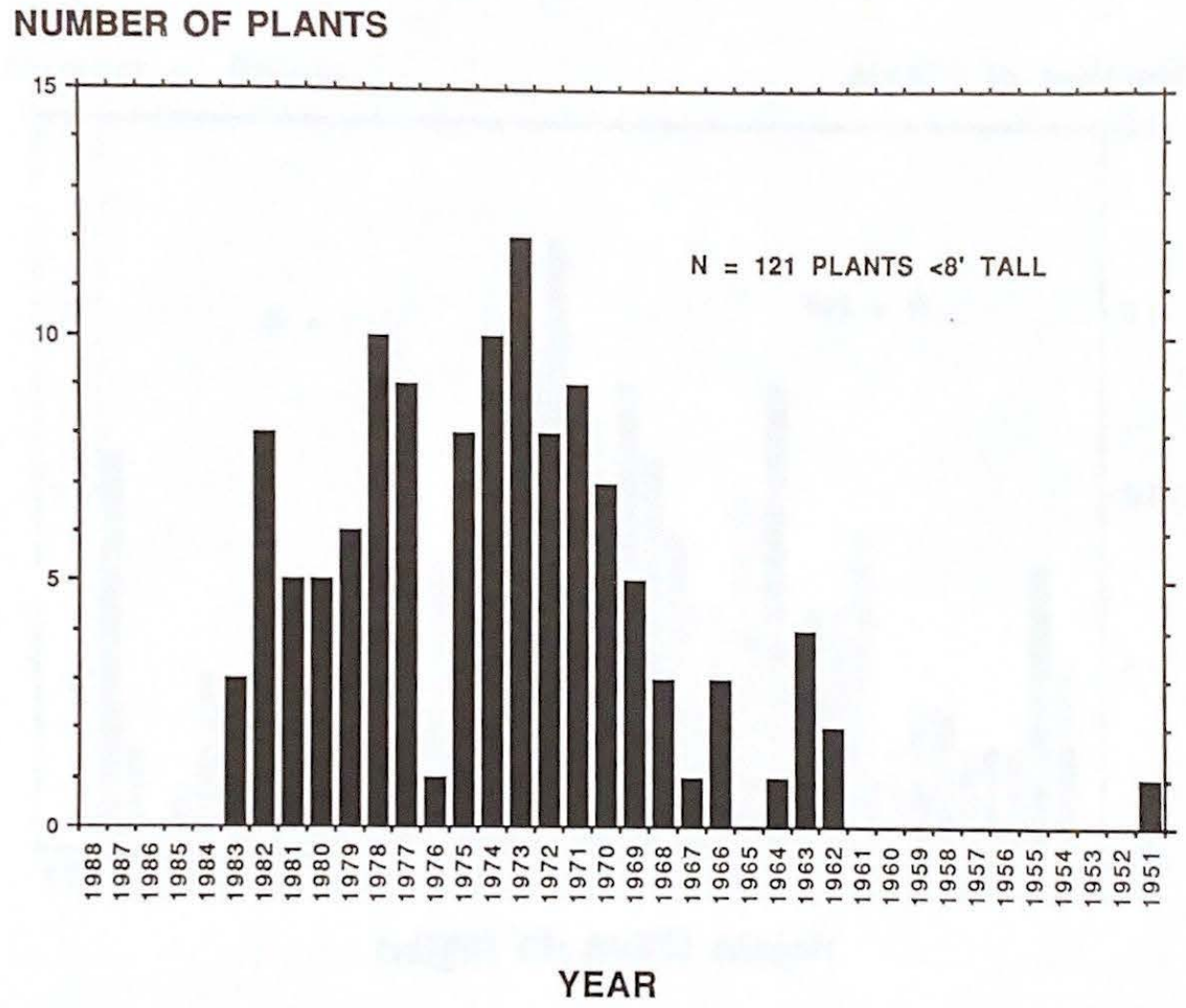


Fig. 3. Age-class frequency of saguaros by year, for plants ≤8 ft at end of 1988 growth year, Rincon Mountain District plot, Saguaro National Monument.

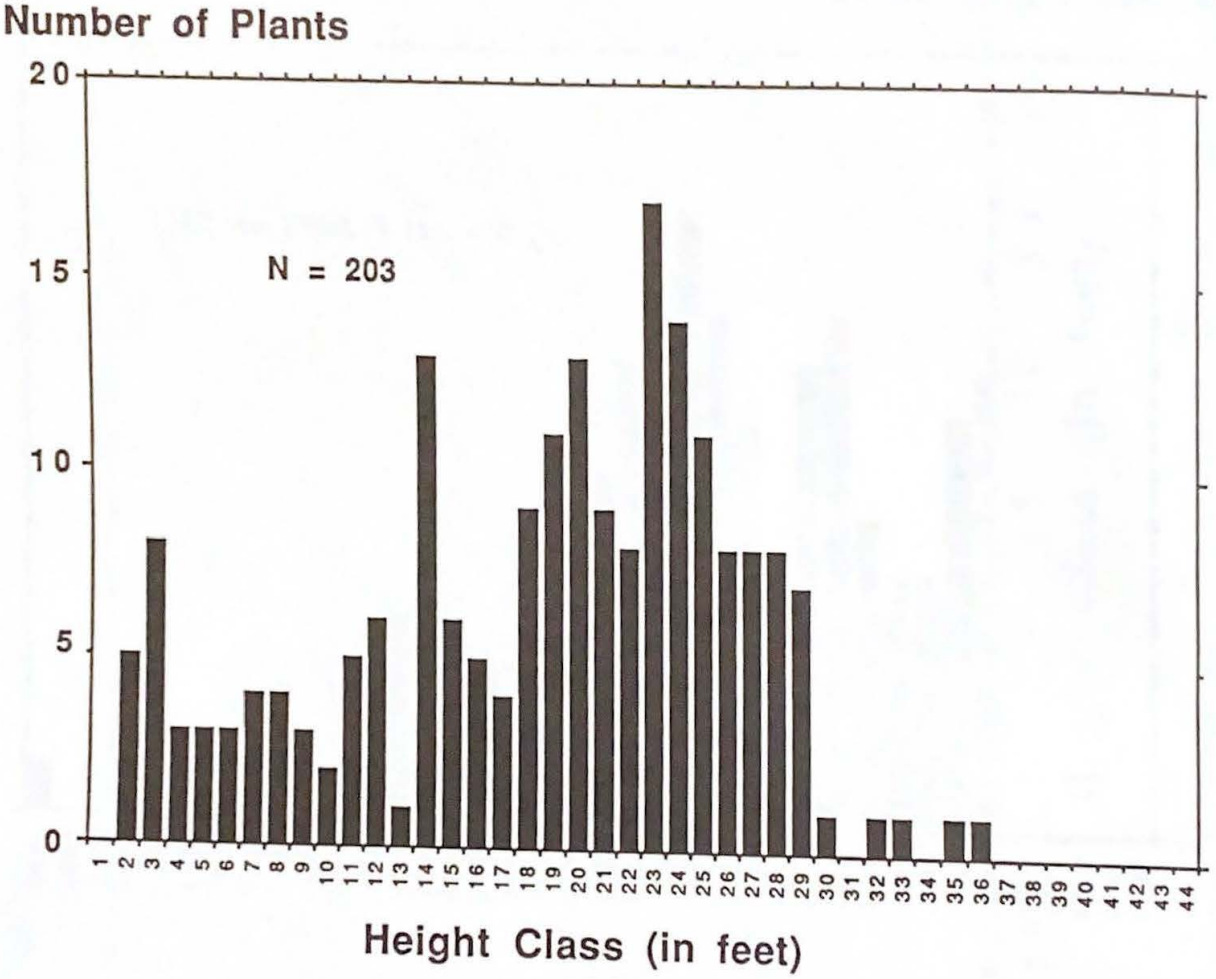


Fig. 4. Height-class frequency of saguaros at end of 1962 growth year, Tucson Mountain District plot, Saguaro National Monument.

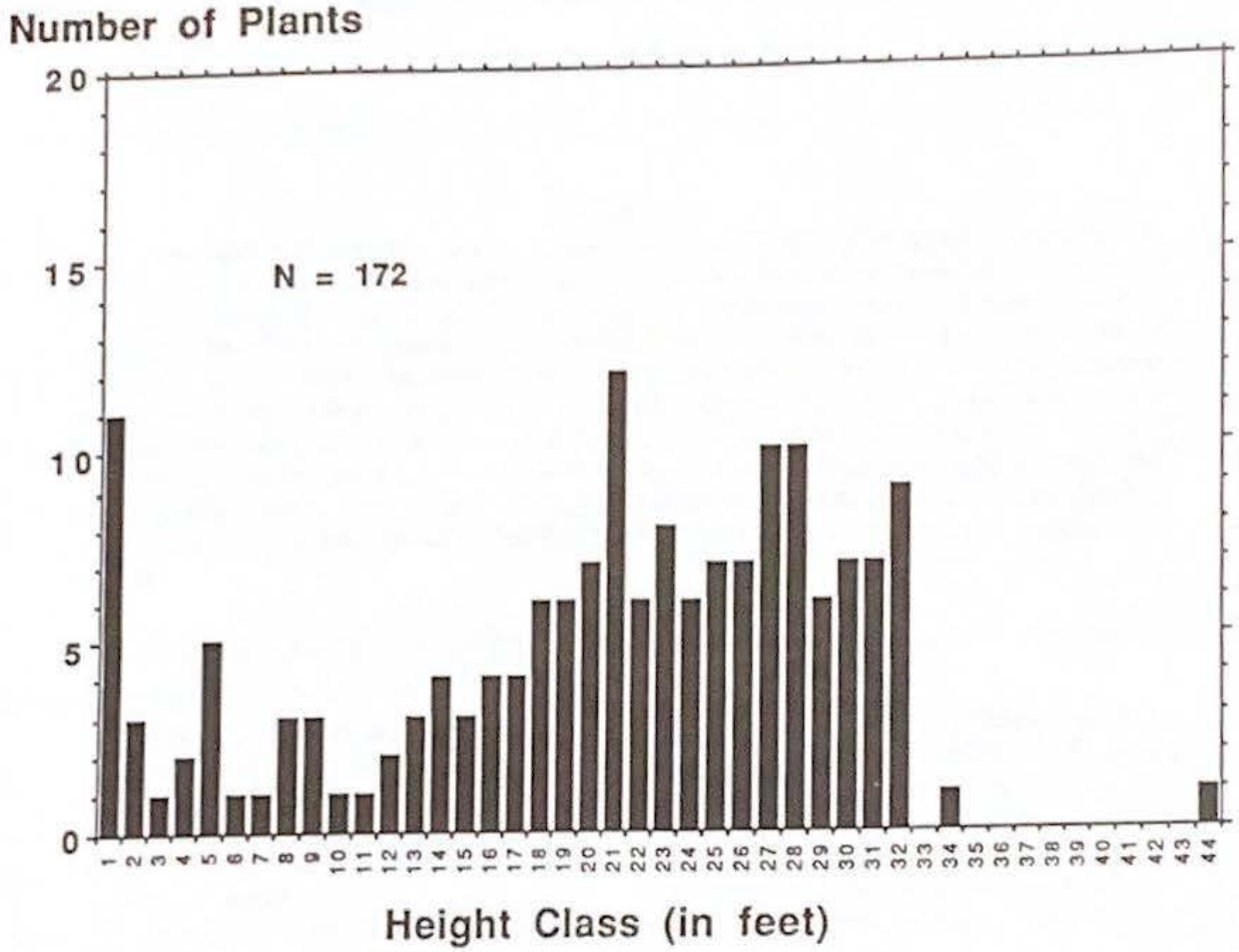


Fig. 5. Height-class frequency of saguaros at end of 1988 growth year, Tucson Mountain District plot, Saguaro National Monument.

Demographic Patterns of Saguaro and Fish-Hook Barrel Cactus Populations in the Cactus Forest of Saguaro National Monument

Thomas Helbsing and Nicole Fischer

ABSTRACT

Natural populations of saguaro (*Carnegiea gigantea*) and fish-hook barrel cactus (*Ferocactus wislizenii*) were studied in the Cactus Forest (Rincon Mountain District) of Saguaro National Monument. On two sampling sites, density, age and/or height distribution, presence or absence of nurse plants, and plant vitality characteristics were recorded. Densities of the barrel cactus stands were 6.2 individuals/1000 m^2 and 6.4 individuals/1000 m^2. Saguaro densities were 5.7 individuals/1000 m^2 and 5.9 individuals/1000 m^2. An unexpectedly large number of very small saguaros was found in this winter-cold habitat: whereas 77.1% of the plants were younger than 20 years on one study site, 84.7% belonged to the youngest age class (0-20 years) on another. All juvenile saguaros were located beneath nurse plants. Regeneration of this once outstanding saguaro population seems possible, provided that all activities adversely affecting the vegetation (e.g., cattle grazing) continue to be excluded.

INTRODUCTION

During the past few years, numerous studies dealing with the ecology of desert succulents have been published (Nobel 1988). Whereas many investigations are focused on such economically important species as certain agaves and prickly pears, a considerable number of papers have been devoted to saguaro (*Carnegiea gigantea*) ecology (Alcorn and May 1962; Niering et al. 1963; Turner et al. 1966, 1969; Steenbergh and Lowe 1969, 1976, 1977, 1983; Soule and Lowe 1970; Brum 1973; Nobel 1980*a*,*b*, 1988; Jordan and Nobel 1982; Helbsing and Kreeb 1985; Helbsing 1989). The dramatic decline of the saguaro population in the Cactus Forest has been of particular interest to environmental scientists. Until now, very different hypotheses dealing with the causes of the population decline have been proposed (Alcorn and May 1962; Niering et al. 1963; Hastings and Turner 1965; Turner et al. 1969; Steenbergh and Lowe 1983). Little is known about the ecology of another large Sonoran cactus, fish-hook barrel cactus (*Ferocactus wislizenii*). In this study, we report on demographic patterns of saguaro and fish-hook barrel cactus in a habitat previously exposed to the impacts of livestock grazing and low temperature stress.

METHODS

Natural populations of the saguaro and fish-hook barrel cactus were investigated in the Sonoran Desert near Tucson, Arizona. Study sites were located in the Cactus Forest (Rincon Mountain District [RMD]) of Saguaro National Monument (SNM). Due to the proximity of two major mountain ranges (Santa Catalina Mountains to the north, Rincon Mountains

to the east), annual precipitation is fairly high in the Cactus Forest ($\bar{x}$ = 312 mm/yr) and winter freezes are common (Steenbergh and Lowe 1977, 1983). Compared with the Tucson Mountain District (TMD) of SNM, the RMD can be regarded as more winter-cold and less arid. Livestock grazing continued even after establishment of the monument in 1933. In the Cactus Forest, grazing ceased in 1958, whereas other portions of the monument were grazed until 1984 (Shelton 1985).

Two study plots were established in the Cactus Forest in 1988 and 1990. Plot I (established in 1988) comprised 0.84 ha and consisted of 21 contiguous 20 x 20 m subplots. Plot II (established in 1990) covered 1.0 ha, and consisted of 25 contiguous 20 x 20 m subplots. For density determinations all saguaro and barrel cacti occurring on the two sampling sites were censused. Special care was taken to detect juvenile individuals, often hidden by other plants and detritus and thus rarely observed in the field. Morphological parameters such as plant heights and diameters were recorded for each plant. Saguaro age classes were based on growth data reported by Steenbergh and Lowe (1983). Plant vitality characteristics such as observable current growth activity, turgescence (swelling) and spination were determined. Freezing damage was identified by stem constrictions indicating previous damage to the apical meristems or by necrotic lesions of the stems (Steenbergh and Lowe 1976, 1983). Presence or absence of nurse plants or rocks was also recorded.

RESULTS

Fish-hook Barrel Cactus

Within the two sampling sites, 52 (plot I) and 64 (plot II) barrel cacti were found, comprising densities of 6.19 individuals/1000 m^2 on plot I and 6.4 individuals/1000 m^2 on plot II. Height distributions of barrel cacti are shown in Figures 1 and 2. On both plots, the barrel cactus populations included numerous small and intermediate-sized plants, with 86.5% of the barrel cacti measuring less than 50 cm in plot I (Fig. 1), and 84.4% in plot II (Fig. 2). Plants of the smallest size classes were most abundant in plot II: 22 individuals measured less than 10 cm in height. Only a small proportion of old plants was found in either plot. The largest barrel cactus, a vigorous specimen measuring 174 cm in 1988, was dead in 1990. Of the barrel cacti investigated in 1988, 61.5% were located beneath nurse plants; in 1990, 65.6% were sheltered by nurse plants.

Saguaro Cactus

Within plot I, 48 saguaros were found in 1988, and population density was 5.71 individuals/1000 m^2. Forty-four of 48 plants were younger than 40 years, 37 individuals being younger than 20 years (Fig. 3). Thus, 77.1% belonged to the youngest age class (0-20 years). Based on the growth rates that Steenbergh and Lowe (1983) observed in the Cactus Forest, the age of the four saguaros taller than 5 m was more than 60 years (Fig. 3). Height distribution of plants measuring less than 250 cm is shown in Figure 4: 23 of 44 juvenile plants were smaller than 20 cm. Only a few juvenile plants were taller than 50 cm. In this winter-cold habitat, 45 of 48 saguaros were recorded beneath nurse plants, mainly mesquite (*Prosopis juliflora*) and foothill paloverde (*Cercidium microphyllum*). No juvenile saguaros were found in exposed microhabitats. Although 32 giant cacti showed no signs of freezing damage, non-lethal freezing injuries were apparent on 10 plants. Lethal freezing damage was observed on six saguaros with turgor losses, necrotic lesions and blackish apical meristems. Whereas three freeze-killed plants were located beneath nurse trees, the remaining three were recorded in exposed microhabitats. Since 59 saguaros were found on the 1.0-ha plot established in 1990 (plot II), the density of the saguaro stand was 5.9 individuals/1000 m^2. On this study site the proportion of very young plants was even greater than in plot I: 50 of 59 saguaros (84.7%) were younger than 20 years (Fig. 5) and 38 (64.4%) were younger than 10 years. Only 5 of 59 saguaros were older than 60 years.

Height distribution of young plants measuring up to 250 cm is shown in Figure 6: 43 of 52 juvenile saguaros (82.7%) were smaller than 10 cm and 35 saguaros measured less than 5 cm. Juvenile saguaros of intermediate height were very scarce: only 2 of 52 juvenile plants were taller than 40 cm (Fig. 6). All juvenile plants were located beneath nurse plants, often hidden completely by grass. Seven adult saguaros were found in exposed microhabitats. Lethal freezing damage was apparent in one old saguaro and non-lethal freezing damage could be observed in 13 plants. Forty-five saguaros showed no signs of freezing damage.

DISCUSSION

Investigations of population structures of barrel and saguaro cactus in the Cactus Forest revealed that both populations are dominated by young plants with only a small proportion of old individuals. The saguaro population, once the main attraction of the monument, is now an unimpressive stand of scattered, senescent plants. Only nine saguaros taller than 5 m were found within the 1.84-ha study site. Freezing damage such as drooping branches is apparent in many of the older cacti (Steenbergh and Lowe 1983), reinforcing the impression of a dying population. Extinction was predicted for this population by the end of this century (Alcorn and May 1962).

Catastrophic freezes, occurring sporadically in winter-cold habitats like SNM, have killed numerous giant cacti since the establishment of the monument in 1933 (Steenbergh and Lowe 1969, 1976, 1977, 1983). In the Cactus Forest, the devastating effects of sub-freezing temperatures are intensified by increased water availability due to fairly high yearly precipitation. Saguaros maintain water uptake during the winter rainy season in spite of low temperatures (Steenbergh and Lowe 1977), so osmotic concentrations parallel an increase in water availability (Soule and Lowe 1970). Thus, plants inhabiting the coldest and least arid sites show lower osmotic concentrations than plants in more arid and warmer environments (Soule and Lowe 1970). This is of particular importance because increased osmotic pressures are correlated with greater tolerances of low temperatures (Helbsing 1989). In laboratory experiments, all well-watered juvenile saguaros were killed by a temperature of -9° C applied for one night. After a 19-week drought, all plants survived the same temperature without any damage. Half of the droughted plants, with osmotic potentials ranging from -0.92MPa to -1.1MPa, survived nighttime temperatures of -10° C without injury (Helbsing 1989). Field observations support these findings: highest freezing mortality rates were recorded in freeze-exposed habitats with improved water availability (Steenbergh and Lowe 1976, 1977, 1983). Thus, in the Cactus Forest winter survival of seedlings is restricted to protected microhabitats created by nurse plants. Prior to 1958, however, the nurse plant cover had been reduced markedly due to grazing (Niering et al. 1963; Shelton 1985), causing the loss of innumerable microhabitats suitable for seedling establishment.

The long recognized absence of saguaro reproduction in the Cactus Forest could be due to interactions of grazing-caused degradation of the vegetation and low temperature stress. Age and height distribution of saguaros in our study plots strongly support this assumption, with an unexpectedly large number of very small plants found beneath the regenerating nurse plant cover. The termination of cattle grazing in 1958 and the recommencement of successful saguaro reproduction show a striking coincidence.

The height distribution of the barrel cactus population shows a similar pattern. Whereas only few large (old) plants were found, small individuals were located in increasing numbers. Turner et al. (1966) hypothesized that non-reproducing saguaro stands would not recover until the nurse plant cover was restored; we agree with this hypothesis. Regeneration of nurse plants occurring since the elimination of cattle grazing (Steenbergh and Lowe 1977, 1983) has been accompanied by increasing rates of germination and establishment of saguaro and barrel cacti. Hence, regeneration of the saguaro stand in the Cactus Forest seems possible, provided that this area is kept under protection.

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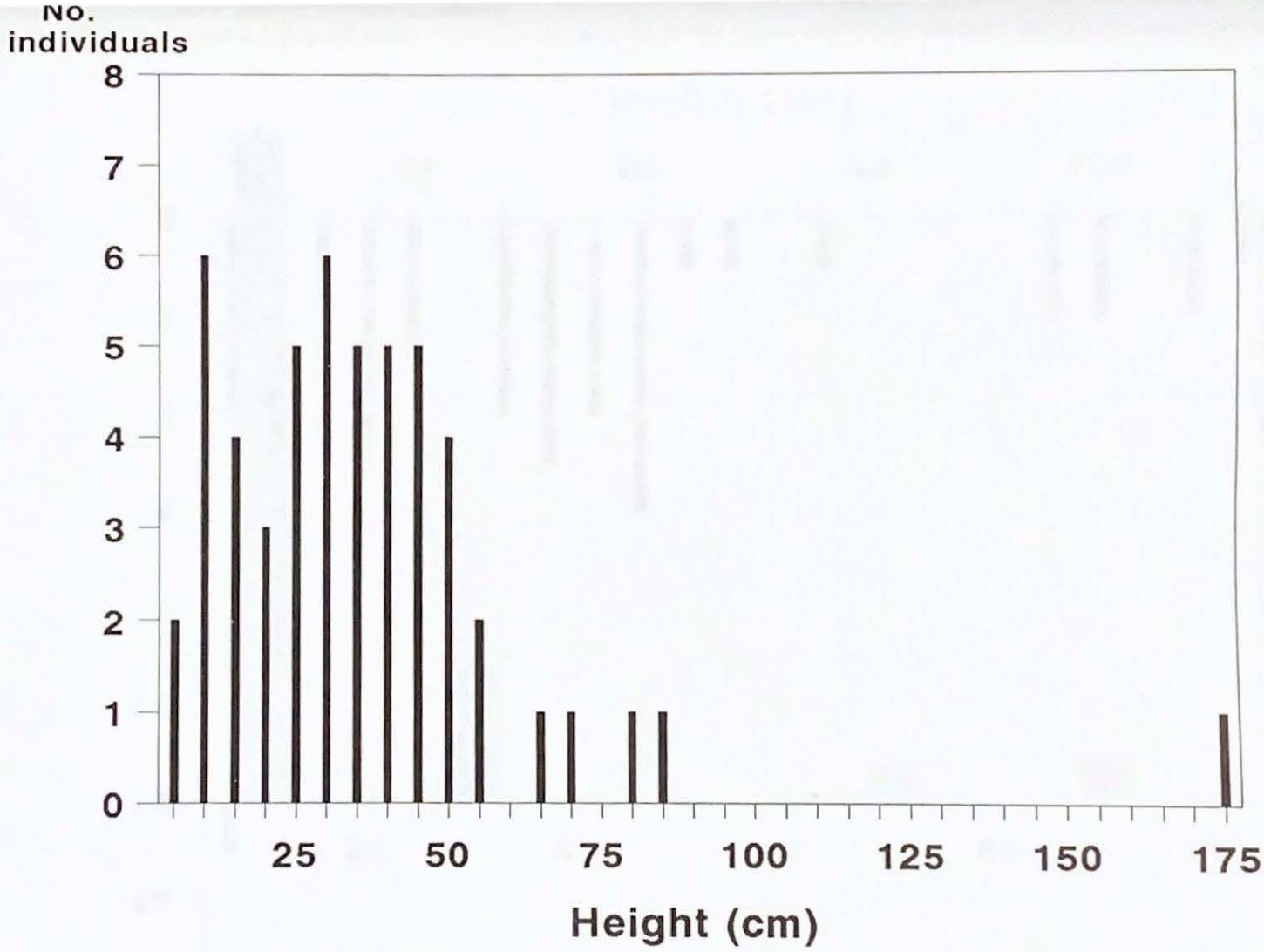


Fig. 1. Height distribution of fish-hook barrel cactus (n = 52) by 5-cm height classes on a 0.84-ha sampling site (Plot I) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

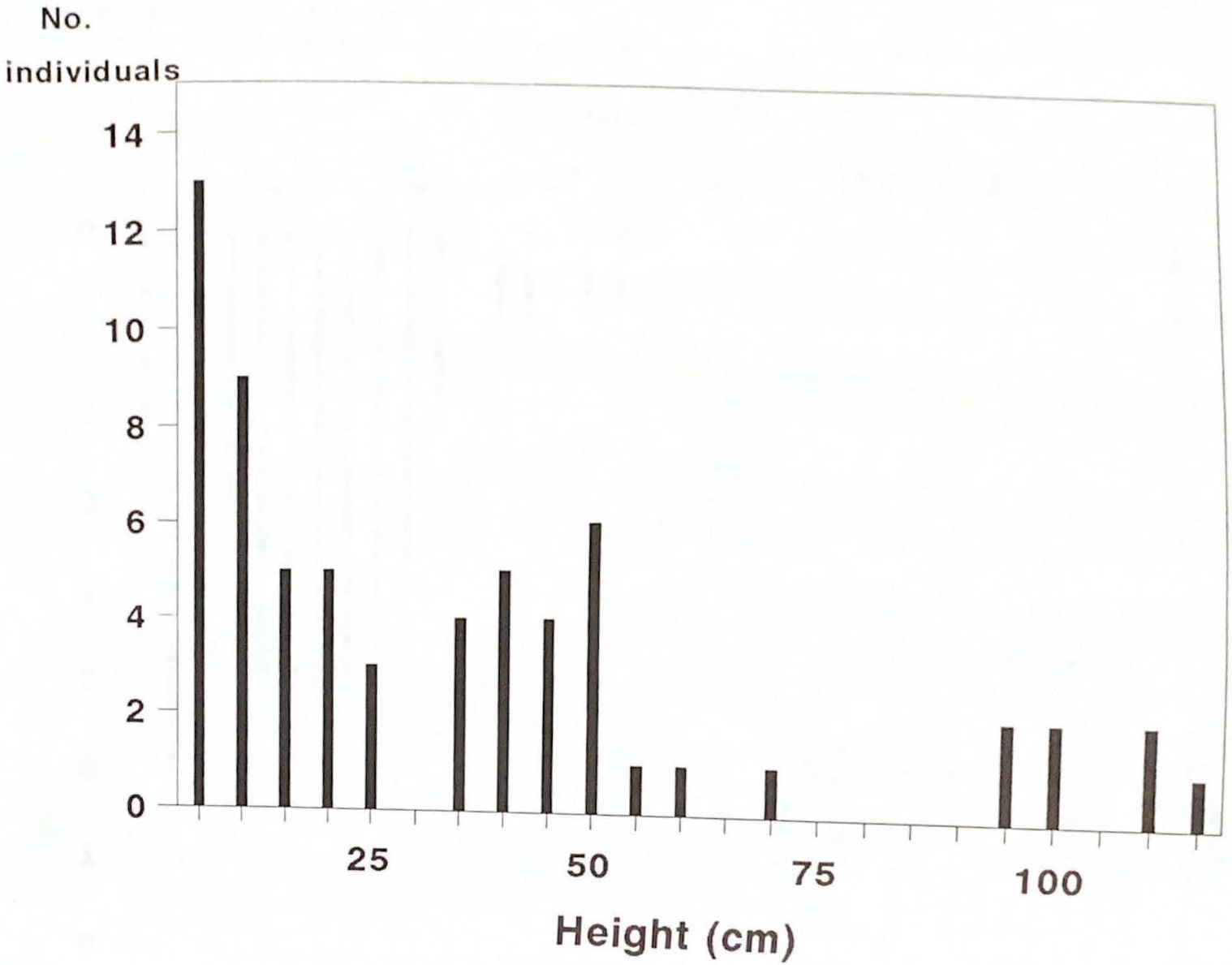


Fig. 2. Height distribution of fish-hook barrel cactus (n = 64) by 5-cm height classes on a 1.0-ha sampling site (Plot II) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

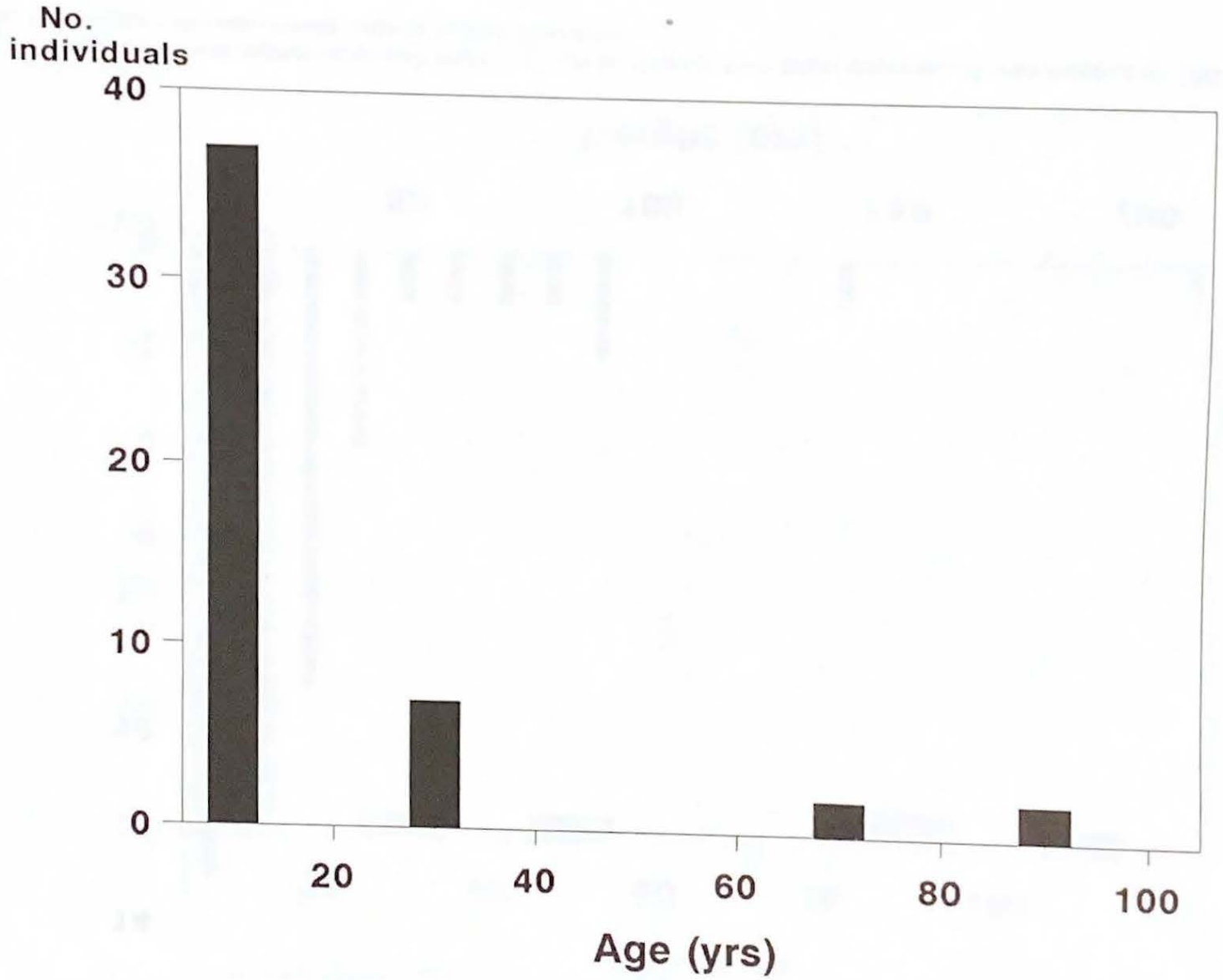


Fig. 3. Age distribution of saguaro cactus (n = 48) by 20-year age classes on a 0.84-ha sampling site (Plot I) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

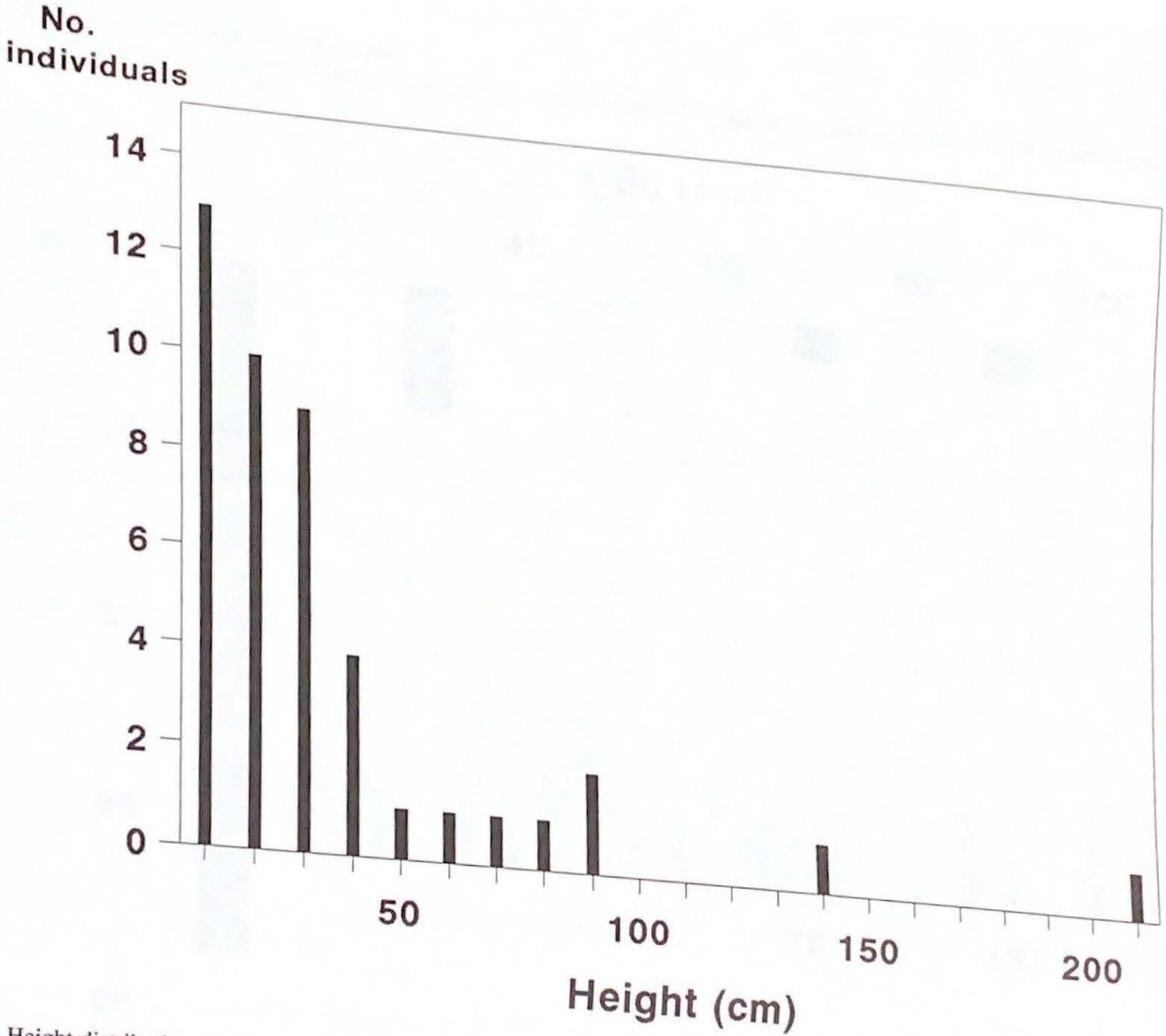


Fig. 4. Height distribution of saguaro cactus with heights <250 cm by 10-cm ($n = 44$) height classes on a 0.84-ha sampling site (Plot I) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

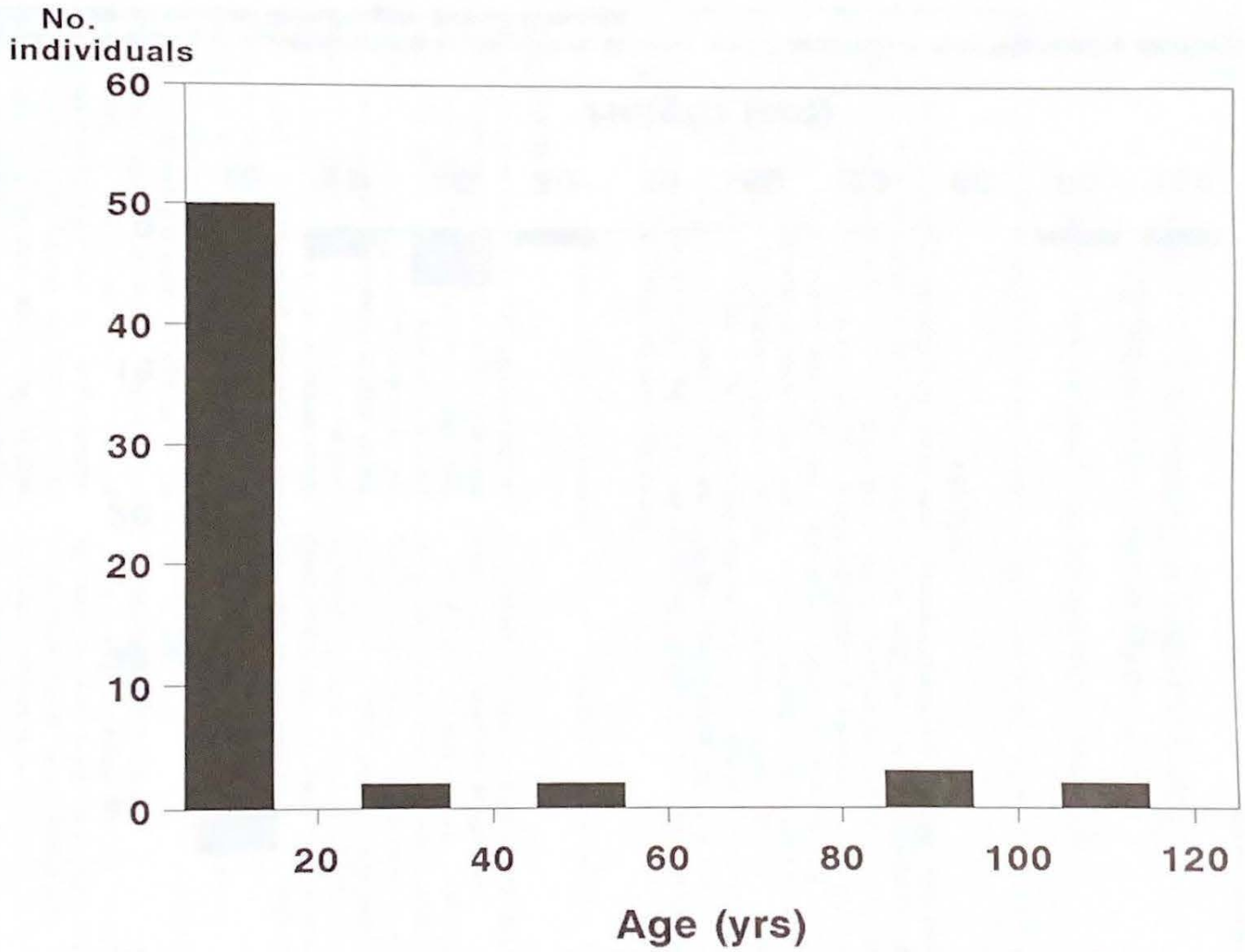


Fig. 5. Age distribution of saguaro cactus (n = 59) by 20-year age classes on a 1.0-ha sampling site (Plot II) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

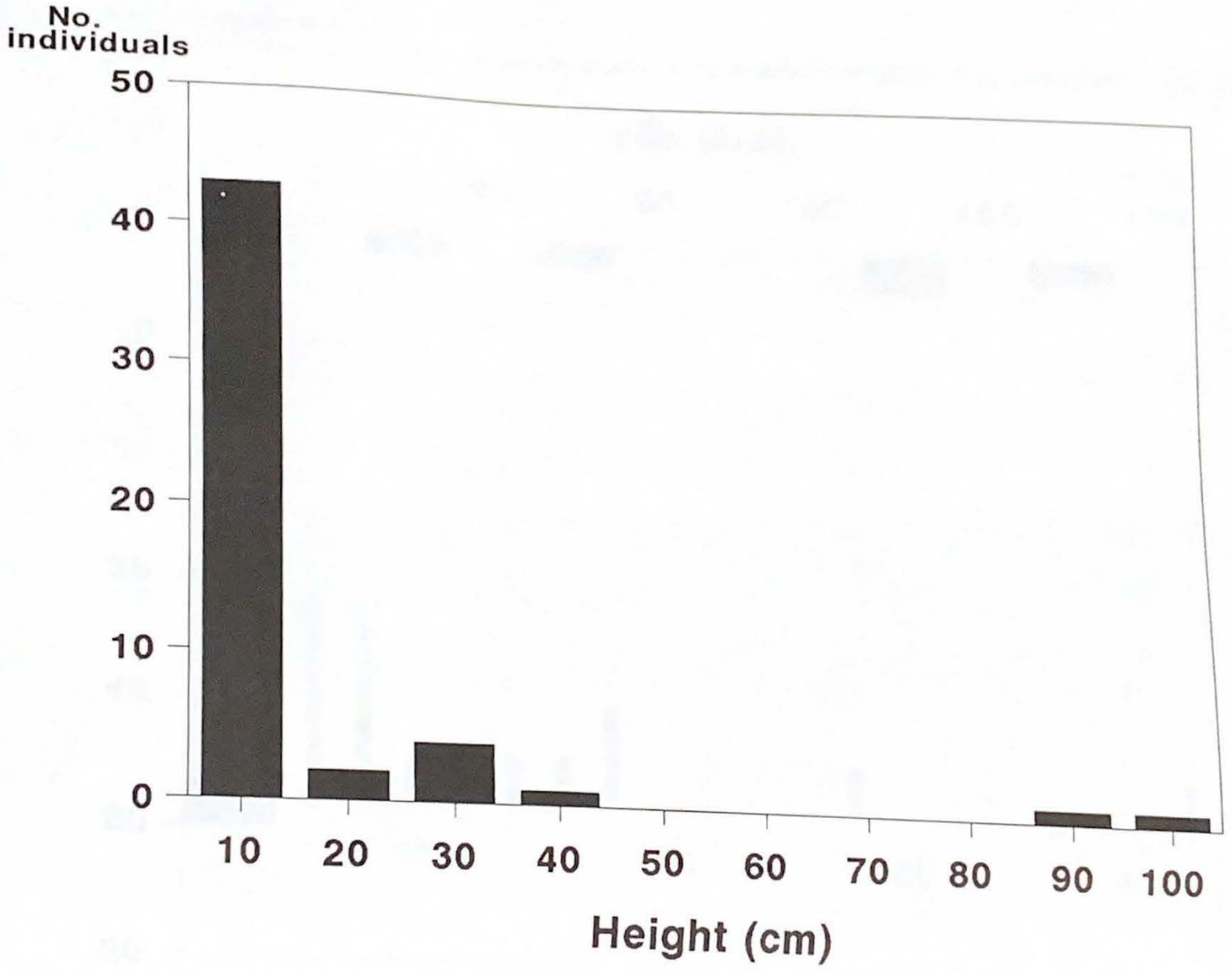


Fig. 6. Height distribution of saguaro cactus with heights <250 cm by 10-cm (n = 52) height classes on a 1.0-ha sampling site (Plot II) in the Cactus Forest, Rincon Mountain District, Saguaro National Monument.

Epidermal Browning of Saguaro Cacti: Is It New or Related to Direction?

Lance S. Evans, Kathleen A. Howard, and Keith H. Thompson

ABSTRACT

Browning of the epidermal surface of saguaro cacti (*Carnegiea gigantea*) is associated with premature death of the species in the northern Sonoran Desert. Analyses of authentic historical photographs demonstrated increased (1) trough (pleat) barking, (2) areole deterioration, and (3) spine loss from mature cacti from 1903 to 1987. Analyses of epidermal characteristics of saguaros at Saguaro National Monument were performed to determine if epidermal browning was related to compass direction. Results showed that both scaling and barking of crests (ridges) and troughs were significantly higher on southern exposures (140-220°) than northern exposures (320-40°). Barking of troughs was tenfold higher on the southern side than on the northern side of cacti. These differences also were apparent for areole scarring and spine loss. The results of this study, coupled with those of previous studies support the hypothesis that UV-B sunlight may be a factor in increased epidermal browning of saguaros during this century.

INTRODUCTION

Recent evidence has shown that epidermal browning is correlated with several other surface and tissue characteristics of saguaros (*Carnegiea gigantea*). Specifically, brown-stemmed cacti have stomata obscured by an epicuticular wax buildup on the epidermis associated with deterioration of other surface characteristics. Surfaces of browning cacti are positively correlated with reduced rates of photosynthesis and a reduced number of chloroplasts in the chlorenchyma, as well as increased browning of parenchyma tissues inside the chlorenchyma (Evans et al., this volume).

Epidermal browning is associated with the decline of the saguaro population at Saguaro National Monument (SNM), and the surface characteristics of healthy and affected cacti have been well characterized (Evans et al., this volume). Are these injuries of recent origin, or can the same characteristics of stem injury be observed for saguaros in the photographic record from many decades ago? In this study, photographs of saguaros from several large collections were used to address this question.

Initial injury appears to occur predominantly on the southern exposures of saguaros. Injury on other exposures appears to follow the initial injury. Analyses of cacti at SNM were used to determine the severity of surface injuries at 20° compass increments around saguaros. These circumferential analyses were then compared with total irradiance values determined from model predictions to ascertain if injury severity is related to solar irradiance.

METHODS

Photographic Studies

Sources of Authentic Photographs.—Three sources of prints and negatives of saguaros were used for this study: (1) the Homer Shantz collection located at the herbarium at the University of Arizona; (2) the collection archived by R. M. Turner of the U.S. Geological Survey at Tumamoc Hill, Tucson,

Arizona; and (3) the collection located at the Arizona Historical Society, Tucson, Arizona. Personnel from these organizations and from SNM stated that these three sources would comprise a representative and authentic historical collection of photographs.

Procedures to Evaluate Photographs.—Only prints and negatives that had verifiable dates were used in the analyses. Criteria for evaluating cacti from photographs were (1) age and number of large (>0.5 m) branches could be determined, and (2) characteristics of crests (ridges) and troughs (pleats) could be evaluated effectively. Each print or negative was viewed under 25x magnification independently by each of four researchers to determine which saguaros in the photograph could be adequately evaluated. Each cactus that fit the above criteria was given a code number for reference. Only saguaros meeting the above criteria were included in the database.

For each cactus to be scored, the following were determined: (1) approximate age, (2) number of branches, (3) presence of scaling or barking on crests, (4) presence of scaling or barking on troughs, (5) condition of areoles (i.e., apparently healthy, or only a scar is present), (6) degree to which spines are present, and (7) condition of growing point (i.e., fuzzy, not fuzzy, or missing).

Not all parameters were scored for each cactus. Sometimes an evaluation could not be made for one or more parameters for a particular cactus.

To insure proper uniformity of evaluation among the four evaluators, a group of 20 saguaros from the Shantz collection was randomly selected for standardization procedures. Each evaluator scored the 20 cacti and the scores were compared. Discussions eventually resulted in similar scores. After standardization procedures were completed, each candidate saguaro was evaluated by two researchers independently. If the evaluations differed significantly, the two evaluators reexamined the specimen again jointly. On rare occasions, a third evaluator was used if marked differences of opinions occurred between the two evaluators. Data were stratified so that parameters scored could be correlated with dates of the photographs.

Researchers observed the physical appearance of both crests and troughs separately. Saguaro surfaces were characterized as exhibiting scaling or barking. Scaling is the appearance of epicuticular wax buildup. Barking refers to a larger buildup of epicuticular waxes with a very dark appearance; areoles are difficult to observe through the waxes. For each crest, the surface was evaluated for scaling and barking, scored independently. A particular crest could exhibit both scaling and barking, one or the other, or neither. A score of 1 was given when a condition was present and a score of 0 when absent. For each trough, the percentage of area that was apparently healthy, covered by scale, or covered by bark was evaluated.

Observations were also made of areoles, including characteristics of spines and the growing points of axillary buds. Areoles were characterized as (1) apparently healthy, (2) having only scar tissues present, or (3) missing completely because of excessive scaling or barking of the crest epidermis. Each crest was characterized as having only one of the three conditions above. A score of 1 was given for only one category, and the other two categories received a score of 0. Spines were characterized as being present or missing. If spines were present, they were characterized as having (1) a full complement of spines, (2) some spines missing, or (3) most spines missing. Each crest was characterized as having only one of these three conditions. A score of 1 was given to only one category. The other two categories received scores of 0. This convention was followed except when no spines were present. When this occurred, the category with most spines missing was given a value of 2.

The growing points of axillary buds were characterized as fuzzy, not fuzzy, or missing. Fuzzy means that epidermal hairs or hair-like tissues are present on the areoles. The fuzzy condition was usually coincident with a swelling of the growing point. The absence of the fuzzy condition was usually coincident with a lack of swelling. When the growing point was absent, it usually reflected the presence of excessive scaling and/or barking of the surrounding crest epidermis.

Studies of Compass Orientation of Injuries

Sources of Cacti.—The saguaros used for the field study were sampled from 1 June through 22 August 1990 at SNM. Cacti were not selected randomly; rather, an attempt was made to sample a wide range

from young cacti with few epidermal injuries to older specimens with brown and black epidermal coverings. Excluded from this study were saguaros with no apparent epidermal problems and those that exhibited extensive barking of all crests and troughs. These two types of cacti would not provide useful information to determine the predominant direction of injury.

Criteria to Evaluate Cacti.—Cacti were evaluated for many stem surface parameters described previously. Compass directions for all crests were recorded for each cactus. Troughs on each side of each crest were also evaluated individually. Relative numbers of spines were recorded for each crest, and the degree of coverage of scaling and barking was estimated for crests and troughs.

Before evaluations began, all four evaluators agreed on the criteria and the degree or extent of the appearance of a certain surface characteristic for randomly selected saguaros. When all four individuals assigned values within 10% of the mean value for each characteristic evaluated, standardization procedures were concluded. Once standardization was accomplished, evaluators worked in pairs. One person was primarily responsible for evaluation while the second person recorded data. The second evaluator also provided technical assistance when necessary, and an independent evaluation on several crests and troughs for each cactus sampled. Observations of characteristics of each crest and trough were taken from 1.5 to 2.0 m above ground level.

After all saguaros were scored, two databases were constructed. One contained data on cacti that exhibited only scaling on troughs, while the second contained data on saguaros that had both scaling and barking on troughs. Compass angles from field data were corrected for azimuth difference from magnetic to true north and then adjusted to the nearest 20°. Some angles had data for two samples while other angles had no data.

Calculation of Irradiance.—The program used to calculate total irradiance was obtained from G. Geller and P. S. Nobel (Nobel 1988). Program inputs were number of days before the equinox and site latitude. All other inputs were default values, which were appropriate for the deserts around Tucson (G. Geller, pers. comm.). The program was modified so that autorotation values were every 20°, and daily amounts of total irradiance for each 20° compass direction were provided. From these daily outputs, total irradiance per annum for each 20° compass direction was calculated.

RESULTS

Photographic Studies

The authentic historical photographs from 1903 to 1987 included 241 cacti. Initial data analysis included all cacti with estimated ages >80 years. Statistically significant ($P = 0.05$) decreases in age and in the average number of branches of cacti occurred with more recent photographs. Spines missing from cacti in later photographs also increased significantly ($P = 0.05$).

A second analysis was performed for cacti that were estimated to be ≥115 years of age (Table 1). Results of this analysis also demonstrated a statistically significant decrease in age ($P = 0.002$) and number of branches ($P = 0.0086$) of saguaros in the photographs. Even though more younger cacti were sampled in more recent years, significant increases in trough barking ($P = 0.046$), growing point missing ($P = 0.034$), and all spines missing ($P = 0.013$) were obtained with later photographs (Fig. 1; Table 1).

Compass Orientation

Trough scaling was highly correlated with compass direction (Fig. 2). Values above 35% of area covered ranged from 100 to 220°. Values on the north side of cacti (340-20°) were below 20%. A similar pattern was present with spines missing on crests (Fig. 3), with highest values (scores >90) present on southern exposures (160-200°) and lowest values (scores <30) on northern exposures (340-20°).

The strong directional responses shown above were supported by the database that included cacti with both scaling and barking of troughs. Trough scaling on southern exposures (>30% of area at 80°) was six times greater than on northern exposures (5% of area at 0°; Fig. 4). This strong relationship was also supported by high levels of crest barking on these cacti (Fig. 5). Barking values were above 0.9 at 180°, and 0.6 at 20°. Scaling of crests was relatively constant so that total injury (both scaling and barking) was higher on southern exposures than on northern exposures. Additional support for a directional effect is shown in Figure 6. Most spines were

missing from southern exposures (values above 1.3 from 140-200°), while northern exposures (320-40°) were above 0.7. Areoles with a whole complement of spines were most prevalent on northern exposures (0.2 at 0°), while values for southern exposures were lower (<0.06 at 180°).

DISCUSSION

The results of this study showed that the extent of epidermal browning (trough barking) has increased 4.5% per decade from 1903 to 1987. The increase in injury suggests that the causative agent may have been present by the 1930s and that the intensity of impact may have increased over the past 60 years.

The results of this study also showed very significant directional effects. Portions of cacti facing compass directions from 120 to 220° (southern exposures) suffered the greatest amount of injury while northern exposures evidenced much less injury. Injury on southern exposures was about six times greater than on northern exposures on trough areas.

Directional effects documented here are not specific to cacti at SNM but are present on saguaros throughout southern Arizona and northern Mexico. The widespread nature of the phenomenon suggests that the causative agent of epidermal browning is not specific to monument areas but is occurring throughout the region.

Calculated total irradiance values of the surface of a vertical cylinder at ground level at 30.12° N latitude, the latitude of SNM, are shown in Figure 7 at 20° increments. These data were calculated from the computer program provided by G. Geller and P. S. Nobel. As a rough approximation, about four to five times as much total irradiance occurs on southern exposures as on northern exposures. If the sun's rays are having an impact on saguaros, it is postulated that UV-B sunlight would be the most damaging. Data from the National Research Council (1989) show that stratospheric ozone levels at 30° N latitude have decreased at the rate of 1.5% per decade between 1930 and 1987. Reduction in stratospheric ozone has allowed an increase in UV-B irradiance. Could this increase in UV-B irradiance explain the increase in epidermal browning of saguaro cacti over the past 60-90 years? This question cannot be answered presently, but a hypothesis that increased UV-B exposure could be the causative agent is consistent with circumstances that relate to epidermal browning of saguaros. These include the following: (1) epidermal browning has increased as total irradiance, including UV-B exposure, has increased; (2) total irradiance on southern exposures is four times that of northern exposures at the latitude of SNM, and scaling of troughs on southern exposures of saguaros is four to six times greater than on north-facing surfaces; (3) crest areas, which receive less shading than trough areas, show injury symptoms of epidermal browning before trough areas; and (4) epidermal browning is not localized but is present on saguaros throughout the northern Sonoran Desert.

The hypothesis that sun exposure, including UV-B irradiance may be involved in saguaro injury is strengthened by unpublished observations by Gloria Montenegro of Santiago, Chile. In Chile, the long-lived columnar cactus, *Echinopsis chilensis* (*Trichocereus chilensis*), exhibits similar epidermal browning characteristics with epidermal browning more prevalent on north-facing surfaces than on southern exposures.

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Table 1. Relationship between characteristics of saguaros estimated ≥115 years of age with date of photograph as the independent variable ($n = 141$).

Dependent variable	Correlation coefficient	*P*	Equation of the linear regression line
Age	-0.462	0.0002	y = 193.01 - 0.92
Number of branches	-0.220	0.0086	y = 8.38 - 0.06
Barking of troughs (pleats)	0.220	0.046	y = -0.0265 + 0.0045
Spines missing	0.273	0.013	y = -0.04 + 0.006
Growing point missing	0.243	0.034	y = -0.0353 + 0.0060
Apparently healthy crests (ridges)	-0.215	0.0493	y = 0.3550 - 0.0044

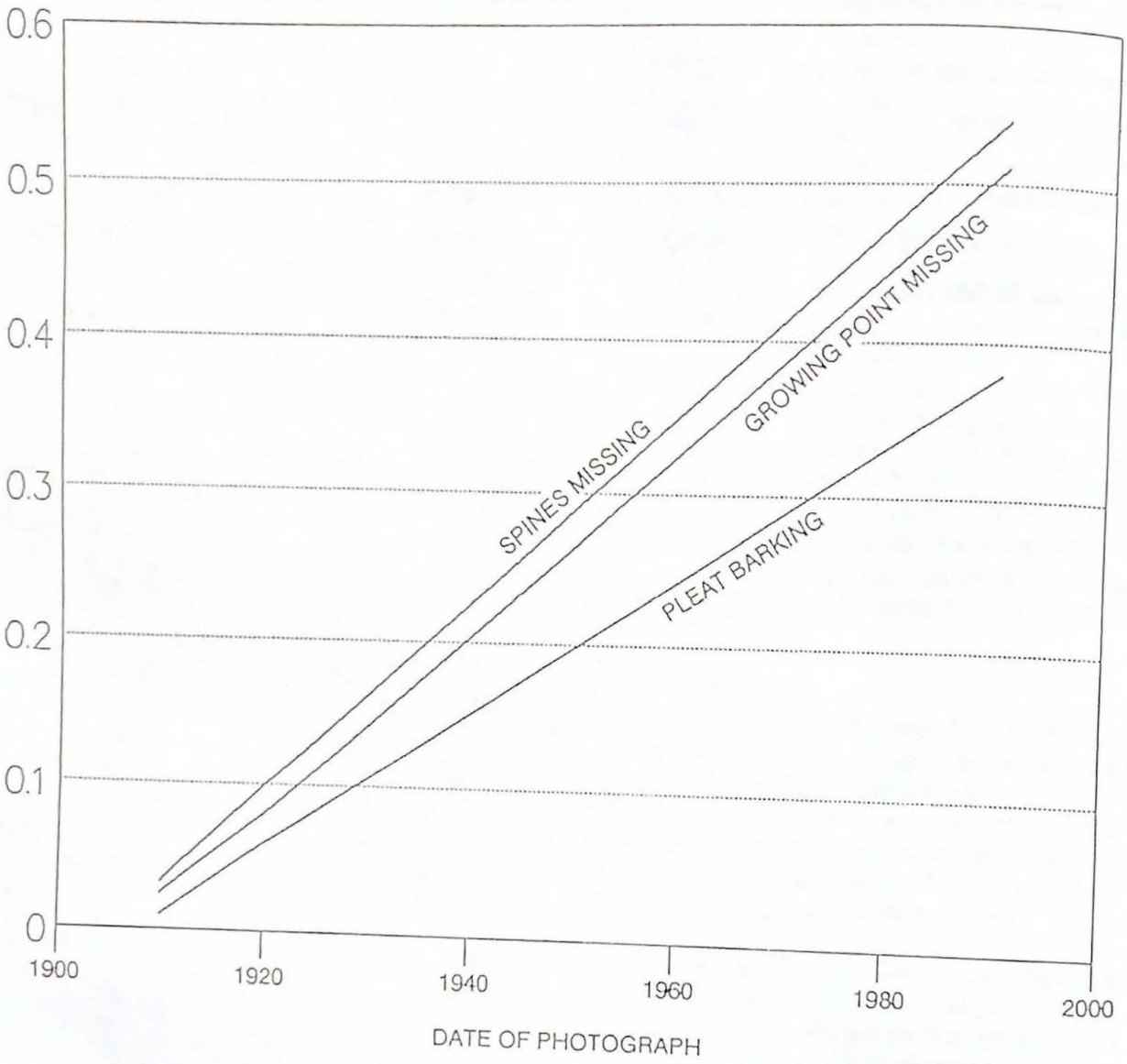


Fig. 1. Relationship between characteristics of saguaros estimated ≥115 years of age with date of photograph. *Y* axis is the proportion of cactus characteristics or area of cactus exhibiting injury symptoms. Statistical evaluations of the regression relationships are shown in Table 1.

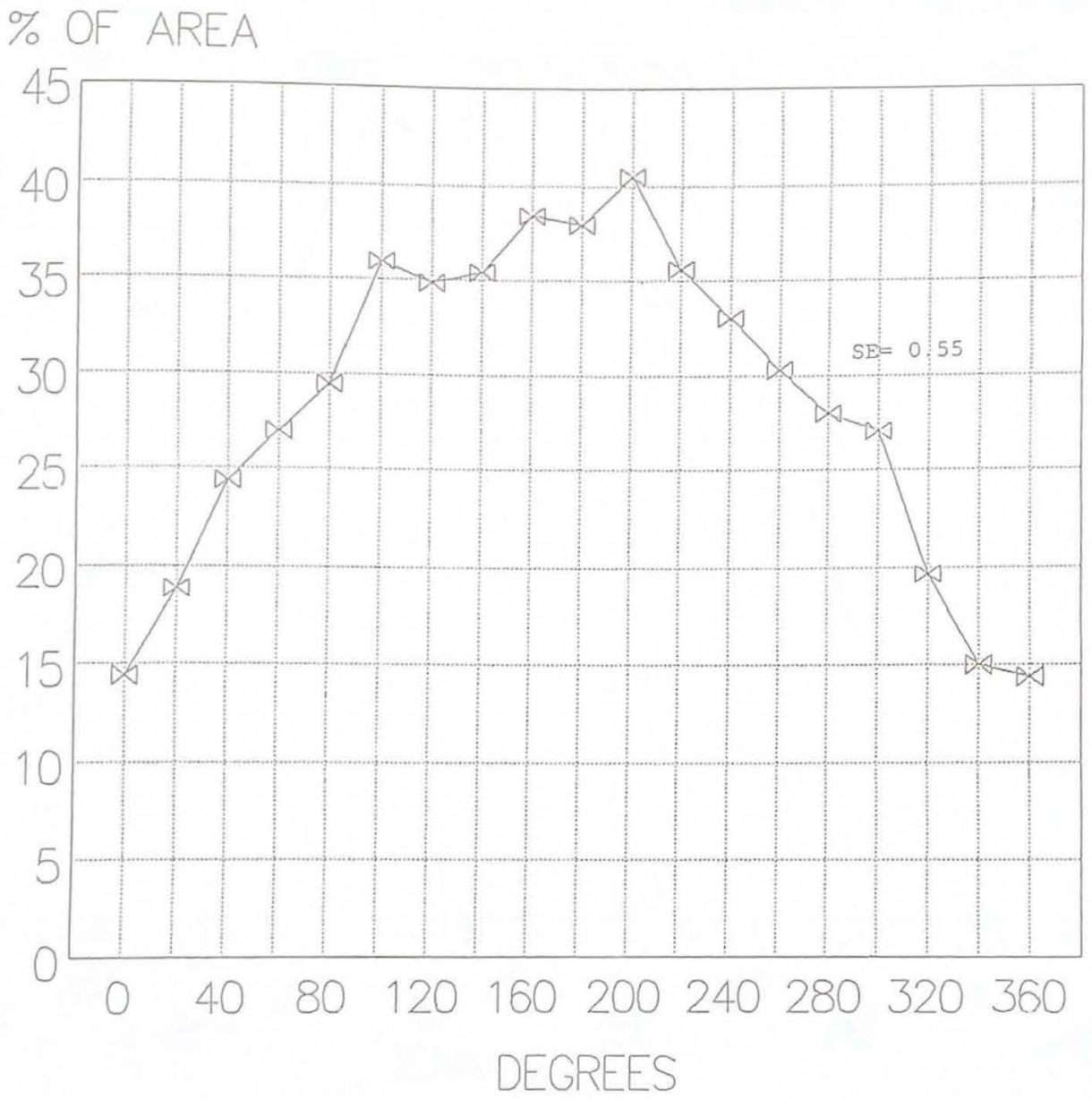


Fig. 2. Relationship between trough (pleat) scaling versus compass direction of the crest (ridge). Data are from saguaros that exhibited only trough scaling. The standard error of the mean for all measurements was 0.55.

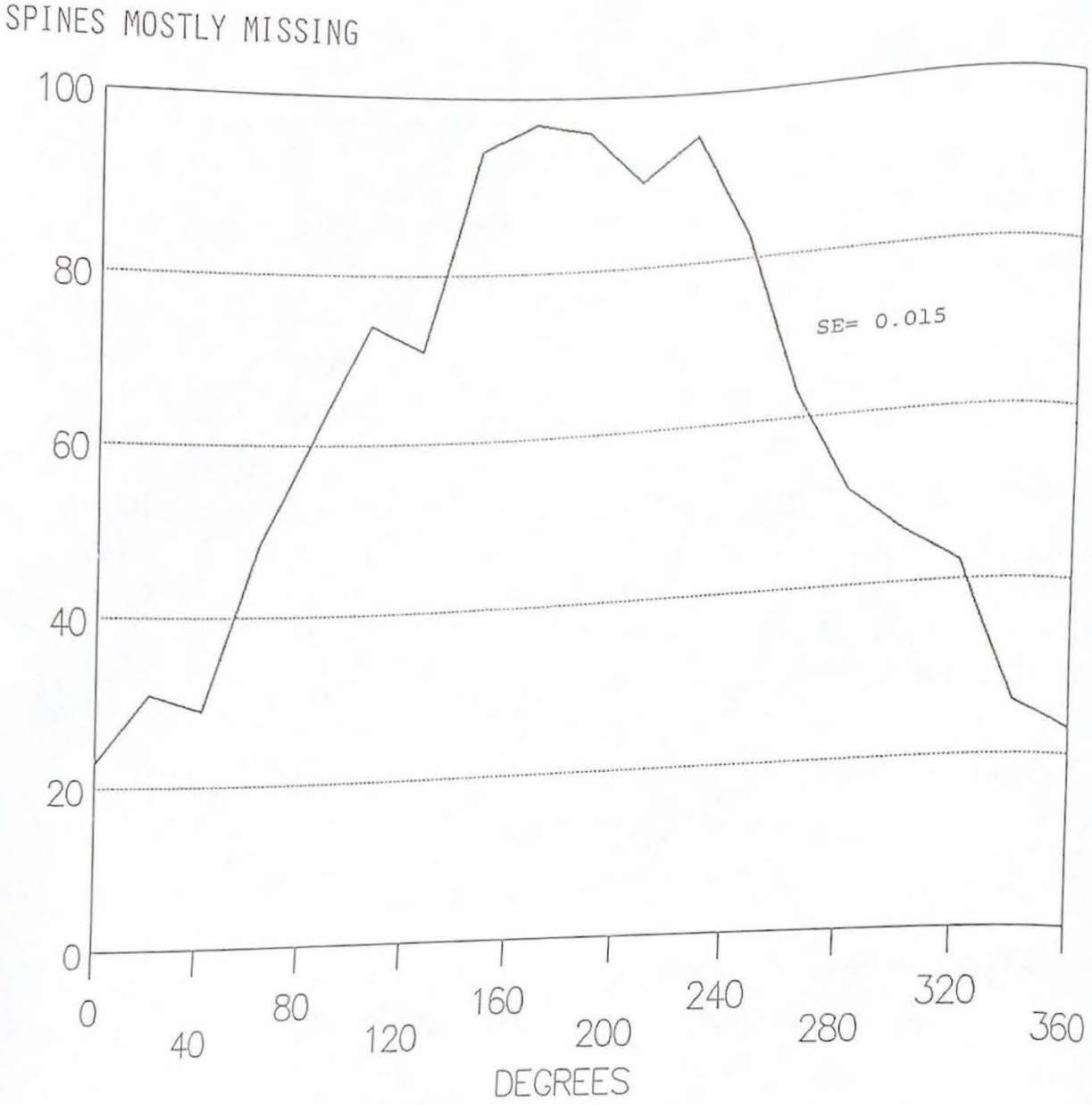


Fig. 3. Relationship between most spines missing versus compass direction of the crest (ridge). Data are from saguaros that exhibited only trough (pleat) scaling. The standard error of the mean for all measurements was 0.015.

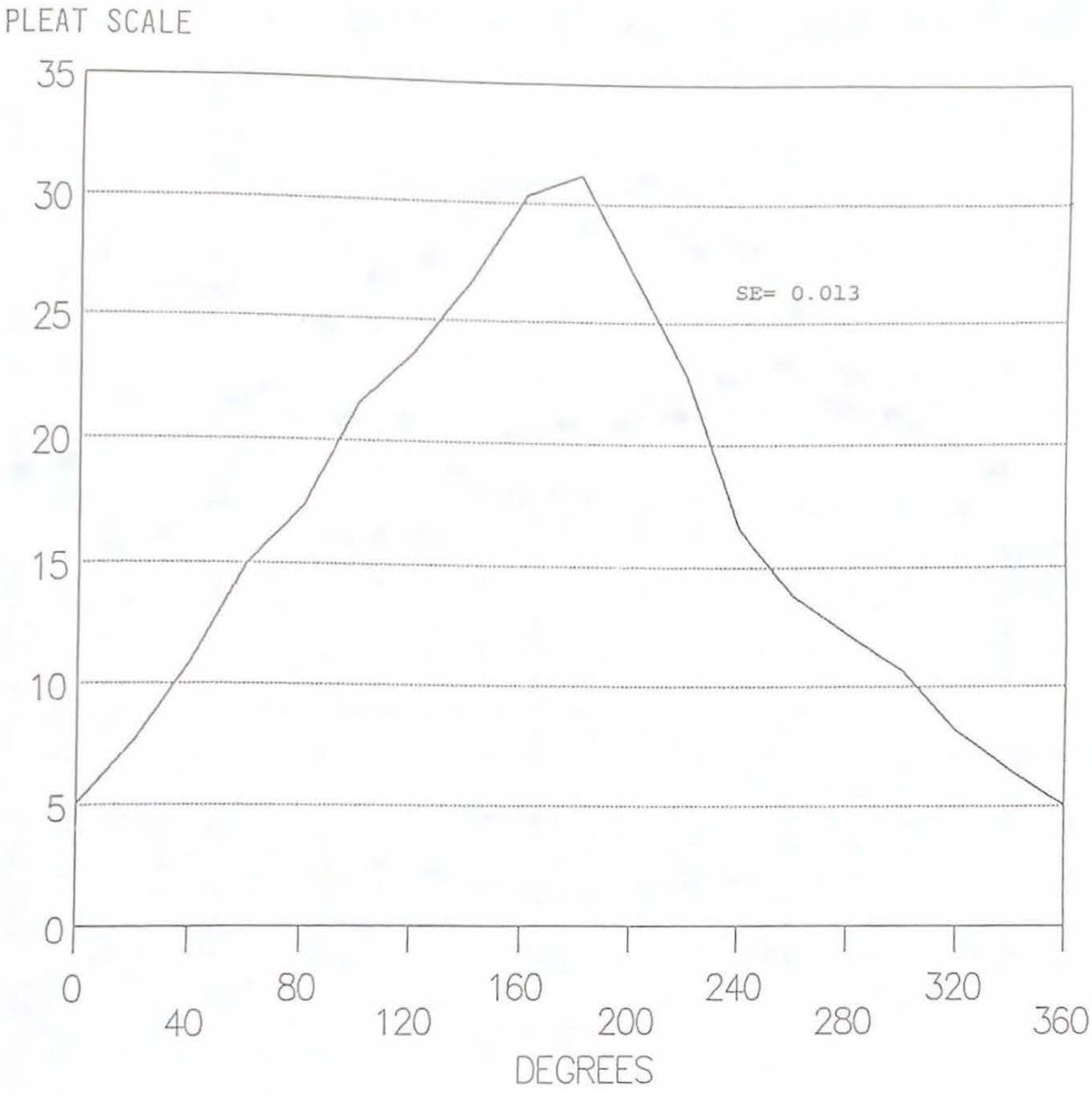


Fig. 4. Relationship between trough (pleat) scaling versus compass direction of the crest (ridge). Data are from saguaros that exhibited both scaling and barking of troughs. The standard error of the mean for all measurements was 0.013.

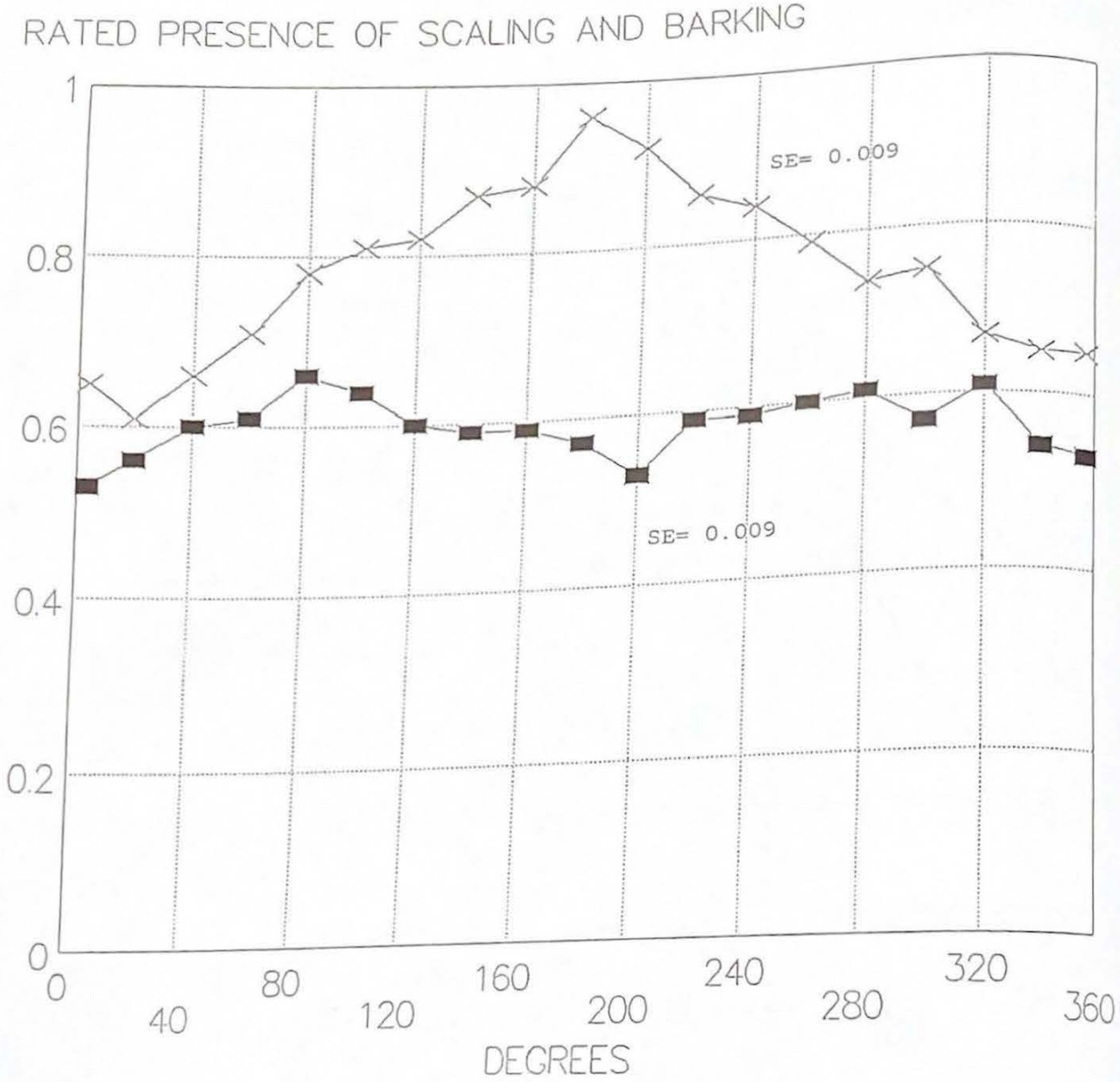


Fig. 5. *Relationship between scaling (lower line) and barking (upper line) on crests (ridges) of saguaros versus compass direction of the crest. Data are from saguaros that exhibited both scaling and barking of troughs (pleats). The standard error of the means for all measurements for barking and scaling were both 0.009.*

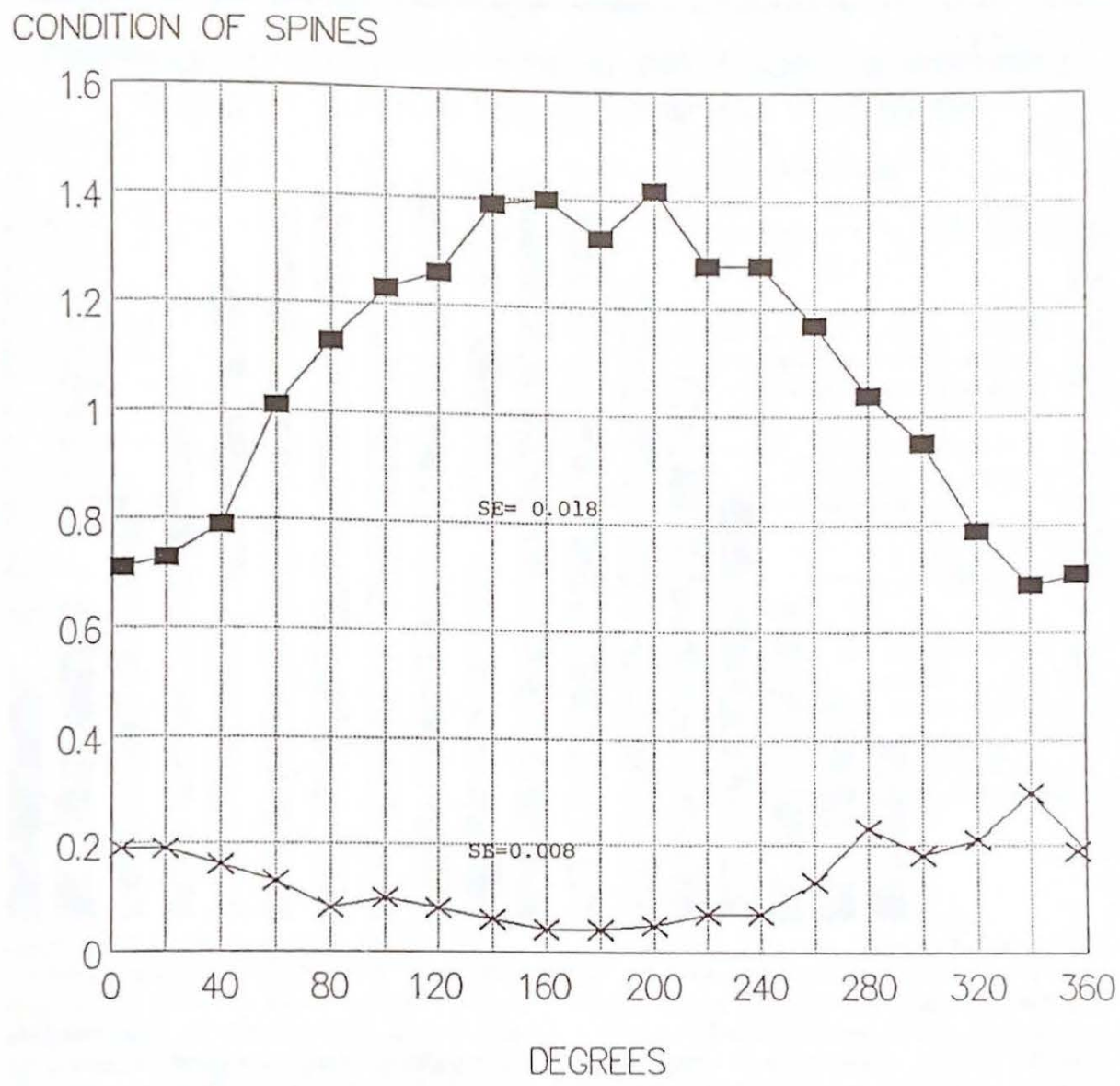


Fig. 6. Relationship between spines mostly missing (upper line) and whole complements of spines (lower line) of areoles versus compass direction of the crest (ridge). Data are from saguaros that exhibited both scaling and barking of troughs (pleats). The standard error of the means for all measurements for most spines missing and whole complement of spines were 0.018 and 0.008, respectively.

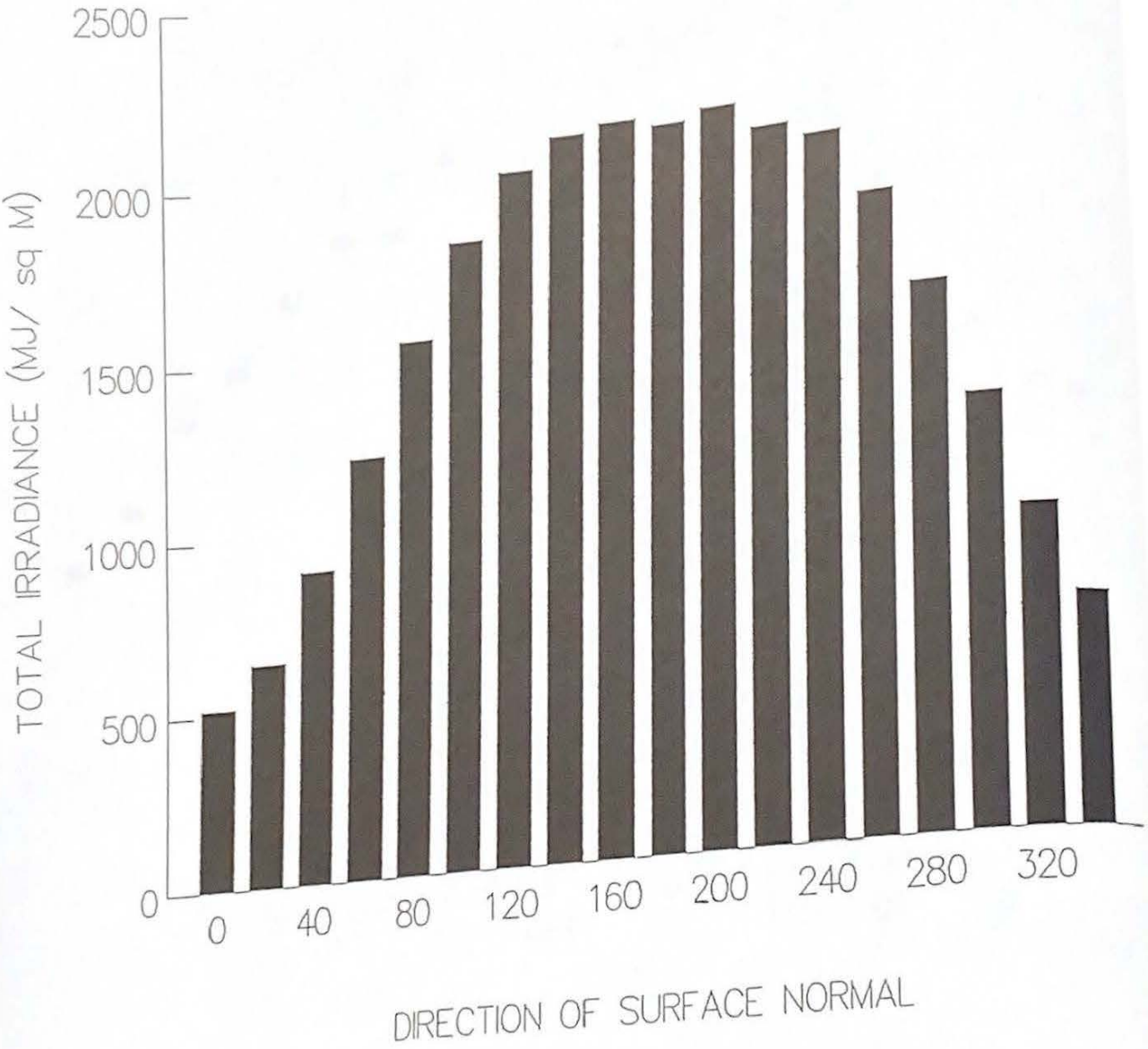


Fig. 7. Relationship between trough (pleat) barking of saguaros versus compass direction of the crest (ridge). Data are from saguaros that exhibited both scaling and barking of troughs. Total irradiance around a vertical cylinder at 30° N latitude calculated from a computer program developed by G. Geller.

Phenological Changes Associated with Epidermal Browning of Saguaro Cacti at Saguaro National Monument

Lance S. Evans, Vincent A. Cantarella, and Kenneth W. Stolte

ABSTRACT

In Saguaro National Monument in Tucson, Arizona, saguaro cacti (*Carnegiea gigantea*) have undergone a noticeable decline characterized by epidermal browning and premature senescence. Green cacti usually show little or no epicuticular wax buildup, numerous spines, greater stomatal density, more axillary buds and areoles, and greater numbers of chloroplasts per cell in the chlorenchyma, than cacti with epidermal browning. It is hypothesized that epicuticular wax ceases to slough off browning cacti, thus hindering gas exchange. Polyphenols are produced as a response to stomatal occlusion, resulting in brown parenchyma and a subsequent browning of stems.

INTRODUCTION

At Saguaro National Monument (SNM) in Tucson, Arizona, population density and recruitment of young saguaro cacti (*Carnegiea gigantea*) have noticeably declined over the past 40-60 years (Hastings and Turner 1980). Saguaros can live to be >200 years old (Hastings and Turner, 1980; Steenberg and Lowe 1983). The most obvious correlate with premature death is the orange to brown to black discoloration that occurs on the surfaces of saguaros that are about 80 years old or more. At present, the cause(s) of epidermal browning is (are) unclear.

Little systematic research has been done to determine the cause(s) of the saguaro decline. Steenberg and Lowe (1982, 1983) attributed the losses to freezing injuries, but no direct evidence has been presented to demonstrate that epidermal browning is related to freezing temperatures. Hastings and Turner (1980) considered the decline of saguaros at the Rincon Mountain District (RMD) of SNM in the context of changes in species dynamics throughout the Sonoran Desert. They discussed such issues as the effects of cattle (*Bos taurus*) and other desert animals, effects of fire suppression, and changes in climate, as possible causes.

The present study was conducted to test the hypothesis that stem tissues of green cacti differ from stem tissues of browning cacti. To test this hypothesis, epidermal characteristics, buildup of epicuticular waxes, depth of chlorenchyma, and depth of tissue browning beneath the chlorenchyma, were related to stem color.

METHODS

Observations on, and tissue samples of, 472 saguaro cacti were collected from March 1988 through August 1990. Cacti from both the RMD and the Tucson Mountain District (TMD) of SNM were sampled. Cacti were not selected randomly. Rather, an attempt was made to sample individual cacti ranging from apparently healthy young plants to older cacti with thick brown to black epidermal coverings. Observations and tissues were taken from 1.5 to 2.0 m above ground on southern exposures. Areas representative of adjacent tissues were also sampled. Scores for the various phenological observations are averages for southern exposures between 1.5 and 2.0 m above ground.

Color Selection

For sample cacti, epidermal color of the southern exposures of stems was quantified through comparison with a Benjamin Moore paint color chart. Color swatches were held next to each stem, making sure that both the specimen and color chart were in direct sunlight. The best color match was chosen by a minimum of four researchers. Each assigned stem color was then subdivided into percentages of cyan, magenta, and yellow through color comparisons with standard color separation procedures (Kneppers 1982) by two commercial artists working in natural sunlight conditions.

The percentages of cyan and magenta each ranged from 0 to 60 and these two surface color components were combined into one color factor using the following formula: color factor = 60 - cyan color + magenta color. Thus, the color factor would be low for cacti with a high cyan color and a low magenta color (green cacti). Conversely, high color factor values would be obtained for scaling and barking cacti with low cyan and high magenta colors (browning cacti).

Tissue Samples

After epidermal color was estimated, tissue samples were taken. Tissue samples (approximately 2 x 2 cm) were cut from southern exposures of stem surfaces. The depth of cut was approximately 2 cm. After the sample was removed, the depth of green color and the depths of the colors of the internal parenchyma were recorded. The cuticle of each sample was removed and both the cuticle and internal tissues were fixed in ice-cold 10% acrolein for a minimum of 20 hours.

Surface Characteristics

Researchers observed the physical appearance of both crests (ridges) and troughs (pleats) separately. Surfaces were characterized as exhibiting pox, scaling, or barking. "Pox" is described as blotches of yellowing blended into the more normal green color of the epidermis. "Scaling" is the appearance of a red-orange epicuticular wax buildup. "Barking" refers to a larger buildup of epicuticular waxes with a red-brown to black appearance.

Observations were also made of areole characteristics, specifically as related to spines and the growing points of axillary buds of areoles on southern exposures. Areoles were characterized as (1) intact, (2) only scar tissues present, or (3) missing completely because of excessive scaling or barking of the crest epidermis. Spines were characterized as to presence or absence. If spines were present, they were characterized as having (1) a full complement of spines, (2) some spines missing, or (3) most spines missing.

The growing points of axillary buds were characterized as fuzzy, not fuzzy, or missing in appearance. "Fuzzy" means that epidermal hairs or hair-like tissues were present on the areoles. The fuzzy condition was usually coincident with a swelling of the growing point. The absence of the fuzzy condition was usually associated with a lack of swelling. When the growing point was absent, it usually reflected excessive scaling and/or barking of the surrounding crest epidermis.

Cuticle Studies

After fixation, cuticles were washed with water for at least 10 minutes, dried with tissue paper and affixed to microscope slides with quick-drying (5-min) epoxy glue. After the cuticles were placed on slides, slides were covered with newspaper. A flat board was placed on the newspaper and lead weights or rocks were placed on the boards to ensure that cuticles remained flat while the glue dried. Care was taken to see that no abrasion occurred that would remove epicuticular waxes or damage the cuticles in any way.

Cuticles were viewed with a microscope at 100x magnification. Five randomly selected views (2.54 mm^2 total area per view) of each cuticle were used to evaluate cuticular characteristics. Cuticles were checked for conditions of epicuticular waxes and stomata. Flaking and sheeting of waxes, as opposed to the lack of epicuticular wax coverings were noted. Stomata were characterized as either visible or obscured by epicuticular coverings. If stomata were visible, stomatal density was determined.

Microscopic Characteristics of Epidermis

Microscopic examination of the epidermis of saguaro cacti was conducted to determine the characteristics of apparently normal cacti and those with scaling and barking of the surface. The visibility and density of stomata on the cuticles were also determined. Characteristics described as flaking and sheeting were observed on cuticle surfaces. "Flaking" is the buildup and partial sloughing of epicuticular

waxes that results in a rough, non-uniform appearance. "Sheeting" is the buildup of epicuticular waxes that results in a smooth appearance. Both conditions result in a decrease in the number of visible stomata. Samples that exhibited both flaking and sheeting were scored as having both conditions.

Values of flaking, sheeting, and the degree to which stomata were visible were rated on a relative scale from 0.00 to 1.00. Low values were given to cuticles with little flaking, sheeting, or when the stomata were clearly visible. Values of 1.00 were given to cuticles with a high degree of flaking of epicuticular waxes, total sheeting of epicuticular waxes, and total obscuring of stomata.

Chloroplast Density Studies

Since the depth of the green chlorenchyma and the amount of internal discoloration (ID) could vary among cacti of various external colors, the number of chloroplasts per cell was determined for various chlorenchyma depths. The depths sampled were (1) 0.0 to 0.9 mm (Tissue A), (2) 0.91 to 1.8 mm (Tissue B), (3) 1.81 to 2.70 mm (Tissue C), and (4) 2.71 to 3.6 mm (Tissue D) from the cuticle. Each cell was classed as having $\leq$5, 6-10, 11-15, or $\geq$16 chloroplasts per cell. Numbers of cells per view within these classes were scored.

Statistical Analysis

Regression analyses were performed for a large variety of presumed independent and dependent variables, and analyses provided levels of significance, correlation coefficients, and best-fit lines for linear and quadratic equations by standard statistical programs (Steel and Torrie 1960). In all cases, linear regression provided the highest level of significance.

RESULTS

Data analyses have been aimed at understanding the changes, both external and internal, that occur as cacti turn from green to the barking condition. Two parameters were used to document the differences, namely color factor (a measure of the green to brown color of the stem surface) and depth of ID.

Depth of ID and color factor are closely related (Fig. 1). The Y-intercept value indicated that green cacti may have 1-2 mm of ID. Internal discoloration increased with increasing color factor values so that with a color factor value of 50, ID was 5.5 mm and with a color factor value of 80, ID was 8.0 mm.

Trough sheeting was positively correlated with color factor and slopes of the lines for sheeting and ID were similar (Fig. 1). The slope of the line for obscured stomata was identical to that for sheeting. The displacement of the line for obscured stomata to the right of that for sheeting suggested that sheeting precedes obscured stomata.

Correlations of flaking, sheeting, and obscured stomata with ID did not provide statistically significant linear relationships. On the contrary, statistically significant quadratic relationships were obtained for all three parameters with ID (Table 1). Results show that flaking was rather low in cactus samples with 1-2 mm of ID (Fig. 2). As ID increased to 3 mm, flaking increased (about 0.70-0.78). At high ID values, flaking decreased, probably as a result of the increase in sheeting. Sheeting values were relatively low (0.4-0.5) for ID values of 2-5 mm. However, sheeting values increased markedly from 0.5 to 0.82 for ID values of 6 to 10 mm. The degree of stomatal obstruction showed a response similar to that of sheeting. For samples below an ID of 6 mm, values below 0.38 were obtained for obscured stomata. However, obscured stomata values increased to 0.63 as ID increased to 9 mm (Fig. 2).

Flaking increased markedly from 0.6 to almost 0.78 as ID increased from 1 to 5 mm (Fig. 2), but thereafter, flaking decreased to about 0.57. At an ID below 5 mm, sheeting levels were below 0.47, but as ID values increased from 5 to 9 mm, sheeting increased from 0.45 to 0.82. The increase in sheeting above 5 mm ID coincided with the decrease in flaking. The increase in sheeting was highly correlated with the degree of obscured stomata. This is not surprising since with a lack of flaking, sheeting of waxes covers the stomata.

Internal discoloration was described in terms of the depth of the discoloration. Since the color of ID ranged from yellow, orangish-yellow, orange, brownish-orange, to brown, and since the gradations of these colorations were difficult to determine in an objective manner, only the depth of the discoloration for each sample was recorded. In general, a depth of discoloration of 1-3 mm reflected a color of orangish-yellow to orange, while a depth of discoloration of $\geq$5 mm was usually brownish-orange to brown.

Field observations suggested that scaling and barking may occur on crests before they occur on troughs. Statistical analyses indicated that crest scaling occurred at relatively low color factor values and increased to about 1.0 for a color factor value of 100 (Fig. 3). In contrast, crest barking usually occurred at lower color factor values. For example, at a color factor of 20, crest barking values were only 0.1 and increased to 0.8 for a color factor value of 100 (Fig. 3).

Relationships between stomatal density and color factor and ID are shown in Figure 4. Stomatal density decreased with increasing color factor values. More than 20 stomata/mm^2 were observed at a color factor of 0 but less than 2 stomata/mm^2 were seen at a color factor of 70. Likewise, stomatal density decreased with increasing ID. At ID values of 1 mm, the stomatal density was about 15/mm^2 while at ID values of 9 mm, stomatal density was about 4/mm^2. The results indicate that stomatal density is highly correlated with color of saguaro stems as well as ID. They support the results above that show that as stems lose green color and turn brown, sheeting occurs and in turn stomata are obscured (Fig. 2).

Chloroplast density was positively correlated with percent cyan in stem color in some tissue classes and negatively correlated with percent magenta in some tissue classes. Statistically significant negative relationships were found for frequency of cells with low numbers of chloroplasts per cell versus cyan content in stem color (Table 2). For example, cyan color was negatively correlated with the number of cells in tissue C that had 6-10 chloroplasts per cell. Three positive correlations between magenta and frequency of cells with low numbers of chloroplasts were found. These results show cyan color in the stem was associated with more cells having higher numbers of chloroplasts per cell, while magenta trunk color was correlated with more cells having smaller numbers of chloroplasts per cell. Significant correlations were found for tissues B, C, and D, but not for tissue A, suggesting that such changes do not occur in cells adjacent to the cuticle but do occur in more internal chlorenchyma.

Relationships between scaling and barking on crests and troughs with degree of ID are shown in Figure 5 and Table 3. Crest scaling was quite extensive at low ID values. Trough scaling occurred after crest scaling, and both crest and trough barking occurred almost simultaneously. These results indicate that crest scaling preceded ID, suggesting that scaling of the crests near the areoles occurred early in the sequence of events that leads to epidermal browning. This sequence of events is supported by data showing that areole scarring (Fig. 6) began about the same time as crest scaling (Fig. 5). These events were followed by loss of most spines and crest barking (Figs. 5 and 6).

Relationships between sheeting, scaling, obscuring of stomata, and barking of troughs are shown in Table 4. Trough sheeting was present at low color factor values. Sheeting of the cuticle preceded scaling. Obscured stomata developed after scaling and preceded barking. Cuticle sheeting preceded scaling and obscuring of stomata of troughs. Since these events in the troughs occurred after changes on crests, it is assumed that cuticle sheeting occurred on crests before scaling, and that obscuring of stomata on crests occurred between scaling and barking of crests. Direct measurements of cuticle flaking, sheeting, and obscured stomata of crests would be very difficult since cuticles of crests are curved and could not be accurately observed.

DISCUSSION

The results of this study demonstrate the sequence of events that lead from green cacti to cacti with epidermal browning. Events on the cactus crests precede similar events on the troughs. Green cacti are characterized by a lack of flaking or sheeting of epicuticular waxes. Cacti with a pale green color showed some flaking of accumulated epicuticular waxes, and this flaking may have resulted in sheeting of the waxes that eventually obscured stomata with scaling on crests. As sheeting occurred, more stomata were obscured and less acid accumulation (photosynthesis) occurred during night periods. Concomitant with these events, the internal parenchyma changed from a pale green or whitish color in the greenest cacti to a yellow, yellowish-orange color. With sheeting and eventual scaling and barking of troughs, the orange discoloration turned brown.

The depth of ID increased from scaling to barking, so that by the time barking occurred, little or no gas exchange was possible. Lack of gas exchange leads to a decrease in the number of chloroplasts per cell, especially in more internal chlorenchyma. The lack

of gas exchange also leads to decreased photosynthetic activity, probably the main causative agent of the extensive internal browning that occurs when troughs are scaled or barked. Internal brown tissues eventually smell decayed when removed from the cacti. The extensive internal browning that occurs with barked troughs probably makes cacti more sensitive to secondary plant pathogens, insect pests, and freezing injuries.

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Table 1. Relationships between trough surface characteristics with amount of internal discoloration.

Dependent variable	*P*	Equation of the line (quadratic functions)
Obscured stomata	0.001	$y = 0.551 - 0.149(x) + 0.015(x^2)$
Sheeting	0.025	$y = 0.678 - 0.119(x) + 0.015(x^2)$
Flaking	0.018	$y = 0.503 + 0.113(x) - 0.012(x^2)$

Table 2. Statistically significant relationships between number of chloroplasts per chlorenchyma cell and stem color.

Tissue*	Stem color	No. chloroplasts/cell	Correlation coefficient	*P*	Equation of the line (linear regression)
B	Cyan	6-10	-0.324	0.0268	$y = 17.07 - 0.30(x)$
B	Cyan	0-5	-0.242	0.047	$y = 1.19 - 0.26(x)$
C	Cyan	11-15	0.238	0.046	$y = 24.35 + 0.35(x)$
C	Cyan	6-10	-0.342	0.034	$y = 20.06 - 0.38(x)$
C	Magenta	0-5	0.274	0.020	$y = 0.582 + 0.034(x)$
D	Magenta	0-5	0.273	0.020	$y = 0.680 + 0.035(x)$
D	Magenta	6-10	0.225	0.040	$y = 12.33 + 0.11(x)$

*Tissue depths: A = 0.0-0.9 mm, B = 0.91-1.8 mm, C = 1.81-2.70 mm, D = 2.71-3.6 mm.

Table 3. Relationships between surface characteristics of saguaros with internal discoloration.

Dependent variable	Correlation coefficient	*P*	Equation of the line
Crest scaling	0.153	0.002	$y = 0.311 + 0.026(x)$
Trough scaling	0.164	0.001	$y = 0.208 + 0.026(x)$
Crest barking		>0.0001	$y = 0.415 - 0.098(x) + 0.011(x^2)$
Trough barking	0.224	>0.0001	$y = 0.083 + 0.034(x)$

Table 4. Relationships between surface characteristics of the troughs of saguaros with color factor.

Dependent variable	Correlation coefficient	*P*	Equation of the line (linear regression)
Sheeting	0.224	0.014	$y = 0.063 + 0.014(x)$
Scaling	0.348	>0.0001	$y = -0.023 + 0.010(x)$
Obscured stomata	0.408	>0.0001	$y = -0.136 + 0.011(x)$
Barking	0.336	0.0001	$y = -0.066 + 0.008(x)$

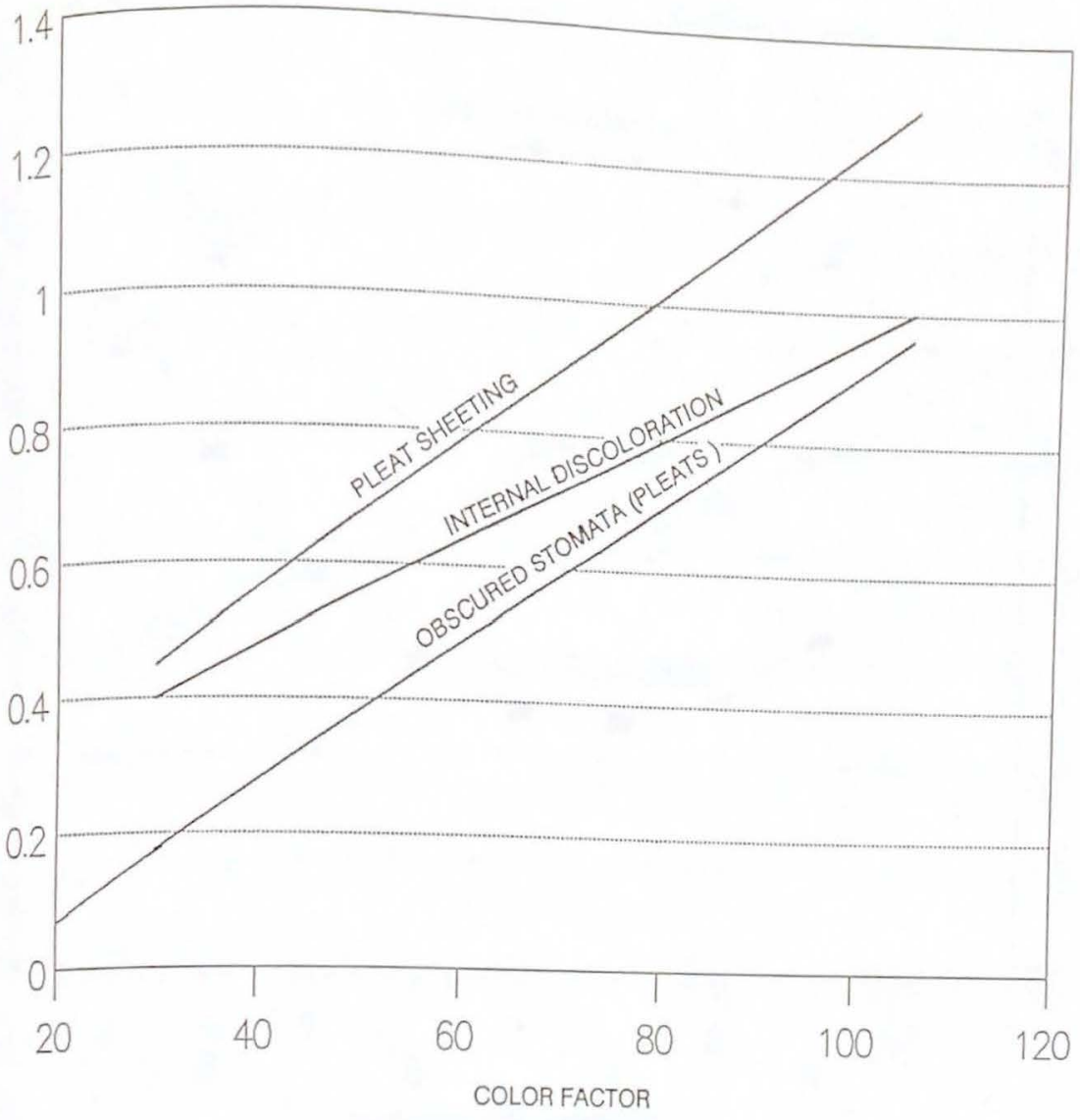


Fig 1. Relationships between depth of internal discoloration (right y axis), trough (pleat) sheeting, and obscured stomata versus color factor (left y axis, units are proportion of cactus area exhibiting injury) for saguaro cacti at Saguaro National Monument.

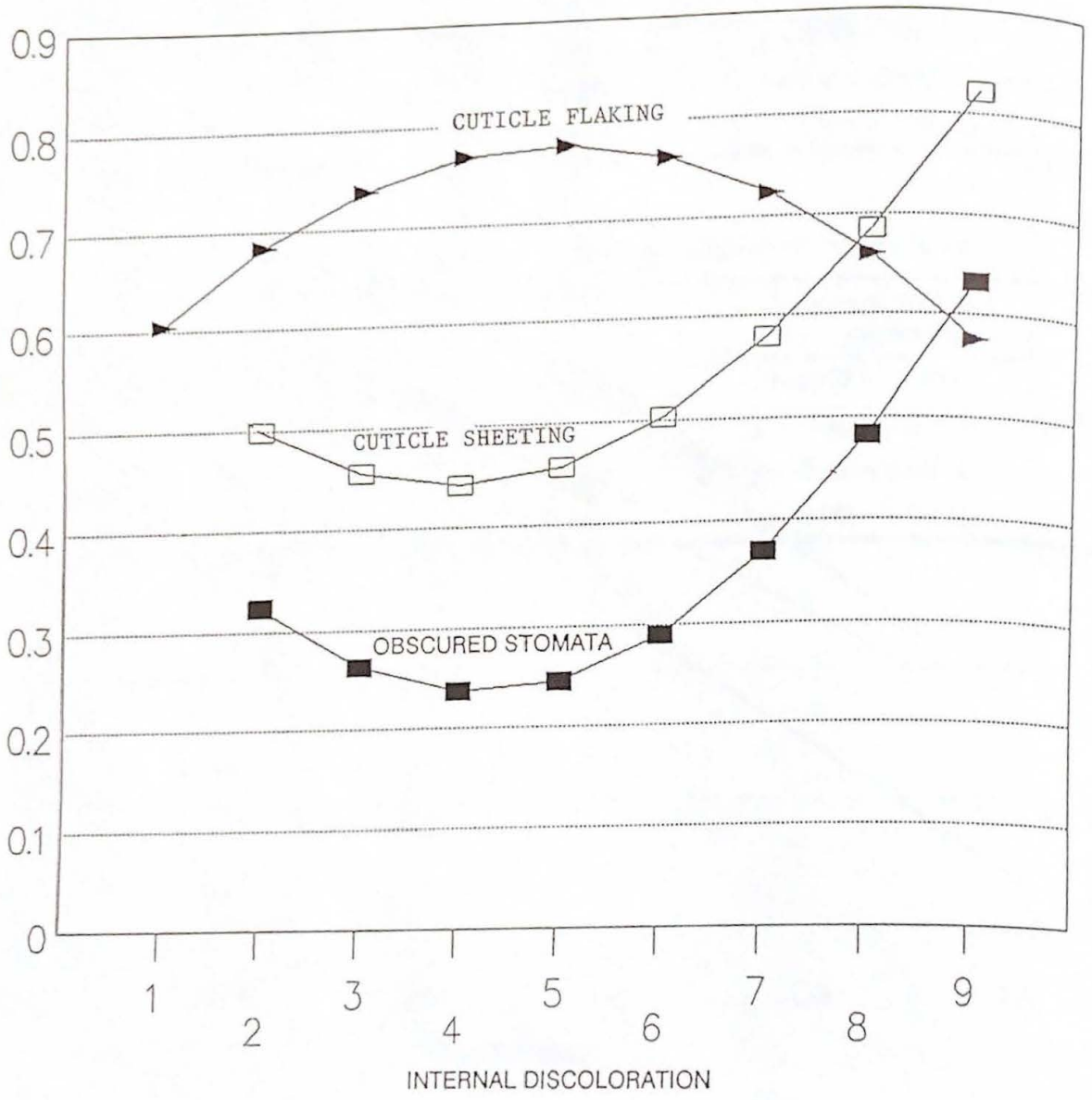


Fig 2. Relationships between cuticle flaking, cuticle sheeting, and obscured stomata (units are proportion of cactus area exhibiting injury) versus internal discoloration (mm) for saguaro cacti at Saguaro National Monument.

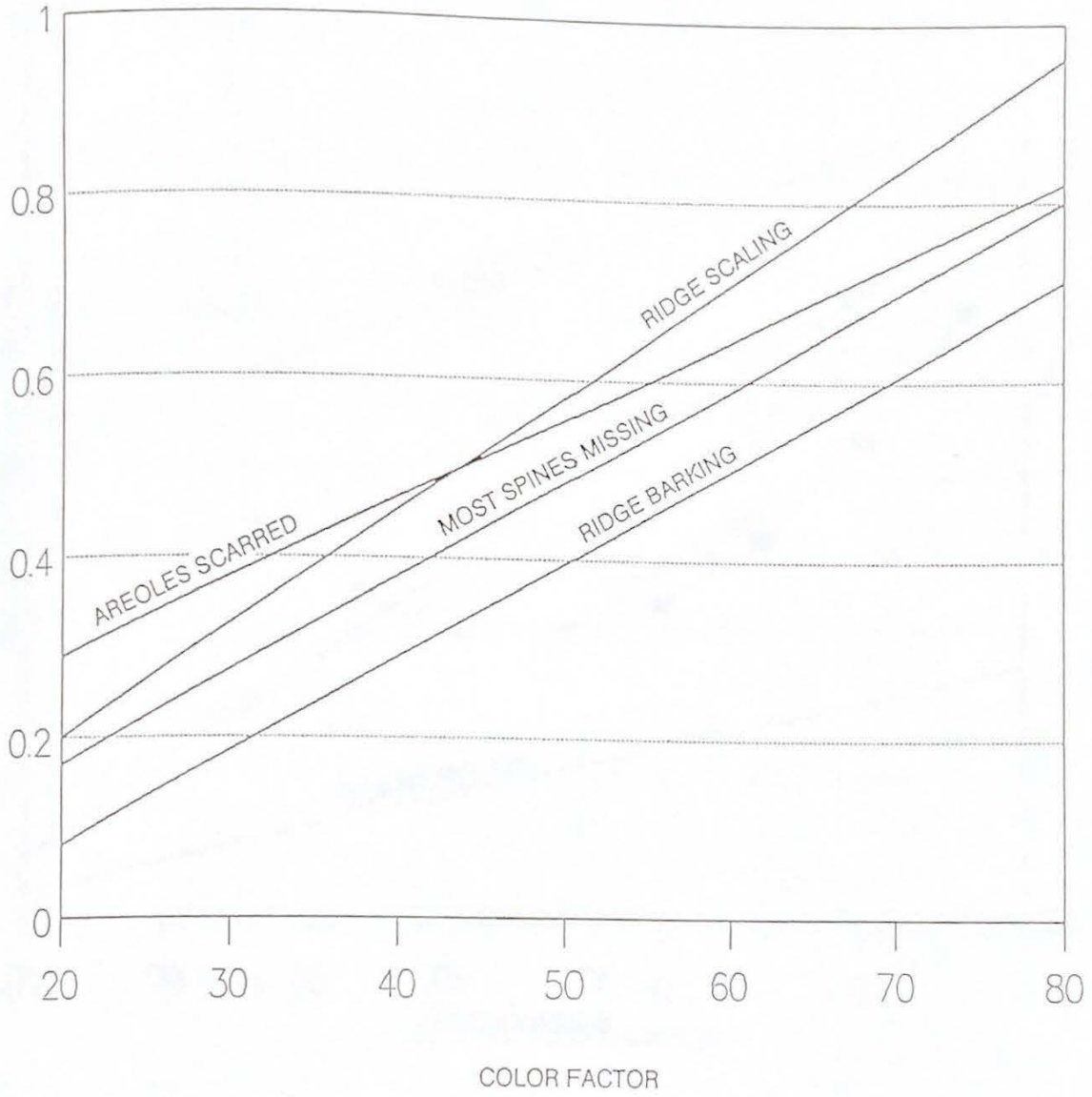


Fig 3. Relationships between crest (ridge) scaling, crest (ridge) barking, areoles scarred, and most spines missing (y axis is the proportion of cactus characteristics or area of cactus exhibiting injury symptoms) versus color factor for saguaro cacti at Saguaro National Monument.

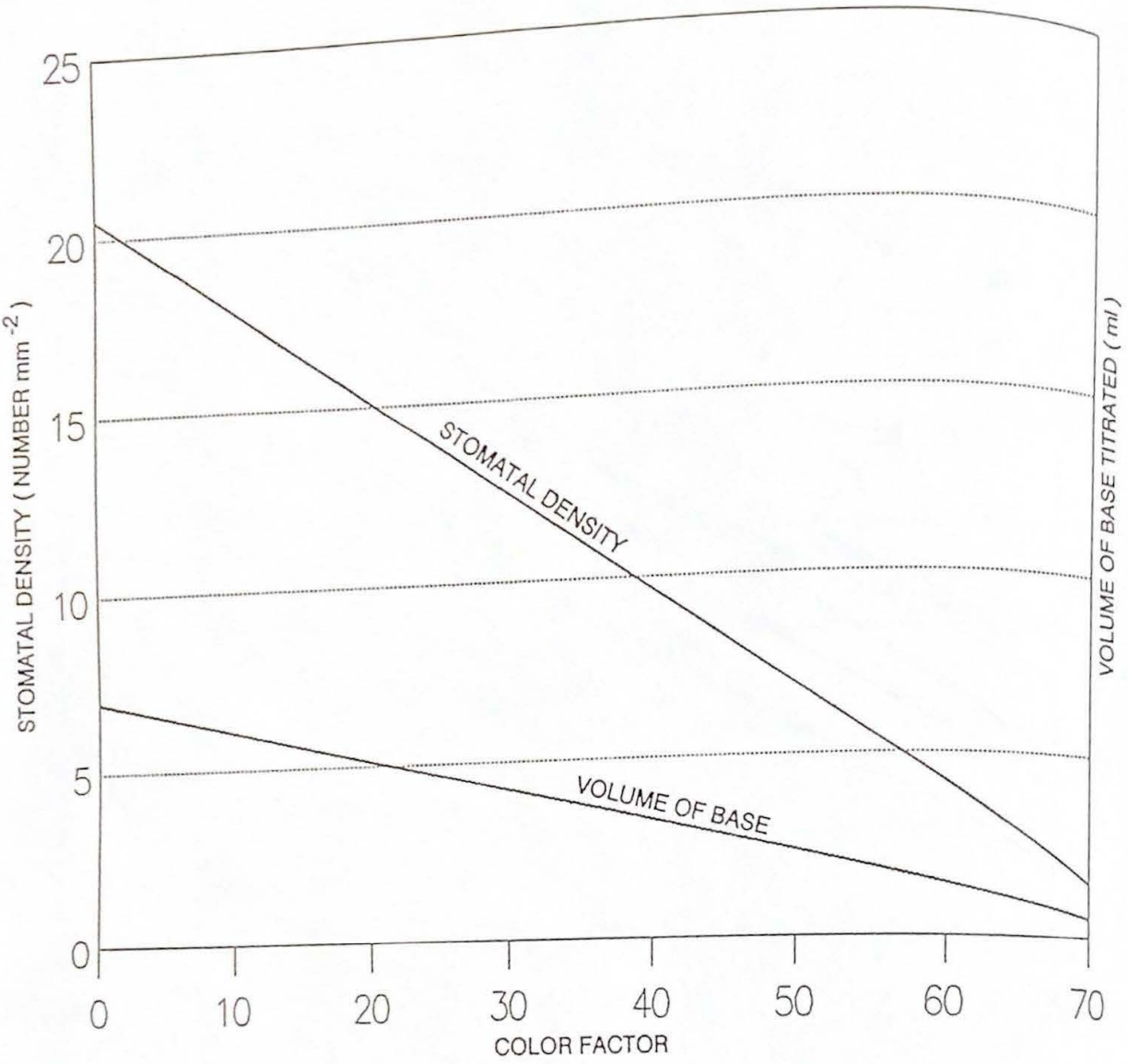


Fig 4. Relationships between stomatal density and volume of base (1 ml of base titrated equals 128mMoles $H+/m^{-2}$) used to titrate stored organic acids versus color factor for saguaro cacti at Saguaro National Monument.

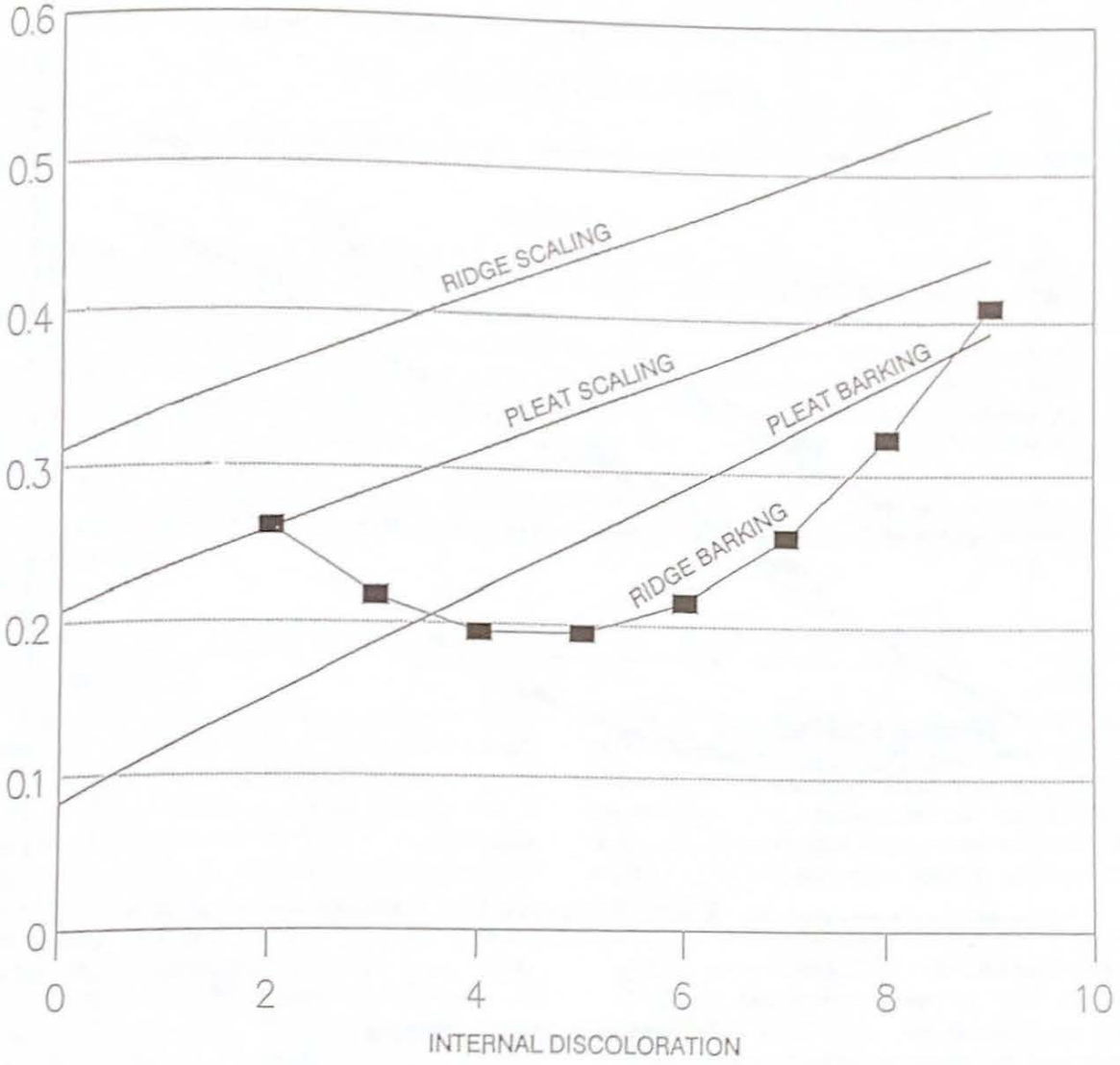


Fig 5. Relationships between scaling and barking of troughs (pleats) and crests (ridges) (y axis is the proportion of cactus surface area exhibiting injury symptoms) versus depth of internal discoloration (mm) for saguaro cacti at Saguaro National Monument.

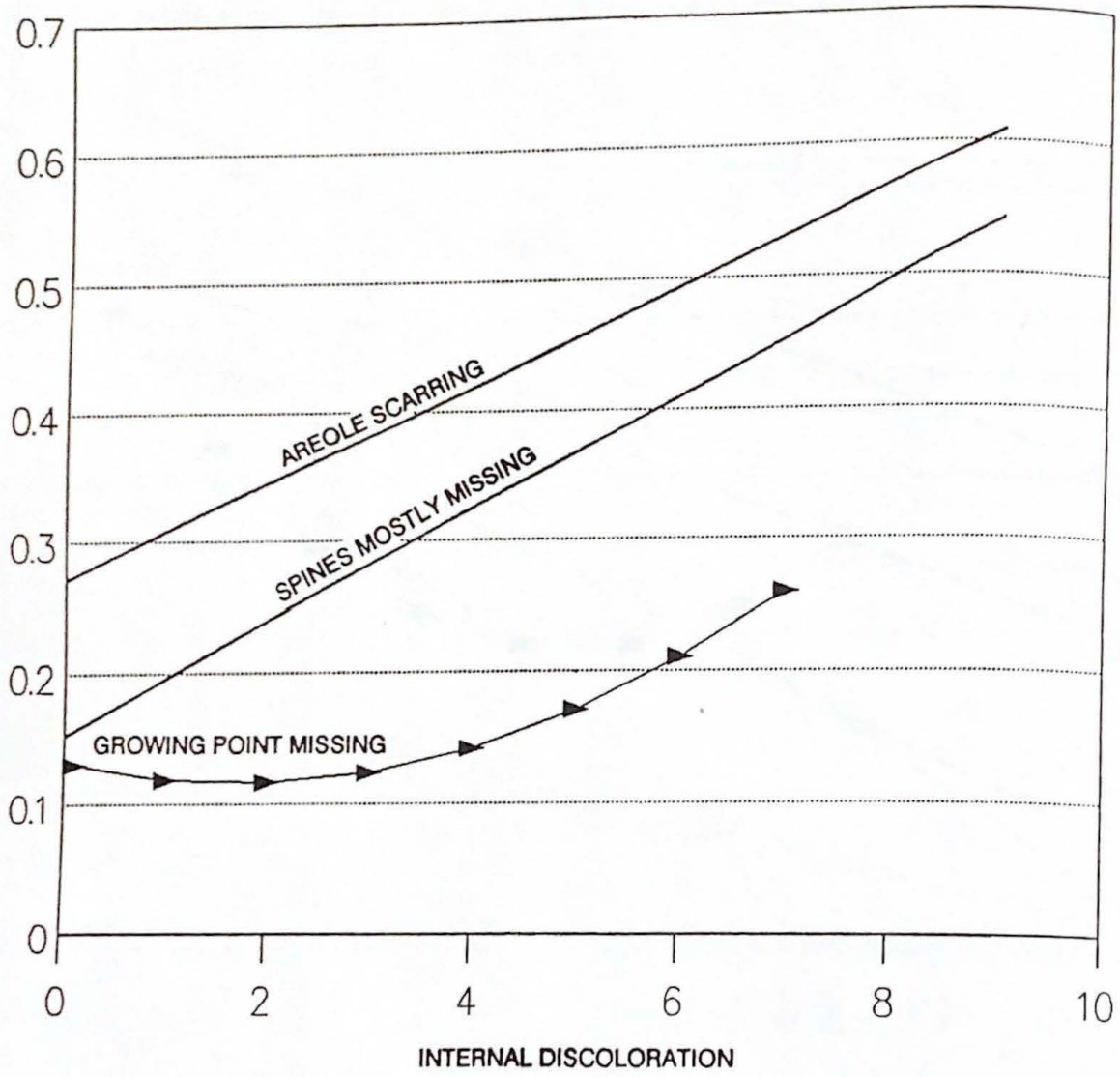


Fig 6. Relationships between areole scarring, spines mostly missing, and growing point missing (y axis is the proportion of cactus surface area exhibiting injury symptoms) versus depth of internal discoloration (mm) for saguaro cacti at Saguaro National Monument.

Ecophysiological and Toxic Element Studies of the Saguaro Cactus in Saguaro National Monument

Kate Lajtha and Kristin A. Kolberg

ABSTRACT

Nutrient relations, gas exchange, and heavy metal chemistry of healthy versus declining saguaro cacti (*Carnegiea gigantea*) were examined in six long-term monitoring plots in the Rincon Mountain District of Saguaro National Monument. Results suggest that decline can first be measured as a loss in maximum carbon dioxide (CO_2) uptake, even before spine loss is observed, during seasons of high water availability and temperature when natural environmental limits on physiological activity are removed. South-exposed tissues are physiologically more active in terms of CO_2 uptake and are the first to show signs of epidermal browning. Water-use efficiency was similar between healthy and declining tissues. Concentrations of heavy metals (lead, cadmium) were well below reported toxicity levels and thus are probably not a factor in the decline. Additional research is needed before definite conclusions documenting the biology and physiology of the saguaro decline can be made.

INTRODUCTION

The saguaro cactus (*Carnegiea gigantea*) in the Rincon Mountain District (RMD) of Saguaro National Monument (SNM) has been declining since the early 1940s. A symptom commonly observed on cacti in affected areas of the RMD is a browning of the epidermis that originates at the areoles near the base of the cacti, beginning on the south-facing ribs and gradually spreading around the cactus to north-facing ribs. Declining cacti also demonstrate epicuticular wax buildup and spine loss (Duriscoe and Graban, this volume). The causal agent of this browning is unknown. Steenbergh and Lowe (1977, 1983) present evidence that this browning is due to natural freeze damage, although links to Tucson urban pollution have more recently been suggested (Stolte 1988).

Other studies in progress sponsored by the National Park Service Air Quality Division are focusing on the possible role of air pollutants in altering ecosystem function (e.g., cyanobacterial-lichen soil crusts [see Belnap, this volume]) and the health and resistance of saguaros to natural stresses. The purpose of this study was to examine nutrient cycling and nutrient chemistry in the ecosystem, and nutrient relations, gas exchange, and heavy metal chemistry of healthy versus declining cacti. Specific goals of this study were to:

1. Document physiological differences between healthy and declining cacti, measured as the diurnal course and maximum rates of nocturnal carbon dioxide (CO_2) uptake and diurnal water loss patterns, and to correlate physiological parameters with visible signs of injury, to determine if decline can first be observed as a physiological decrease in CO_2 uptake and/or an increase in transpired water loss;
2. Determine if decline begins first in the physiologically most active tissues, in part to examine the alternate hypothesis that light radiation (such as elevated ultraviolet [UV-B] wavelengths) could

have a direct negative effect on cactus health;
3. Determine if heavy metal pollution (lead, cadmium) from precipitation-borne smelter emissions is a cause of the saguaro decline, by comparing trace metal concentrations in both healthy and declining tissues to known levels of toxicity and injury.

METHODS

Site Selection

During August 1990, six intensive study sites were chosen in the RMD from those established by Duriscoe and Graban (this volume). Plots were chosen to span the range of calculated injury indices (Table 1). At least seven cacti from within each plot that had not already been tagged for long-term monitoring were marked for physiological studies and tissue nutrient analyses.

For cacti chosen during 1990, ribs were chosen from around the entire circumference and specific locations at breast height were permanently marked for gas-exchange analysis. Rib surface azimuth was measured with a compass. During 1991, six sample locations were selected on each cactus to reflect tissues facing true north (345°) and true south (165°), and azimuths at 60° increments in between.

Gas Exchange Analyses

Gas exchange measurements were conducted with a LI-COR closed-system Infrared Gas Analyzer (IRGA) that had been fitted with a custom plexiglass chamber top that was lined with clear teflon tape. Measurements were made during an unusually wet summer (1990) as well as an unusually dry summer (1991). Carbon dioxide and hygrometer calibration was conducted using standard gases by LI-COR, Inc., prior to the field season. Seals between the chamber top and the marked surface of each cactus were made with double layers of closed cell foam. "Breath tests" were performed before each logged run to ensure that a full seal had been obtained between chamber and plant as outlined by LI-COR, Inc.

Because cacti use the CAM (Crassulacean Acid Metabolism) photosynthetic pathway and thus open stomata and have active CO_2 uptake during the night, initial measurements during the summer of 1990 were made to determine the nocturnal timing of gas exchange. Measurements were obtained from ca 6:00 pm to 8:00 am the following day for four cacti at one site (Mica), and six at another (plot 2) to monitor the time course of nocturnal CO_2 uptake and to determine if a maximum rate was maintained for a length of time that could be used for between-plant comparative measurements. Initially only nocturnal CO_2 uptake and the timing of morning stomatal closure was measured, rather than daytime respiration measurements after stomatal closure. Once a time interval for maximum CO_2 gain was determined, cacti within other plots were measured during this time frame in order to compare tissues and different cacti. At least two measurements were made of each rib chosen on each cactus during the night's run, and were averaged. One control plant at one site (plant 3, Mica) was used as a reference plant, and was measured at a predetermined time after each night's plot run to be able to assess the validity of pooling data from different days.

Nutrient/Elemental Analyses

At the end of the sampling season, tissue samples were taken from the north and south sides of selected cacti for trace metal chemistry. All tissues were frozen and sent to Boston University for processing. Tissues were freeze-dried for four days, separated from cuticles, and divided into chlorenchyma and parenchyma. Tissues were ground in an agate mortar. Samples and NBS (National Bureau of Standards) citrus leaf standards were digested in teflon vessels using a nitric acid flux on a hotplate using cleanroom techniques, stored in virgin-resin HDPE bottles, and analyzed using graphite furnace atomic absorption. Ultrapure acids, deionized water, and pyrogen-free pipette tips were analyzed for purity against standards. Concentrations were determined using standard additions to eliminate matrix effects.

Calculation of an Injury Index

An injury index was chosen to reflect the percent damage on tissue surfaces within the areas chosen for gas-exchange analysis. Surfaces were rated for percent orange to orange-brown scaling (the appearance of a red-orange epicuticular wax buildup), with chlorenchyma still visible through the cuticle, as well as for the more severe barking (a larger buildup of epicuticular waxes with a red-brown to black appearance) of tissues. Tissues were ranked first for percent

cover of damaged area, which could include either barking or scaling; this percentage was divided by 10 to become the first number in the injury index. The second number corresponds to the percentage of barking in the total cover. Thus an injury index of 2,05 means that 20% of the total surface area was damaged, with 5% barking.

Statistical Analyses

Statistical analyses were performed using SAS procedures on a Boston University mainframe computer. Comparisons between cacti and correlations among variables were performed using analysis of variance (PROC ANOVA) and reported as significant at the 0.05 level.

RESULTS

In general, the more south-facing tissues (azimuths 165°, 105°, 225°) had significantly higher injury indices than north-facing tissues, a fact also reported by Duriscoe and Graban (this volume). Thus gas-exchange measurements were compared both by tissue orientation as well as the estimated injury index.

During August of 1990, CO_2 uptake rates in healthy saguaros became positive at ca 4:00 to 8:00 pm, and either increased slowly or remained relatively constant at a maximum rate at least two hours on each side of midnight (Fig. 1). Thus all rates to compare different cacti within plots were made during these hours, with each saguaro's ribs measured twice over this span. During this season of greatest water availability, tissues on the south side of healthy saguaros had higher CO_2 uptake maxima and remained active longer than healthy tissues on the north side (Fig. 1). In saguaros with visible browning and injury indices over 2,00, south-facing ribs had lower rates of uptake than north-facing ribs (Fig. 2). The extent of decreased uptake from south-facing ribs was directly related to the extent of browning as measured by the injury index. During this season, there were significant correlations ($P < 0.01$) between CO_2 uptake maxima and both injury index and rib azimuth.

Because we had initially hypothesized that decline symptoms might represent injury to stomatal function that would be reflected in rates of water-use efficiency (WUE), we calculated a measure of instantaneous WUE, defined as the ratio of photosynthesis to transpiration. No correlation was seen between WUE and injury index even in plants with a wide range of injury indices and CO_2 uptake rates (Fig. 3).

During the dry summer of 1991, CO_2 uptake rates were clearly limited by the availability of water and were significantly lower than 1990, and many plants did not show positive CO_2 gain at any time during the night. For all plants measured during this season, daytime respiration losses were greater than nighttime CO_2 accumulation. However, CO_2 uptake was still marginally related to injury index (Fig. 4), although this effect was not as pronounced as during the summer of 1990, when CO_2 uptake rates would be expected to be at a maximum of physiological potential.

Heavy metal concentrations in both green and browning tissues were very low, well within the range of concentrations seen in plants considered to be free of trace metal contamination. Brown tissues had slightly, although not significantly, higher levels of lead and cadmium than green tissues (Table 2).

DISCUSSION

Results suggest that saguaro decline can first be measured as a loss in maximum CO_2 uptake, even before spine loss is observed, during seasons of high water availability and temperature when natural environmental limits on physiological activity are removed. This decrease appears to be due to a general stomatal closure during the night, as water loss appears to be similarly reduced, with WUE not directly related to injury index.

It has been suggested that elevated ultraviolet (UV-B) radiation might be the cause of decline in saguaros, which would fit in well with observed patterns of epidermal browning beginning on south-exposed tissues (L. S. Evans, pers. comm.). An alternate hypothesis would be that decline begins first in the physiologically most active tissues, as is common for tissues exposed to both natural and anthropogenic stresses, and that light radiation per se is not the proximate cause of saguaro decline. Research results reported here do indeed confirm that in healthy saguaros, south-exposed tissues are physiologically more active in terms of CO_2 uptake during seasons of high water availability. However, it could

not reliably be determined if water loss was also greater on south-exposed tissues. To definitively distinguish between hypotheses, analysis of plants both with and without UV-B screens that were in place for several years would need to be made.

Heavy metal concentrations were well below reported toxicity levels. Although levels were marginally greater in declining than in healthy tissues, this is probably a concentration effect due to chlorophyll loss, rather than due to metal toxicity. However, the only way to truly assess the respective roles of potential atmospheric pollutants such as heavy metals is to compare levels in these declining populations to levels in populations of healthy saguaros. Similarly, the only way to truly assess the role of nitrogen deficiency/saturation in these saguaros is to compare levels to populations far from atmospheric sources of nitrogen, or at least in populations observed to be healthy. Levels of sulfur were not measured in these tissues; due to smelting operations and reported low pH's for rain at nearby weather stations, toxicity due to high levels of sulfur are the next most likely culprit.

CONCLUSIONS

It is recommended that the following research be completed before definite conclusions documenting the biology and physiology of the saguaro decline be made:

1. Nutrient analysis (specifically, tissue nitrogen concentrations) of healthy populations of saguaro to establish a baseline for analysis of declining populations;
2. Analysis of sulfur concentrations and sulfur isotope ratio analyses in saguaro tissues to determine if excess sulfur deposition is a cause of premature senescence;
3. Tissue analyses of reference plants (e.g., *Larrea tridentata* [creosotebush], *Prosopis velutina* [velvet mesquite]) to expand the analysis of air pollution effects to the entire desert community;
4. Regional analyses over the entire range of the saguaro to assess population structure, tissue browning, and physiological activity;
5. Physiological analysis (e.g., CO_2 uptake) of saguaros protected from ultraviolet (UV-B) wavelengths (by glass shields) to determine if light, or some component of light radiation, directly causes premature senescence in saguaro tissues, or if decline symptoms are simply first observed in the physiologically more active tissues, and is directly caused by some other, yet unknown agent.

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Table 1. Study sites chosen from those established by Duriscoe and Graban (this volume). Plots were chosen to span the range of calculated injury indices.

High injury index:	Intermediate injury index:	Low injury index:
Plot 15 (39.6)	Plot 2 (12)	Plot 10 (5.2)
Plot 5 (22.1)		Plot 9 (4.1)
		Mica (no calculated index)

Table 2. Comparisons of lead (Pb) and cadmium (Cd) concentrations in ppm (μg/g) found in saguaro chlorenchyma tissues to published values of other plants from both contaminated and uncontaminated sites.

Plant tissue	Pb		Cd	
	range	$\bar{x}$	range	$\bar{x}$
saguaro (green tissues)	0.05-0.30	0.157	0.01-0.03	0.022
saguaro (browning tissues)	0.12-0.59	0.285	0.01-0.04	0.025
cereal grains, edible	0.10-1.00	0.36	0.01-0.10	0.03
plants from contaminated sites	27-1506		1-7	

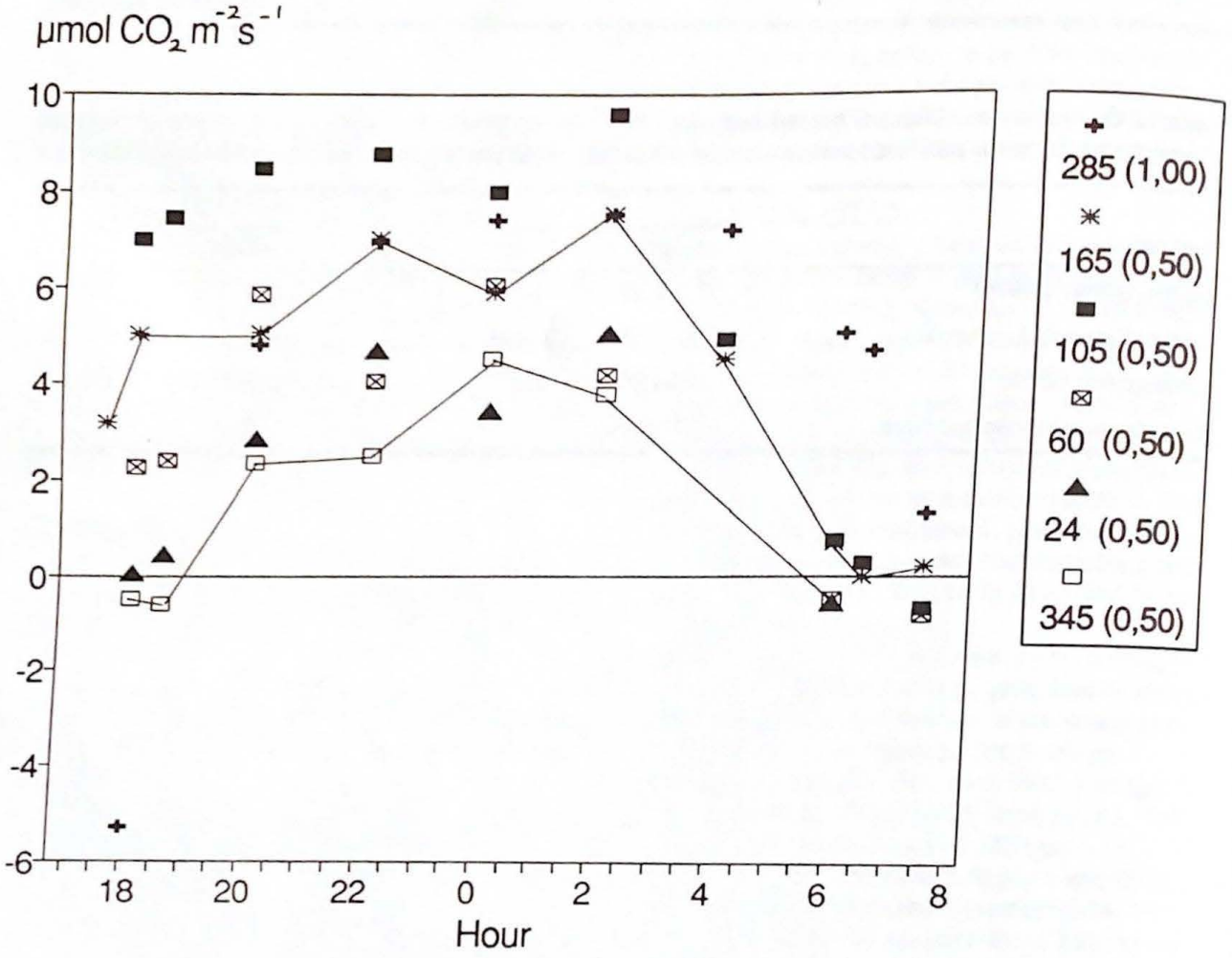


Fig. 1. Daily time course of photosynthesis in a healthy saguaro during the wet (Aug 1990) season. Legend values are azimuth (injury index), with 345° as true north and 165° as true south.

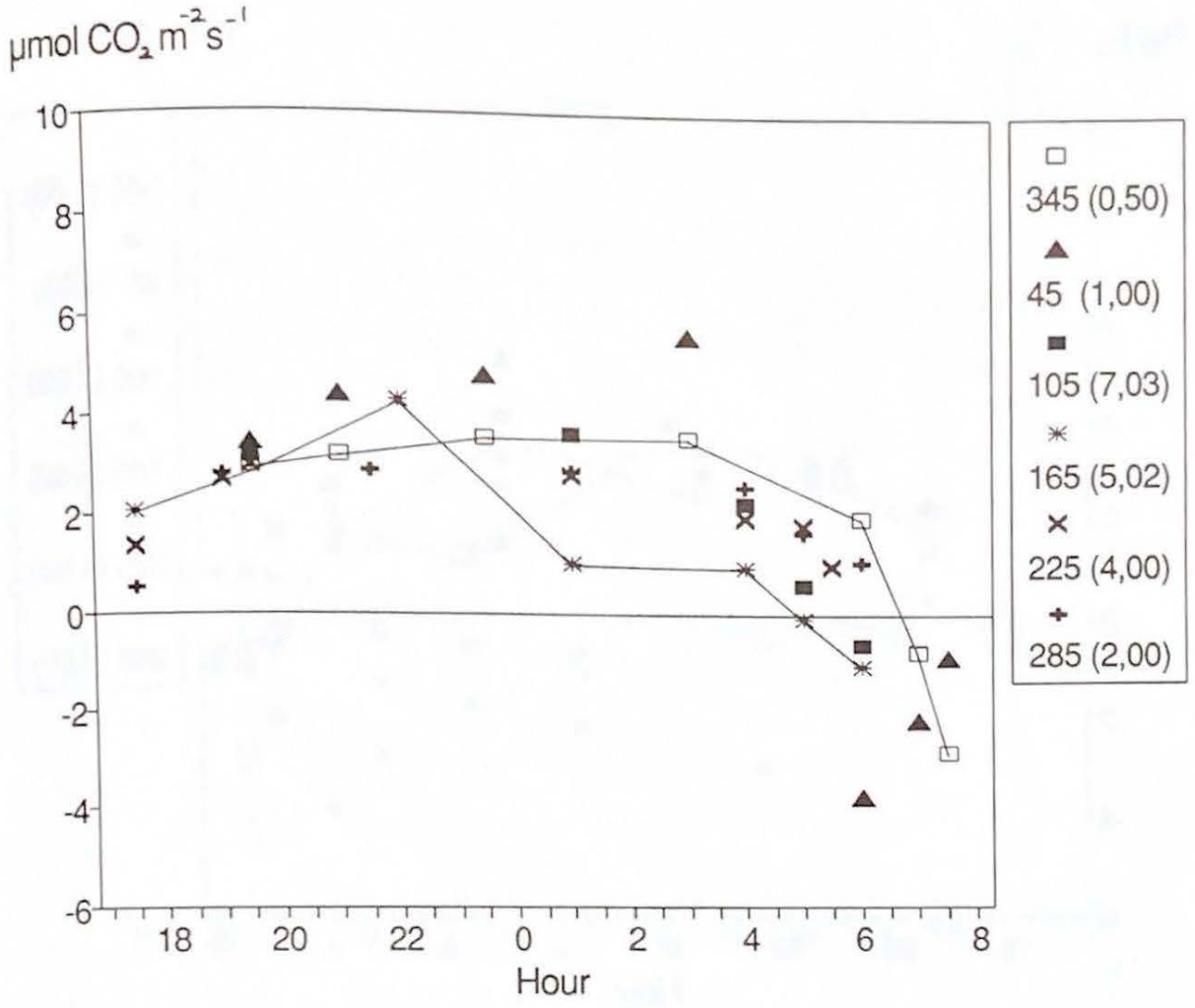


Fig. 2. Daily time course of photosynthesis in a declining saguaro during the wet (Aug 1990) season. Legend values as in Figure 1.

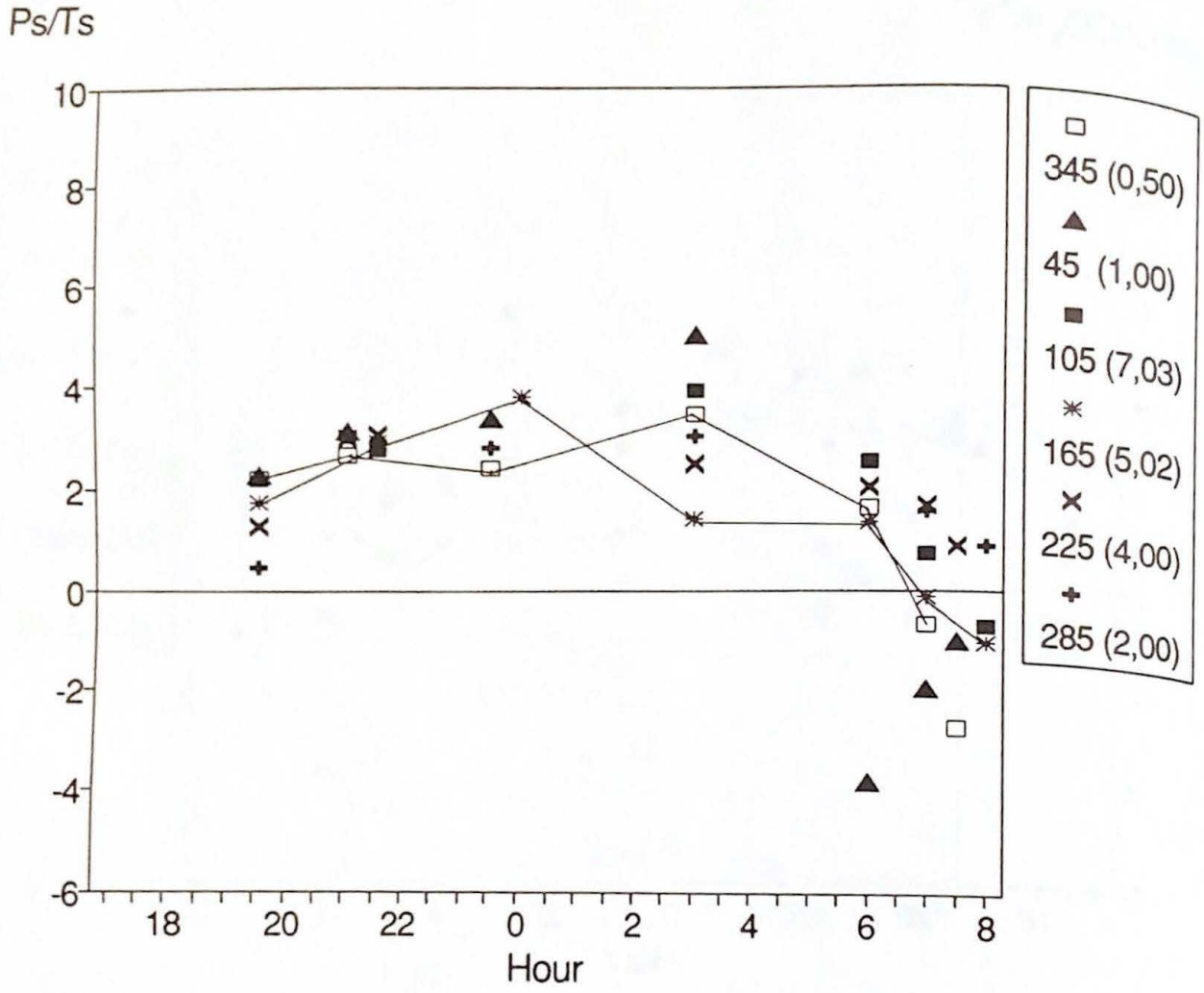


Fig. 3. Water-use efficiency, measured as the ratio of photosynthesis to transpiration, in a declining saguaro during the wet (Aug 1990) season. Legend values as in Figure 1.

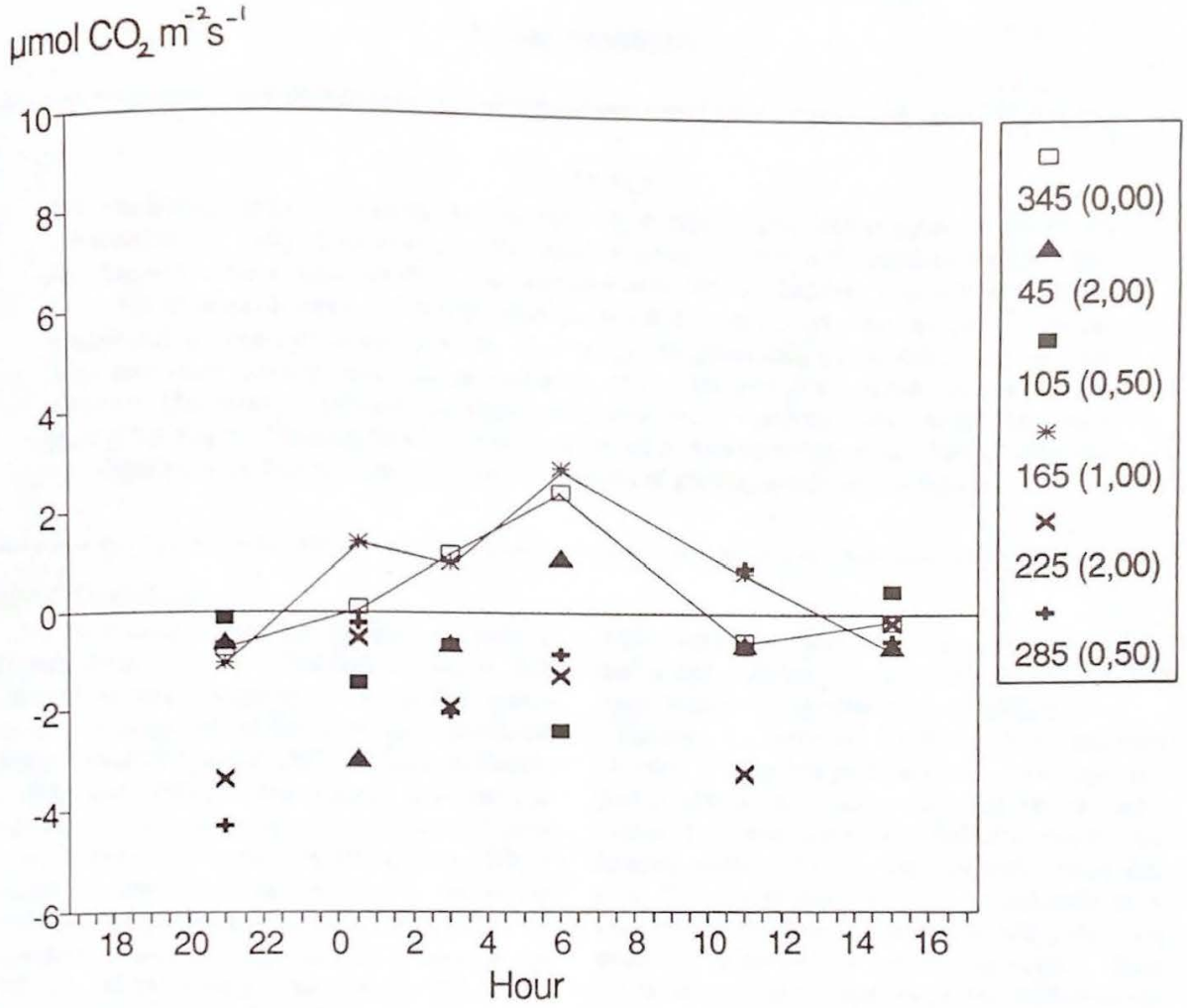


Fig. 4. Daily time course of photosynthesis in a healthy saguaro during the dry (Aug 1991) season. Legend values as in Figure 1.

Influence of Livestock Grazing on Saguaro Seedling Establishment

Fareed Abouhaidar

ABSTRACT

The relationship between livestock grazing and young saguaro (*Carnegiea gigantea*) plants was examined in this study. Field work was conducted in Saguaro National Monument (Rincon Mountain District) where a fence divides a homogeneous area into two portions, grazed until 1958 and 1978. The hypothesis tested was that if cattle grazing had no effect, then the number of saguaros and/or their age distribution would be the same on the two differently grazed areas. Ten belt transects were established on each area parallel to the fence. Saguaros were probed for, counted and measured. Data analysis indicated that significantly more young saguaros existed on the area free of grazing the longest (20 years longer). Grazing appeared to influence saguaro population age structure. Saguaros should be considered in the management of grazing in some desert habitats.

INTRODUCTION

The giant saguaro cactus (*Carnegiea gigantea*) is the most distinctive plant of the Sonoran Desert. It is a drought-adapted, tropically-derived species that is sensitive to severe freezes like those that occur in the Rincon Mountain District (RMD) of Saguaro National Monument (SNM), where saguaros grow close to their eastern range boundary. The saguaro is highly responsive to environmental change and offers insight into past and present ecology of associated desert plants (Steenbergh and Lowe 1977). Generally, saguaro populations have been declining since the early part of this century, resulting in the loss of spectacular dense stands of large plants. These stands contained few young saguaros to replace dying older plants. A series of hard freezes early in the century caused much of the damage (Steenbergh and Lowe 1977).

Surprisingly little is known about the effect of cattle grazing on saguaros. Cattle (*Bos taurus*) have been suspects in the saguaro decline, and have been eliminated from SNM. Yet no study has compared a grazed area to an adjacent ungrazed one. Such a study would likely eliminate variables such as pollinating bats, rodents, pollution, climate, and soil that might mask the long-term effects of grazing.

Grazing may have had subtle effects on long-term survival of saguaro populations. Seedlings and young plants are usually found growing under "nurse" trees and shrubs that shelter saguaros from foraging wildlife, drought and cold during their first years (Steenbergh and Lowe 1977). Saguaros grow very slowly the first two decades; when they are small they might be very vulnerable to cattle. Grazing on the monument began in the late 1800s and the present study aimed to examine effects of past cattle grazing on saguaros (Abouhaidar 1989).

Field work was conducted on the RMD where a fence divides an environmentally homogeneous area into two portions, one grazed until 1958 ("ungrazed" area), and the other until 1978 ("grazed" area). The limited width of the study area (100 m) helped reduce risk of variation as one moved away from the base of the mountains. This also minimized the possibility of cattle use tapering off from east to west

with increasing distance from a nearby spring and salt lick.

METHODS

Ten transects were placed on each area. Transects were 2 m wide, 220 m long and 3 m apart, and parallel to the fence at right angles to washes. Proximity to the base of the mountain mandated that transects be placed close together. Twine was laid to represent the center of the transect. Straightness was checked by sighting down the twine as well as measuring distance to the previous transect. Wherever the transect ran through a large, low tree, the twine was laid around it. At the other side, the path was picked up by sighting through the tree.

The surface, within a meter of the twine, was closely examined for small saguaros by walking the length of the transect. Where the twine went around a tree, its intended path through the obstacle was sighted and examined. Small saguaros were measured with a tape measure, larger ones with an Abney level.

To estimate the age of each saguaro, growth rates established by Steenbergh and Lowe (1983: Tables 2-10) were used. Growth of saguaros varies with climate, especially rainfall, and with habitat (rocky, non-rocky, exposure, etc.). The growth rate table was derived from saguaros from non-rocky habitats in the RMD, which approximate those of the study site. Any inaccuracies that might have resulted apply to all saguaros on both sides of the fence and thus did not affect the final outcome.

For each side of the study area, the saguaros were divided into 10-year age categories (11-20, 21-30, etc.), except for those scarce ones >70 years old, which were combined into one category. The population in the ungrazed area was considered to be the control with the expected distribution, and the grazed population was compared to it (Table 1). The log-likelihood ratio test was used to assess goodness-of-fit without bias (Zar 1984).

RESULTS

Thirty-four saguaros of various size were found on the transects of the ungrazed area, and 29 on the grazed area. Statistical analysis indicated that the grazed sample of saguaros came from a population with different age distribution than the ungrazed sample. A plot of saguaro numbers by age class indicated that the major difference between the two populations was in the youngest class (11-20 years). Saguaro numbers in older classes appeared similar (Fig. 1).

A new set of hypotheses was proposed to test the possibility that saguaros ≥ 21 years of age had the same age distribution in the two plots. Statistical analysis indicated that among saguaros in this age class, the grazed sample came from a population similar in age distribution to the ungrazed sample ($P = 0.05$). This means that all the significant variation among the two samples was caused by the difference in the number of saguaros in the youngest age class (11-20 years).

DISCUSSION

The difference in the saguaro population age structure between the grazed (east) and ungrazed (west) areas seems to point toward cattle grazing or some other unknown factor(s). Germination and survival of new saguaros was probably largely suppressed with grazing. In 1958, the fence was built and cattle removed from the west side, providing the area a chance to recover for >30 years. With no grazing, the habitat improved for saguaros, which germinated and survived at a higher rate than previously. Few saguaros (three) appeared during the first decade (1958-68) while the habitat was still recovering. In the following decade (1968-78), a marked increase in saguaro germination and growth occurred, as evidenced by the 15 individuals that are now (1988) 11-20 years old. In the third decade (1978-1988), this trend may or may not have continued depending on climatic and/or other conditions. Plants germinating during this period are still too small to be reliably detected.

If the same scenario applies to the grazed plot, then the following has taken place or will, assuming other variables do not change. Grazing stopped in 1978. A lag in saguaro recovery occurred during the first decade (1978-88). Between 1988 and 1998, more saguaros should germinate and survive, and a large increase will be visible by 2008. At present (1988), 10 years after grazing was discontinued, the east side of the fence is in the same condition that the west side was in in 1968. Only two small saguaros 11-20 years old were found there, compared to 15 on

the west side. These two germinated and grew while grazing was still taking place. Thus, 13 small saguaros may have been "lost" to grazing, a significant loss according to the statistical tests. A test excluding the youngest age category revealed no difference between the two populations of older saguaros (≥21 years). Thus, grazing does not seem to affect older saguaros.

Survivorship of saguaros decreases with time. Not all 15 young saguaros found on the west side of the fence will survive to adulthood. Natural elements will take their toll. But more saguaros are likely to survive from 15 (ungrazed area) than from 2 (grazed area) small plants. Grazing has probably destroyed most of the young saguaros needed for population stability over time. It is possible that grazing may affect old saguaros, perhaps through erosion or other factors. If so, a 20-year difference in grazing termination is apparently not enough time for differences in the two adult populations to be expressed.

The results of this study apply only to areas similar to the study site—areas close to the cold-affected boundary of the saguaro's range, where small saguaros are dependent on nurse plants for protection from freezing temperatures. Also, results apply only to relatively flat areas that are heavily grazed; steep rocky areas experience less use by cattle, and large rocks often shield small saguaros from trampling.

Cattle may have damaged saguaros (especially young ones) on the site in several ways. In hot weather, cattle tend to rest more often in the shade, possibly intruding on the habitat of small saguaros that require nurse plants in their first years of life (Arnold and Dudzinski 1978). Cattle may also graze on nurse plants and reduce their protective cover (Steenbergh and Lowe 1983), cause erosion, and directly trample small saguaros. Occasionally, young saguaros are eaten by cattle (Niering and Whittaker 1965).

MANAGEMENT IMPLICATIONS

The surest and easiest, but most controversial, way of protecting saguaro populations from cattle grazing is to simply eliminate grazing from saguaro habitats. This may not be possible on most public lands, but less drastic measures can also be taken to protect significant saguaro populations. Saguaro National Monument has properly taken the conservative course by removing all cattle. Even if saguaros were totally immune to the effects of grazing, cattle do not belong in a location where efforts are being made to maintain natural processes unaffected by outside influences. Due to resistance by ranchers, cattle grazing was removed piecemeal, inadvertently allowing for comparisons between adjacent areas.

The area that was used for this study should be monitored in the future to observe changes in the number of young saguaros, especially on the more recently grazed (east) side of the fence. If the fence is removed in the future, its location should be marked for the obvious reason of continuing such studies. Exhibits at the SNM visitor center should mention cattle as one of the agents that may have decimated saguaros in the RMD. Exhibits should also mention that grazing should be carefully regulated in saguaro habitats outside the monument.

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Table 1. Saguaro numbers on the constantly grazed site and the site at which grazing was removed. Numbers of saguaros on the site ungrazed since 1958 were adjusted to give the same total sample size (expected distribution) as on the site grazed until 1978. Actual number of saguaros found on the site ungrazed since 1958 was 34.

Age category (yrs)	Observed No. (Site grazed until 1978)	Expected No. (Site with grazing removed in 1958)	
		>10 years	>20 years
11-20	2	12.8	—
21-30	5	2.6	4.3
31-40	2	2.6	4.3
41-50	3	2.6	4.3
51-60	6	5.1	8.5
61-70	6	1.7	2.8
>70	5	1.7	2.8
Totals	29	29.1	27.0

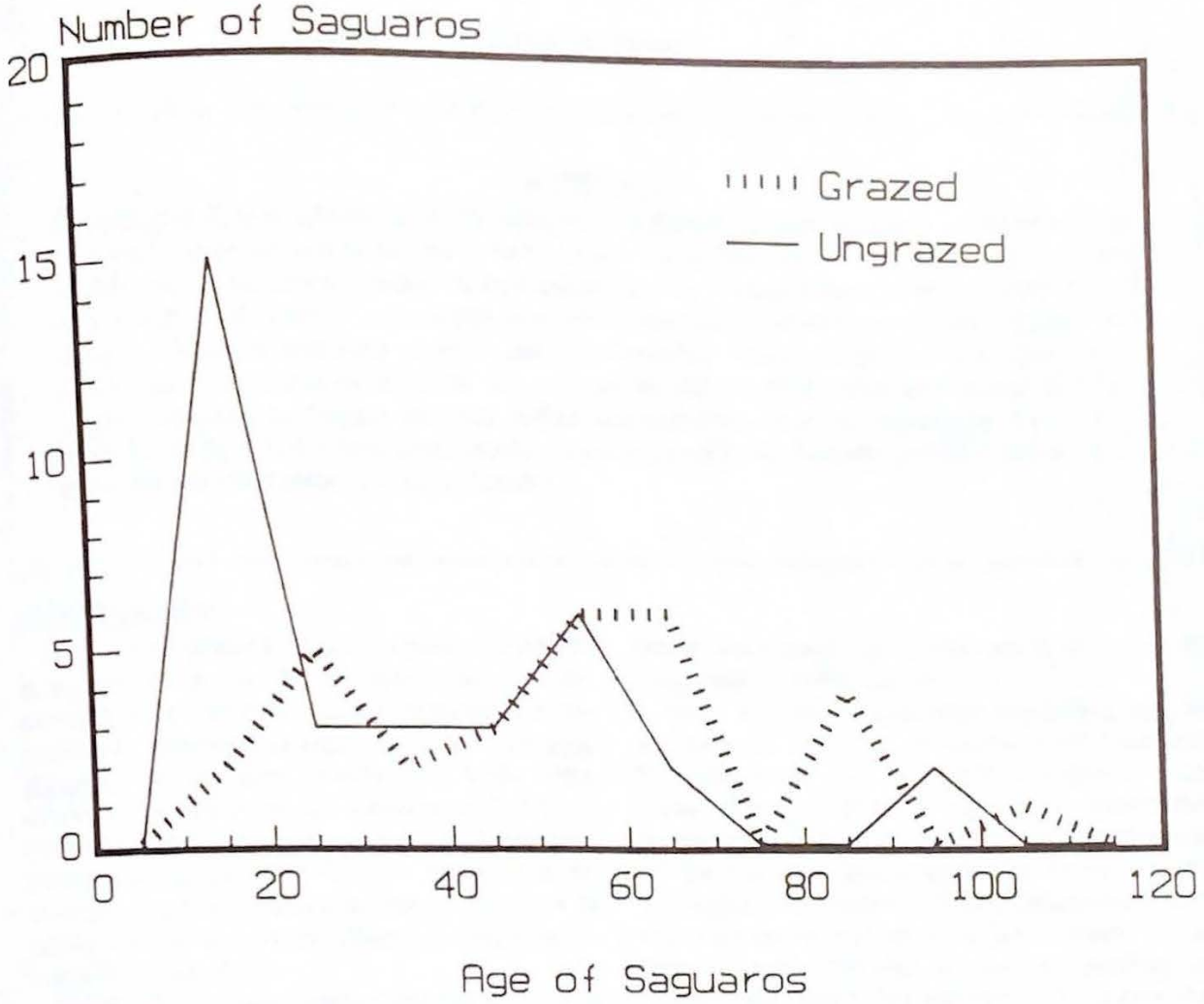


Fig. 1. Plot of saguaro numbers by age class in grazed and ungrazed areas.

Effect of Infrared Reflectance on Stem Temperatures of Saguaros

Mark W. Smith

ABSTRACT

The role of high near-infrared (near-IR) reflectance in the temperature regulation of saguaro cactus (*Carnegiea gigantea*) was investigated. Two independent methods were used to determine the effect of high near-IR reflectance on saguaro stem temperatures: (1) measurement of surface temperatures of two individual plants of comparable size and health, one of which was partially shaded by a canopy of loose sun-screening material; and (2) a numerical solution of the time-dependent energy balance (or heat transfer equation) for saguaro was determined. High reflectance at near-IR wavelengths was found to decrease the peak surface temperatures reached by saguaros by 3.2 ± 1.5° C under the fairly mild environmental conditions encountered in the Sonoran Desert at 940 m elevation during late September and early October.

INTRODUCTION

The research described in this paper was conducted to answer two specific questions related to the role of high near-infrared (near-IR) reflectance in the temperature regulation of saguaro cactus (*Carnegiea gigantea*): (1) How large, quantitatively, is the effect of high reflectance at near-IR wavelengths (0.7-1.5 μ [microns]) in reducing the peak daytime surface temperatures of saguaros, and (2) How important is the IR reflectance in comparison to other factors such as convective cooling and reemission of longer wavelength IR radiant flux?

Radiant flux of wavelengths from 0.4 to 0.7 μ is sometimes referred to as photosynthetically active radiant flux (PAR), since it is capable of promoting photosynthesis. Photosynthetically active radiant flux corresponds roughly to visible radiant flux, or light, since the human eye is also sensitive to these wavelengths. Infrared radiant flux of wavelengths from 0.7 to 1.5 μ will be referred to as "near-IR" flux, since it is near in wavelength to visible light. Infrared radiant flux at still longer wavelengths, from about 5 to 25 μ, will be referred to as "thermal-IR" flux. Thermal-IR flux is emitted by all objects, including clouds, the ground, and plants, and is related to the temperature of these objects.

About 40% of the total solar output is at near-IR wavelengths. Since this radiant flux is not photosynthetically active, it would serve primarily to warm plants, if it were absorbed. One might suspect that the rejection of near-IR flux is especially important for desert plants, which must tolerate intense sunlight and high air temperatures while simultaneously limiting evaporative cooling to conserve water. Thick-stemmed succulents such as agave and cacti do not transmit any radiant flux and can limit the heat load imposed by the sun only via high reflectance.

Absorptance as a function of wave number, or inverse wave length, is shown in Figure 1 for saguaro, *Agave americana*, and *Opuntia laevis*. The product of absorptance times solar irradiance is plotted in Figure 2 for saguaro and *Agave lecheguilla*. High near-IR reflectance reduces the total amount of solar energy absorbed by saguaros by 15-20%.

In addition to reflection, absorption and/or reradiation of radiant flux, various other factors influence the temperature of saguaros. Convective cooling by

the air, heat conduction into and out of the stem, and heat storage within the massive fleshy stem are all important. All may be related to energy balance. Conservation of energy requires that any difference between the energy flowing into and out of a fixed body of matter be balanced by an increase or decrease in the stored energy of the body. The change in the stored energy is given by the product of heat capacity and temperature change. The basic terms important for saguaro in the equation for energy balance are: solar input + thermal-IR input – thermal-IR output ± convection = heat capacity x temperature change (Gates 1980).

METHODS

Field Measurements

The field measurement site was located approximately 50 m east of the National Park Service (NPS) air quality station at the Rincon Mountain District (RMD) of Saguaro National Monument (SNM) at latitude 32° 10' N, longitude 110° 44' W at 940 m elevation. All data sets were collected between 27 September 1988 and 2 October 1988, very shortly after the autumnal equinox, so days and nights were about equal. No rain fell during the period of measurements and very few clouds were present. Overall, the weather was extremely stable.

The saguaro chosen for study had no arms and stood on level ground free from the shade of neighboring plants. The cactus was 2.25 m in height, with mean diameters of 27.5 cm at a height of 0.5 m above ground, 29 cm at a height of 1 m, and 31 cm at 1.5 m. The cactus had 18 ribs over its upper section, each 4 to 4.5 cm deep.

Temperatures of the cactus were measured at 38 locations with type-T (copper-constantan) thermocouples. Temperatures were measured at 29 locations inside the cactus with 36-gauge wire and at 9 locations on the surface with 30-gauge wire. The thermocouples were located to provide cross-sectional temperature distributions at heights of about 0.5, 1.0, and 1.5 m. The output voltages of the thermocouples were digitized, converted to temperature readings, and recorded automatically at 30-min intervals. The error in the thermocouple measurements was estimated at ± 0.8° C in accordance with standard error values published by Omega Engineering, Inc.

Hemispherical solar irradiance, air temperature, and wind direction data were obtained from the NPS air quality station at RMD. These values were available at 5-min intervals. Wind speed was measured at 1 m above ground level with an anemometer located approximately 3 m from the cactus chosen for study. The wind speed was sampled at 10-sec intervals and averaged over a 15-min period. Ground surface temperatures were measured at 15-min intervals with a 36-gauge type-T thermocouple covered with a thin layer of soil at the surface of the ground, 2 m west of the cactus.

An awning to provide partial shade for the saguaro under study was erected from 28 September 1988 to 30 September 1988. The framework was made from 0.5 in. diameter electrical conduit. The shading material was lightweight plastic netting obtained from a local nursery. The framework and the netting were painted white so that they would not be unduly heated by the sun. An Eppley model 8-48 radiometer was used to monitor the amount of shade provided by the awning. Two layers of netting produced approximately a 15% decrease in the amount of direct normal solar irradiance falling on the plant.

An Everest 112C pistol grip infrared thermometer (IRT) was used to measure temperature variations over the surface of a single rib and to make comparisons between the surface temperature of the saguaro under study and a reference saguaro. The thermometer had a 3° field of view. An emissivity setting of 0.98 was used. The reference saguaro was located near the air quality station and was about 4 m in height.

Computer Model

To develop a computer model of the time-dependent temperature distribution of saguaro, the equation of energy balance was first differentiated with respect to time to yield an equation describing the dynamics of energy flow or heat transfer. The saguaro under study was approximated by a tapered cylindrical solid, and this solid was divided into a grid of finite volume elements. The differential equation for heat transfer was then converted into a finite difference equation using a Crank-Nicholson finite differencing method (Press et al. 1988). The total differential operator was split into radial, vertical, and angular components. The resulting equations all have

the form of tri-diagonal matrices. This approach allowed the integration to be replaced by the much simpler process of inverting tri-diagonal matrices (Press et al. 1988). Each element of the grid was allowed to exchange heat energy by conduction with its nearest neighbors. Surface elements also exchanged energy by convection and radiative exchange with the environment.

Calculations were conducted on a grid containing typically 36 radial divisions, 24 angular divisions, and 8 vertical divisions, or a total of nearly 7,000 points. Time steps of typically 100 seconds were used. Calculations were carried out in double precision. The calculations were started using the measured 6:00 am temperature distribution of the cactus. The temperature at the 38 measured points was interpolated to fill out the calculational grid. Energy flow and temperature changes were then calculated for the next 24 to 72 hours using the measured environmental data as inputs.

The following values were used for the basic physical parameters in the model: saguaro surface emissivity = 0.98 (based on values for eight other cacti published by Idso et al. 1967); net solar absorption coefficient = 0.70 (average of values published by Gates et al. 1965 and Nobel 1978); stem thermal conductivity = 0.58 W/m/°C; stem density = 924 kg/m^3; and stem heat capacity = 3,885 J/kg/°C. The thermal conductivity, density and heat capacity of the stem were based on values published for compass barrel cactus (*Ferocactus acanthodes*) and were all set equal to 93% of the corresponding values for water at 35° C (Lewis and Nobel 1977).

Thermal-IR flux emitted by the sky was calculated from air temperature using a published formula (Idso and Jackson 1969). Thermal-IR flux emitted by the ground and other plants was calculated using the blackbody formula with emissivities of 0.95 and 0.97 (Wolfe and Zissis 1985). The thermal-IR flux re-emitted by the saguaro was also calculated using the blackbody formula. The convective heat transfer coefficient was calculated as a function of wind speed using published formulas (Lewis and Nobel 1977; Nobel 1978). To account for ribbing, the surface area available for convective exchange was set equal to 1.7 times the surface area of a smooth cylinder of the same diameter as the cactus.

RESULTS AND DISCUSSION

Field Measurements

Measured ground temperatures reached lows of 14-18° C near dawn and peaked at 50-55° C within one half to one hour after solar noon (time at which the sun reaches its highest point in the sky). Air temperatures ranged from lows of 17-22° C near dawn to highs of 32-34.5° C in midafternoon. Wind speeds followed a pattern of being nearly zero in the hours from midnight to just after dawn, increasing steadily after dawn to a high of 2.0-2.5 m/s in midafternoon, decreasing to near zero again after sunset, and picking up again to 0.5-1.0 m/s from 9:00 or 10:00 pm to midnight or 1:00 am. The measured hemispherical solar irradiance peaked at 920-940 W/m^2 at solar noon. The calculated value of direct normal solar irradiance peaked at 1,000-1,020 W/m^2 at solar noon.

Surface temperatures of west-facing sections of the saguaro with thermocouples implanted were measured between 3:00 and 6:00 pm and compared statistically with those of a reference saguaro. On two days when the 15% shade awning was not set up, the surface temperatures of the saguaro with thermocouples implanted averaged 1.4° C lower than those of the reference saguaro. On two days when the awning was set up, the average temperature differential was 3.1° C. This implies that a 15% reduction in direct solar irradiance produced an average decrease of 1.7° C in afternoon surface temperatures. The reduction in peak core temperature was only about 1° C. The standard deviation of the differential surface temperature measurements was 0.7-0.8° C. The maximum variation of temperature over the surface of a single rib was measured to be 1.0-1.5° C for sections of the cactus not receiving direct sunlight.

Calculated versus Measured Temperatures

The difference between calculated and measured values of the core temperature and average surface temperature was less than about ± 3° C for the period from sunrise to sunset. The model tended to underestimate midmorning temperatures and overestimate midafternoon temperatures. The agreement during the night was better than ± 1° C. The close agreement for night temperatures indicates that the calculated

values for convective cooling and thermal-IR exchange are probably very good. The calculated daytime response, which is dominated by solar input, was not as accurate.

Calculated and measured temperatures for selected times on 27 September 1988 and 28 September 1988 are plotted in Figure 3. A transect from the west-facing surface to the core at a height of 1 m is shown. The calculations were begun at 6:00 am on 27 September 1988 and ended at 6:00 am on 28 September 1988. The surface temperatures reached a minimum at 6:00 am. The core temperature fell about another 1° C and reached a minimum about an hour later. Surface temperatures on the west side of the plant peaked at 4:00 pm. The core temperature peaked at 8:00 pm. The error bars for the measured surface temperatures were set at ± 1.5° C in accordance with the measured variation in temperature over the surface of a single rib in late afternoon. The standard thermocouple errors of ± 0.8° C were used for the interior temperatures.

Calculated Effects of Varying Radiative and Convective Properties

The following parameters were varied in the computer model and temperatures were recalculated. The average solar absorption coefficient was decreased by 15%, from 0.70 to 0.60, to mimic the cooling effect of the 15% shade awning. The solar absorption coefficient was next increased to 0.85, to predict how warm the cactus would grow if its absorptance at near-IR wavelengths were equal to its absorptance at photosynthetically active wavelengths. The solar absorption coefficient was further increased to 0.98 to predict how warm the cactus would become if its absorptance at solar wavelengths were equal to its absorptance at thermal-IR wavelengths. The solar absorption coefficient was then reset to its normal value and the ribs were artificially removed by treating the cactus as a smooth cylinder. This decreases the surface area available for convective cooling, but leaves the area available to collect direct normal solar irradiance almost unchanged. Finally, the cactus was treated as a smooth cylinder and the solar absorption coefficient was increased to 0.85 simultaneously. The calculated effects of these changes on peak surface temperature and peak core temperature are summarized in Table 1.

The calculated increase in peak surface temperature produced by increasing the solar absorption coefficient from 0.70 to 0.85 was 3.2-3.3° C. Since the average absorption coefficient at photosynthetically active wavelengths is 0.85, this 3.2-3.3° C change may be interpreted as the temperature reduction attributable to high reflectance at near-IR wavelengths. The estimated uncertainty in this value is ± 1.5° C based on the measured variation in temperature over a single rib. The change in peak core temperature was only about 0.9° C.

Artificially removing the ribs produced a calculated 4.0-4.7° C increase in peak surface temperature. Simultaneously removing the ribs and increasing the absorptance produced a calculated increase of 8.0-8.8° C in peak surface temperature and a 2.0° C increase in peak core temperature. These results indicate that the enhancement of convective cooling due to the ribs is somewhat more important in minimizing peak temperatures than is the decrease in absorbed solar irradiance due to the high reflectance at near-IR wavelengths. Together, the two properties are very important in minimizing the peak surface temperature.

Calculated energy balance terms for a west-facing saguaro surface at a height of 1 m are plotted in Figure 4. As shown, convective cooling of a given section of the saguaro stem is at a maximum when absorption of incident solar flux is at a maximum. Convective cooling is proportional to the temperature difference between a given section of the surface of the plant and the surrounding air. The maximum temperature differential, and therefore maximum convective cooling, occur when the surface is facing the sun directly.

Emitted thermal-IR also peaks when the surface temperature of the plant peaks. However, absorbed and emitted thermal-IR are always in approximate balance. The value of the absorption coefficient at thermal-IR wavelengths is therefore a fairly neutral property in terms of energy balance. Decreasing this coefficient from 0.98 to 0.50 produced only a 0.3-0.7° C decrease in peak surface temperature and a 0.6° C decrease in peak core temperature.

Temperature fluctuations at the saguaro's surface propagate inward towards the core, with a time lag and with dampened magnitude. The core temperature of the saguaro under study was observed to peak near

8:00 pm. This was two hours after sunset and well after surface temperatures had peaked and begun to decline. Gates reported that the core temperature of saguaro peaks near midnight (Gates 1988). The time lag is expected to be greater for larger stem diameters. From Figure 3 we see that over a 24-hour period, temperature fluctuations at the surface were 25-31° C. However, temperature fluctuations at the core were only 7-10° C.

Air temperature is the greatest controlling factor for the saguaro's temperature, averaged over a 24-hour period. The average air temperature from 6:00 am on 27 September to 6:00 am on 28 September was 33.3° C. The average core temperature during the same period was 33.7° C. Lewis and Nobel reported that air temperature is the factor which exerts the greatest influence on average surface temperatures of various species of cacti over a 24-hour period (Lewis and Nobel 1977; Nobel 1978).

The exact values reported for various temperatures, both measured and calculated, are of course valid only for the relatively mild conditions encountered during the period of field measurements. However, the conclusions about the relative importance of various terms in the energy balance equation probably remain valid for a much wider range of conditions.

MANAGEMENT IMPLICATIONS

No specific recommendations are made at this time for further research or monitoring. However, an explanation of energy balance and plant temperatures would make an interesting topic for public education. The possibility of developing an educational display was explored previously, but not pursued due to a lack of available funding.

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Table 1. Calculated and measured effects of changing various physical parameters that affect the energy balance of *Carnegiea gigantea*.

Property changed	From	To	ΔT (°C) surface	ΔT(°C) core
Net solar absorption (with awning)	0.70	0.60	-(1.0 to 2.4)	-1.0
Net solar absorption	0.70	0.60	-(2.0 to 2.2)	-0.9
Net solar absorption	0.70	0.85	+(3.2 to 3.3)	+1.3
Net solar absorption	0.70	0.98	+(5.8 to 6.2)	+2.6
Thermal-IR absorption	0.98	0.50	-(0.3 to 0.7)	-0.6
Geometry	ribbed	smooth	+(4.0 to 4.7)	+0.6
Net solar absorption Geometry	0.70 ribbed	0.85 smooth	+(8.0 to 8.8)	+2.0

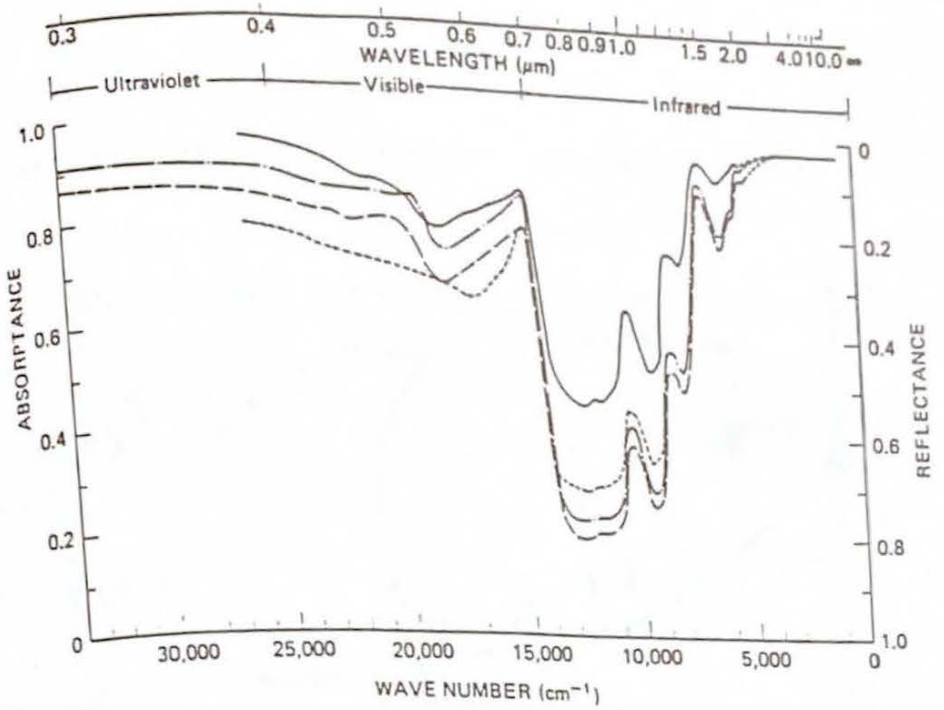


Fig. 1. Absorptance and reflectance as a function of wave number for: *Cereus giganteus* [*Carnegiea gigantea*] (——); *Agave americana*, lower surface (— ·), and upper surface (— —); *Opuntia laevis* (- - -). Reproduced by permission from Biophysical Ecology by D. M. Gates (Springer-Verlag 1980).

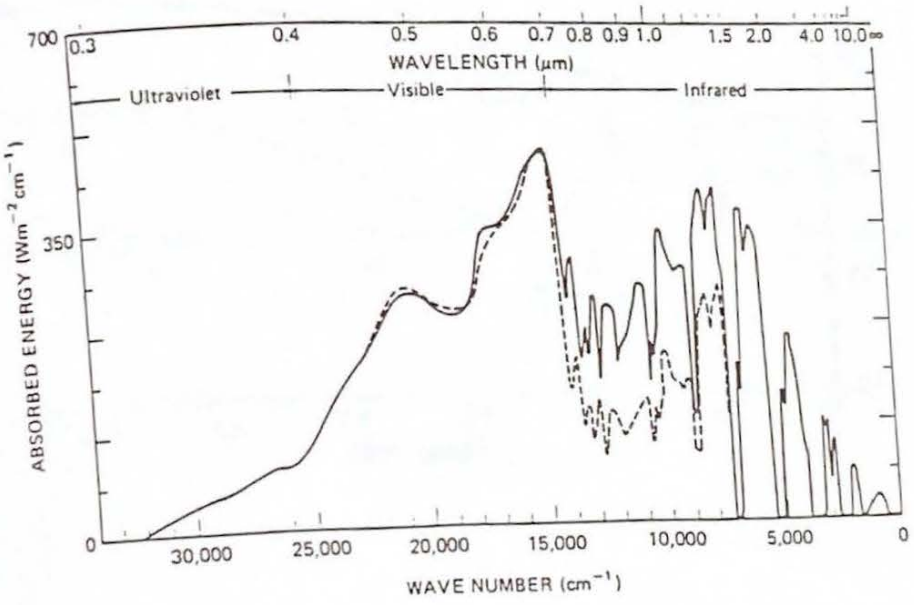


Fig. 2. Sunlight absorbed as a function of wave number for: *Cereus giganteus* [*Carnegiea gigantea*] (——); *Agave lecheguilla* (- - -). Reproduced by permission from Biophysical Ecology by D. M. Gates (Springer-Verlag 1980).

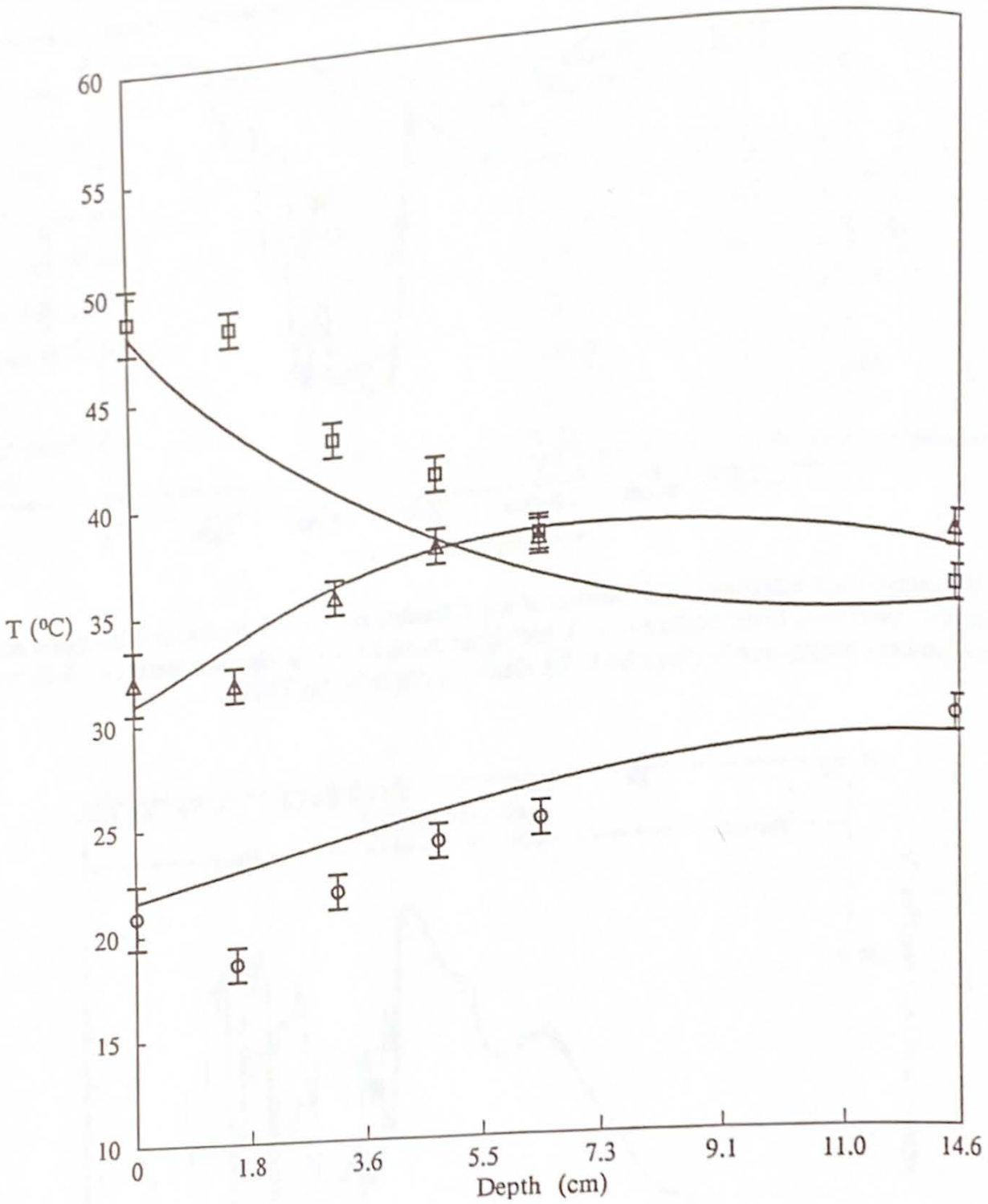


Fig. 3. Transect of calculated and measured temperatures on west-facing surface of *Carnegiea gigantea* at 4:00 pm on 27 September 1988 (squares); at 8:00 pm on 27 September 1988 (triangles); and at 6:00 am on 28 September 1988 (circles).

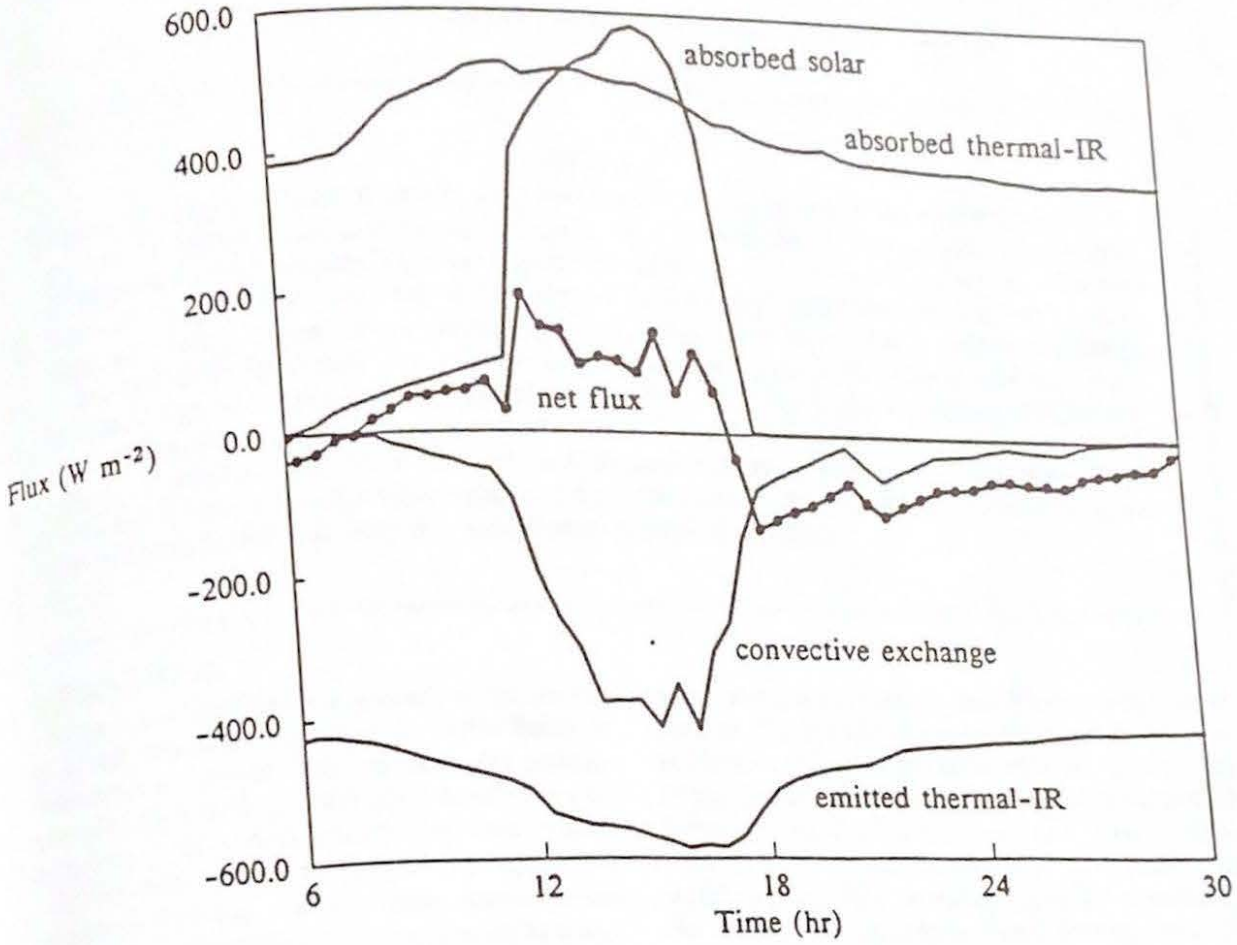


Fig. 4. Calculated energy balance terms for a west-facing surface of *Carnegiea gigantea*. Thirty minute averages of absorbed solar radiant flux, absorbed and emitted thermal-IR radiant flux, convective exchange, and the sum of these four processes. Positive values indicate energy flow into the plant.

Saguaro and Cardón Cacti: Nectar Sources *Par Excellence* for Native and Honey Bees

Justin O. Schmidt, Stephen L. Buchmann, and Steven C. Thoenes

ABSTRACT

Saguaro (*Carnegiea gigantea*) flowers are a nutritional bonanza for a diversity of pollinators. Average flowers contain enormous rewards: 115 mg nectar sugar and 266 mg pollen. In Saguaro National Monument, the main animals that use saguaro floral resources are the native cactus bee (*Diadasia opuntiae*), the imported honey bee (*Apis mellifera*), and to much lesser degrees a variety of native large and small bees, bats, doves, and beetles. Cactus bees start foraging before sunrise and rapidly collect pollen for larval food. They collect nectar more slowly than pollen. Honey bees collect nectar (mainly for honey production) and pollen, removing both within the first several hours after sunrise. The nectar and pollen resources of saguaro and cardón (*Pachycereus pringlei*) cacti, a near relative of saguaro, were determined and the pollination biology of the two cacti compared. Honey bees appear not to adversely affect saguaro cactus pollination or reproduction, but they likely reduce or exclude populations of other native pollinators through competition.

INTRODUCTION

Saguaro cacti (*Carnegiea gigantea*) bloom during the hottest and driest time of year in the Sonoran Desert. This is a period of intense stress for pollinators and a period during which other floral resources are scarce or unpredictable (O'Neal and Waller 1984). For these reasons, saguaro flowers represent a particularly important source of nectar and pollen for floral visitors. The goals of this study were to determine the quantity and sugar concentration of nectar produced by saguaros and their relative, the cardón (*Pachycereus pringlei*) and to determine how saguaro nectar and pollen are utilized by honey and native bees.

METHODS

Nectar from freshly removed saguaro flowers was carefully extracted with 100 µl (microliter) calibrated micro-capillary tubes (Kimble micro-capillary pipettes). Floral nectar sugar concentration was measured as total dissolved solids based on refractive index using a Bellingham and Stanley hand refractometer. The amount of pollen produced by individual flowers was determined, after removal of the nectar, by carefully removing the basal portion of the flower containing the nectaries with a razor blade, followed by inverting the flower in an aluminum foil weighing dish. After standing overnight, or until near the normal midafternoon floral closing time, the anthers were vibrated with a 256 Hz tuning fork to remove any remaining pollen, and the pollen weighed.

To obtain information on the rates of nectar secretion and pollen and nectar removal by pollinators, hourly measurements of nectar and/or pollen were recorded over major periods of the night and day. Some flowers were "bagged" with large plastic bags to prevent loss of nectar and pollen to pollinators. Study sites for the saguaro bloom were: Saguaro National Monument (SNM), Rincon Mountain District (RMD) near the northwestern area of the Cactus

Forest Loop Drive (May 20, 1984 and May 23, 1986); on the property of Mervin Larson on the border of SNM, Tucson Mountain District (TMD) (May 12 and 13, 1987); and on Tumamoc Hill, Tucson just above the Desert Laboratory (May 27 and 28, 1987).

Pollinators were identified by visual observation and collection of voucher specimens. The Larson site was chosen partly because the major pollinators at that site were the native cactus bee (*Diadasia opuntiae*), and the Tumamoc Hill site because primary pollinators there were the imported honey bee (*Apis mellifera*).

Cardón floral nectar and pollen quantities were determined as described for saguaro. Cardón study sites were: Sierra Cirio mountains near Puerto Libertad, Sonora, Mexico (April 17, 1987), and near the beach on the mainland across from Tiburon Island, Sonora, Mexico (April 18, 1987).

RESULTS

Saguaro flowers typically open between 9:00 pm and 11:00 pm (Mountain Standard Time) and remain open throughout the night and into the early afternoon of the next day. By 5:00 pm most are closed. No pollinating bats were observed at any of the sites on observation nights nor was any of the typical floral disruption caused by bat feeding observed on any of the flowers. The first pollinators to arrive at the flowers were the cactus bees, which arrived about 45 minutes before sunrise, followed by honey bees, which began arriving about 15-30 minutes later. These two species accounted for almost all of the floral visits (>98%). Minor floral visitors included large and small bees (carpenter bees [*Xylocopa californica*], and sweat bees [Halictidae spp.], plus occasional other species) and doves, which typically arrived later in the morning.

Pollen is fully available to pollinators upon floral opening. Unlike pollen quantity, which cannot increase with time, nectar is present in varying quantities during the one-day floral lifetime. Nectar secretion usually begins shortly after the flower opens and nectar volume continues to increase until about 9:00 am. After this, the flower begins to resorb the nectar, with complete resorption by the time the flower closes. Nectar production at its peak varied over a large range of about 100 to 1,000 µl per flower with a mean of 519 ± 228 (SD) µl based on 10 flowers from each of the four saguaro sites taken at the time of peak nectar volume. Nectar volume appears to vary depending upon the year, season, site and other unknown factors. On average, saguaro nectar contains 22.2 ± 3.1% sugar (range = 15-26%). Total nectar floral reward (weight of sugar per flower) is 115 ± 51 mg (n = 40), with a maximum of 236 mg. Based on a sample of 130 flowers obtained from the various study sites, pollen weight per saguaro flower is 266 ± 135 mg, with a maximum of 670 mg.

As soon as light is sufficient for flight, bees begin visiting the flowers. A typical standing crop curve of pollen removal by honey bees over time is shown in Figure 1. On this day sunrise occurred at 5:33 am; the first bee was observed exiting a hive at 5:00 am, and very few other pollinators were observed in the area. By 6:00 am and within 30 min of sunrise, over 50% of the original pollen standing crop had been removed. One hour later over 75% of the pollen was removed and the trend continued until 10:00 am, by which time very little pollen remained. Evidence of even one bee visit was obvious: the usual smooth uniform texture of the cone-shaped ring of anthers around the pistil was disrupted. Within a short time, heavily-visited flowers began looking ragged and the creamy yellow appearance of the anthers imparted by the pollen was lost.

Nectar removal by honey bees began soon after initial pollen removal. Unlike pollen, which is readily available on top of the flower, nectar is deep in the floral corolla and the bees must struggle through the bed of stamens to get to it. Nectar removal by honey bees followed a similar pattern as shown for pollen in Figure 1.

Cactus bees exhibited a different saguaro floral resource removal pattern than did honey bees (Table 1). Unlike honey bees, which after an initial removal of a portion of pollen, removed nectar and pollen in parallel, cactus bees emphasized pollen collection at the partial expense of nectar collection. For example, at the cactus bee sites at 8:00 am, only 17% of the nectar was removed, while 75% of the pollen was removed. At sites predominantly visited by honey bees, both nectar and pollen were about 75% removed by 8:00 am. This trend for the cactus bees continued, with half of the nectar remaining at 9:00

am and almost all of the pollen removed. By 1:00 pm nearly all the pollen was gone, while much nectar still remained in the flowers.

The population of cardón cacti studied was in a much drier and harsher environment than the saguaros. Cardón flowers opened at night about the same time as saguaro flowers, but closed much earlier (around 10:00-11:00 am). During the study period, no honey bees were observed visiting cardón flowers or anywhere else and, presumably, they were absent from the sites. Furthermore, no other bees or pollinators were observed, although the observation period was short. We observed no evidence of floral visitation to any cardón flower during night or day. Floral resources of cardón and saguaro exhibited striking differences (Table 2). The amount of pollen produced by the two species was similar, but cardóns produced almost twice as much nectar (nectar volumes measured at the 9:00 am peak volume time for saguaro and at 7:00 am for cardón). In addition to yielding more nectar, cardón flowers produced a nectar that was about 40% more concentrated in sugars. Combined, these figures reveal that cardón flowers produce three times the nectar sugar of saguaro.

Another difference between cardón and saguaro floral resources was observed in the different strategies of pollen production. Nearly all saguaro flowers we have ever observed produce pollen. Of the 24 cardón flowers sampled in the two sites and from 10 different individual plants, only six flowers contained pollen. Supporting evidence of the absence of pollen in the remaining 18 flowers was provided by the nectar. The nectar of flowers without pollen was clear and pollen-free; in contrast, the nectar of all six pollen-producing flowers was slightly to moderately cloudy and contained pollen grains. The information in Table 2 for cardón pollen production was based on only the six pollen-producing flowers. If the pollen produced by all 24 flowers is combined and averaged, then an average flower contains only 64 mg pollen, less than one-quarter that of saguaro. Cryptic, male sterile flowers may be present in cardón populations.

DISCUSSION

Both saguaro and cardón are columnar cacti that are typically considered to be bat-pollinated (McGregor et al. 1962). Evidence for this assumption is that the flowers open at night when bats are present, are white and readily visible to bats on starlit nights, and are large and shaped appropriately for bat muzzles to become covered with pollen and thereby pollinate distant flowers. Both species also produce abundant nectar, which is essential to provide sufficient energy to maintain a large pollinator such as a bat. Although bats might be the most significant pollinators of these related cacti from an evolutionary standpoint, other saguaro visitors also play pollination roles. The evidence is that saguaro flowers remain open well into the afternoon with receptive stigmas. During the morning and early afternoon period the nectar and pollen are available for bees, other insects, and birds. Saguaro nectar and pollen are highly attractive to a variety of potential pollinators as well as being highly nutritious (Schmidt 1984; Schmidt and Johnson 1984; Schmidt and Buchmann 1986).

Honey bees are not native to the Americas and therefore played no role in the evolution of the pollination systems of either saguaro or cardón. Now, however, this cosmopolitan, generalist, tramp species is perhaps the major pollinator of saguaros in SNM, and presumably affects the pollination of both saguaro and cardón in other areas where honey bees and the cacti coexist. Honey bees appear to be effective pollinators of saguaros (McGregor et al. 1962) and are probably now the most important pollinators along with cactus bees. No data are available for cardón pollinators. Thus, from the point of view of the saguaro, the honey bee is not deleterious. In fact, humans have reduced bat populations by destroying roosting sites, habitat, and food sources; therefore, honey bees might be beneficial replacement pollinators.

The effects of honey bees on native pollinators of saguaro is unclear. Bees do not have a direct effect on bats because bats exploit the resources only at night and before bees enter the scene. Direct evidence of honey bees competitively reducing or excluding diurnal pollinators is difficult to obtain. Indirect evidence of competitive exclusion is derived from observations (Fig. 1 and Table 1) that within a few hours of sunrise and well before floral closure, most nectar and pollen have been removed by honey bees. Nectar and pollen, therefore, are unavailable for other pollinators, particularly those that might be active after 9:00 am in the morning.

Honey bees may well impact some diurnal pollinators more than others. Doves and other birds likely were major visitors to saguaros before the advent of honey bees and when nectar remaining after bat foraging was available. At midday, a time of great water and heat stress for birds, available saguaro nectar might be especially valuable since birds cannot readily forage on the ground due to high surface temperatures. We speculate that saguaros might well have been an important food and moisture source for birds at midday, a source now largely unavailable due to honey bees.

The pollination biology of cardón cacti is almost unknown; although cardóns are bat-pollinated, little else is known. In the cardón study areas, insect pollinators were scarce, and that situation is likely to exist in other extreme cardón habitats. Thus, during the evolution of the cardón pollination system, the main selective forces were probably those generated by bats. Evidence for this is the enormous production of nectar and sugar by the flowers and the relatively low (compared to saguaro) overall production of pollen. Bats rely much more heavily on nectar than pollen for food. Therefore the nectar-rich provisions of cardón are ideally suited for a bat-cactus pollination system. Although we have no evidence, it is interesting to speculate about the possibility of competition between cardóns and saguaros for pollinators. If, in areas such as our cardón study sites, pollinators other than bats are rare, and if bats are a limiting factor in the pollination biology of columnar cacti, it is conceivable that cardóns outcompete saguaros for these rare bat pollination services. This could occur simply because cardóns provide about three times the sugar per flower that saguaros provide. If pollen is relatively unimportant for bats and if a superabundance of columnar cactus flowers exists relative to bat needs, then bats likely would visit predominantly cardón flowers for the rich nectar reward and ignore the saguaros. This could be a driving force for the competitive exclusion of saguaros in some areas.

SUMMARY AND MANAGEMENT IMPLICATIONS

This study has revealed that the introduction of feral honey bees into SNM should have little deleterious effect on saguaro cacti and their reproduction. Honey bees could, however, have a significant impact on native pollinators and other organisms such as some birds that use saguaro floral resources. Although direct evidence is lacking, we believe that honey bees reduce the populations of native bees in some situations. This problem might be exacerbated in the future with the introduction of Africanized honey bees (*Apis mellifera scutellata*) that are known to be active earlier in the day than European honey bees, to form denser feral populations, and to nest in small cavities such as saguaro boots. These combined factors might place added stress on native pollination systems within the monument and other natural areas. Africanized bees are also a greater threat to human visitors and might need to be controlled in some natural areas that are particularly biologically sensitive, or are heavily visited by the public.

ACKNOWLEDGMENTS

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Table 1. Rate of nectar and pollen removal from saguaro cacti at sites visited primarily by native cactus bees or by honey bees.

	% removed			
	Cactus bee sites		Honey bee sites	
Time	Nectar	Pollen	Nectar	Pollen
6:00 am	—	—	0	0
7:00 am	9.6	34.1	0	28.9
8:00 am	16.9	74.7	73.6	84.3
9:00 am	51.4	92.1	88.3	94.6
1:00 pm	76.8	97.7	—	—

Table 2. Comparison of nectar and pollen production by saguaro and cardón cacti. Variance is given as ± SD.

Floral Production	Saguaro	Cardón	Ratio: Cardón/Saguaro
Nectar volume (µl)	519 ± 228 (n = 40)	958 ± 300 (n = 6)	1.85
Nectar sugar concentration (%)	22.2 ± 3.1 (n = 40)	31.3 ± .8 (n = 6)	1.41
Nectar sugar (mg)	115 ± 51 (n = 40)	339 ± 100 (n = 6)	2.95
Pollen weight (mg)	266 ± 135 (n = 6)	256 ± 49 (n = 6)	0.96

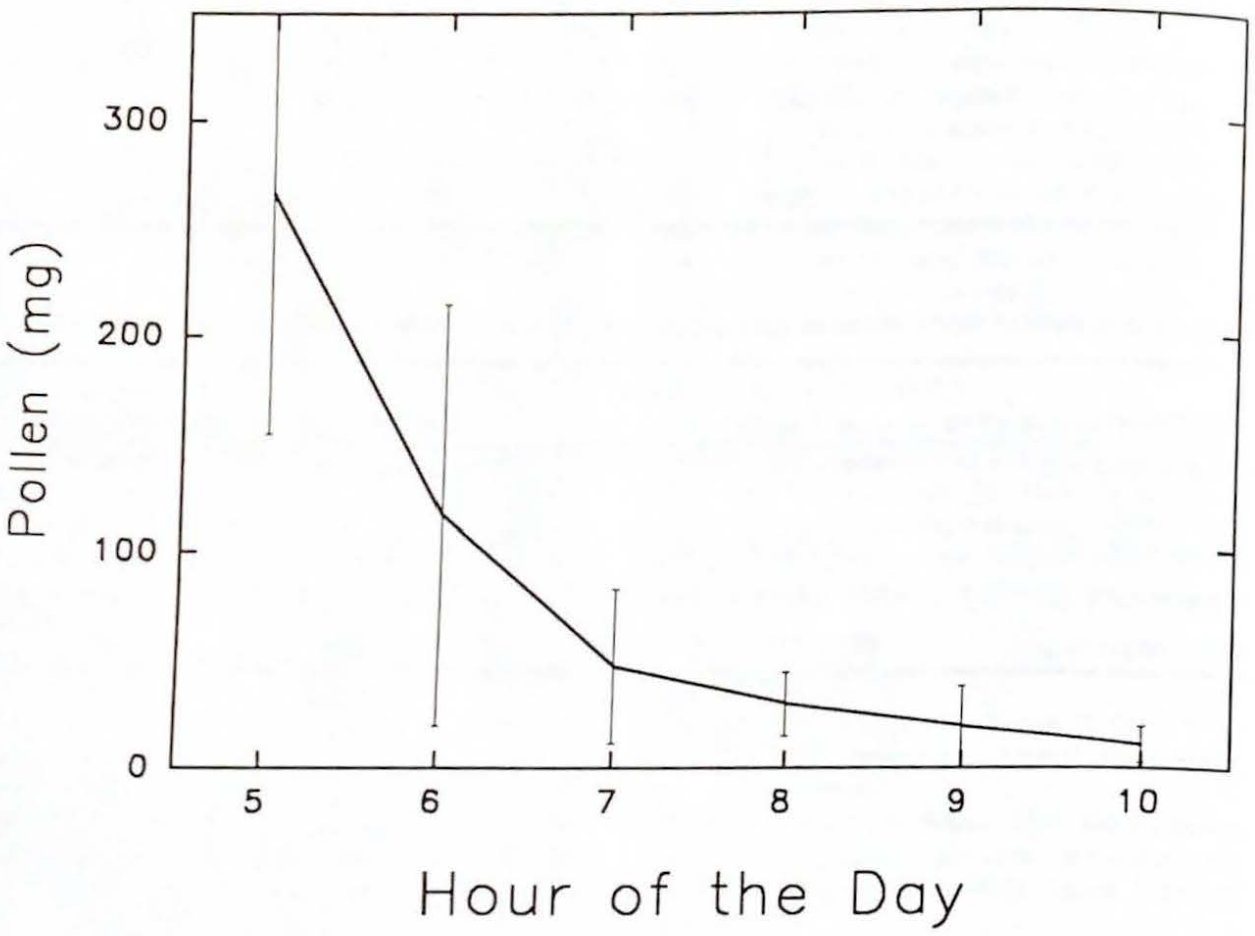


Fig. 1. Pollen removal by honey bees from saguaro flowers, Rincon Mountain District, Saguaro National Monument, 1986.

Behavioral Characteristics and Reproductive Traits of Saguaro-Breeding *Drosophila*

Henar Alonso-Pimentel and William B. Heed

ABSTRACT

The behavior and reproductive traits of the two *Drosophila* (pomace fly) species (*D. mettleri* and *D. nigrospiracula*) that use saguaro (*Carnegiea gigantea*) as a host plant, are presently under study. The location of the oviposition (egg-laying) substrate is the most remarkable difference between the two species, but laboratory studies have shown other marked differences in behavior. Field research is being performed to corroborate laboratory findings. Preliminary data illustrated a differential distribution of sexes and species in feeding versus non-feeding areas on the cactus. The developmental stage of the eggs differs significantly in the females of the two species and it appears to be correlated with specific ecological conditions. A temporal succession of the species was also observed. This work illustrates the adaptability of behavioral and reproductive characteristics to the ever-changing conditions of cactus necroses.

INTRODUCTION

The cactus-yeast-*Drosophila* system is considered a model for evolutionary and genetic studies (Barker and Starmer 1982). The three components of the system have been extensively investigated and their interactions can be briefly described: *Drosophila* (pomace flies) take nutrients from the yeasts and from the cactus tissue that is decomposing due initially to stressful conditions such as lightning strike or freezing temperatures (Steenbergh and Lowe 1983). The yeasts feed on the decaying tissue also and are transported by the flies to newly formed and very aromatic necroses originated by bacterial action. The ecology of the host plant, the cactus, sets the stage for life history characteristics of the microorganisms and the *Drosophila*.

In the Sonoran Desert this system is characterized by a high specificity between endemic species of *Drosophila* and the species of their host cacti (Heed and Mangan 1986). Saguaro (*Carnegiea gigantea*) and cardón (*Pachycereus pringlei*) have been identified as the main host plants of *D. mettleri* and *D. nigrospiracula* in the desert. A remarkable difference in the ecology and behavior of the two fly species is the location of the oviposition (egg-laying) substrate (Fogleman et al. 1981): *D. nigrospiracula* females lay eggs in the necrotic tissue of the cacti while *D. mettleri* females lay eggs in the soil that has been soaked with liquid dripping from the cactus as it ferments (Heed 1977, 1978). Recent behavioral studies in the laboratory have shown marked differences between the two species; however, it is important to determine whether these differences may also be encountered in nature, and that is the focus of this research. The field work was begun very recently; therefore, only preliminary data from saguaros near the monument are presented.

METHODS

Flies were observed and collected from three different rotting cacti in the vicinity of Tucson, Arizona.

One rotting saguaro was located on the Sonoran Arthropods Studies, Inc. (SASI) land near the Tuscon Mountain District (TMD) of Saguaro National Monument (SNM). The other two were located at Ironwood Hills Picnic Area (Tucson Mountain Park). Collections and observations were conducted in the morning for eight days during late October through late November 1990. Collecting was accomplished by mouth aspirators connected to a vial. The vial of flies was placed in a small cooler with ice to stop activity. Two different areas were identified on each rotting cactus: (1) feeding areas where liquid was dripping down the ribs and where flies were observed feeding, and (2) non-feeding areas on externally healthy parts of the cactus where flies were also present. Flies from both areas were taken to the laboratory and examined under a microscope to identify the species and the sex. A number of females were dissected in order to record the state of their reproductive organs. The presence of sperm in the female and the developmental stage of her eggs, as outlined by King (1970), were recorded.

FIELDWORK

A clear difference was found in the distribution of the two species of flies and in the habits of males and females with respect to feeding and non-feeding areas. Most of the males and females of *D. mettleri* were found in the feeding areas. Almost 60% of *D. nigrospiracula* males, however, were captured in the non-feeding areas, and close to 20% of females of this species were also found in non-feeding areas.

The percentages of females in each species with clearly different developmental stages of the eggs are shown in Figure 2. We dissected 103 females (39 *D. mettleri* and 64 *D. nigrospiracula*). The majority of *D. mettleri* females had immature eggs representing stage 9, where half of the developing egg is occupied by nurse cells (King 1970). In *D. nigrospiracula*, almost 40% of the females had fully mature eggs. The data were collected from rotting cacti with no wet soil present; therefore, we lack comparative information from cacti with oviposition substrate for *D. mettleri*. Even so, an important physiological difference seems to exist between the two species under these conditions.

Collections were also made from a single rotting cactus five times during a 10-day period from 31 October to 11 November (Fig. 3). A temporal succession of both species is evident. As the necrotic tissue became older, the number of *D. mettleri* flies increased and the number of *D. nigrospiracula* decreased. The number of flies collected every day was quite similar; therefore, a real change in absolute numbers of these two species over time exists.

LABORATORY WORK

Two main differences in behavior between *D. mettleri* and *D. nigrospiracula* have been found in the laboratory: the movement of the wings by the males during courtship and the degree of severity of aggression against females and males of the same species. *D. mettleri* males vibrate their wings during courtship. One wing is laterally extended from the resting position and is rapidly moved up and down. The wing in the resting position may also vibrate. This display, in which males alternate the extended wing, is typical of a number of species (Spieth 1952). The extended wing is always the one closest to the female (Fig. 4b). *D. nigrospiracula* males "scissor" their wings instead of vibrating them. Wing scissoring is a laterally symmetrical, rapid and simultaneous opening and closing of both wings (Spieth 1952) (Fig. 4a). Both types of wing movements in the two species produce a high frequency sound, the love song, that females receive through their antennae (Ewing and Bennet-Clark 1969). The love song is known to play an important role during courtship (Spiess 1987). The marked difference in the pattern of wing movements suggests a significant difference in the love songs of *D. nigrospiracula* and *D. mettleri*.

Male aggression is another distinctive difference between these species. *D. mettleri* males are very aggressive towards their own females and among other males. Occasionally in the laboratory we have observed males engaged in direct combat. The males butt heads, go into an upright position for a few seconds and then fall over (Fig. 5a). The motive for the fight is unknown; however, combats have been observed immediately following copulation in mating chambers where a high ratio of males to females exists, suggesting a relationship with mate procurement. *D. nigrospiracula* males are not as aggressive towards females nor among other males. Markow (1989) described *D. nigrospiracula* males commonly found in non-feeding areas of saguaros that are

uniformly spaced with respect to each other. Males waited in their small territories for females to arrive in order to court them. If other males were encountered, the defending male flicked its wings vigorously, chasing the other males (Markow, 1989; Fig. 5b). This behavior has also been observed in the laboratory. Our results on the distribution of the flies (Fig. 1) support Markow's observations. We observed *D. mettleri* males continuously courting feeding females, which suggests that the mating behavior of the two species determines their unique spatial arrangement on the cactus.

DISCUSSION

Egg development and female mating behavior are coordinated factors according to Kambysellis and Cradock (1991). *D. mettleri* females feeding on rotting cacti without suitable oviposition substrate had immature eggs (Fig. 2). Therefore, mating behavior might be greatly affected by the developmental stage of the eggs. Lack of data from rotting cactus with wet soil prevents us from speculating about how the presence or absence of oviposition substrate affects the physiological state of the flies. Even so, this observation raises interesting questions concerning behavioral regulation of oogenesis (egg formation). Are females controlling oogenesis because the oviposition substrate is not present, or are they feeding in a non-substrate cactus because of the immature nature of their ovaries? An answer to this question can help us understand the relationship between physiology and ecology.

Heed and Mangan (1986) suggested that "*D. mettleri* is adapted to feeding in soils that have been partially produced by the activity of *D. nigrospiracula* larvae in the tissue of *Carnegiea*." Our results in Figure 3 support this hypothesis. The densities of *D. mettleri* flies should be low at the initial stages of the rotting process and increase as *D. nigrospiracula* larvae work through the cactus tissue. The decline in *D. nigrospiracula* can simply be the consequence of the drying of the tissue over time. A temporal succession of the two species, determined by the rotting cactus stage, could affect behavioral patterns. Fluctuations in population density may create variations in male aggressiveness and mating behavior (Ewing and Ewing 1987).

SUMMARY AND MANAGEMENT IMPLICATIONS

This work represents one of the few comparative behavioral studies being conducted with several species of *Drosophila* under entirely natural conditions. Our preliminary data clearly illustrate how observations under natural conditions are vitally necessary for the interpretation of behavioral patterns. The role of the monument in permitting basic research to be conducted is of considerable value and will be even more valuable in the future.

Cactophilic *Drosophila* undoubtedly play an important role in nutrient cycling in the Sonoran Desert. Although these flies are not the initial cause of saguaro decay, their larvae are important decomposers of the tissue that is no longer useful to the cactus.

ACKNOWLEDGMENTS

We thank Eric Dyreson for his assistance in the field and Sonoran Arthropods Studies, Inc. (SASI) for the use of their land and facilities. This work was supported by a Center for Insect Science trainee grant.

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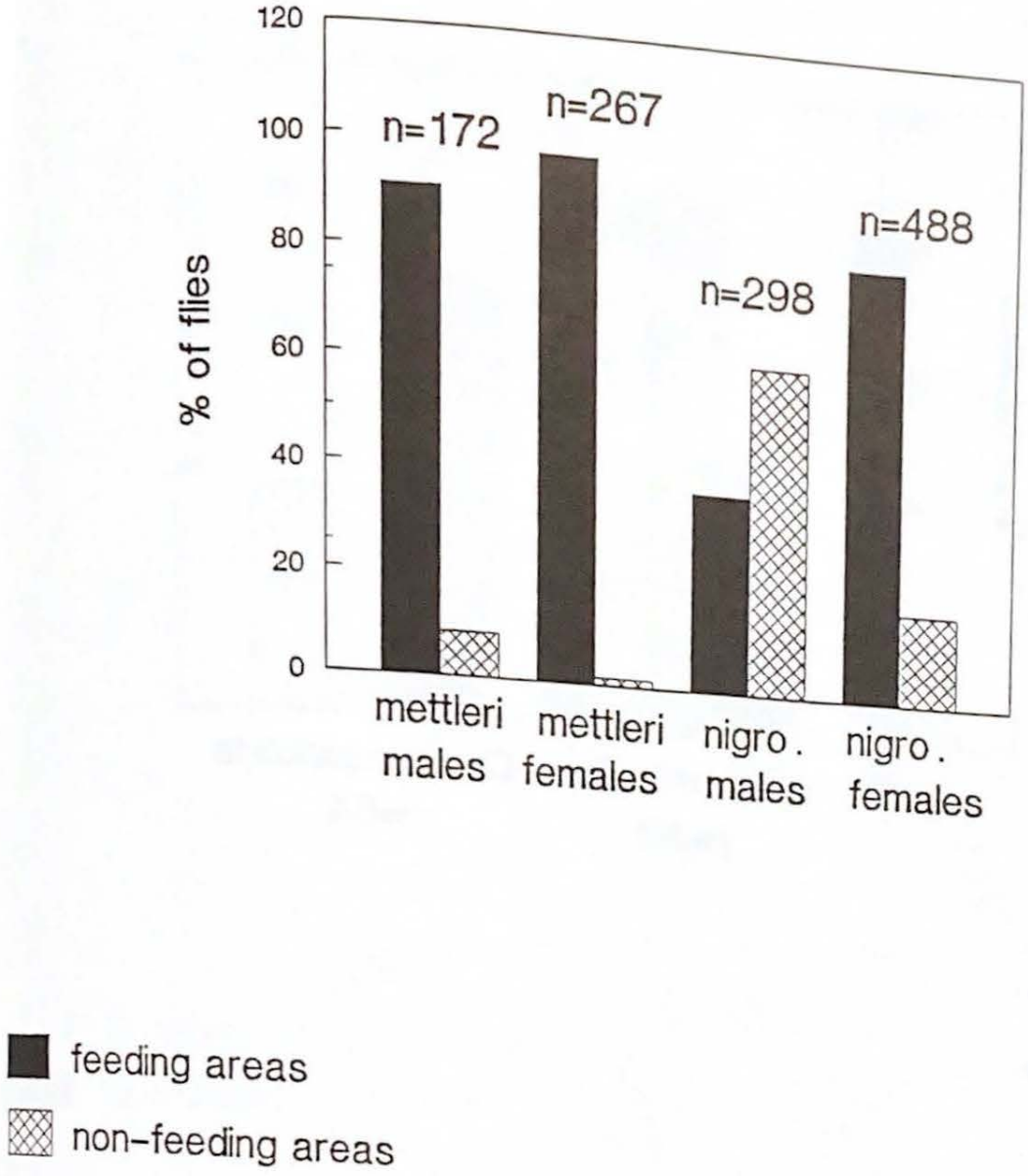


Fig. 1. Distribution of the flies. Percentages of males and females of *D. nigrospiracula* and *D. mettleri* collected in the feeding and non-feeding areas of rotting saguaros.

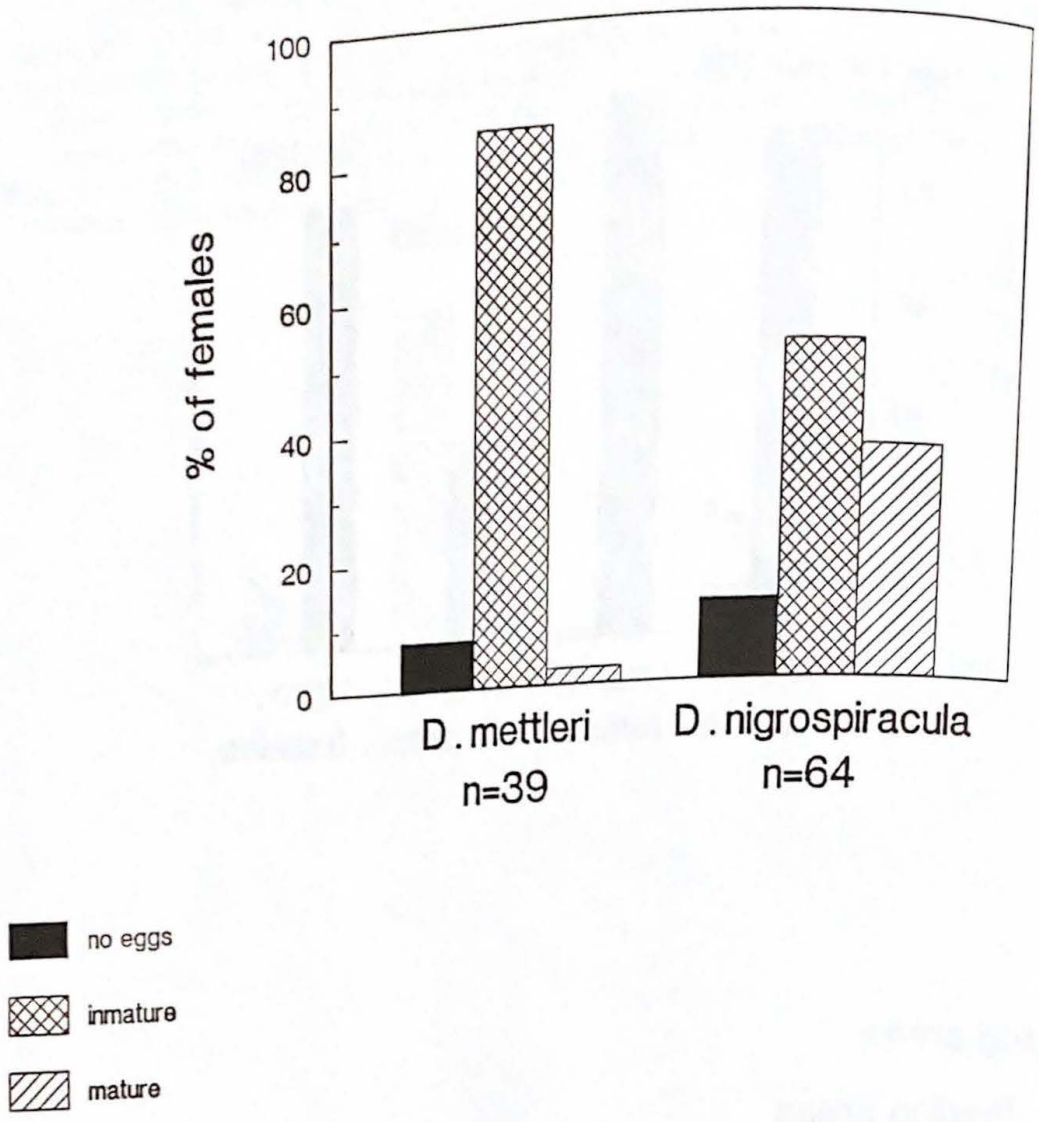


Fig. 2. Developmental stage of eggs. Percentages of *D. mettleri* and *D. nigrospiracula* females in three different developmental stages of their eggs: no eggs, immature and fully mature.

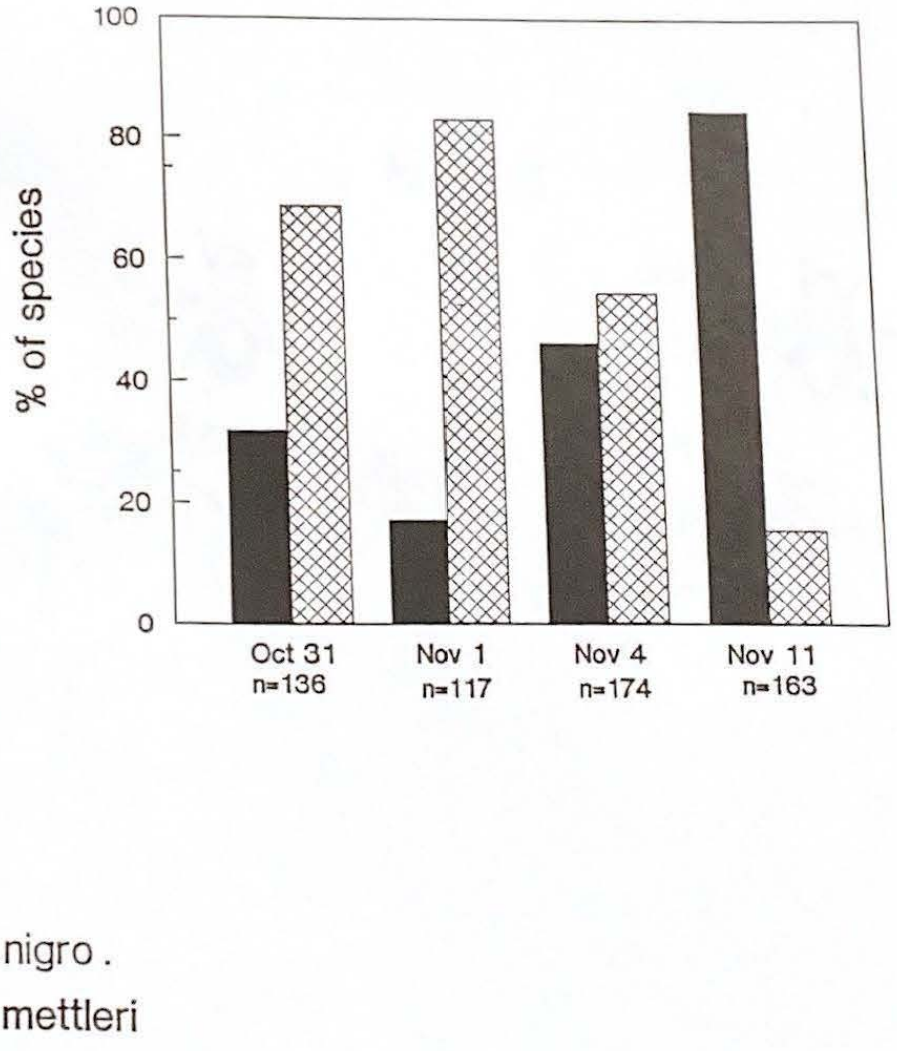


Fig. 3. Temporal succession. Flies collected from a single rotting cactus over a 10-day period. Bars represent the percentage of each species collected on the given dates.

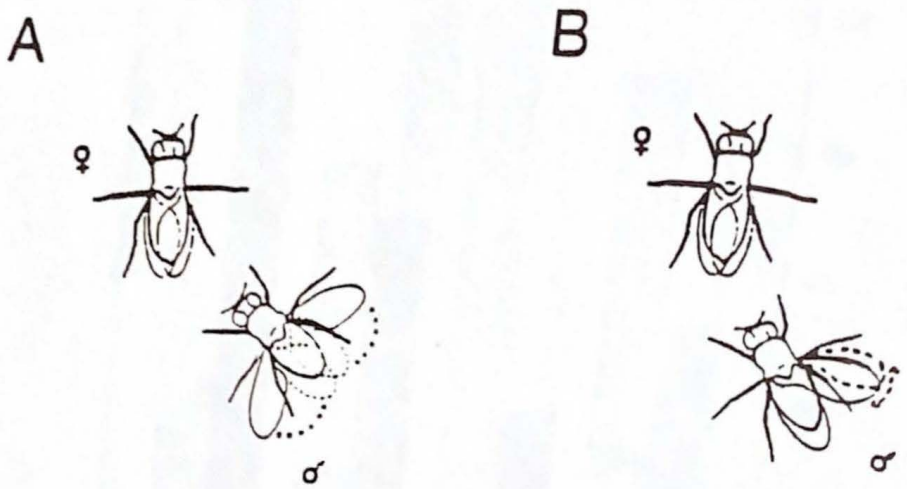


Fig. 4. Male wing display. Patterns of wing movement displayed by the males during courtship: **a.** *D. nigrospiracula*, wing scissoring; **b.** *D. mettleri*, wing vibration.

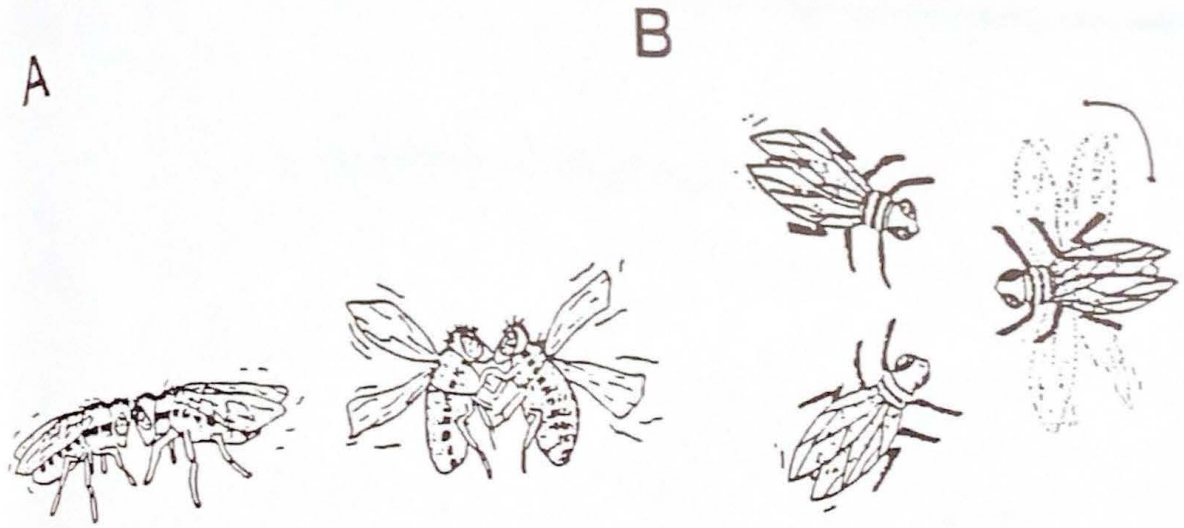


Fig. 5. **Male aggression.** Agonistic displays among males: **a.** *D. mettleri* males butt heads and get into an upright position; **b.** *D. nigrospiracula* males scare off other males from small protected areas in the cactus.

II.
Monument Flora and Fauna

On the Biogeography of the Herpetofauna at Saguaro National Monument

Charles H. Lowe

ABSTRACT

The known monument herpetofauna of 57 species is briefly addressed. Explanatory biogeography is discussed for desertscrub taxa at lower elevations, and woodland and forest taxa at higher elevations on the monument and beyond. Specific aspects of desert ecosystem structure underlying the presence/absence of potential Sonoran Desert lizard and snake congeners are discussed. Within this biogeographic framework lies the explanation for the situation at Saguaro National Monument where the most xeric-adapted taxon in a given species pair is the one that is missing from the monument herpetofauna. Species in the rattlesnake genus *Crotalus* illustrate especially well biogeographic aspects of the south-north Madrean Archipelago and the east-west Madrean Line in southeastern Arizona and adjacent New Mexico. The Madrean Line divides in two the mountain island Madrean Archipelago between the Sierra Madre Occidental (south) and the Rocky Mountains (north). This Southwest biogeographic line is as sharp as the world's most famous one, Wallace's Line, which divides the Malay Island Archipelago in two.

INTRODUCTION

The space allotted is, of course, insufficient to discuss the entire herpetofauna at Saguaro National Monument (SNM). Hence, my focus will be on fascinating biogeographic stories in which parts of the herpetofauna of the monument participate. A brief summary of the amphibian and reptilian taxa that occur on the monument is followed by a look at two biogeographic patterns involving (1) the herpetofauna of the lower elevations, which lives wholly or predominantly in desertscrub and desert-grassland communities, and (2) the herpetofauna of the upper elevations, which lives wholly or predominantly in woodland and forest communities.

THE HERPETOFAUNA

Four worldwide groups of vertebrates are represented in the monument herpetofauna, the anurans (frogs and toads), the turtles, and the lizards and snakes (Table 1). Ecological and distributional information for these species is provided in Lowe (1964*a*), Black (1982), Lowe and Holm (1986, 1991), Lowe et al. (1986), and Stebbins (1985). Only one reptilian species, the blacktailed rattlesnake (*Crotalus molossus*), is found throughout the 6,600 ft (1.25 vertical mi) elevational range of the monument.

In the discussion that follows for the lower monument, desertscrub species-pairs of iguanid lizards and colubrid snakes are examined as present-or-absent congeners in the herpetofauna. A biogeographic explanation is given for the distribution pattern that is observed.

Six rattlesnake species occur in the herpetofauna at SNM, most of which are not high mountain species (Table 2). As noted, only one of the six, the blacktailed rattlesnake, occurs throughout the elevational range of both districts of the monument. One

of them, the sidewinder (*Crotalus cerastes*), occurs only in the desert Tucson Mountain District (TMD), which is the western unit of the monument.

One of the six, the Arizona black rattlesnake (*Crotalus viridis cerberus*), is found only in the forested Rincon Mountain District (RMD), where it reaches its southernmost distribution on the continent. As discussed below, this rattlesnake is of particular importance in one of several interesting and scientifically important Southwest biogeographical patterns that involve the herpetofauna and other vertebrate groups at the monument.

Three other species of rattlesnakes ("Mexican mountain rattlesnakes") that occur in other nearby mountain ranges in southeastern Arizona do not occur in the Catalina-Rincon Mountains and thus are not included in the monument herpetofauna (see detail maps in Lowe et al. 1986). A discussion for the upper elevation forest and woodland taxa centers on the biogeography of the forest and woodland rattlesnakes in southeastern Arizona and adjacent Mexico. The Rincon Mountain fauna, which includes the Arizona black rattlesnake, participates in this Southwest biogeographic story that involves present-and-absent congeners.

THE LOWER ELEVATIONS: SONORAN DESERTSCRUB AND DESERT-GRASSLAND

Recent discussions of natural habitats may be found in Niering and Lowe (1984), Bowers and McLaughlin (1987), and Lowe and Holm (1991). The Sonoran Desert communities are primarily creosotebush (*Larrea*) desertscrub, paloverde-saguaro (*Cercidium-Carnegiea*) desertscrub, and their ecotones that predominate on site from 2,020 ft upward to ecotones with desert-grassland at 3,700 ft and above.

The desert-grassland (or semidesert grassland) communities are climax mixtures of native perennial grasses, native dry-tropic shrubs and stem-succulents, mesquite (*Prosopis*) and other often disclimax weedy perennials that prevail on widely altered native dry-tropic grasslands between 3,700 and ca 5,000 ft. At and above ca 4,500 ft, savanna-like ecotones are formed with oaks of the evergreen woodland above.

Desert Ecosystem Structure

When one travels through the deserts of the world and looks at them comparatively, it becomes apparent that deserts are comprised of three underlying features: (1) rockpiles, (2) bajadas[1], and (3) valley bottom fill (Fig. 1). The three components are contiguous and more or less subtly continuous subsystems of a collective ecosystem unit.

Superimposed on these three primary landscape features is (4) a pattern of drainage lines produced primarily by water, and (5) sandpiles that are produced primarily by wind. These five principal features are, of course, not peculiar just to deserts. They are simply more naked, if not more obvious, and thus perhaps more quickly if not more accurately assessed in the world's deserts and grasslands.

The Substratum

Both inside and outside of desert ecosystems, the nature of the natural substratum or "substrate" (bark, rock, sod, et al.) is one of a half-dozen critical controls that determines the presence or absence of a given reptilian or amphibian species on a particular site. In deserts especially, the soil texture (rock, gravel, sand, silt, clay, et al.) is one of the most important characteristics of the substratum for a large and diverse array of amphibians and reptiles.

Resulting primarily from weathering and the erosional forces of water and gravity, there is a downward gradient in soil particle size distribution that extends across the entire ecosystem unit. That is, from the rock parent material above, downward across the bajada slope to the finer textured soils of the flatter valley bottom fill below (Fig. 2). Accordingly, many of the severest desert conditions are

[1]The bajada is the flanking detrital skirt that surrounds the rockpile (mountain, rocky butte, etc.) of its source; the familiar alluvial fan is a portion of a bajada. Earlier in the upland erosional cycle, bajadas are steeper and, partly as coalesced fans, are composed of relatively deep alluvial soil as in Figs. 2 and 3 representing the study area in basin and range topography. Later in the erosional cycle, bajadas are less steep and may exhibit relatively shallow soil across outward sloping bedrock from the base of the rockpile. The latter bedrock surface, with essentially no soil nor vegetation, is also called a pediment, which term (meaning sloping surface) is borrowed from classical Greek architecture, where the triangular space forming the gable of a roof is the pediment. Bajada evolution—from the fanform bajada to the pediform bajada—in the erosional cycle in aridlands is illustrated in *Putnam's Geology* (Birkeland and Larson 1978) and elsewhere.

reached for both plants and animals on the fine textured soils between desert ranges, where the least plant-available soil moisture is due to finer soil particle size. Thus it is not unexpected that some of the most highly specialized adaptations for desert living, such as extremes in sand swimming and drought resistance, are associated with fine textured soils located in the valley fill component of desert ecosystems.

It may be only somewhat less expected, when the observer comes upon desert specialists that are adapted for rock-dwelling. Indeed, in deserts some of the most extreme desert specialists live at one or the other of two most extreme substratum types on the gradient—rockpiles and sandpiles—at opposite ends of the substratum particle size distribution. Such extreme specialists are few in number and spectacular in adaptation. Among their representatives in the Sonoran Desert are the chuckwalla (*Sauromalus obesus*) specialized for life on and in desert rockpiles, and the fringe-toed lizard (*Uma notata*) specialized for life on and in shifting sandpiles.

Most reptilian and amphibian desert taxa, however, are centered adaptively at varying ecological positions away from these extreme substratum conditions of continually moving sand, and solidly positioned pilerock. Therefore, not surprisingly, we find that most of the amphibian and reptilian desert taxa of the world are adapted to relatively less extreme substrata that usually characterize the bajada-valley fill gradient.

Sonoran Desert Biogeography in Arizona

A simple diagramatic profile of SNM as shown in Figure 3, illustrates that the monument area contains a truncated desert ecosystem lacking one of the three principal ecological subsystems. The missing subsystem is valley bottom fill, which supports desertscrub biotic communities dominated by creosotebush-white bursage (*Ambrosia dumosa*) and their few associates on primarily flatland fine-textured soils (Figs. 1 and 2). An examination of species-pairs that are present-or-absent congeners, shows that the Sonoran Desert reptilian taxa absent ("missing") from SNM are those species and genera requiring desert microenvironments peculiar to the missing subsystem.

All of these taxa absent from SNM are present, for example, in the herpetofauna at Organ Pipe Cactus National Monument (ORPI), which area contains desert ecosystem units with all principal ecological subsystems represented (Figs. 1 and 2). Organ Pipe Cactus National Monument is at a lower base elevation in southwestern Arizona and SNM is at a higher base elevation in southeastern Arizona. In the cases where paired-species combinations are examined in herpetofaunal comparisons for the two monuments (Table 3), the result is as predicted: the most xeric-adapted species of the species pair is the one that is missing from the herpetofauna at SNM.

The taxa absent from SNM occur in flatland communities dominated by creosotebush-white bursage at ORPI, more or less throughout Shreve's (1951) Lower Colorado Valley subdivision of the Sonoran Desert that extends eastward into the Avra Valley and to within a short distance of SNM (Fig. 3). Thus, in fact, all the listed desert elements of the herpetofauna absent from SNM reach to the western doorstep of, but do not enter, the monument.

Saguaro National Monument could have included a representative portion of the historically and biologically significant Avra Valley within its boundaries with relative ease 50-60 years ago, perhaps even 30-40 years ago. The then essentially pristine and little known area of Avra Valley that lies directly below the western boundary fence of SNM has since become variously occupied, and is now largely destroyed. Saguaro National Monument was established by presidential proclamation in 1933 and the TMD portion was added in 1961.

One would think that since President Hoover in 1933 proclaimed all of the forested Rincon Mountains (to Rincon Peak at 8,482 ft) to be included in SNM, which he did amid little protest, surely he could have proclaimed a small part of the huge and nearly unoccupied Avra Valley to be included, if not some part of the Santa Cruz Valley. A President in the 1940s or 1950s could have still accomplished the task for the National Park Service (NPS), certainly for a part of the Avra Valley area. But such thinking today is with the clarity of hindsight in a much more knowledgeable world. The problem in the early 1930s was ecological. Ecology was then a young and little-known science, and a fully coherent concept of the *ecosystem* much less the *Sonoran Desert*, was not at hand. The problem later in the 1960s was political; it was too late.

THE UPPER ELEVATIONS: FOREST AND WOODLAND

The Southwest evergreen woodlands in the Rincon Mountains are oak (encinal) and pine-oak woodlands. At the lower woodland limits of 4,000-4,500 ft according to slope exposure, the encinal is an evergreen oak woodland of Emory oak (*Quercus emoryi*), Mexican blue oak (*Q. oblongifolia*), and Arizona oak (*Q. arizonica*) with the occasional presence of juniper and pinyon representation in the woodland. With gradual increase in elevation into the pine-oak woodland above, Chihuahua pine (*Pinus leiophylla*) joins with Mexican pinyon (*P. discolor*), alligator-bark juniper (*Juniperus deppeana*), and several evergreen oaks—principally silverleaf oak (*Q. hypoleucoides*), Arizona oak, Emory oak—and others. Mexican pine-oak woodland above 7,000 ft gradually merges with the montane conifer forest above.

The montane conifer forest is a mixed conifer forest with primarily pine and fir dominance varying according to slope exposure and elevation from approximately 7,000 ft to the top near 8,600 ft. Ponderosa pine (*P. ponderosa*) is the principal forest conifer, providing a pine forest with Gambel oak (*Q. gambeli*), madroño (*Arbutus arizonica*) and others. This forest usually becomes a mixed conifer community at increasing elevations, with presence of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and white pine (*Pinus strobiformis*). These three coniferous trees reach their greatest stature and density on north-facing slopes above 7,800 ft.

Mountain Islands

In the four-corners area of Arizona-Sonora-Chihuahua-New Mexico, as elsewhere throughout much of the Southwest, the mountain island character of conifer-clad and other high wooded mountains is unmistakable (Fig. 4). Because of significant differences in base level to well over a thousand feet on different sides of a mountain in the Southwest, different biotic communities may contribute to the surroundings of the mountain at base level. Grassland is the single most prevalent formation at mountain base level in this four-corners area, as shown in Figure 4.

Dating from early in this century these mountain islands have been called "desert mountains," "desert mountain islands," "mountain islands in desert seas," etc. But for these conifer-clad "sky islands" (Heald 1951), such desert names "are inappropriate because they are not surrounded by desert" (Lowe 1964*a*), as Shreve (1915) first pointed out years ago. *The bases of these mountain islands are either primarily grassland, or these ranges are completely surrounded by grassland, not desertscrub* (Shreve 1915, 1919; Nichol 1937; Marshall 1957; Lowe 1964*b*; Martin and Mehringer 1965; Brown and Lowe 1977, 1980); see Gehlbach 1981 and Davis 1991 for the contrary view.

The grassland versus desert distinction again noted, is of basic importance to species dispersal and the explanatory biogeography of the mountain island archipelago. These lowlands have been involved, from full glaciation to the present time, in a series of community replacements from forests to woodlands to grasslands, and, locally, to desertscrub. The current grassland connectors (grassland seas) between the mountain islands in the archipelago have been *in situ* approximately 9,000 years (Van Devender 1990*a*,*b* and elsewhere).

Mexican Mountain Biogeography in the Borderlands

As in the case for certain desert species pairs that are present or absent in the herpetofauna at SNM, an interesting biogeographic story is associated with certain high mountain species that are present-or-absent congeners in the monument's forested Rincon Mountains. This is the story of the high Sierra Madrean fauna and flora that barely enters the United States, where it variously adjoins southernmost elements of the Rocky Mountain fauna and flora. The rattlesnake genus *Crotalus* is exemplary in this story of Madrean ("Mexican Mountain") biogeography in Arizona.

The Arizona black rattlesnake reaches its southernmost distributional limit on the continent in the Rincon Mountains of SNM, just short of the Arizona-Sonora boundary line. The current late Holocene distribution of rattlesnake species on high mountain islands in southeastern Arizona, and in adjacent southwestern New Mexico in the Sierra San Luis, Animas Mountains, et al. is illustrated in Figure 5. It is a biogeographic pattern that is repeated in many other taxa.

The rattlesnake genus *Crotalus* provides a glimpse into vicariance biogeography in an island archipelago. The pattern involves a distinctive south-north

mountain island deployment of principal groups of taxa (Fig. 5). One group is "southern" in origin with its ecological metropolis in the Sierra Madre Occidental of northwestern Mexico (Madrean); the other is "northern" in origin in the Rocky Mountains of the southwestern United States (Petran).

Two of the most interesting early findings for the herpetofauna and avifauna are indicated in Figures 4 and 5. One of these findings is the occurrence of a sharp biogeographic boundary line that divides in two the montane island archipelago—the Madrean Archipelago—lying between the Sierra Madre Occidental proper and the Colorado Plateau proper. The geographic position of this Madrean Line that divides the archipelago in two is approximated by the present location of Interstate Highway 10 (I-10) in southeastern Arizona and adjacent southwestern New Mexico (Fig. 4). This Southwest biogeographic boundary line—the Madrean Line—is as sharp as the world's most famous one, Wallace's Line, which divides the Malay Island Archipelago in two (Wallace 1859, 1863). Wallace's Line is unarguably the boundary line of greatest interest and prominence in biogeography.

The other especially interesting finding illustrated in Figures 4 and 5 is for the Sierra Pinaleño (Graham Mountains), the highest mountain range involved in the system. The Pinaleños provide an enigmatic situation that parallels that of the enigmatic Celebes (now Sulawasi) in the Malesian theater of Wallace's Line. The Pinaleño enigma, as illustrated here by rattlesnakes in the genus *Crotalus* (Fig. 5), results from the anomalous presence of Madrean (southern) taxa north of the boundary line ("I-10") on what is presumably a mountain island outlier of the Rocky Mountain (northern) massif.

We conclude for the Pinaleños, as Wallace (1876) did for the Celebes, that the Pinaleños were not earlier united by extensive lands (highlands) to either the northern or the southern massif. Rather, as indicated best by the packrat midden data (Van Devender 1990*a*,*b*), faunal connections with dispersal under secular climatic change, came through woodland and forest communities across what are currently grasslands in the archipelago lowlands (Fig. 4). Thus, what is clear beyond reasonable doubt is that during the last dozen-odd glacial and interglacial faunal and floral dispersions, the Pinaleños have witnessed the comings and goings—during the last dozen-odd glacial and interglacial faunal and floral dispersions—of Madrean taxa and Rocky Mountain taxa during the cyclical waxing and waning of their northern and southern distributional limits.

Thus, certainly the anomalous Pinaleños in the Southwest, like the anomalous Celebes for Wallace and those who followed in Malesia, speak clearly to the theory first proposed by Wallace (1876 and elsewhere) that present regional biogeography reflects events of the past—the geological floral and faunal history of the area.

These findings for the Madrean-Rocky Mountain montane archipelago system were made in the 1950s and 1960s by field zoologists at the University of Arizona engaged in detailing the ecological and geographical distributions of the Sierra Madrean and Rocky Mountain vertebrate faunas in southern Arizona and adjacent Mexico. We conducted a part of this field work in the Rincon Mountains of SNM. The first and most thorough field-based investigation of Madrean-Petran montane island distributional patterns is Marshall's (1957) Birds of the Pine-Oak Woodland. The most recent examination is by Davis (1991), who is studying the Madrean-Petran montane sedentary mammal fauna, inclusive of those in Saguaro National Monument (Davis et al., in press).

What about the plants? One of the striking similarities of the Southwest Madrean-Petran case to the classical one in Malesia is the nonconformity of many plant distributions to those of the animals. Many plant taxa including major dominants do not adhere nicely to the faunal boundary lines in either area, while some do fit the pattern. For the Malesian case, see contributors in Whitmore 1981, 1987; for the Southwest case see Shreve 1915; Marshall 1957; Lowe 1961; Whittaker and Niering 1964; Bowers and McLaughlin 1987.

For the Santa Catalina-Rincon Mountains and other ranges *north* of the Madrean-Petran boundary (Fig. 4), the *southern* representation of plant taxa is relatively weak in terms of the abundance (population densities) of major community dominants. This is true however strong may be the Madrean percentage of the total taxa in the flora (Shreve 1915 to Bowers and McLaughlin 1987). Major Madrean plant dominants and others dwindle in population densities northward of the Madrean Line reaching

extinction at or before the Mogollon Rim, which is a major boundary in the archipelago. The northward population diminution of Madrean plant taxa to extinction is controlled primarily by deficient winter heat—as in the case of their northward truncated physiognomy—in annual concert with progressively-northward deficient summer precipitation.

Between the Pacific and Atlantic coasts are five major south-north biotic corridors that extend in latitude across and beyond the Mexico-United States borderlands. The Madrean Archipelago lies within one of these corridors. The plant and animal populations in all of these south-north corridors obviously respond individually and differentially to the environmental constraints that determine taxon distributional limits. It is beyond reasonable doubt for the subtropical and tropical taxa, that winter-deficient heat northward, and summer deficient rainfall northward, provide major direct and indirect constraints on population distribution and population dispersal across the several degrees of latitude within each of the five corridors (Fig. 6). This conclusion was confirmed long ago by relevant data from many observers stationed in southern Arizona, beginning with Forrest Shreve (e.g., 1911) and John Thornber (e.g., 1911).

The Wilderness Act of 1964 defined wilderness as *an area of land untrammeled by man, with opportunity for solitude, containing ecological, geological, educational, scenic, and historical values*. In closing these brief remarks on investigations into what G. G. Simpson (1964) called "explanatory biogeography," it should be underscored that our field investigations have included studies at SNM, which fortunately protects within its boundaries several presently untrammeled Sonoran Desert biotic communities. And, because of the mission of the NPS, the monument protects what will be the last untrammeled montane forest island—the Rincon Mountains—in all of the Madrean-Rocky Mountain island archipelago.

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Table 1. The amphibians and reptiles at Saguaro National Monument. From Lowe and Holm (1986, 1991).

Phylum Chordata
- Subphylum Vertebrata
  - Class Amphibia (8 species in 4 genera)
    - Order Anura—Frogs and Toads (8)
      - Family Bufonidae—Toads (3)
      - Family Hylidae—Treefrogs (1)
      - Family Pelobatidae—Spadefoot Toads (2)
      - Family Ranidae—Frogs (2)
  - Class Reptilia (49 species in 35 genera)
    - Order Testudines—Turtles (3)
      - Family Emydidae—Pond and Box Turtles (1)
      - Family Kinosternidae—Mud and Musk Turtles (1)
      - Family Testudinidae—Tortoises (1)
    - Order Squamata (46)
      - Suborder Sauria—Lizards (19)
        - Family Helodermatidae—Beaded Lizards (1)
        - Family Gekkonidae—Geckos (1)
        - Family Iguanidae—Iguanids (12)
        - Family Scincidae—Skinks (1)
        - Family Teiidae—Whiptails and Allies (3)
        - Family Anguidae—Alligator Lizards and Allies (1)
      - Suborder Serpentes—Snakes (27)
        - Family Leptotyphlopidae—Blindsnakes (1)
        - Family Colubridae—Colubrids (19)
        - Family Elapidae—Coralsnakes and Allies (1)
        - Family Viperidae—Vipers and Pit-Vipers (6)

Table 2. The six rattlesnake species at Saguaro National Monument.

Crotalus cerastes	Sidewinder
C. atrox	Western Diamondback Rattlesnake
C. tigris	Rattlesnake
C. scutulatus	Mohave Rattlesnake
C. molossus	Blacktailed Rattlesnake
C. viridis cerberus	Arizona Black Rattlesnake

Table 3. Species-pairs in the Sonoran Desert that are present-or-absent congeners in the herpetofauna at Saguaro National Monument (SNM). The four congeners absent within the boundaries of SNM are present a short distance off site, on the nearly-adjoining Avra Valley bottom fill to the west of the monument boundary fence in the Tucson Mountain District (Fig. 3).

Organ Pipe Cactus National Monument		Saguaro National Monument
Phrynosoma solare	Regal Horned Lizard	*Phrynosoma solare*
Phrynosoma platyrhinos	Desert Horned Lizard	Absent
Urosaurus ornatus	Tree Lizard	*Urosaurus ornatus*
Urosaurus graciosus	Longtailed Brush Lizard	Absent
Phyllorynchus browni	Saddled Leafnosed Snake	*Phyllorynchus browni*
Phyllorynchus decurtatus	Spotted Leafnosed Snake	Absent
Chilomeniscus cinctus	Banded Burrowing Snake	*Chilomeniscus cinctus*
Chionactis occipitalis	Western Shovelnosed Snake	Absent

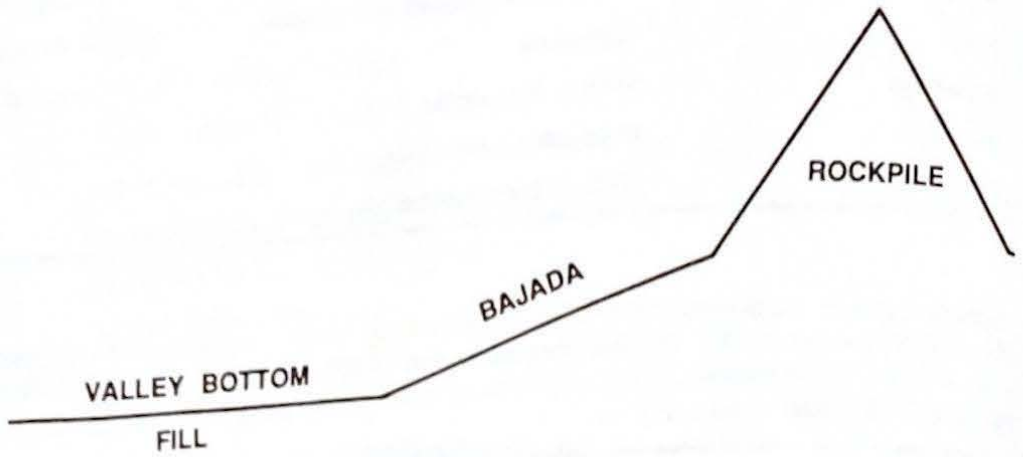


Fig. 1. Three major underlying features of desert landscape structure—the rockpile, its bajada, and the valley bottom fill, of a desert ecosystem.

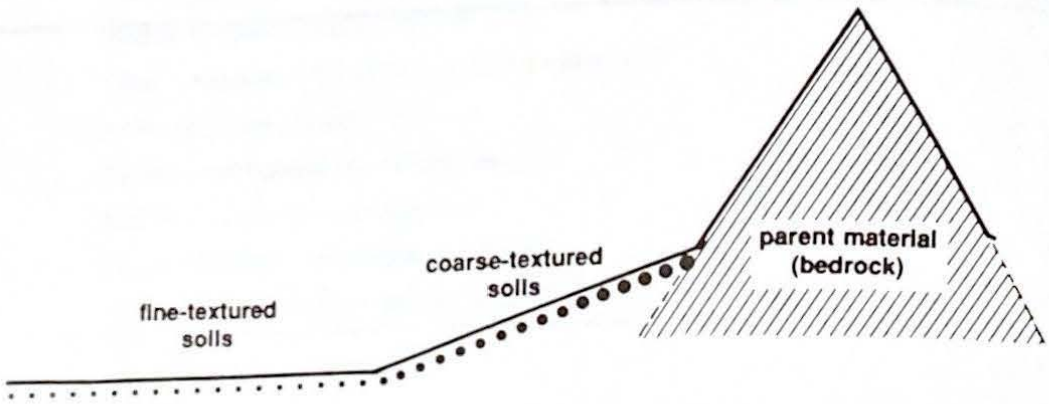


Fig. 2. Predominating soil textures are indicated in their relative positions (coarse to fine, not to scale) on the gradient of soil particle size distribution in the three subsystems of a desert ecosystem unit.

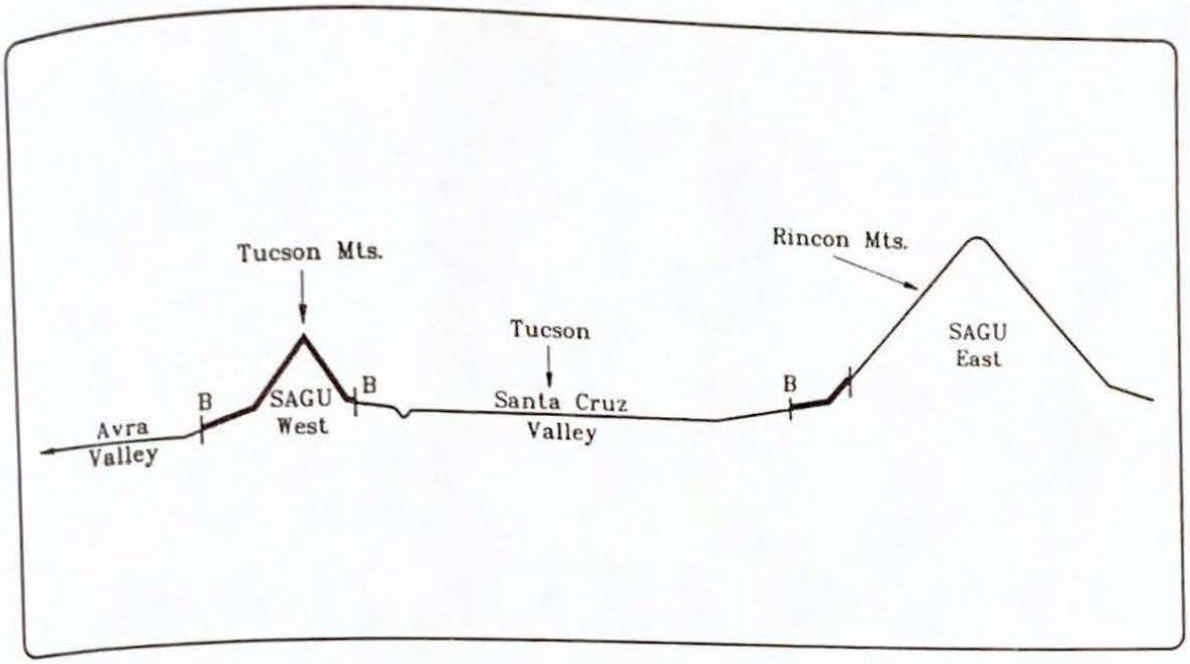


Fig. 3. Saguaro National Monument and environs in diagrammatic profile, not to scale. Sonoran Desert areas *within the monument* are indicated by bolder lines between hash marks. A complete three-part desert ecosystem unit does not occur within the boundaries of Saguaro National Monument. The monument includes bajada (B) and rockpile (RP) subsystems, while falling shy of the basin subsystem of fine-textured valley bottom fill (VF). Accordingly, members of several paired-taxa congeners in the Sonoran Desert herpetofauna do not occur on the monument (see Table 3).



Fig. 4. Part of the vegetation map at scale 1:1,000,000 representing biotic communities in the North American Southwest (Brown and Lowe 1980). Mountain islands are shown in the Madrean-Rocky Mountain archipelago (or Madrean Archipelago) both north and south of the Madrean Line, a major Southwest biogeographic line with which today's Interstate Route 10 (I-10) coincides; this is the Southwest equivalent of Wallace's Line.

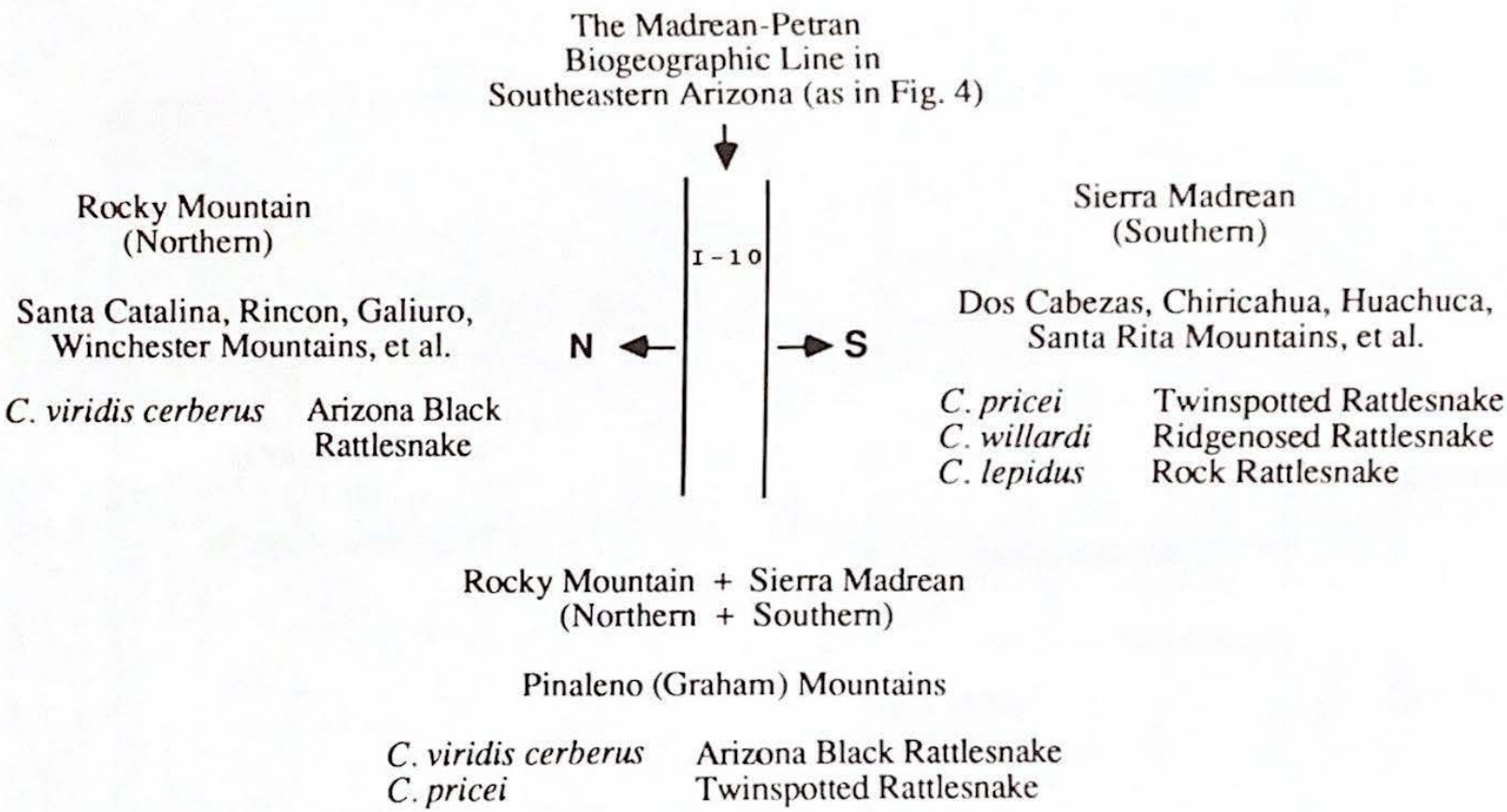


Fig. 5. The distribution of four species of mountain rattlesnakes (genus *Crotalus*) in southeastern Arizona. A fifth species, the blacktailed rattlesnake (*C. molossus*), occurs both north and south of the line. The enigmatic Pinaleños lie north of it (see Fig. 4).

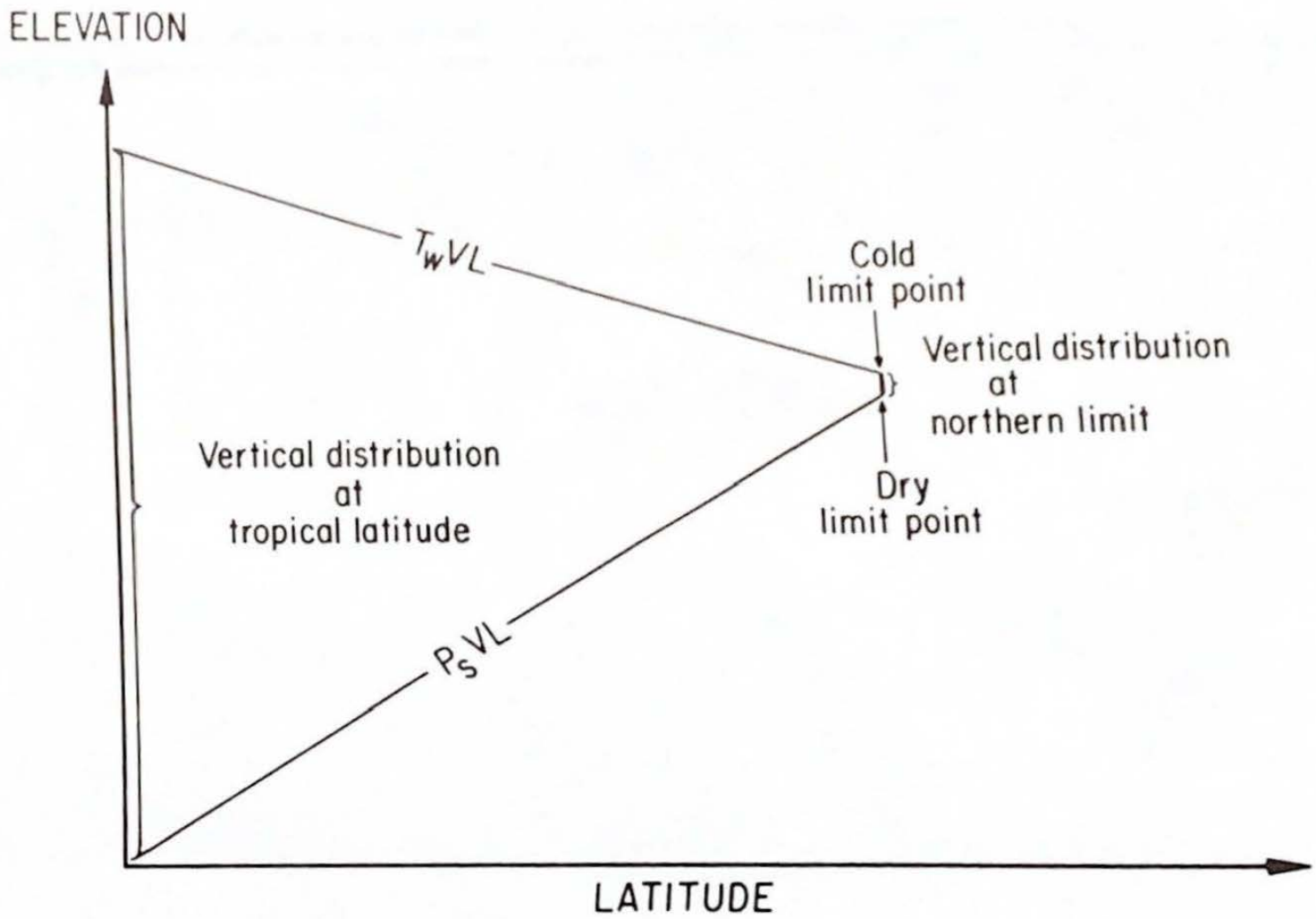


Fig. 6. Conceptual model of the pattern of northward limiting winter-deficient heat and summer-deficient rainfall—*the climatic constraints that gradually restrict (to extinction) the northward distribution of tropical and subtropical taxa along the Madrean Archipelago, as within the other four S→N distributional corridors out of northern Mexico (see text).*

The Importance of Xeroriparian Ecosystems to the Wintering Avifauna of Saguaro National Monument

R. Roy Johnson and Lois T. Haight

ABSTRACT

A xeroriparian study plot for wintering birds, consisting of a 30 x 800-m belt transect, and an upland control plot of the same dimensions, were established near the base of Tanque Verde Ridge in the Rincon Mountain District of Saguaro National Monument. Counts conducted on the xeroriparian plot in winter 1990-1991 averaged 19.67 species/census, with 167 individuals. In contrast, counts on the upland plot averaged 11 species and 47.5 individuals/census. Thirteen of the 27 species observed were recorded on only the xeroriparian plot, 14 occurred on both, but none occurred only on the upland plot, thus illustrating the importance of xeroriparian ecosystems to wintering birds.

INTRODUCTION

Riparian ecosystems have been recognized as some of the most important and most endangered ecosystems in the desert Southwest since at least the 1970s (Johnson and Jones 1977). Ecosystems associated with dry desert watercourses have also been considered important habitat for many species of plants and animals, including birds, for several decades (Lowe 1964). These drainageways, formed by intermittent and ephemeral streams, and their associated xeroriparian ecosystems (Johnson et al. 1984*a*), provide critical avian habitat in arid and semi-arid desert regions. A number of studies begun in the southwestern United States in the late 1960s and early 1970s first established the value of riparian lands as avian habitat. These early investigations quantified riparian bird population densities and species richness in desert lowlands along the Verde, Salt, and Gila rivers and tributaries in central Arizona (Johnson and Haight, in press). The earliest quantitative riparian avian studies were for breeding birds in cottonwood-willow (*Populus-Salix*), mixed deciduous broadleaf (*Platanus-Fraxinus-Populus*), cottonwood-mesquite (*Prosopis*), and associated riparian scrub (Carothers and Johnson 1971; Johnson 1971; Carothers et al. 1974). These studies used time-cost intensive spot map methodology, and provided highly accurate figures regarding population densities and species richness for breeding birds on plots approximating 4 ha (10 a) in size (Carothers et al. 1974).

The value of xeroriparian ecosystems was recognized at Organ Pipe Cactus National Monument (ORPI) by the 1950s (Hensley 1954). However, attempts to quantify the importance of these ecosystems to birds were not undertaken until 30 years later, during the 1980s, more than a decade after avian populations along perennial and wetter intermittent streams were first quantified, in 1969. Findings for xeroriparian studies have been similar to those for more mesic riparian areas, and demonstrate the importance of riparian areas as avian habitat in comparison to adjacent drier upland areas (Johnson and Haight 1985, 1988).

The earliest xeroriparian studies were conducted on both National Park Service (NPS) and non-NPS plots in the Sonoran and Chihuahuan deserts in the

United States and on Sonoran Desert plots in Mexico. The studies reported here are the first xeroriparian population studies for wintering birds on Saguaro National Monument (SNM).

STUDY AREA

The study was conducted in the Arizona Upland subdivision of the Sonoran Desert. The upland plot was established in a Sonoran desertscrub/scrub-grassland (semidesert grassland) ecotone (Brown et al. 1979). Dominant trees and shrubs were foothill paloverde (*Cercidium microphyllum*), velvet mesquite (*Prosopis velutina*), bush muhly (*Muhlenbergia porteri*), grama grasses (*Bouteloua* spp.), three-awns (*Aristida* spp.), numerous cacti (e.g., saguaro [*Carnegiea gigantea*], cane-fruit cholla [*Opuntia fulgida*], christmas cactus [*O. leptocaulis*], pricklypear [*O. phaecantha*]) and numerous other shrubs, grasses, and cacti. Vegetation on the upland plot was exceptionally lush, especially for an upland desert site.

The xeroriparian plot was in a lush stand of the mixed shrub-*Prosopis velutina* association (Brown et al. 1979). Dominant trees and shrubs were velvet mesquite (*Prosopis velutina*), catclaw acacia (*Acacia greggii*), netleaf hackberry (*Celtis reticulata*), desert hackberry (*C. pallidum*), desert broom (*Baccharis sarothroides*), graythorn (*Ziziphus obtusifolia*), chuperosa (*Anisacanthus thurberi*), canyon ragweed (*Ambrosia ambrosioides*), and several other woody species, as well as numerous grasses on floodplain terraces. The wash channel was incised, often bordered by banks 2 to 3 m high. In several places vegetation grows on xeroriparian islands separated by a braided streambed, typical for higher order ephemeral washes throughout the monument.

WASH ORDER

Wash order is a system for classifying drainageways formed by ephemeral and drier intermittent streams (Johnson et al. 1984*b*). The system was adapted from the stream order system originally devised for classifying running streams (Horton 1945). A headwater wash is first order until its confluence with another first order wash, then it becomes a second order wash (Fig. 1). As washes progress downslope, order increases each time there is a confluence between washes of like order—two second order washes form a third order wash, etc. Lower order washes entering higher washes do not result in an increase in order; thus a first order wash entering a second order wash does not form a third order wash, etc. Studies by Johnson et al. (1984) and Warren and Anderson (1985) at ORPI demonstrated a close relationship between wash order and plant species occurrence, presumably related to varying moisture availability. Higher order washes tend to support larger trees and shrubs and have a wider xeroriparian belt on the banks of the wash.

METHODS

Study plots consisted of two belt transects located near the base of Tanque Verde Ridge, at the southernmost part of the Cactus Forest Loop Drive in the Rincon Mountain District (RMD) of SNM (T14S, R16E, S32). We modified our earlier censusing methodology (Johnson and Haight 1985, 1988) to provide a maximum amount of information with the minimal resources available. A xeroriparian census plot consisted of a 30 x 800-m belt transect, with actual width in a given area determined by the width of the wash, including channel and riparian vegetation on each side. An upland plot was designed for paired plot comparison, and was also 800 m in length and an average of 30 m wide. Care was taken to separate the upland plot from the xeroriparian plot by at least 200 m, preferably 400 m, but this is not as critical for winter as for spring and summer censuses when birds are on breeding territories.

The upland plot originated 50 m southwest of the "Cactus Forest Trail" sign located approximately 0.25 mi northwest of the Javelina Picnic area turnoff. The plot continued along the crest of the ridge to its end, then turned 90° to the southeast (directions approximate) and continued to the next ridge, turned 90° to the northeast, continued across the road and then roughly paralelled the one-way road. It ended approximately 50 m from the road and 250 m south of the large wash that was used for the xeroriparian plot (Fig. 2). The xeroriparian plot began 100 m west of the loop drive in the largest wash in the area (approximately 4th order), and continued 800 m downstream to a couple of hundred meters from the point where the Cactus Forest Trail drops from a hill into the wash.

Originally, attempts were made to conduct paired censuses on the same mornings in December 1990 and January 1991; however, the combination of late sunrise and cold mornings made it nearly impossible to accomplish this. Little avian activity occurred before sunup, which occurred about 30 min. earlier on the upland plot than the xeroriparian plot. Approximately the same length of time was spent on each plot, generally 40 to 60 min. Birds on the upland plot were comparatively easy to detect and identify. However, censusing the xeroriparian plot often required more time because of additional effort required to count larger numbers of sparrows (Table 1) and because the denser vegetation resulted in greater difficulty in detection and identification of birds. The census taker whistled an imitated call of the ferruginous pygmy-owl (*Glaucidium brasilianum*) at regular intervals of approximately 50 m during the xeroriparian census to attract certain species, e.g., ruby-crowned kinglets, hermit thrushes, and Bewick's wrens, that otherwise often go unnoticed (scientific names of birds observed are given in Table 1). Ideally, if censuses are conducted two days in a row, reversing the direction traveled on the second day increases the probability of observing certain birds, especially those near the end of the count that may have short activity periods. If two plots are censused on the same day, the order of census for the plots should be reversed on the second day. For standardization, only the birds observed by one person were counted, even if two or more individuals were involved in walking the transect.

We conducted most of our censuses on relatively sunny, windless days. Attempts to census on a couple of cloudy and/or rainy days were largely unsuccessful. Wind, rain, and other environmental factors often lead to decreased avian activity and/or reduction in observer sight and/or hearing of avian activity (Johnson et al. 1981; Ralph and Scott 1981). The xeroriparian area was censused three times, and the upland area was covered twice.

We began censusing as soon as morning avian activity began. Most of the sparrows became active when the sun started warming the area and the sparrows then left to feed in the grasses of the adjacent uplands within an hour after sunrise. This necessitated censusing of the xeroriparian plot first, so we covered each plot on a different day to standardize both the length of time and time of day for upland and xeroriparian censusing. The high degree of accuracy attained for breeding bird studies by Carothers et al. (1974) in spot-mapping breeding birds exceeds the limits of our methodology. However, comparative figures for upland and xeroriparian species richness and population densities established by our methodology are relatively reliable.

RESULTS AND DISCUSSION

Three xeroriparian censuses averaged 19.67 species/census with 167 individuals, in contrast to upland averages of 11 species and 47.5 individuals/census (Table 1). Thus, the xeroriparian plot supported approximately 3.5 times the number of individuals and twice the number of species as the upland plot. Four species were recorded on each of the five censuses, six species on four censuses, eight on three censuses, four on two censuses and five on only one census.

Of perhaps greatest significance is the almost equal split of species occurrence in the two areas, with 13 of the 27 species recorded only on the xeroriparian plot, 14 on upland plots also, but none only on the upland plot. The critical importance of xeroriparian ecosystems is clearly illustrated, since all species occured at some time in the xeroriparian ecosystem, but no species were restricted to the uplands. However, it would be a mistake to assume that the upland habitat is not essential. For example, although several species of sparrows roosted and rested on the xeroriparian plot, they were dependent on the extensive upland semidesert grassland ecosystem for food.

Even though there is appreciable contrast in our findings between upland and xeroriparian ecosystems, the differences are not as great at SNM as for most other areas we have studied during the past 11 years in the Sonoran and Chihuahuan deserts. Our other studies tend to show 5 to 10 times the numbers of species and/or individuals on all types of riparian plots as on adjacent upland plots, with few exceptions (Johnson and Haight 1985, 1988). We credit the relatively low contrast between upland and xeroriparian plots in the present study to three main factors:

1. The ecotonal nature of the SNM area, which shows characteristics of both desertscrub and semidesert grassland, discussed earlier.

2. The large number of drainageways distributed throughout the Rincon Mountain foothills make it difficult to establish a transect of more than a couple of hundred meters without crossing a wash. Our 800 m long upland plot crossed several first order washes (see below) and relatively heavily vegetated swales.
3. The Sonoran Desert is the only arboreal desert in North America. Saguaros are extremely important nest sites for some species and several species of birds use saguaro nest cavities throughout the year.

Although winter birds are not generally as territorial as breeding birds, certain species are relatively regular in their habits, especially in winter roosting and feeding patterns. The unidentified, mid-sized owl (Table 1) was found along the same section of the wash on several days. The large flock of Brewer's sparrows roosted in approximately the same area on floodplain meanders along the wash each night of the census period and left at approximately the same time each morning to feed in the upland grasses. Permanent residents, e.g., curve-billed thrashers, cardinals, and pyrrhuloxias maintained semblances of territories throughout the year. Several winter residents, e.g., ruby-crowned kinglets, hermit thrushes, and Bewick's wrens maintained winter territories. Thus, the more often one censuses an area the more familiar one becomes with the locations of individual birds. This also is the rationale for censusing at least two or three days in a row. The census taker becomes more familiar not only with the terrain and vegetation but also with the location of individual birds.

CONCLUSIONS

Extensive losses of riparian habitat have led to great concern about associated impacts on breeding birds, especially in the lowland North American Southwest (Johnson et al. 1985; Johnson et al. 1987; Knopf et al. 1988). The importance of riparian habitat to migrating (Stevens et al. 1977) and wintering birds (Johnson and Haight 1985, 1988) is becoming increasingly apparent. For, although reproduction is a critical event in the maintenance of a species, if birds do not survive migration and overwintering, whether due to loss of habitat or other causes, they may be extirpated as surely as when breeding conditions are not adequate.

National Park Service lands provide protected areas for wintering as well as breeding and migrating birds. The Tucson Basin foothills are rapidly becoming part of the Tucson urban environment (Duncan et al. 1986). Examination of aerial photography shows that approximately 10% of the basin is xeroriparian ecosystems. Saguaro National Monument is an important natural "island" in this setting and its well vegetated stream courses are a dominant aspect of the natural landscape. Even first order washes show a decidedly lush aspect on the monument in relation to the surrounding uplands; increasingly higher order washes show an even more marked contrast in comparison to upland plant communities.

MANAGEMENT IMPLICATIONS

Winter bird studies at Saguaro National Monument demonstrated that SNM's avian population is highly dependent on xeroriparian ecosystems. Similar findings from extensive studies in ORPI and other sites throughout all three North American deserts of the United States and Mexico have demonstrated the critical importance of xeroriparian habitats, compared to upland habitats. A disproportionate number of species of plants and animals are components of xeroriparian ecosystems, areas that constitute critical habitat for wintering, migrating, and breeding birds (Johnson and Haight, in press).

The great diversity of riparian habitats varies from permanently moist situations along perennial streams to bare sand or rock along dry desert washes. Although nearly all upland species exist in one or more of these diverse riparian habitats, many species of riparian plants and animals do not exist in upland ecosystems. Additionally, riparian ecosystems constitute only a small spacial percentage of the total land mass for most regions, especially in arid lands. Thus, one may find approximately 70-90% of the individuals and more than 50% of the avian species of a region along riparian corridors constituting less than 10% of the region's space.

Non-resilient upland ecosystems, especially in arid regions, may be relatively resistant to damage, but once damaged usually take considerable time to recover. By contrast, riparian ecosystems, including

vegetation, are generally comparatively resilient. Lusher vegetation and higher moisture assist riparian ecosystems in the recovery process. Thus, damaged riparian areas can often be successfully rehabilitated (Carothers et al. 1989).

The same characteristics that make riparian areas prime wildlife habitat also make them attractive to humans for development and recreational purposes. Riparian lands commonly receive disproportionate use by humans as well as wildlife (Johnson and Carothers 1982). Management strategies for park lands need to account for this disproportionate importance of riparian lands by active monitoring of these areas and by providing for their protection from overuse or inappropriate use by humans and domestic animals. Additionally, development and maintenance of facilities, roads, trails, and other management activities should be minimized in riparian areas.

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Table 1. Saguaro National Monument avian census, 1990-91.

	12-27-90 Xero-riparian	12-27-90 Upland	12-28-90 Upland	12-31-90 Xero-riparian	01-21-91 Xero-riparian
Gambel's quail *Callipepla gambelli*		16			3
Mourning dove *Zenaida macroura*	5			2	8
Great horned owl *Bubo virginianus*					1
*Owl spp.				1	1
Gila woodpecker *Melanerpes uropygialis*	4	2	1	3	3
Northern flicker *Colaptes auratus mearnsi*	1		1	1	2
Verdin *Auriparus flaviceps*	6	3	3	7	2
Cactus wren *Campylorhynchus brunneicapillus*	3	3	6		1
Bewick's wren *Thryomanes bewickii*	5			4	2
Ruby-crowned kinglet *Regulus calendula*	4	1		5	4
Black-tailed gnatcatcher *Polioptila melanura*	3	1	1	1	
Hermit thrush *Catharus guttatus*	4			3	3
Curve-billed thrasher *Toxostoma curvirostre*	1	2	2	1	1
Northern cardinal *Cardinalis cardinalis*	2	1		1	
Pyrrhuloxia *Cardinalis sinuatus*	2				
Green-tailed towhee *Pipilo chlorurus*	3		1	2	3

*Short-eared, long-eared or spotted owl.

Table 1. Continued.

	12-27-90 Xero-riparian	12-27-90 Upland	12-28-90 Upland	12-31-90 Xero-riparian	01-21-91 Xero-riparian
Canyon towhee *Pipilo fuscus*		2	4		2
Rufous-winged sparrow *Aimophila ruficeps*	2			2	
Chipping sparrow *Spizella passerina*					19
Brewer's sparrow *Spizella breweri*	99+	2	21	121	95+
Black-chinned sparrow *Spizella atrogularis*	2			1	
Vesper sparrow *Pooecetes gramineus*	5	13		1	
Black-throated sparrow *Amphispiza bilineata*	2	2	7		9
Savannah sparrow? *Passerculus sandwichensis*	1				
White-crowned sparrow *Zonotrichia leucophrys*	6			4	17
Lincoln sparrow *Melospiza lincolnii*	1				
House finch *Carpodacus mexicanus*	1			1	2
Total No. Individuals	162	48	47	161	178
Total No. Species	22	12	10	18	19

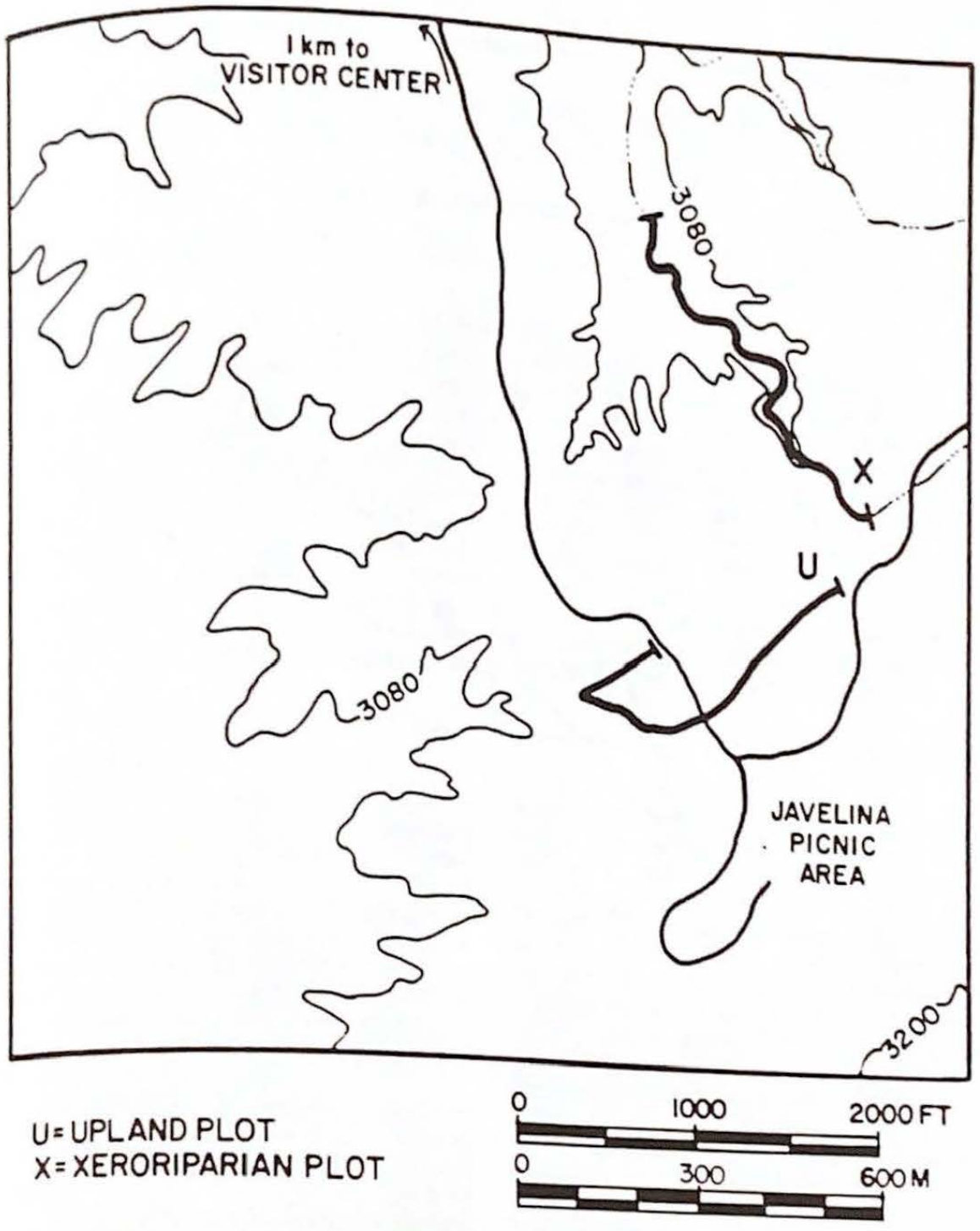


Fig. 1. Wash order system for classifying drainageways formed by ephemeral and drier intermittent streams.

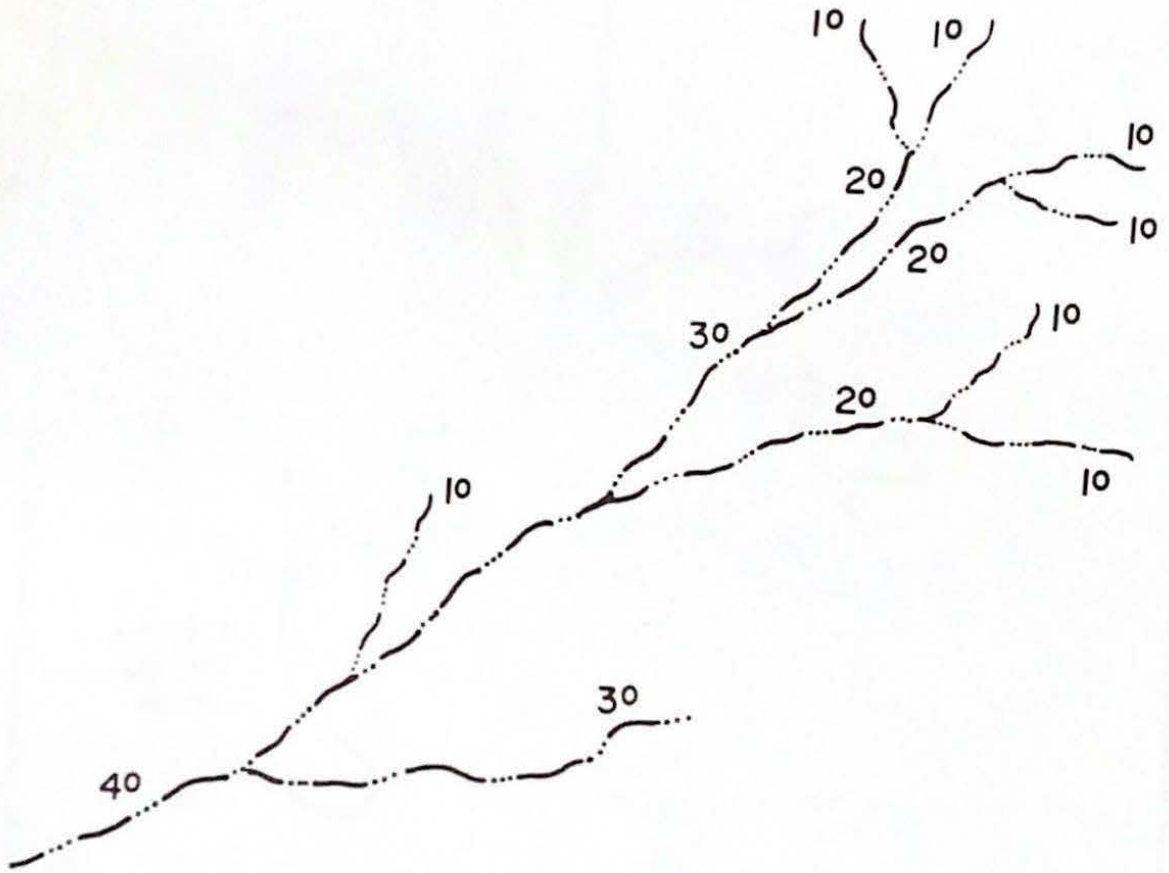


Fig. 2. Location of study plots, Rincon Mountain District, Saguaro National Monument.

Unexpected Mammalian Distributions in the Rincon High Country

Ronnie Sidner and Russell Davis

ABSTRACT

Trapping and observation of small mammals in the high country of the Rincon Mountains from 1983 to 1988 have yielded several species new to Saguaro National Monument. Two of these small mammal species provide evidence that contemporary colonization (ongoing movement of species across less suitable habitat separating mountain islands from each other and from the source of the species) has occurred. The yellow-nosed cotton rat (*Sigmodon ochrognathus*) exemplifies such colonization and suggests movement, sometime within the past 50 years, into a vacant niche in the Rincon high country. Abert's squirrels (*Sciurus aberti*) dispersed across semidesert grassland from the Catalina Mountains (where they were introduced in the 1940s) and offer another example of contemporary colonization—in this case with a very precise arrival time. Desert shrews (*Notiosorex crawfordi*) provide the first records of shrews from the Rincons and were found at record elevation and habitat. Eight species are added to the list of bats from montane conifer forest. Suggestions are given for protection of the monument for future environmental health and scientific endeavor.

INTRODUCTION

The Rincon Mountains, one of the isolated mountain ranges in southeastern Arizona, are examples of mountain "islands" in a "sea" of semidesert grassland. The island in this case is relatively small; the high country portion, at elevations ranging from about 1,525 to 2,640 m, consists of approximately 40 km^2 of Madrean Evergreen Woodland (mixed oak and oak associations), and approximately 20 km^2 of Madrean Montane Conifer Forest (ponderosa pine [*Pinus ponderosa*] and pine associations; Brown and Lowe 1983).

Despite proximity to Tucson and the University of Arizona, the Rincon Mountains have been studied by few animal ecologists, undoubtedly because access to the high country has been confined to foot trails since the early 1900s. Limited mammal collections were made by H. Brown in 1911 and by L. M. Huey in 1932. However, a complete list of mammals has not been compiled, nor has there been a rigorous study of mammals done in the high country since Huey's work, nor since most of the Rincon's woodland and forest habitats were included within the boundaries of Saguaro National Monument (SNM) at its establishment in 1933 (Cockrum 1960; Hoffmeister 1986). To correct this difficiency, we began hiking into SNM to live-trap small mammals in the oak woodland and montane forest, and we compiled previously gathered information to compose a more thorough list of mammal species diversity and distribution within SNM (Davis et al. 1986; Doll et al. 1989).

Island biogeographical theory has been applied to mammals on desert mountains. According to this theory, species richness should result from the opposing forces of colonization and extinction. The rate of colonization should decrease as the distance increases from the source of distribution of the species, while the rate of extinction should increase with a decrease

in island size. However, biogeographers generally have favored the idea that once these mountain islands were colonized (at some time in the past when the climate was cooler and wetter and when the mountains were interconnected by forest habitats), extinction since then has played the only significant role in determining the current species pattern (Davis and Dunford 1987). However, we report here two examples of the distribution of mammal species that do not fit this previously accepted biogeographical explanation. In addition to these unexpected examples of geographical distributions, we also report two cases of unexpected ecological distributions of mammals.

METHODS

We hiked into SNM to observe small mammals and trap them with live traps, pit-fall (can) traps, and mist nets in the fall of 1983, the spring of 1985, and during the summers of 1984 through 1988. We spent six days in the oak woodlands during April, September, and October, and 41 days in the montane conifer forest during May, June, and August. We also compiled information about mammals of the high country from records at the University of Arizona Mammal Collection, the Museum of the San Diego Society of Natural History, and from observation records kept by personnel of SNM. Mammal names used in this report follow those of Jones et al. (1986).

RESULTS AND DISCUSSION

Yellow-nosed Cotton Rats

Within forest habitats in Arizona are patches of subalpine grasslands (Brown and Lowe 1983) suitable for grass-eating, runway-making rodents such as members of the vole genus, *Microtus*. In southern Arizona today, however, a species of this genus, the long-tailed vole (*M. longicaudus*), currently occurs only in high mountain meadows of one mountain range, the Pinaleños (Graham Mountains). Fossil deposits with *Microtus* from late Pleistocene age, including one from the northeastern side of the Catalina Mountains, suggest the possibility that this genus once occurred on most mountains of southeastern Arizona but became locally extinct. In the Rincon Mountains, small grass-fern meadows can be found at elevations from 2,226 to 2,640 m, surrounded by ponderosa pine-oak (*Pinus ponderosa-Quercus* sp.) and ponderosa pine-Douglas-fir (*Pseudotsuga menziesii*) forest that would be appropriate for *Microtus*, but none exist there today. This niche for grass-eating, runway-making rodents is now occupied by the yellow-nosed cotton rat, *Sigmodon ochrognathus* (Davis and Ward 1988).

The presence of these rats in these montane meadows was first verified in August 1984, when we were surprised by the capture of five in just 20 traps set in Manning Camp meadow at 2,440 m elevation. Although the Rincons were within the range of this species, yellow-nosed cotton rats had not been recorded from them, and relatively few specimens had been previously taken in Arizona (Hoffmeister 1986). None had been reported above 1,860 m (Cockrum 1960) nor above oak woodland habitat (Hoffmeister 1986). In August 1985, we found yellow-nosed cotton rats again in Manning Camp meadow, Spud Rock Cabin Site meadow (2,226 m), on top of Spud Rock (2,621 m), and in Mica Meadow (2,561 m). However, during the earlier and drier season of that year, in May and June, we did not find any yellow-nosed cotton rats at these localities. All of the northern records of this species have been recent; these rats were not known much north of the border mountains until after 1960 (Cockrum 1960; Hoffmeister 1986; Davis and Ward 1988).

It appears that yellow-nosed cotton rats have colonized northward in the last 50 years from their origin along the eastern slopes of the Sierra Madre Occidental. To reach their typical habitat in the rocky, grassy slopes of the oak belt in the southeastern mountains, these rats had to move through less suitable semidesert grassland habitats. Such colonization efforts are striking exceptions to the previous biogeographical explanation for the distribution of small mammals in woodland and forest habitats on the mountains of southern Arizona. When the climate became warmer and drier after the Pleistocene, leaving woodland and forest habitats isolated on mountaintops, the mammals of these habitats all were thought to have been left stranded on mountains, with only the possibility of extinction (or speciation) to alter species composition on any mountain (Davis and Dunford 1987). The dispersal of yellow-nosed cotton rats northward within the past 50 years or so provides evidence of contemporary colonization. In addition, because they are the ecological equivalent of *Microtus* in its grass-eating, runway-making habit, yellow-nosed cotton rats have moved in to fill this

vacant niche in several southeastern Arizona mountains including the Rincons (Davis and Dunford 1987).

Abert's Squirrels

In 1941, Abert's squirrels (*Sciurus aberti*) were introduced into the Catalina Mountains, where they have become common. In 1959, a SNM employee recorded having seen one of these squirrels near Spud Rock in the Rincon Mountains. Abert's squirrels do not appear to be common yet in the Rincons, but they now have been recorded from many forest localities, and we saw them several times at and near Manning Camp (Davis et al. 1986).

None of the early sight records of Abert's squirrels mention the significance of their sudden appearance in the Rincons. The possibilities that might occur to someone upon first seeing them here are that this species had been present all along but had been overlooked, or that it had been introduced. It is unlikely that these conspicuous squirrels were overlooked for very long, and it is highly unlikely that someone illegally went to the logistical difficulty of capture, maintenance, and backpack transport to release them into a mountain range lacking road access or hunting possibilities. The much more likely explanation is that these squirrels dispersed from the Catalinas sometime between 1941 and 1959.

As with the yellow-nosed cotton rat, this is another example of what has been termed contemporary colonization (Davis and Dunford 1987)—the ongoing movement of a species from a source across non-typical and less suitable habitat to isolated patches of suitable habitat. In this case, squirrels moved from ponderosa pine forest in the Catalina Mountains, across 23 km of woodland and semidesert grassland in Redington Pass, to ponderosa pine forest in the Rincons. Several similar movements by Abert's squirrels across less suitable habitat to colonize new territory in Arizona have been documented by Davis and Brown (1989). A similar situation must have occurred with Abert's squirrels on the North and South Rim of the Grand Canyon.

It had previously been thought that Abert's squirrels were widely distributed during the Pleistocene in the vast coniferous forest which covered much of Arizona, and that they were left stranded in high elevational islands with the increase in environmental aridity after the Pleistocene. It was presumed that these squirrels were left in their islands like prisoners unable to move beyond their confines and that the Kaibab squirrel, a subspecies of Abert's squirrel, was left on the North Rim with resulting population changes accumulating because gene flow with other high elevational populations was stopped. We know now, from plant fossil evidence, that this was not the case. Abert's squirrels depend upon ponderosa pines for long-term survival, and no ponderosa pine forest occurred on the North Rim before the early Holocene. In consequence, these squirrels must have colonized northward with, or after, the establishment of ponderosa pine. To have reached the North Kaibab required that they move across non-montane habitat—perhaps that occurring within the Grand Canyon (Davis and Brown 1989).

Desert Shrews

No species of shrew had previously been recorded from the Rincon Mountains. The montane shrew (*Sorex monticolus*) occurs in the montane conifer forest in the Catalina Mountains, and was expected to be present in the Rincon high country meadows. In 1985, Davis found a desert shrew (*Notiosorex crawfordi*) dead atop a boulder on Spud Rock (2,621 m), but he postulated that an owl could have carried it there. However, three years after the placement of pit-fall traps in Manning Camp meadow (2,440 m), a desert shrew was caught verifying the presence of this species in the Rincon high country (Davis and Sidner 1989).

The desert shrew that was found in Manning Camp meadow not only represents a new locality record (i.e., the Rincon Mountains), it is also a habitat and elevational record for the species. Previous observations are from arid to riparian habitats in desertscrub up through the oak belt below 1,830 m (Cockrum 1960). The absence of the "appropriate" shrew for this locality (the montane shrew) and the presence instead of a species found at lower elevations, might suggest another example of a species moving in to fill a vacant niche in montane forest (Davis and Sidner 1989).

Bats of Manning Camp Meadow and Pond

Bats have been captured at three localities in the Rincon high country. In July 1911, H. Brown collected two big brown bats (*Eptesicus fuscus*) at Manning Camp (2,440 m). In June 1932, L. M. Huey collected two big brown bats, one southwestern myotis (*Myotis*

auriculus), and one long-legged myotis (*Myotis volans*) at Spud Rock Cabin Site (2,226 m). These ecologists used shotguns to collect bats as did most early collectors, but guns are not now allowed in the monument and are no longer appropriate for the capture of bats anywhere because of the possibility of indiscriminate injury or death of a federally protected bat species. In August 1966, B. Lund collected four fringed myotis (*Myotis thysanodes*) at Manning Camp (no field notes are available, but these specimens were probably from a roost in the cabin). We captured a single big brown bat in a net over Chimenea Creek at Grass Shack (1,659 m) in September 1983. In June 1988 we netted over Deer Head Spring (2,195 m) where bats were seen flying, but we caught none. Capture success at the pond at Manning Camp, however, was often surprisingly high; from 1984 to 1988 we netted 136 bats.

Our technique was to set mist nets over water to sample bats that came to drink or to forage on concentrations of flying insects. Nets were left open from one to approximately nine hours (all night). Freezing temperatures and steady rain were associated with the absence of bats. Evenings that followed days of high temperatures and bothersome flying insects saw increased bat activity. During the rainy season (August-October), few bats were caught. For example, at Grass Shack on 9 September and 29 October 1983, a net left open all night yielded only one bat. One net set all night at Manning Camp pond in August 1984 produced no bats, and during 32 hours of netting there in August 1985, only five bats were captured. Netting during drier months such as May and early June was much more productive. For example, during May-June 1985, 38 hours of netting at Manning Camp produced 58 bat captures.

Prior to 1988, only three species of bats had been recorded from the Rincon high country (Hoffmeister 1986; Sidner et al. 1988). Twelve species of insectivorous bats have now been netted at Manning Camp pond (Table 1). This is the highest recorded species density (number of species per unit area) of mammals on the monument. The high species diversity of bats at Manning Camp is a result of the drinking water provided by the pond, and the abundance of insect prey attracted to both the water and the nearby meadow. The presence of a large number of species sharing a single resource would be expected to cause the selection of resource allocation patterns to minimize competition. Resource allocation involving temporal spacing has been suggested for the two most abundant species at the pond, big brown bats and silver-haired bats (*Lasionycteris noctivagans*) (Davis et al. 1986).

SUMMARY AND MANAGEMENT IMPLICATIONS

Two species of mammals (yellow-nosed cotton rats and desert shrews) found in Manning Camp meadow are unusual and rare at that elevation and habitat type. The meadow should be protected from any change; for example, continuation of the policy against grazing by pack animals in the meadow is warranted.

Twelve species of bats have been discovered drinking or feeding over the Manning Camp pond. Because the pond is the source of water for field personnel, it will of course be protected, but it is important that this be accomplished in a way to preserve its present conditions in terms of open access, depth, natural purification, and any other parameters affecting the natural insect communities. Additional field work is warranted to learn more about community structure of these bats.

The encroaching development of homes and businesses near SNM borders will impact wildlife either as a result of visits to homes by wandering or enticed wildlife, or as human and pet visitors discover wildlife and their resources on the monument. For this reason, public participation in educational programs about environmental and ecological principles will become increasingly important. Additional symposia and other educational programs should be offered.

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Table 1. Bats netted at Manning Camp pond. Numbers of each species are tabulated by month and year. Species marked with an asterisk had been captured previously in the Rincon high country. A question mark designates two unidentified myotis bats (one escaped, and one was eaten by a raccoon).

		1985		1986	1988
Common name	Scientific name	Jun	Aug	Jun	Jun
Vespertilionid Bat Family	Vespertilionidae				
Southwestern Myotis*	*Myotis auriculus*	6		4	1
California Myotis	*Myotis californicus*			1	1
Western Small-footed Myotis	*Myotis ciliolabrum*			2	
Fringed Myotis*	*Myotis thysanodes*	6		2	1
Long-legged Myotis*	*Myotis volans*	4		4	1
Yuma Myotis	*Myotis yumanensis*			1	
Myotis ?	*Myotis* spp.	1	1		
Hoary Bat	*Lasiurus cinereus*	3		6	3
Silver-haired Bat	*Lasionycteris noctivagans*	4		11	6
Townsend's Big-eared Bat	*Plecotus townsendii*		1		1
Big Brown Bat*	*Eptesicus fuscus*	34	3	12	14
Pallid Bat	*Antrozous pallidus*			1	
Molossid Bat Family	Molossidae				
Brazilian Free-tailed Bat	*Tadarida brasiliensis*				1

A Long-Term Study of Natural Selection in a Natural Population of the Tree Lizard

Donald B. Miles

ABSTRACT

A long-term mark-recapture analysis was initiated in the spring of 1987 to assess the selective significance of body size in a population of *Urosaurus ornatus* (tree lizard) inhabiting a mesquite (*Prosopis juliflora*) bosque at Saguaro National Monument. Over 1,000 lizards were captured during the four-year study period. Average body size of both male and female lizards exhibited a significant decline over the four years. This pattern is attributed to a reduction in food resources as a result of low rainfall from 1987 through 1989. Rainfall patterns in the Tucson region showed a correlation with El Niño-Southern Oscillations, suggesting a global influence on local climate. The decline in lizard body size also affected the patterns of natural selection operating on body size. Overall, recurring and oscillating patterns of selection likely affected body size. Males and females showed strong, but opposite differentials which may be evidence for separate selection pressures acting on the sexes.

INTRODUCTION

The process of natural selection is a major evolutionary force responsible for molding the shape of phenotypic traits in natural populations (Futuyma 1986). Because of its prominence in evolutionary biology, natural selection has been intensively studied from a variety of perspectives and approaches. Many of the studies demonstrating selection have involved indirect estimates, such as correlations between a phenotypic trait and an environmental variable (e.g., Fleischer and Johnston 1984; Endler 1986). Few investigators have adopted available alternative approaches (e.g., cohort analysis, comparisons among age classes or life-history stages, and perturbations of natural populations), to provide a more direct estimate of the magnitude and direction of selection (Endler 1986; Schluter and Smith 1986). Even fewer researchers have followed populations for several years (e.g., Grant and Grant 1990).

In this paper, I describe direct estimates of the temporal patterns of natural selection on body size in a resident population of *Urosaurus ornatus* (tree lizard) over a four-year period. The description of such patterns will enhance our understanding of the ecological significance of fluctuating environmental conditions on phenotypic traits. In each year of the study, I analyzed the data for evidence of selection at a single life history stage—overwinter survivorship. Determination of selection over several years provides an opportunity to assess the frequency and magnitude, as well as the form of selection, i.e., directional or stabilizing. Previous studies of natural selection have focused on breeding bird populations in dramatically fluctuating environments (e.g., Grant 1986; Grant and Grant 1990; Price et al. 1984; Gibbs et al. 1988). This study is one of the few to present the selection regime operating on an ectothermic vertebrate.

Factors Affecting Body Size

Body size is a critical ecological trait for many species (Peters 1983). Increased body size may have important effects on reproductive success, acting through dominance relations in males or larger clutches in females (Dunham 1981, 1982; Dunham and Miles 1985). As lizards increase in size (e.g., from juveniles to adults), advantages in avoiding predators may occur (Peters 1983). Two proximate factors acting to determine body size of lizards are: (1) levels of food availability, and (2) length of the growing season (Ballinger 1977; Dunham 1978). Both may act to limit growth rate and hence ultimate size at adult stage (Ballinger 1977). Food availability may be indirectly estimated by rainfall and length of growing season by calculating the number of degree days per year.

Demographic Profile of *Urosaurus ornatus*

The Saguaro National Monument (SNM) population of this species has a cohort generation time of 1.5 years and an average annual adult survivorship of 0.20 (D. B. Miles, unpubl. data). The maximum life span in the field (i.e., age of the oldest captured individual) is at least five years. The age of first reproduction for both sexes is eight months at a snout-vent length (SVL) of 46 mm. Maximum recorded adult body size is 53 mm for females and 58 mm for males. Potential predators at the SNM site include the lizards *Sceloporus magister* (desert spiny lizard) and *S. clarki* (Clark's spiny lizard), at least one snake (*Masticophis flagellum*, coachwhip snake), and several bird species.

METHODS

Study Site

A study transect was established near the northeastern boundary of SNM along the Speedway Alignment. A 2-ha study site was delineated in a mesquite (*Prosopis juliflora*) bosque along the length of an arroyo. All trees within the study area were uniquely numbered and their locations mapped on an x,y coordinate grid following the sampling design of Dunham (1981).

Mark-Recapture Analysis

I employed a cohort (longitudinal) design for estimating the selection statistics. Individuals were marked, released at the site of capture and followed over time. The techniques for conducting a long-term mark-recapture study necessary for investigations of natural selection are well established (e.g., Dunham et al. 1988). In this project, which lasted from 1987 through 1990, the study site was monitored for at least three months (June, July and August) each year. However, I also surveyed the study site during the months of April (1989), and May (1989, 1990). The study plot was repeatedly censused each year during these periods. At the start of the field season (April, May or June) we searched the habitat every day for the first 14 days. Thereafter, censuses were conducted weekly or biweekly. All numbered trees were assiduously examined for individuals of *U. ornatus*. Captured lizards were brought to the laboratory for subsequent tests and measurements. The SVL of each lizard was recorded to the nearest 0.5 mm using a metal ruler. Individuals were also weighed to the nearest 0.01 g on an electronic balance. After the measurements were taken, the individuals were uniquely marked by toe clipping and a paint symbol at the pelvis. Lizards were then returned to the site of capture. On subsequent censuses only lizards that lacked a paint mark were captured for processing. When an individual with a paint mark was located, we recorded the tree number, time of day and location in tree for use in our survivorship estimates.

Rainfall Data

Desert habitats are characterized by unpredictable rainfall patterns, both in space and time. Because of the important association between the amount of rainfall and arthropod abundance, I recorded monthly rainfall estimates from the National Oceanic and Atmospheric Administration climatic summaries. I used data from the Tucson Magnetic Observatory as a reasonable estimate of the rainfall for the Speedway site. Rainfall amounts were lumped to provide seasonal totals for winter and summer.

Selection Statistics

I followed standard formulae for estimating the natural selection coefficients (Endler 1986). For the purposes of this paper, I present the results for the directional selection coefficient. This is defined as the change in the mean value of a trait before and after an episode of natural selection. The magnitude of change in a trait is given by:

$$i = X_a - X_b / (v_b)^{1/2}$$

where i is the directional selection coefficient, X_a is the mean of the trait after selection, X_b is the mean of the trait before selection, and $(v_b)^{1/2}$ is the standard deviation of the trait before selection (Endler 1986). The value i is known as the standardized selection differential (Falconer 1981)

RESULTS

Rainfall Patterns

Seasonal variation in rainfall for the years 1972 through 1990 is presented in Figure 1. Total rainfall in the Sonoran Desert usually is apportioned into two equal seasons; roughly half the total rainfall occurs in winter and half in summer (Lowe 1965). However, roughly 42% of the years had substantially more rainfall in summer (>100 mm difference), 16% had more rainfall in winter and 44% of the years showed no difference between seasons. A strong correspondence was observed between occurrence of El Niño-Southern Oscillation (ENSO) events (denoted by asterisks above rainfall data in Fig. 1) and those years with high summer rainfall (1972, 1982, 1983, 1984, and 1988). During the first three years of the study, rainfall levels were below normal, especially the winter rainfall for 1989. The period of low rainfall was interrupted by an exceptionally wet summer season in 1990

Temporal Variation in Body Size

Yearly and monthly trends in average body size are presented in Figures 2 (males) and 3 (females). Both sexes show similar patterns. Average body size tended to increase from April to August; mean size increments varied from 1-5%. Large increases in size were evident for males (growth increment = 5.4%) between July and August 1990. However, mean adult body size declined from 1987 to 1990 (Table 1).

Patterns in Selection

The selection differentials, which may be interpreted as the covariation between survivorship and body size, are presented in Figure 4. Two patterns were evident: (1) the population experienced recurring episodes of directional selection, and (2) the magnitude of selection oscillated between the sexes. Surviving individual males and females had, on average, a smaller body size than the population as a whole before selection in the period between winter 1987 and spring 1988. Interestingly, in the next period surviving males were larger and females smaller than the non-survivors. Between 1988 and 1989, the selection differentials switched; smaller males on average and larger females on average survived in 1989. In all years, evidence was also found for stabilizing selection, i.e., a cropping of extreme individuals with a consequent reduction in the variation before and after an episode of selection.

DISCUSSION

Studies of populations over a number of years and through several periods of selection are rare (e.g., Grant 1986; Schluter and Smith 1986; Grant and Grant 1990). Putative agents of selection are infrequently known in such studies. In contrast, this study demonstrated recurring and oscillating patterns of natural selection operating on a resident population of *U. ornatus* within SNM. The observed trend of declining body size among years can be indirectly tied to lowered rainfall levels during the study period. Previous evidence has shown a strong correlation between rainfall and arthropod abundance (e.g., Dunham 1978, 1981).

Of particular interest is the impact of the ENSO events on the local patterns of rainfall in the Tucson Basin. Other studies have shown a correlation between ENSO and biological phenomena in the tropics (e.g., Grant 1986; Glynn 1988; Grant and Grant 1990). Past ENSO events have been tied to massive reproductive failures in seabird colonies. Other tropical populations have been affected as well, e.g., Darwin's finches (Boag and Grant 1981) and lava lizards of the Galapagos (H. Snell, pers. comm.). Thus, ENSO may act as a major selective event through its influence on local and global climatic patterns.

The correlation between ENSO events and the summer rainfall pattern in the Tucson Basin may also be an important component affecting the population dynamics of *U. ornatus*. Recently, Swetnam and Betancourt (1990) found a relationship between incidence of fires in the Southwest and the ENSO. This is the first study to demonstrate such a correlation between a temperate population and ENSO. The link between rainfall and body size is manifested by the large correlation (Spearman rank correlation = 0.80); however, the small sample size precludes any probability level being assigned. Still, the decline in average body size with lowered rainfall and the dramatic

increase in body size after the heavy summer rainfall of 1990 suggests a strong connection.

The periodicity and fluctuation in the operation of selection on the population of *U. ornatus* may be tied to ENSO as well as other biotic factors. Because *U. ornatus* at the SNM site is polygamous, i.e., one male may have two mates or more, the responses of each sex to variation in environmental conditions is not unexpected. Previous studies have demonstrated recurring incidences of natural selection (e.g. Price et al. 1984) as well as selection favoring small body size (Price and Grant 1984). Therefore, within this population of *U. ornatus*, females may be pursuing a bet-hedging strategy in which energy apportioned to reproduction and growth are shunted to maintenance and survivorship.

SUMMARY AND MANAGEMENT IMPLICATIONS

Long-term study of variation in *U. ornatus* at SNM demonstrated significant temporal variation in body size. Temporal variation in the magnitude and intensity of selection affecting the population was also evident. The data indicate that these patterns are a manifestation of abiotic and biotic factors. Most importantly, the trend of body size variation is likely to be attributable to local rainfall patterns, which affect the abundance of arthropods, i.e., the lizards' food supply. Evidence links the patterns of local rainfall to a global climatic event, the El Niño-Southern Oscillation. Thus, global weather patterns may have a great affect on local conditions, which in turn affect local biotic systems and population dynamics.

Natural resource managers at SNM should be aware of the influence that global conditions can and do have on the processes within the monument. Also, every effort should be made to protect natural ecosystem dynamics within SNM. As habitat fragmentation within the Tucson Basin and the surrounding region increases, SNM may be the only locality which provides the luxury of pursuing long-term ecological research.

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Table 1. Analysis of temporal variation in body size.

Source	df	*F*	*P* > *F*
Males			
Month	4	17.56	0.001
Year	3	9.28	0.001
Month x Year	6	3.85	0.001
Females			
Month	4	31.39	0.0001
Year	3	32.87	0.001
Month x Year	6	1.77	0.09

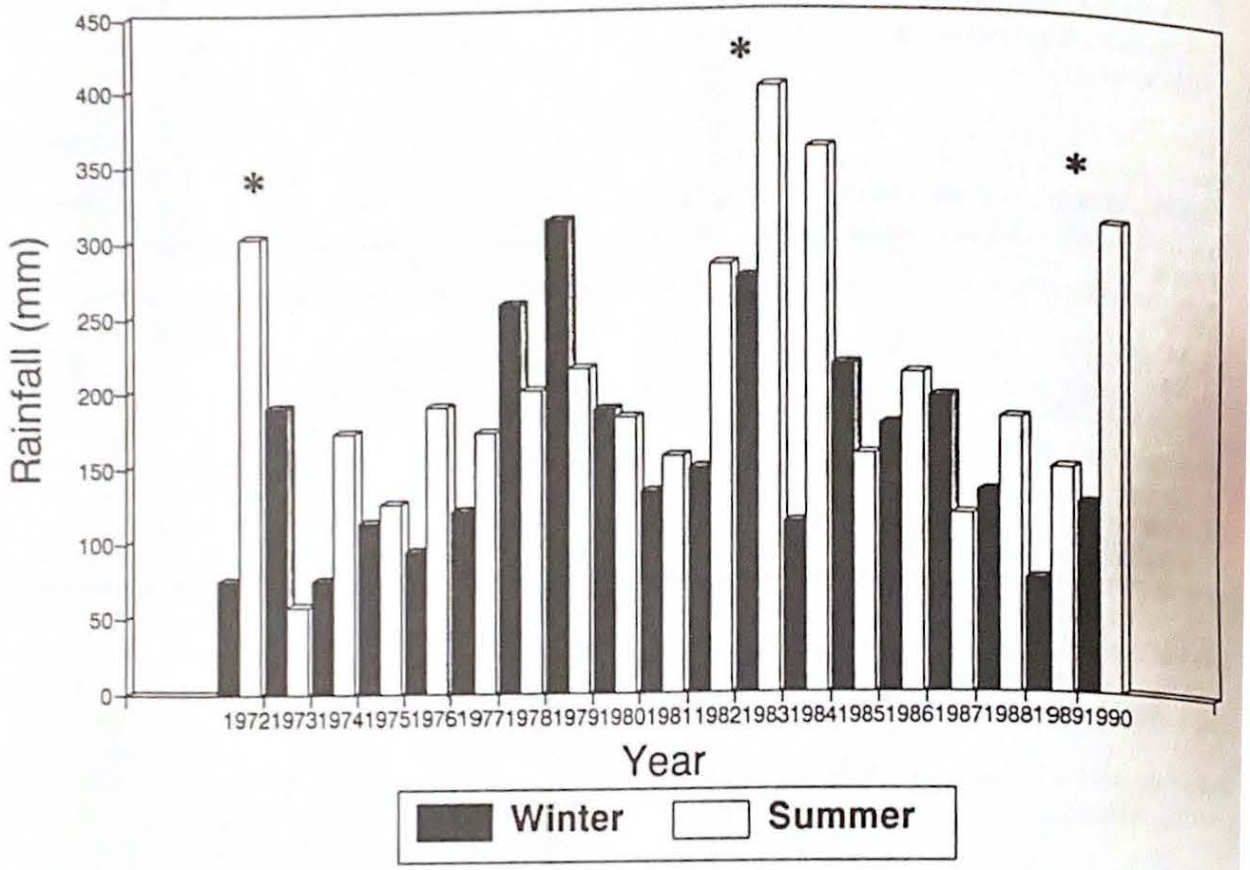


Fig. 1. Seasonal rainfall patterns near Saguaro National Monument. Years marked with an asterisk denote El Niño events.

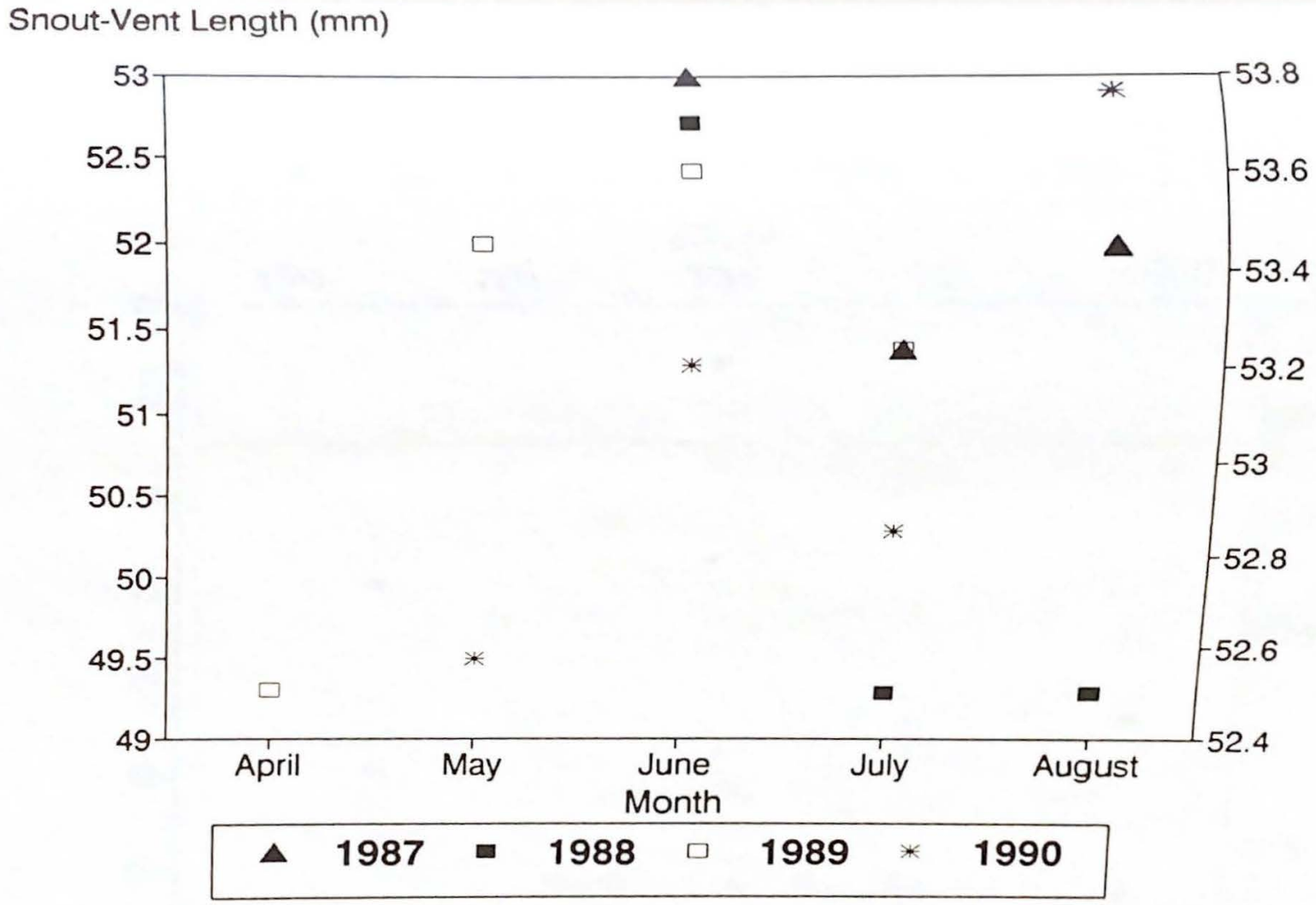


Fig. 2. Yearly and monthly variation in male snout-vent length.

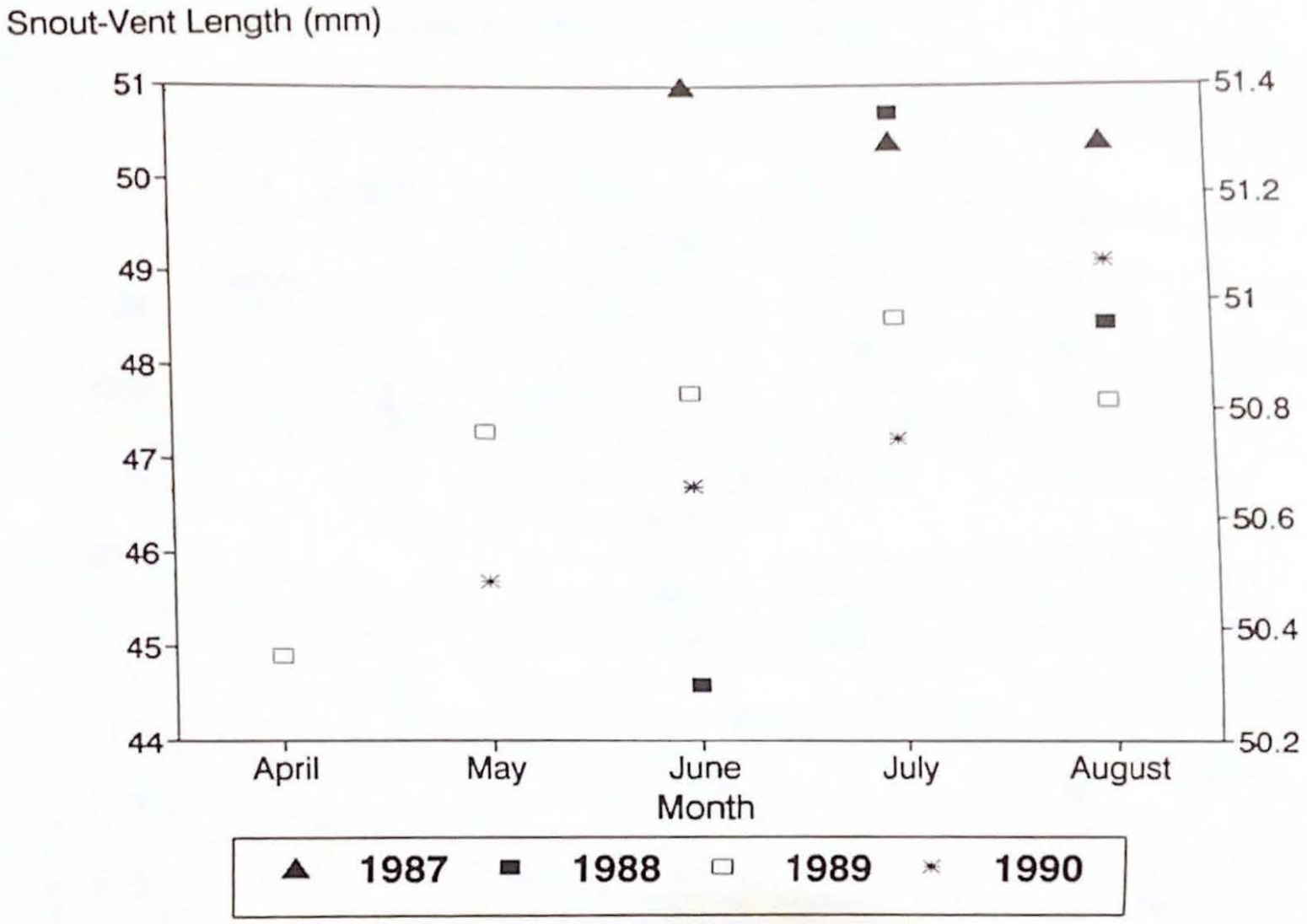


Fig. 3. Yearly and monthly variation in female snout-vent length.

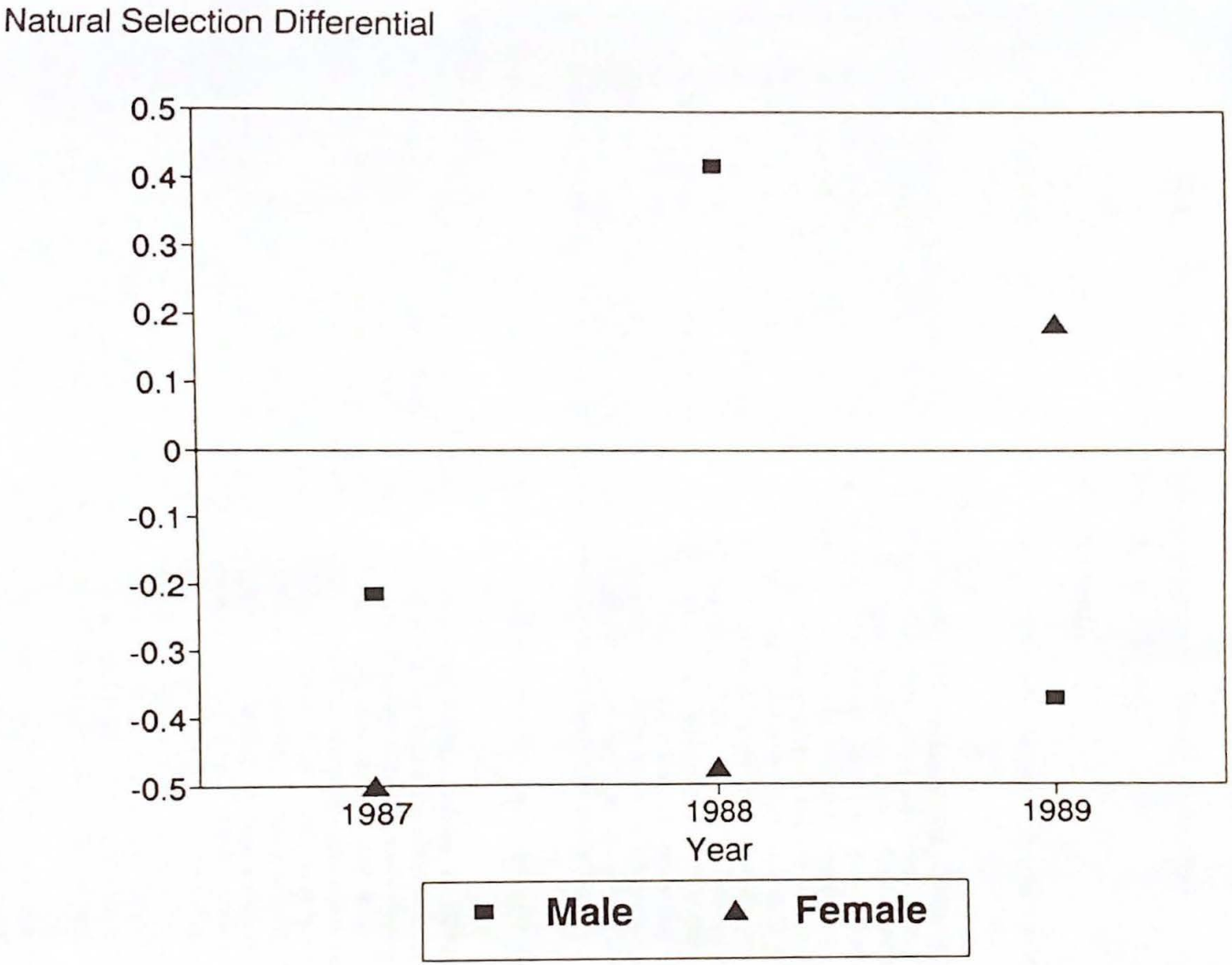


Fig. 4. Pattern of temporal variation in natural selection differentials. Selection differentials calculated for snout-vent length.

The Currency of Competition in Tree Lizards: Food, Habitat, or Mates?

Robert T. M'Closkey

ABSTRACT

A combination of surveys and small-scale experimental studies were conducted from 1983 to 1988 at the Rincon Mountain District, Saguaro National Monument, in order to characterize the density and distribution of a common lizard species (Iguanidae, *Urosaurus ornatus*, tree lizard). Tree lizard numbers were higher in dry wash than surrounding flatland desert. Males defended territories that included the home ranges of females, and the mating system was variable, with bachelor, monogamous, and polygynous males in the same population. Polygyny was habitat dependent and prevailed in wash habitats. Polygynous males were larger than monogamous males, and territory owners could not be displaced from territories by intruders. Territory defense by males was tenacious, and mates were the objects of defense. This conclusion was substantiated by showing that males abandon their territories following removal of the resident females. In contrast, food resource abundance was not important in determining lizard numbers, territory quality, or home range selection. Females maintained home ranges in the absence of males, and cues for site selection included the structural characteristics of habitats. Transplant experiments with adult females suggest that successful reintroduction of species into habitats previously occupied requires careful attention to the age class of the transplants.

INTRODUCTION

Ecologists are interested in discovering those factors that control the distribution, abundance, and variety of organisms in natural populations and communities. Because the answers to some questions about ecological processes are elusive, it is important to select organisms for study that are numerous and found in a variety of habitats. In this sense, lizards are model organisms (Huey et al. 1983) because they are abundant, defend space, are easy to observe and catch, and occur in different combinations of species in many types of habitat. Field studies of lizards have added substantially to our knowledge of basic principles of population biology. Numerous demonstrations of the limiting effects of food and space on lizard growth, reproduction, and population size have been published (Ballinger 1977; Stamps 1977; Dunham 1978, 1980; Pacala and Roughgarden 1982).

At Saguaro National Monument (SNM), Arizona, the lizard family Iguanidae exemplifies the characteristics of the model study organisms referred to above. In 1983, I initiated investigations on the behavioral, population, and community ecology of iguanids at the Rincon Mountain District (RMD) of the monument. The initial focus of the work was to assess the significance of interspecific competition and predation among the lizard species. Most certainly, the larger spiny (*Sceloporus* spp.) and collared (*Crotaphytus collaris*) lizards include smaller species (*Urosaurus ornatus*, tree lizard) in their diets. In addition, because several species of lizard occupy the same habitat, interspecific competition for limited resources is possible.

The focus of our initial research soon changed. We found no evidence for competitive interactions

between spiny and tree lizards (M'Closkey and Baia 1987), and we never observed reduced survivorship or growth rates of tree lizards whose territories were contained within the territories of spiny lizards. By virtue of their cosmopolitan distribution and high density, tree lizards have been the subject of most of our research at SNM.

I employed two different approaches to investigate patterns of tree lizard distribution and abundance. First, data from comparative surveys were used to provide information on territorial behavior, the mating system, the role of food in determining lizard distribution, and the pattern of habitat and microhabitat use. Second, I have used small-scale, nondestructive experimental studies (removal and introduction of tree lizards) to provide a mechanistic basis for understanding what governs the interactions among individual lizards in their quest for resources. The experimental studies have important implications for the reintroduction of species into habitats they formerly occupied. Such experimental work can provide management guidelines, but is best approached by manipulation of common, widespread species prior to implementation on rare, threatened, or endangered species.

In this paper I summarize the primary results of our investigations on tree lizards. This work is contained in a series of papers, and for economy of space I cite them once (M'Closkey et al. 1987*a*,*b*; M'Closkey and Baia 1987, 1990; M'Closkey et al. 1990*a*,*b*,*c*).

METHODS

Lizard surveys relied heavily on detailed censuses to provide data on relative numbers among habitats and the mating status of different individuals. At each site we estimated the standing crop of arthropods (lizard food) and measured structural attributes of habitats. Details are given in the papers cited above and are summarized here.

Lizard Census

We spent from two to five months in the field each summer from 1983 through 1988. Lizards were live-captured, marked, measured, and released. After a few censuses, recapture rates of previously marked lizards were >90% and on many occasions reached 100%. Therefore, we had nearly complete enumeration of the lizards at each study site. Because tree lizards spend most of their activity time above ground, mesquite trees (*Prosopis juliflora*), dead saguaro (*Carnegiea gigantea*), and dead paloverde (*Cercidium microphyllum*) are focal points for male territories and female home ranges.

Mating System

The census work provided detailed maps of the locations of individual lizards. We used the territory (male) and home range (female) maps to classify the mating status of males as either bachelor, monogamous, or polygynous. In addition, we observed courtship and mating of many individual lizards. Male territories do not overlap so we could assign females to territorial males with little error. Females did not move among male territories.

Food Resources

During both dry and wet seasons on each study plot, we estimated arthropod numbers by placing construction paper cards (15 x 15 cm) at sites or trees occupied by lizards and nearby vacant sites. Cards were placed both on the ground and in mesquite trees and were coated with "Tangle-Trap" adhesive. Most feeding by tree lizards occurs above ground but we observed occasional strikes at prey on the ground. Sample effort varied among sites, but overall we counted more than 100,000 arthropods on 900 cards.

Habitat Assessment

The census work was conducted primarily in two habitats, flatland desert and dry washes. Four wash plots and three flatland plots ranged in size from 0.1 to 1.8 ha and contained from 11 to 67 mesquite trees or other sites occupied by lizards (e.g., dead saguaro and paloverde). Not all plots were surveyed in each year. On each plot we measured tree size and spacing, distance to the nearest woodrat (*Neotoma albigula*) nest, and soil penetrance (with a Brainard-Kilman pocket penetrometer).

Experimental Studies

In 1984, to test the hypothesis of mate defense in tree lizards, we removed 40 females and 41 males from their territories and home ranges. The removed lizards were transported to nearby sites and released in mesquite trees that were not occupied by tree

lizards. In 1985, we conducted 30 trials on male tree lizards to test the hypothesis that territories could be invaded by a nonresident male. Males were captured and released in "strange" territories. Since they were each evicted by the resident male, we recaptured each intruder and returned him to the original territory. In 1988, we conducted transplants of 20 female lizards in order to test the hypothesis that females recognize other females in selecting home range sites.

RESULTS AND DISCUSSION

Density and Distribution

The primary seasons of lizard activity are spring, summer, and early fall. In April and May, courtship and mating are obvious and active territory defense by males occurs. Two clutches of eggs are deposited by females in late summer and hatchlings emerge by late August. During our census work we marked >500 lizards, and we recorded >2,000 total captures. Beginning with censuses in 1983 a clear pattern of tree lizard distribution emerged. Dry washes with large, closely-spaced mesquite trees had high lizard density (1.1-2.2 lizards/tree or site) compared to flatland habitat (0.3-0.8 lizards/tree or site). Lizard numbers were highest in the spring, followed by a gradual decline through the summer in all habitats.

Mating System

The tree lizard mating system is variable, with bachelor, monogamous, and polygynous males occurring together in the same population. However, the degree of polygyny is dependent on habitat type (Table 1). In dry washes, polygyny is always more common than in flatland habitat. In washes, over half the males may guard two or more females within their territories. However, monogamy prevails in flatland habitat, and isolated mesquite trees will usually support only one pair of resident lizards.

One obvious correlate of the polygyny pattern is the degree to which females aggregate at mesquite trees or other sites. Because females lack the aggression shown by territorial males, large trees may contain the home ranges of several females. Hence polygyny increases with the proportion of trees occupied by two or more females (Table 1). In addition, closer spacing of trees or sites permits males to monopolize mating opportunities. The seasonal decline in polygyny (from dry to wet season) is a consequence of the general decline in lizard numbers and the more even distribution of females.

For males, polygyny provides clear advantages and dry washes appear to afford the greatest opportunities for multiple mates. Because mating opportunities represent a potentially limiting resource, I partitioned the data to determine whether polygynous males are somehow different from monogamous or bachelor males. In both 1984 and 1985, significant differences were found in male body size (Table 2). Although the sample sizes were small, the data suggest that larger males fare better in gaining access to multiple mates than smaller males.

Additional evidence for the role of body size in determining mating success in males is provided by the relationship between body size and survivorship. Territory contests are evident in April and May and fights for space frequently result in tail loss and severe injuries (e.g., skin broken by cactus spines). Body size is clearly advantageous in determining winners and losers. Males that survive to late May and successfully find mates are significantly larger than males not surviving (Table 3). Females neither defend space nor compete with one another for home range sites. Consequently, body size has no influence on female survivorship (Table 3).

Experimental Studies

I determined the tenacity of territory defense by challenging resident males with nonresident intruders. Thirty trials were conducted in which an adult male intruder was placed within the territory of a resident adult male. The typical pattern of response by the resident was to threaten, attack, and evict the intruder. Many of the trials were reciprocal. After the intruder was evicted we captured it and returned it to its original territory. After a period of time, the original resident was captured and introduced to this strange male's territory. Once again, the resident evicted the intruder. Prior ownership of a territory is important, and once territories are established even a larger intruder could not evict a smaller resident.

Sex-removal experiments (1984) were designed to determine if the primary function of territory defense was the defense of resources (food, safe sites from predators) or the defense of mates. On one plot females (n = 40) were removed, on another males

($n = 41$) were removed, and a third was an unmanipulated control. This simple experiment provided dramatic evidence of the differences between the sexes in their use of space. Thirteen resident males abandoned their territories on the female-removal plot. No resident males remained. In contrast, 15 females remained resident on their home ranges on the male-removal plot. The difference between the removal and control plots was significant for males but not for females. In other words, males clearly defended mates, but females were content to remain on their home ranges even with no resident male present.

By late August 1984, the female-removal plot contained no lizards after abandonment of territories by males. In addition, because females were removed prior to oviposition (egg laying), no hatchling recruitment occurred. How quickly is a lizard-free habitat colonized by immigrants? Censuses in spring 1985 revealed no difference among control (0.96 ± 0.07 lizards/tree), female-removal (1.02 ± 0.15), and male-removal (0.89 ± 0.05) plots. No significant deviation from a 1:1 sex ratio was found. Therefore, recovery is fast and unbiased with respect to sex.

Food Resources

The availability of food resources may be important in affecting animal numbers, distribution, and mating systems. Several questions are of interest in the context of tree lizard ecology. Are wash habitats superior to flatland in terms of food resources? Do polygynous males occupy food-rich territories compared with monogamous and bachelor males? Do females select home ranges on the basis of food abundance? Answers to these questions would provide clues to the pattern of lizard numbers in different habitats and could explain why females remain in their home ranges in the absence of males.

In 1984, we compared arthropod numbers between wash and flatland habitat. We detected no differences in arthropod numbers at the level of habitat, but seasonal differences are apparent (Table 4). Similarly, in 1986 we could find no difference between habitats in the number of arthropods trapped on the cards.

Differences Within Habitats

Even though habitats appear uniform in arthropod distribution, patchiness within habitats may produce variation in arthropod numbers. However, within the wash in 1984, trees occupied by lizards and vacant trees did not differ in arthropod numbers (Table 5). No difference was observed in either dry or wet season.

On a finer scale, we investigated whether males differing in mating status maintained territories of different food abundance. In both 1984 and 1986, no differences were found among males in the quality of their territories (Table 6). This pattern held for both dry and wet seasons, but the data are shown only for the dry season when active territory defense was apparent. Therefore, polygynous males did not defend territories containing more food resources.

The final analysis dealt with the question of whether females use arthropod numbers as cues in selecting home ranges and oviposition sites. Home ranges in which oviposition occurred were identified with certainty because of the reproductive condition of the resident females and the subsequent appearance of hatchlings. However, home ranges in which oviposition occurred were no better (or worse) than vacant neighboring sites (Table 7). The arthropod sampling detected significant seasonality in both 1986 and 1987, but no difference in arthropod numbers between female home ranges and vacant sites was found (Table 7).

Site Selection by Females

The preceding analysis showed that females do not maintain home ranges, either for the choice of mates or for concentrations of food resources. What cues determine home range selection and maintenance by females? We have discovered that significant tree size selection by females occurs. In wash habitat, mesquite trees on which females settled are significantly larger ($P < 0.001$) than vacant trees. Larger trees may provide refuges from predation or basking sites. Once females establish residence in these trees they are defended by males. In flatland habitat the presence of woodrat nests near the base of mesquite trees increased the likelihood that females would settle. In 1986 and 1987, woodrat nests were present in 16 of 19 female home ranges. For neighboring vacant sites nests were present in only 8 of 30 cases. The presence of nests was significantly ($G = 22.9$, $P < 0.001$) associated with the location of female home ranges.

In addition, soil resistance (to penetration) was significantly less (1.43 ± 0.14 g/cm^2) in female home

ranges compared with vacant sites (1.81 ± 0.12 g/cm^2; $P < 0.005$, Wilcoxon signed-ranks test). Oviposition is highly synchronized and may be triggered by summer precipitation which facilitates digging in the soil. For example, 16 females oviposited on the afternoon of July 21, 1986, following delayed summer rains. The loose soil beneath woodrat nests is especially conducive to digging in preparation for oviposition.

Experimental Studies

Does the presence of females on home ranges affect the choice of those sites by other females? Two or more females were frequently observed sharing the same tree or site, with no apparent aggression. Transplant experiments with females were conducted in 1988 to answer this question. Eleven of 13 sham-transplanted female lizards (controls) were present after one week and six of 13 were still resident after 70 days. In contrast, females transplanted to new sites (with 0 or 1 female already present) quickly abandoned these sites. Only one of 20 transplants maintained residence at the transplant site after 70 days. The difference between transplant and control lizard residence is significant ($G = 5.8$, $P < 0.025$).

CONCLUSIONS

Surveys of tree lizards at the RMD of SNM revealed differences in density between two major habitats. Wash habitats supported higher densities of tree lizards than flatland habitats. Larger and more closely spaced wash trees may provide refuges from predation and this may explain the pattern in lizard numbers. Stamps (1983) has provided experimental evidence of refuge effects in juvenile lizards and Howard (1978) has shown a relationship between habitat selection and mortality in bullfrogs (*Rana catesbiana*). In wash habitats, nearly all foraging by tree lizards is within the tree canopy, whereas flatland lizards do strike prey on the ground. This difference in feeding behavior may lead to greater risks of predation in flatland habitat and produce the pattern in lizard density we observed.

An important consequence of tree distribution and size in wash habitats is that female aggregations are more common there. In contrast, flatland females are more uniform in distribution. This difference in female distribution (Table 1) permits some males to monopolize or guard more than one mate. The result is a variable mating system, with bachelor, monogamous, and polygynous males in the same population. Emlen and Oring (1977) demonstrated how resource distribution can affect the degree of polygyny in animal mating systems. Two observations suggest that competition among males for mates is important. First, polygynous males are larger than monogamous or bachelor males (Table 2). Second, males that survive to establish territories are larger in body size than males that eventually disappear (Table 3). These observations are consistent with scenarios of competition for mates (Trivers 1976). In addition, two lines of experimental evidence demonstrate the significance of competition for mates. First, the territories of resident males are resistant to invasion by intruders. Owners attack and evict intruders, and intruders retreat from threats and attacks of owners. Second, males abandon their territories when females are removed.

This experimental result permitted us to distinguish two types of polygyny. First, several studies have demonstrated the role of food distribution and abundance on mating systems (e.g., Davies and Lundberg 1984), territory size (Simon 1975; Guyer 1988*a*,*b*), and animal distribution (M'Closkey 1983). Where females are attracted to and aggregate at resources defended by males, the resulting mating system is resource defense polygyny (Emlen and Oring 1977). Alternatively, males may defend mates, per se, independent of food or other resources. If some females aggregate, the resulting mating system is mate defense polygyny, and this is clearly shown in tree lizards.

Food abundance plays no role in the quality of male territories (Table 6) and does not determine their mating status. Food abundance does not provide any cues to habitat (Table 4) or territory quality. Because females remain on their home ranges following male removal, the basis for habitat selection in females is not linked to mate choice. Rather, female home range selection is probably related to the selection of oviposition sites within their home ranges. The presence of loose soil beneath woodrat nests may be very important in site choice. Tinkle et al. (1962) also showed a close association between the home ranges of another iguanid lizard and the presence of woodrat nests.

Finally, transplant experiments with adult female tree lizards suggest that female aggregations are not caused by female-female recognition. This contrasts with experimental studies of Stamps (1987), which demonstrate conspecific cuing in another iguanid lizard.

SUMMARY AND MANAGEMENT IMPLICATIONS

The RMD of SNM contains a variety of habitats exploited by a diverse lizard fauna. Tree lizards are the most common iguanid and censuses revealed higher numbers and greater frequency of polygyny in wash compared with flatland habitat. In contrast with much published work on birds, food resources available to tree lizards have no affect on lizard numbers, territory quality, or home range selection. Instead, the mating system is variable, is based on mate defense polygyny, and body size confers a polygyny advantage to some males.

Defining habitat and microhabitat requirements of small animals is a major research activity (Szaro et al. 1988), with applications in habitat restoration, definition of indicator species, and reintroduction of species into areas previously inhabited. Two of our experimental results have implications for developing management guidelines.

Our female-removal site was devoid of lizards by midsummer. However, no recolonization of the site occurred for the remainder of the summer. In addition, no juvenile recruitment occurred. By the following spring, the female-removal site did not differ from the control or male-removal site in terms of lizard numbers. Recolonization was quick and complete, and must have occurred in the early spring following emergence of lizards from winter inactivity. By inference, the timing of reintroduction experiments may be critical in the successful establishment of populations. One might be inclined to conduct reintroductions of animals late in the summer when territorial aggression is lower and individuals have accumulated food resources. However, territory establishment occurs in early spring and this may be the best time to conduct introduction experiments.

The transplant experiments were also revealing. Females were not aggressive toward one another and home ranges often overlapped extensively. Because transplanted adult females failed to establish residence at trees occupied by other females, it appears that home range tenacity develops early in life, perhaps in juveniles. This result presents an interesting paradox for the implementation of reintroduction experiments. Individuals with high reproductive value (mature females prior to their first reproduction) may prove to be unsuccessful subjects for introductions. In contrast, juveniles have lower reproductive value because they face a substantial period of mortality prior to reproduction. However, colonization of vacant habitat, dispersal, and home range and territory choice may only occur in juveniles. Hence, the ages of animals must be examined closely in the context of introduction experiments.

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Table 1. Polygyny, tree spacing, and the percent of trees or sites with two or more females during wet and dry seasons.

Habitat	No. of males	Polygyny (%)	Trees or sites with ≥2 females (%)	Mean distance between trees (m)
Wash-dry	78	53-67	24-33	4.4-4.6
Wash-wet	18	33	6	
Flatland-dry	50	0-33	3-8	12.2-13.6
Flatland-wet	46	7-20	2-9	

Table 2. Polygyny and body size (snout-vent length [SVL] in mm) in wash habitat.

	SVL (mm) ($\bar{x} \pm 1$ SE)	
Male status	1984[a]	1985[b]
Monogamous	47 ± 0.9	51 ± 0.3
Polygynous	54 ± 0.5	54 ± 0.4

[a]1984: $t = 7.21$, $n = 24$, $P < 0.001$.
[b]1985: $t = 5.43$, $n = 26$, $P < 0.001$.

Table 3. Size of lizards ($\bar{x} \pm 1$ SE snout-vent length [SVL] in mm) captured before 12 April 1984, and either surviving or not surviving to late May.

Sex	Surviving	Not surviving	D[a]	P
Male	49 ± 1.1	46 ± 1.0	0.45	<0.01
Female	41 ± 1.1	40 ± 1.2	0.21	0.2

[a]Kolmogorov-Smirnov test.

Table 4. Density of arthropods ($\bar{x} \pm 1$ SE; N/100 cm^2/d) trapped on "Tangle-Trap" cards in wash and flatland habitat during dry and wet seasons, 1984.

Season[a]	Wash[b]	Flatland[b]
Dry (Apr-Jun)	12.9 ± 2.40	9.2 ± 1.59
Wet (Jul-Aug)	25.7 ± 2.79	29.0 ± 3.72

[a]Season, $F = 43.4$, $P < 0.001$.
[b]Habitat, $F = 0.53$, $P > 0.25$.

Table 5. Density of arthropods ($\bar{x} \pm 1$ SE; N/100 cm^2/d) trapped on "Tangle-Trap" cards in wash habitat at occupied and vacant trees, 1984.

	Trees				
Season	Occupied	Vacant	t	n	P
Dry	13 ± 1.1	13 ± 1.0	0.02	51	>0.9
Wet	25 ± 1.5	26 ± 1.7	0.78	51	>0.4

Table 6. Density of arthropods ($\bar{x} \pm 1$ SE; N/100 cm^2/d) on "Tangle-Trap" cards in wash habitat among males differing in mating status, dry season.

Male status	1984[a]	1986[b]
Bachelor	16.3 ± 3.59	7.8 ± 0.91
Monogamous	13.1 ± 1.09	7.6 ± 0.90
Polygynous	11.7 ± 0.72	9.4 ± 0.76

[a]1984: $F = 2.29$, $P > 0.1$.
[b]1986: $F = 0.93$, $P > 0.25$.

Table 7. Density of arthropods ($\bar{x} \pm 1$ SE; N/100 cm^2/d) on "Tangle-Trap" cards within home ranges and at vacant sites.

Year	Season	Home range	Vacant
1986[a]	Dry	7.8 ± 0.73	7.7 ± 0.36
	Wet	4.7 ± 0.29	4.6 ± 0.29
1987[b]	Dry	3.0 ± 0.41	3.9 ± 0.45
	Wet	6.4 ± 0.35	6.6 ± 0.51

[a]Habitat: $F = 0.00$, $P > 0.75$; season: $F = 14.76$, $P < 0.005$.
[b]Habitat: $F = 0.85$, $P > 0.25$; season: $F = 51.27$, $P < 0.001$.

Extirpated Plant Species of the Tucson Mountains

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ABSTRACT

The Tucson Mountains form a small range located west of Tucson, Pima County, Arizona, in the Arizona Upland subdivision of the Sonoran Desert. Our compilation of a regional flora for the mountain range shows changes in the abundances of certain species during this century. Twenty-seven species collected prior to 1950 have not been taken since, in spite of more collecting effort. Extirpated and extant (existing) species differed significantly as to the fraction of plants that were winter/spring annuals (many have been lost). A change in climate, competition from introduced species, and habitat destruction are all possible explanations for the loss of these species. The annual winter rainfall was above average in the early part of the century followed by a drought of some 40 years. Introduced species have increased since the early part of the century. Competition, especially from introduced annuals, which tend to germinate and bloom earlier than native species, coupled with lack of rainfall could account for the high percentage of winter annuals lost in the latter half of this century.

INTRODUCTION

The Tucson Mountains form a small range west of Tucson, Arizona (Fig. 1), in the Arizona Upland subdivision of the Sonoran Desert (Shreve 1964; Turner and Brown 1982). Approximately 40% of the range is in protected areas, mainly Saguaro National Monument-Tucson Mountain District (SNM-TMD; 8,750 ha) and Tucson Mountain Park (7,075 ha). Saguaro National Monument was set aside in 1961 to "preserve and interpret a remarkable display of relatively undisturbed Sonoran Desert vegetation, including a saguaro (*Carnegiea gigantea*) stand, which equals or surpasses saguaro stands elsewhere in the nation." Saguaro National Monument occupies the majority of the high peaks and ridges as well as major washes, canyons, and bajadas of the study area. Tucson Mountain Park is a county park established in the 1920s as a nature preserve. It protects large areas of foothills as well as peaks, ridges, and washes. The purpose of this study was to identify changes in the plant species composition in the Tucson Mountains within the 20th century.

METHODS

Most of the field work was conducted from 1987 to 1990, throughout each year, although greater effort was applied during the seasons of greater plant reproductive activity. A 335-km network of trails, ridges, washes, canyons, and peaks was surveyed for plants by the authors. In addition, vegetation along all major roads and many minor roads was investigated. Many of the sites were revisited several to many times (e.g., Sendero Esperanza Trail to Wasson Peak was visited 19 times in 1989). All major washes, canyons, trails, and peaks (except Safford Peak) were visited at least two times (spring and fall). Special attention was given to examination of all distinct rock types and habitats. We recorded the elevation, habitat, rock type, habit, and reproductive status of

each observed plant species, and collected at least one voucher for each taxon.

The herbarium surveys entailed searching the following herbaria: University of Arizona, Arizona-Sonora Desert Museum, Saguaro National Monument, and Rancho Santa Ana Botanical Garden in Claremont, California (the repository of Lyman Benson's cactus collection). Label data from approximately 3,500 specimens representing all Tucson Mountain plant taxa were entered into a computerized database.

For each of the 27 extirpated species, case histories were developed that included geographical and elevational range, habitat preference, life form, and flowering time. Identifications of all specimens were verified.

RESULTS

Collecting effort in the Tucson Mountains has fluctuated throughout the 20th century; the first 20 years and the last 30 years were the most active periods for plant collecting (Fig. 2). Until recently, the most intensively collected area was the Desert Laboratory area on Tumamoc Hill (Thornber 1909; Bowers and Turner 1985).

In the early part of the century (1901-1933), J. J. Thornber, botanist and curator for the University of Arizona Herbarium, was the primary collector, with over 600 botanical specimens taken between 1901 and 1915 from the Tucson Mountains or "mesas, Tucson" (Thornber considered the area around Tumamoc Hill as mesas [Thornber 1909]). His efforts apparently were directed at the lower elevations and little if any collecting was done on the high peaks and ridges. Forrest Shreve, a plant ecologist with the Desert Laboratory (Bowers 1988) collected more than 75 specimens from the Tumamoc Hill region in the years 1908-1941. Lyman Benson, a southwestern botanist, collected 30 specimens, mostly from the "A" Mountain, Gates Pass, and Rattlesnake Pass region. From 1960 to the present, the major collections have been made by J. E. Bowers, A. E. Garwood, P. S. Martin, R. M. Turner, D. K. Warren, and the authors.

Although a substantial number of specimens were collected from the Tucson Mountains during the early part of this century (Fig. 2), just over half (301 of 587) of the species were documented at that time. Nonetheless, 27 species that were reported as present or common and that are documented with voucher specimens, have not been reported since 1950. A list of these 27 species is presented in Table 1.

Most extirpated species are annuals (75%), of which 85% are obligate spring annuals (growing only in spring) (Fig. 3). In contrast, the species still found in the area consist of 41% annuals, of which 60% are obligate spring annuals. A G-test (Sokal and Rohlf 1981) showed this difference in proportions of spring to summer annuals to be highly significant ($G = 6.49$, 1 df, $P = 0.002$); the difference in proportion of annuals to perennials is also significant ($G = 9.869$, 1 df, $P = 0.011$).

DISCUSSION

It is difficult to argue from negative evidence; although these species have not been collected since 1950, they may still occur somewhere in the range. Nevertheless, we have made a diligent search and in spite of a much greater sampling effort than that expended previously (Fig. 2), these species still have not been located. Possible explanations for these local extirpations include misidentification (by earlier researchers or the authors), habitat destruction, competition from introduced species, and climatic change.

All specimens were checked for proper identification; any extirpated species with similar morphology to extant species were marked for special attention in field observations. Habitat destruction has resulted from urbanization and industrialization since the first half of the century and might have contributed to the loss of some of these species. It is difficult to know how many may have been lost to habitat destruction, since many of the labels from the specimens are vague in terms of location. At least one species was likely eliminated due to habitat destruction; *Cheilanthes parryi* was collected from "Picacho de Calero" (Twin Peaks) in 1931, and since then the mountain has been removed for its limestone. No one particular habitat is common to the extirpated species. Former habitats include rocky slopes, flats, low elevation, high elevation, washes, etc. Most habitat destruction has been limited to the bajadas on the eastern side of the mountains. Therefore, habitat destruction is not likely to be the major cause of extirpations.

Competition from introduced species could play an important role in extinctions (Groves and Burdon 1986). Bowers and Turner (1985) showed an increase in the number of taxa from 238 to 346 over 75 years for the flora of Tumamoc Hill. Many of the additions resulted from changes in habitat, especially from disturbance associated with construction of roads, pipelines, a clay quarry, and a sanitary landfill on the property. Forty percent of the 126 taxa added to the flora were introduced species, and the majority are closely associated with disturbance. In some cases, introduced species may successfully compete against native species when resources are in short supply. Many introduced spring annuals germinate and flower before the native annuals, and strongly compete with the natives for water and pollinators.

It is likely that decreases in winter rainfall through this century (Sellers and Hill 1974) may have caused the ranges of annuals to contract to the north and west. The annual winter rainfall was above average in the early part of the century followed by a drought of some 40 years. Although both summer and winter rainfall were below average for the 40-year period, the decline in winter precipitation was more severe. A combination of competition from alien species and a 40-year drought may explain the high loss of winter annuals. Although species associated with the Chihuahuan, Mohave, and Sonoran Deserts are represented in these extirpated species, those from the Mohave Desert region are the most common (26%); all other regions are fairly evenly distributed (Table 1). Mohave Desert rainfall occurs predominately in winter, and the Mohave region has the highest percentage of winter annuals among the regions represented. A decrease in winter rainfall would be expected to have a greater impact on winter annuals and species from the Mohave Desert.

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Table 1. Characteristics of locally extirpated species collected prior to 1950 (from Rondeau 1991).

Family/species name	Collector and date	Spring annual	Biogeographical region
Adiantaceae			
Cheilanthes parryi	Humphrey s.n. Feb 1931	No	Mohave Desert
Boraginaceae			
Plagiobothrys pringlei	Thornber 533 March 1903 Thornber 2206 April 1908	Yes	Sonoran Desert
Compositae			
Chaenactis carphoclinia	Thornber s.n. March 1906 Thornber 5306 April 1905	Yes	Mohave Desert
Hemizonia kelloggii	Thornber s.n. April 1905 Thornber 386 May 1903 Thornber s.n. April 1905 Thornber s.n. May 1905	Yes	Introduced
Lasthenia californica	Thornber 7734 April 1915	Yes	California
Layia glandulosa	Benson 10112 April 1940	Yes	Mohave Desert
Malacothrix coulteri	Thornber 387 April 1903 Thornber 4621 April 1905	Yes	Mohave Desert
Prenanthella exigua	Thornber s.n. May 1903 Spalding & Thornber s.n. April 1906	Yes	Sonoran/ Mohave Deserts
Stylocline psilocarphoides	L. Benson March 1945	Yes	Mohave Desert?
Cuscutaceae			
Cuscuta salina	Thornber 7516 September 1913	No	Saline Soils
Euphorbiaceae			
Chamaesyce serrula	Thornber 47 October 1903 Thornber 8948 August 1917 Gould 2552 September 1944	No	Sonoran Desert
Gramineae			
Lamarkia aurea	Mrs. Thornber March 1903	Yes	Exotic
Vulpia myuros	Thornber s.n. March 1906 Thornber s.n. March 1907	Yes	Exotic
Hydrophyllaceae			
Phacelia popei	Mrs. Thornber 4013 March 1903	Yes	Desert-grassland

Table 1. Continued.

Family/species name	Collector and date	Spring annual	Biogeographical region
Leguminosae			
Lotus greenei	Hinkley s.n. March 1931	No	Chihuahuan/ Desert-grassland
Lotus salsuginosus	Benson 10620 March 1941 Benson 10700 March 1941	Yes	Sonoran/ Mohave Deserts
Malvaceae			
Eremalche exilis	Benson 10622 March 1941 Thornber 4884 April 1903 Thornber 5326 April 1905	Yes	Mohave Desert
Sphaeralcea hastulata	Fulton & Harris 6818, 6824 6825 April 1930	No	Chihuahuan/ desert-grassland
Onagraceae			
Oenothera caespitosa	Shreve s.n. March 1931	No	Montane
Papaveraceae			
Argemone ochroleuca	Peebles 6951 May 1930	Yes	Tropical
Plantaginaceae			
Plantago bigelovii var. *californica*	Darrow s.n. March 1937	Yes	Widespread
Polemoniaceae			
Gilia capitata	Thornber s.n. May 1905 Thornber s.n. March 1903	Yes	Northern
Ipomopsis longiflora	Thornber 4439 August 1901 Thornber s.n. March 1903 Thornber 4988 April 1903 Thornber 4987 April 1903	No	Chihuahuan/ desert-grassland
Linanthus aureus	Mrs. Thornber 1903	Yes	Sonoran/ Mohave Deserts
Polygonaceae			
Eriogonum reniforme	Thornber s.n. April 1906 Thornber s.n. April 1908	Yes	Mohave Desert
Rhamnaceae			
Condalia corellii	Blumer; March 1911	No	Tropical
Solanaceae			
Lycium macrodon	Benson 10617a March 1941	No	Sonoran

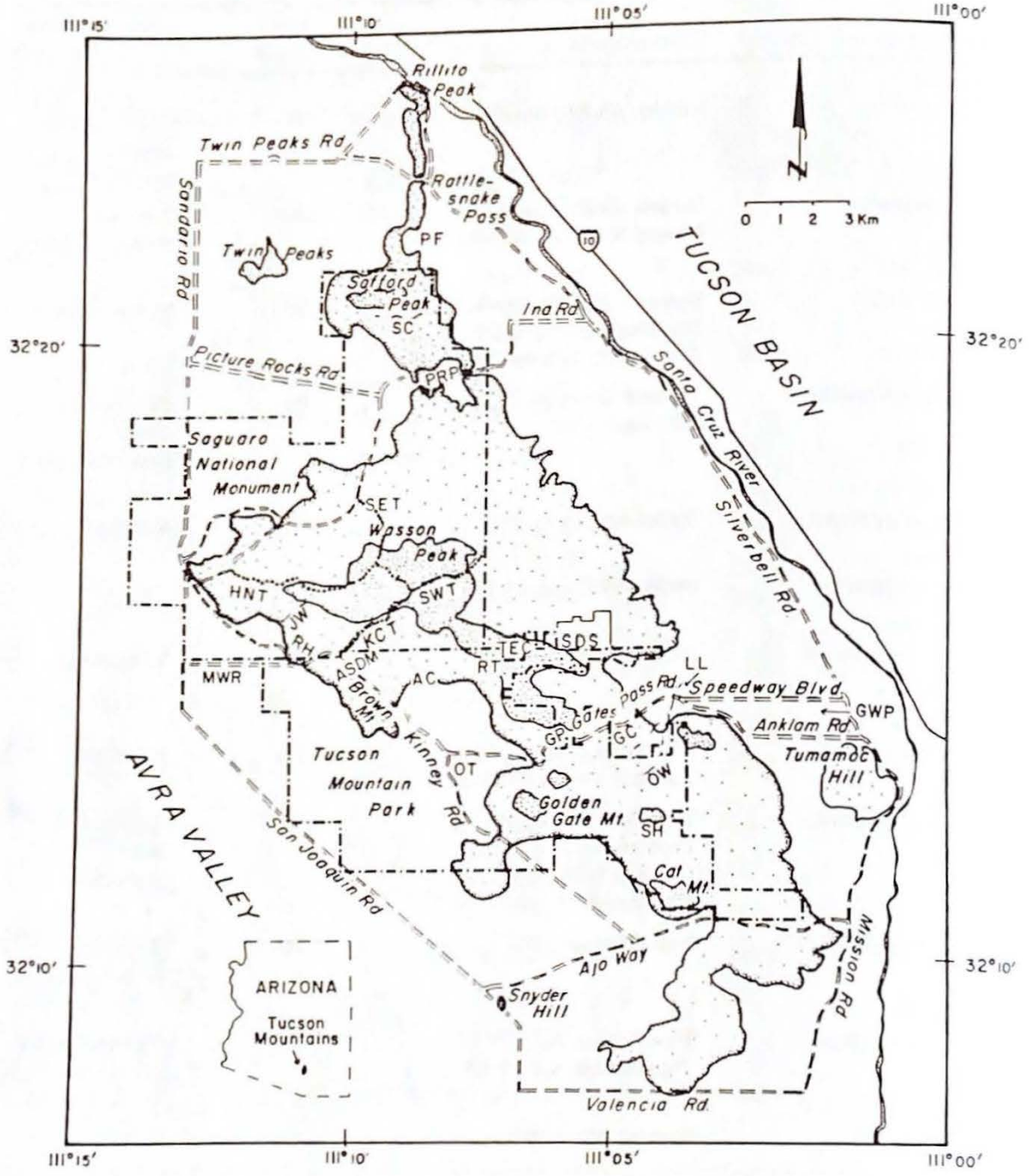


Fig. 1. Location of the Tucson Mountain study area. The denser the stippling, the higher the gradient and elevation.

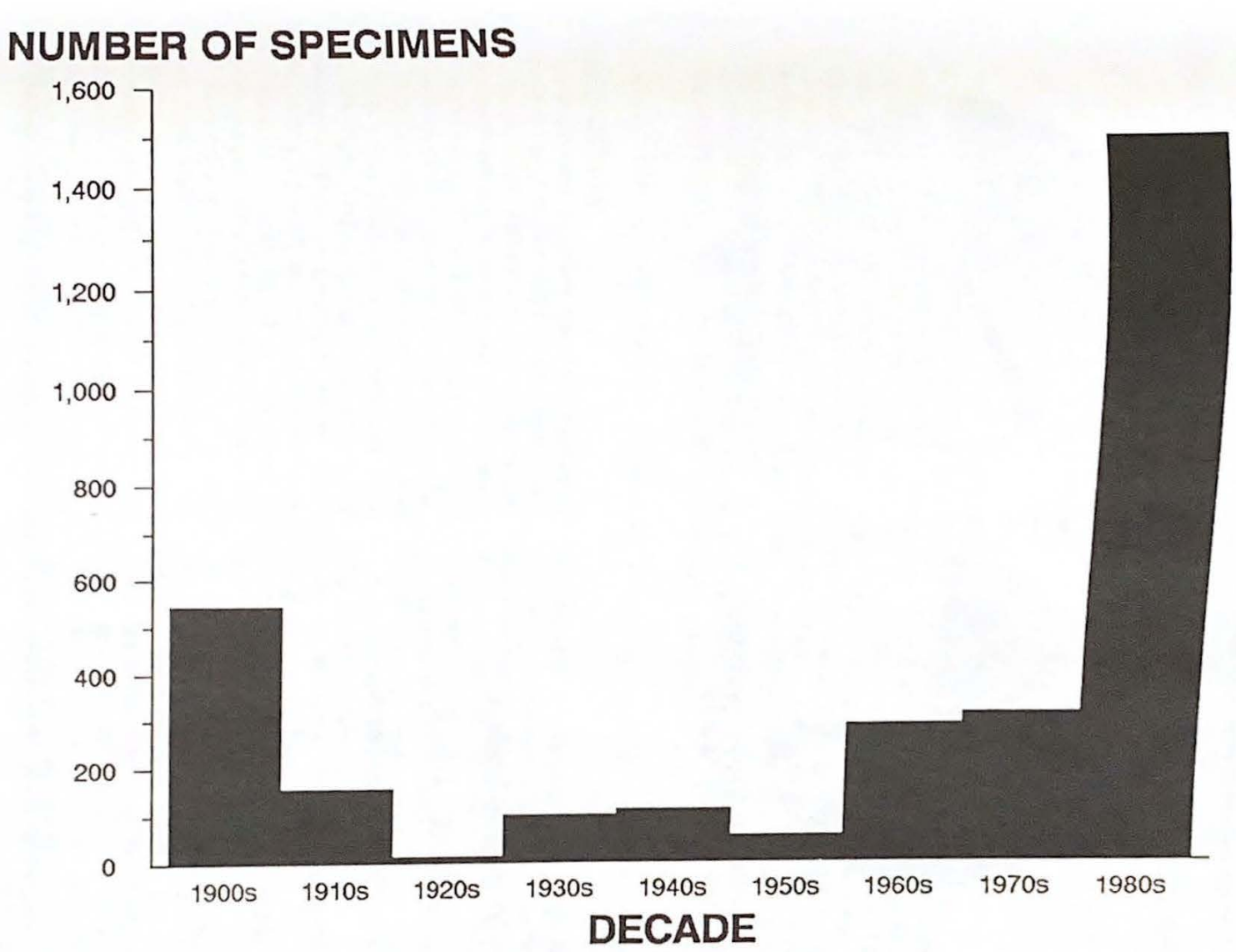


Fig. 2. Number of specimens collected per decade from 1900 to 1990 (from Rondeau 1991).

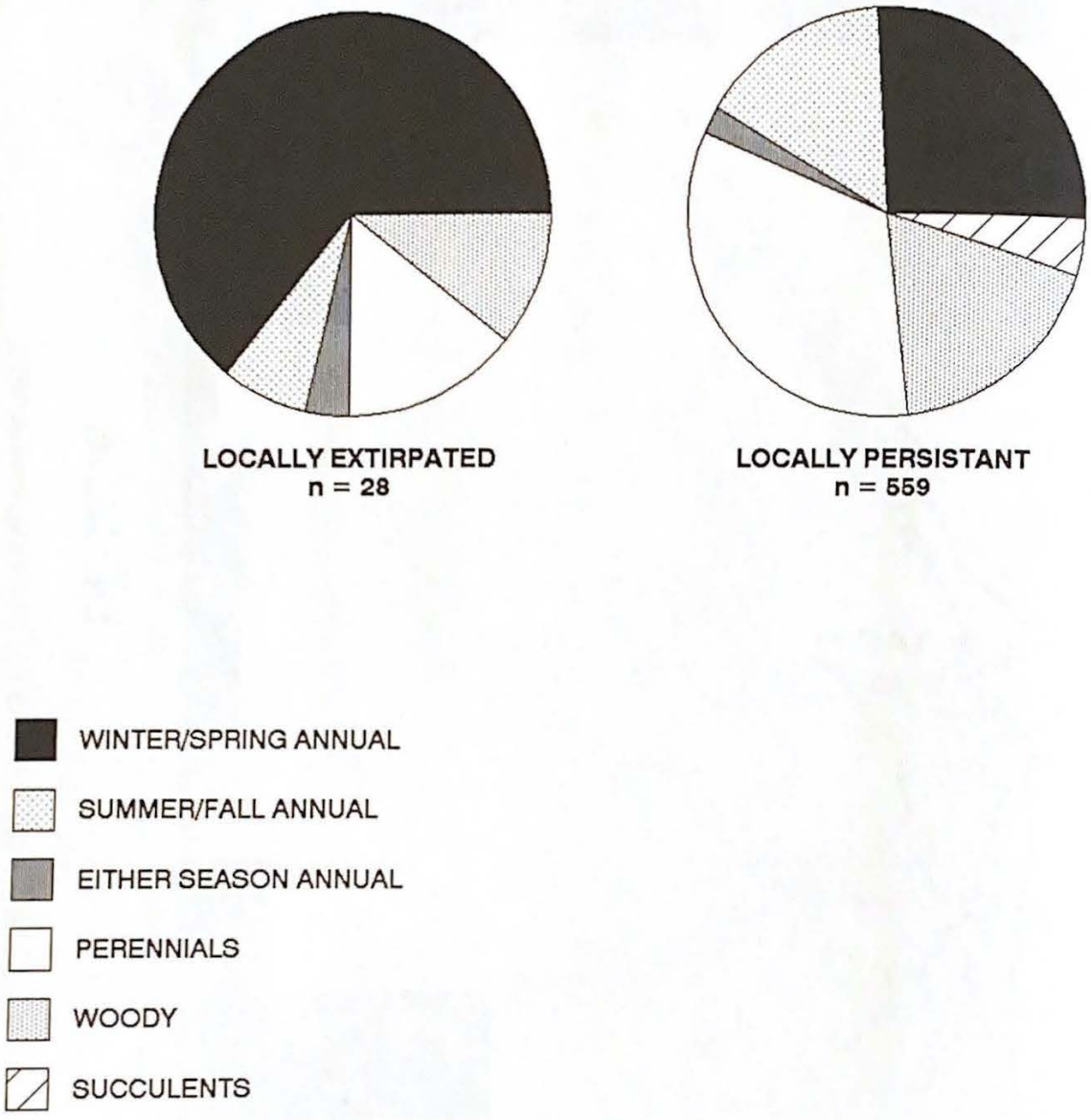


Fig. 3. Comparison of life forms between locally extirpated species and locally persistent species (from Rondeau 1991).

Pollen Harvest by Honey Bees in Saguaro National Monument: Potential Effects on Plant Reproduction

Stephen L. Buchmann, Mary K. O'Rourke, Charles W. Shipman, Steven C. Thoenes, and Justin O. Schmidt

ABSTRACT

A research apiary of five honey bee (*Apis mellifera*) colonies was established in the Tucson Mountain District of Saguaro National Monument during April 1987. The hives were fitted with modified Ontario Agricultural College (OAC) pollen traps and monitored weekly from April 1987 until January 1991. Amounts of pollen trapped ranged from 10.2 to 23.7 kg annually. Daily pollen amounts ranged from 0 to 282 g with a mean of 61.1 ± 9.0 (95% CI) grams/colony/day. Four major periods of pollen availability were found, with concomitant bee harvesting, during each of the four years. Pollen diet breadth was quantified for nearby areas and extrapolated for managed and feral bee colonies within the monument. Honey bees are extreme pollen generalists consuming pollen from 20-30% of all angiosperms within their foraging area (80-100 km^2). This generalist strategy likely has significant but unknown effects on the reproduction of native flora.

INTRODUCTION

True honey bees, the genus *Apis*, are comprised of about seven species not native to the New World. One species (*Apis mellifera* L.), however, is now nearly pandemic due to intentional introductions to new lands, transport by beekeepers for honey and wax production, and recent introductions for pollination. Such a worldwide distribution has brought *Apis* into contact with almost all of the world's terrestrial flora. The Italian race or subspecies, *A. m. ligustica* is the most popular for beekeeping in the United States. With purposeful introduction into the Mexican Plateau/Mexico City area in the 16th century by Spanish conquistadors (Brand 1988), a highly efficient bee competitor was unleashed onto floral landscapes. Descendants of these Spanish honey bees (*A. m. iberica* or *A. m. mellifera*) escaped from naive local beekeepers near Mexico City and migrated northward into more temperate climates. Purposeful introductions into northern Mexico, Sonora, and southern Arizona were probably made by Franciscan and Jesuit missionaries during the 17th and 18th centuries (S. L. Buchmann, unpubl.). Thus, the exotic honey bee rapidly naturalized and has been a part of our arthropod biota for at least 200 years. Since introduction, about 3,500 generations of bees have had adequate time to colonize hollow cavities in all available Sonoran Desert habitats below 2,500 m.

Apis probably has the greatest pollen dietary breadth (i.e., polylecty) of any bee genus, or at least shares this distinction with some neotropical bees in the genus *Trigona*. Several biological characteristics of these highly social bees make this possible. Unlike native ground or twig-nesting solitary bees, which are active briefly as seasonal dietary specialists (mono- or oligolecty), honey bee colonies cannot afford to specialize upon one or a few flowering plants due to their perennial life history strategy. Honey bees are active every day when weather allows bee flight, and their colonies are nearly immortal if successful queen replacement occurs.

Honey bees have a particulate diet that includes pollen, spores and some pollen-like substances providing protein and lipid needs. *Apis* is known to collect pollen from almost all angiosperm groups, many gymnosperms, and some ferns and a few other spermatophyte groups. Honey bees have been observed collecting such bizarre non-pollen particulates as mites, flours, coal dust and sawdust (see references in Schmalzel 1980). Animal-pollinated (zoophilous) and wind-pollinated (anemophilous) flowers are visited for pollen. Wind-pollinated plants have no floral nectar but this does not deter honey bees from stealing pollen and exploiting these plants (Schmidt and Buchmann 1983). Honey bees sequester carbohydrate reserves (honey) in their hives not only for winter food, but as "flight fuel" making the stripping of pollen from anemophilous blossoms energetically possible. *Apis mellifera* can exploit both periodic and random (rare) floral pulses of desert nectar and pollen due to its efficient scouting, communication and recruitment abilities. Several studies have determined that *Apis* routinely collects pollen from 20-30% of all available species of flowering plants within flight range (often 100-200 km^2) of their colonies (Roubik 1989; S. L. Buchmann, unpubl. data). For better or worse, honey bees have intimate reproductive contact with one-fourth of all flowering plant species in natural and human-altered plant communities.

All bees, including honey bees, harvest floral pollen as proteinaceous food for themselves and their larvae. None are "helpful mutualists" purposefully delivering pollen to receptive stigmas as do yucca moth (*Tegeticula* spp.) adults. Bees are more appropriately viewed in an evolutionary context as persistent plant enemies simply taking pollen and nectar for their own nutritional uses (Roubik 1989). We do not know the relative pollination efficiency of introduced honey bees versus native bees as pollen vectors of the native flora in Saguaro National Monument (SNM) or other protected habitats (Schmidt and Buchmann 1986; Scott et al. 1991). It is clear, however, that honey bee visits to native flowers can be damaging, and the long-term consequences of such exotic pollination and pollen predation to plant community maintenance are unknown (Schaffer et al. 1979, 1983).

In this paper, we report on pollen gleaned from SNM on a seasonal and annual basis, based on pollen trap data. Further, we indicate which flowering plant genera and species are most heavily used by *Apis*, and thus at greatest risk to reproduction or lowered seed quality.

METHODS

Pollen Trapping

On April 7, 1987, we moved five full-size colonies of Italian honey bees housed in two deep and two shallow Langstroth "supers," to the Tucson Mountain District (TMD) of SNM. The pollen trap apiary was located alongside a wash 200 m west of Sandario Road and approximately 1.6 km southwest of the Sus Picnic Area (T13S, R11E, S28). At establishment, the colonies contained from 22,000 to 26,000 adult bees. The colonies were given minimal management with infrequent inspections only for diseases and healthy, laying queens. Each hive was placed upon a metal stand with legs in cans of motor oil to dissuade ants. All colonies were positioned in the shade under large paloverde trees (*Cercidium microphyllum*) but otherwise unprotected. All five hives were fitted with bottom-type wood and screen-modified Ontario Agricultural College (OAC) pollen traps (Smith and Adie 1963; Waller 1980) with deep drawers. This type of pollen trap is less efficient at removing pollen loads from returning foraging bees than most pollen trap designs, and can remain in place for several years without adverse effects on brood-rearing (O'Neal and Waller 1984; S. L. Buchmann, unpubl. data). These traps removed 60-65% of incoming pollen corbicular loads, which were then available for later weighing and sampling (O'Neal and Waller 1984; S. L. Buchmann, unpubl. data). In the first few months of the study, bees in one of the colonies died out. The colony was not replaced, so all data reported herein are from the four colonies that survived during the approximately 4-year study period.

Almost every Friday afternoon from April 7, 1987, to January 1, 1991, the apiary was visited and pollen collected. Drawers were emptied into separate paper bags for each colony and returned to the laboratory within 1-2 hours following collection. Pollen samples were sifted to remove unwanted non-pollen debris and immediately weighed to the nearest 0.1 g.

After repeating this procedure for all colonies, the four weekly samples were placed into one paper bag and vigorously shaken to thoroughly mix the pollen. From this pooled sample was drawn a homogeneous 100 g subsample. This procedure was repeated weekly and all subsamples were archived (frozen at -20°C) for eventual chemical (nitrogen and crude protein) or palynological determinations. All weight data presented represent fresh pollen weights as found in the traps.

Pollen Preparation and Palynological Methods

To date, no chemical analyses or microscopical taxonomical determinations of the 1987-1991 frozen pollen samples have been made. The Arizona Upland subdivision of the Sonoran desertscrub (Turner and Brown 1982) plant community that surrounds the apiary is very similar in vegetation structure (floristic richness including abundance and diversity) to other sites in the Tucson Mountains and Pima Canyon (Santa Catalina Mountains) where we have established other long-term OAC pollen trap apiaries. We (Buchmann and O'Rourke, in press) are beginning to identify pollen grains recovered from trap samples from a site in Tucson Mountain Park (Arthropod Discovery Center operated by Sonoran Arthropod Studies, Inc.). For this reason, we infer from these and other unpublished studies, that previously analyzed samples from our Pima Canyon site are qualitatively similar, in terms of annual bee pollen diet, to SNM samples. Therefore, palynological determinations of plant taxa as *Apis* dietary elements for the Pima Canyon site are generalized as probable dietary elements for the SNM trap apiary. Methods for pollen preparation, chemical extraction, identification and quantification are given elsewhere (O'Rourke and Buchmann 1991). Further technical details of bee pollen dietary studies and quantification, especially the importance of pollen volume calculations and simple numerical abundance counts, are presented elsewhere (Buchmann and O'Rourke, in press).

RESULTS

A total of 196 weekly samples were collected at the SNM apiary between April 1987 and January 1991. Because time intervals between sampling dates were not always seven days apart, we report average pollen influx into the apiary as grams/colony/day as illustrated in Figure 1 (see also O'Neal and Waller 1984).

Pollen harvest by the four colonies living in this rich paloverde-saguaro (*Carnegiea gigantea*) upper bajada slope, was characterized by dramatic weekly fluctuations in amounts of pollen trapped. The variability in weekly pollen amounts is diagrammed as vertical error bars representing one standard deviation (Fig. 1). Dramatic periodic shifts are the result of times of pollen abundance in the floral community, and favorable (sunny, warm and not windy) or unfavorable meteorological conditions for active flight by worker bees. In general, the histograms are strikingly similar to others we obtained for different southern Arizona sites. Four periods of pollen availability are evident (one or two in the spring months, one in summer during the seasonal monsoon precipitation, and a sharp narrow fall peak). The striking pollen dearth in early July each year occurs during hot, dry weather and floral community inactivity prior to the onset of summer rainfall. The amount of pollen trapped for all colonies varied from a low of 10.2 kg in 1987 (partial year record) to 23.7 kg in 1989, with a mean of 18.9 ± 6.0 (SD) kg. On a grams/colony/day basis (combined values), the amount of trapped pollen ranged from 0 to 282 g with a mean of 61.1 ± 9.0 g (95% CI) (Table 1). The habitat was rich in pollen produced and used by the honey bee colonies. Based on 60% trap efficiency, colonies actually amassed 14.3 to 33.7 kg per annum during the four years.

The average annual precipitation for this part of SNM is 280-300 mm. The precipitation from 1987 to 1990 was 221 to 413 mm, with a mean of 300 ± 90 (SD) mm (Table 1). Unexpectedly, although 1989 was a dry year and 1990 wetter than average, no positive correlation was found between wet years and more honey bee-collected pollen. Such a relationship has been observed in other long-term trapping apiaries (S. L. Buchmann, unpubl. data).

Pollen Diet Breadth

Other pollen trapping and palynological investigations at nearby Sonoran Desert sites indicate that managed and feral honey bee colonies routinely

harvest pollen from 35-55 species of angiosperms (Buchmann et al. 1990; S. L. Buchmann, unpubl. data). At the Pima Canyon, Santa Catalina Mountains foothills apiary (during 1980-1989), pollen from 55 flowering plant species in 40 genera and 25 families was used by the honey bees. Numerically, the dominant pollen types were: *Aster* (22.7%), *Prosopis* (17.1%), Liliaceae (9.5%), *Larrea* (6.6%), *Simmondsia* (6.6%), *Ambrosia* (6.4%), *Phoradendron* (4.8%) and Cruciferae (1.6%). These taxa contributed 75.3% of the annual pollen diet. Pollen from 35-55 angiosperm species, representing about 18-28% of the native flora within flight range, was used by bees at this site from 1980-1989. Anemophilous plants (e.g., *Ambrosia*, *Ephedra*, *Simmondsia*) were heavily used and the overall contribution from wind-pollinated plants during this time was 5-28%. Surprisingly, dominant plants such as saguaro and foothills paloverde only represented 0.8 ± 0.4% and 1.1 ± 0.7% of the mean annual diet (Buchmann and O'Rourke 1988, in press; Buchmann et al. 1990). Another OAC trap study conducted previously in SNM, Rincon Mountain District (Schmidt and Buchmann 1986) indicated that saguaro and mesquite are often major pollen sources for *Apis* during their blooming periods.

DISCUSSION

The Arizona Upland subdivision of the Sonoran desertscrub plant association, especially on uppermost bajadas encircling isolated desert mountain islands in southern Arizona, is extremely rich in legumes and other zoophilous (animal-pollinated) annual and perennial plants. The area receives periodic and regular summer precipitation promoting a plant assemblage rich in trees, shrubs, annuals, and succulents, with much vegetative and floral biomass. Floral production, and therefore, pollen availability to bees, is largely absent in December and early January. At all other seasons, native bees and exotic honey bees have a diverse bouquet of flowers as their pasture. A conservative estimate for this region at the former International Biological Program, Silverbell, Arizona, site indicated that every hectare of plants produces at least 10.7 kg of pollen annually (Simpson 1977). It is not surprising, therefore, that the Arizona Sonoran Desert supports the world's richest (comparable to some Mediterranean areas) native bee fauna. Approximately 3,500 described bee species are found in the United States, and as many as 1,000 species may be present within 50 km of Tucson. Native plant bee pastures this rich in pollen and nectar-producing plants support competing populations of managed and feral honey bees in addition to native taxa.

Numerous feral colonies of *Apis* live in rock cavities in the Tucson Mountains. No surveys have been conducted to determine the average number of colonies present in any of the 340 km^2 area that SNM protects. One estimate made for a riparian area near Cottonwood, Arizona, suggested a range of 2.9 to 5.1 feral colonies/km^2 (Taber 1979). If we assume that each of the 340,000 ha within SNM produces 10.7 kg of pollen each year (based upon the Silverbell site estimate of Simpson 1977), then the entire monument may produce 36,380,000 kg/yr. The hypothetical 1,358 colonies at a density of 4.0/km^2 (not including numerous managed colonies in apiaries within flight range of the monument) would, therefore, harvest 54,320 kg, or 1.5% of the estimated potential annual pollen production from this area.

Sonoran Desert plant communities produce large amounts of carbohydrate-rich floral nectar, which is efficiently exploited by *Apis* colonies. Conservative estimates of nectar production by a Sonoran plant community (Simpson 1977) indicated that at least 4.4 kg/ha is available each year. Since honey is 20% water, this suggests a honey equivalent production of 5.3 kg/ha/yr. Measurements of honey production by managed *Apis* colonies in Tucson during the period 1973-78 showed a yearly average gain of 18.5 kg, although some colonies collected 47.3 kg. An upper bajada site with pollen trap-managed colonies averaged 83 kg stored honey, with a probable annual harvest and consumption rate of 193 kg of honey each year (S. L. Buchmann, unpubl. data). Assuming that smaller feral colonies use 97 kg/yr, 1,358 feral honey bee colonies collect 131,726 kg (7.3%) of the entire (1,802,000 kg) annual nectar production available to all nectarivores from the monument.

Nearly four years of OAC pollen trapping data indicate overall plant community richness in pollen and striking temporal variability. Four major periods of pollen abundance occur, including two peaks in

the spring months, a pronounced June/July dearth, followed by a recovery after the summer rains, and a fall (October-November) pulse due to native and introduced Compositae species (Fig. 1). At this site, community pollen abundance is too low to support bee reproduction during December and January. The average daily pollen availability, indicated by trapped pollen, was surprisingly stable, at 61 ± 9 g (95% CI). Surprisingly, lower-than-average precipitation in 1989 (only 221 mm) (Table 1) produced unusually high pollen harvests (33.2 kg) by our trap colonies. We have no explanation for this negative correlation. Pollen trapping of *Apis* colonies is labor-intensive and not the easiest way to acquire pollen diet breadth information. Since colonies are long-lived, much of the harvested larval-ingested pollen becomes part of hive architecture. Pollen grains become incorporated into propolis (plant resins), old dark brood combs, and for old protected feral colonies, as a blackened debris midden. These materials can be processed to reveal quantitative floral choices made by entire colonies over annual multi-year periods (O'Rourke and Buchmann 1991).

Because *Apis mellifera* likely has the greatest pollen dietary breadth of any insect, and because it has an anthropogenic-derived cosmopolitan distribution, the species directly affects the reproductive biology of about 25% of the world's flowering plants. Honey bees are often a powerful disruptive floral herbivore and selective agent. Although honey bees are supreme floral generalists (polyleges), and their fidelity per foraging bout makes the species a good pollinator, more often their effect on natural plant communities is negative. *Apis* foragers, due to their effective massive recruitment and immense colony size, rapidly diminish nectar and pollen standing crops, even from wind-pollinated genera. This undoubtedly reduces floral rewards available to specialist and generalist native bees, and in turn, lowers population sizes. Even if community-wide pollen and nectar are not limiting in this Sonoran habitat, for certain solitary bees there could be indirect effects of honey bee floral visitation on individual plant species. For example, stigmas can become clogged with foreign or less viable pollen. No documented cases have been made for *Apis* causing any native bees to become extinct in modern times. Conversely, any equilibrium that now exists between native bees and exotic *Apis* probably does not represent native bee foraging activity levels or floral preferences, prior to honey bee introduction or natural migration into the Sonoran Desert several hundred years ago. We can never return to pre-*Apis* conditions and even the most remote Sonoran Desert sites have introduced Eurasian immigrant honey bees.

SUMMARY AND MANAGEMENT IMPLICATIONS

Although commercial and hobbyist beekeeping is not allowed within monument boundaries, the potential effects of possibly 1,358 feral *Apis* colonies on floral resource extraction/depletion and angiosperm reproduction are likely great and heretofore unappreciated. Even if we wanted to eliminate all feral and managed honey bee colonies from the monument, it would be economically and logistically impossible. As in almost all other areas of the world, since late in this century honey bees have been omnipresent floral visitors. Attendant ecological dangers may even exist in a plan for massive eradication or colony control, especially in relation to impending Africanization of feral honey bee colonies.

Australia has recognized the potential dangers of intensive beekeeping within state and national parks and has enacted legislation to control apiculturists in native park lands. In the Northern Sandplains of western Australia, imported honey bees used 30% of 413 native plant species as sources of nectar and pollen (Wills 1989; Wills et al. 1990). In western Australia many parks do not allow any beekeeping within their borders. Through lobbying of beekeepers, however, some areas have been set aside as designated beekeeping, honey-producing reserves. No stated policy has been developed in Australia for removing feral colonies.

In the United States, park managers and rangers are being increasingly called upon to selectively remove and/or kill aggressive feral colonies located near visitor centers, trails and other much visited public areas. This can be rapidly and economically done using a number of existing techniques. In one or two years when Africanized honey bees (*Apis mellifera scutellata*) reach Arizona, the problem of feral colonies in national parks and monuments will worsen, since the

Africanized bee population can use much smaller cavities as nesting sites than honey bees. Africanized bees will undoubtedly compete with native birds for access to "boots" and other cavities in saguaro cacti. Many or all of the resident feral honey bees nesting in rock cavities may be replaced by the invaders, likely creating a greater feral colony density within the monument. To forestall or ameliorate this invasion, it would be best to leave present feral colonies alone, as they provide the only potential biological barrier to Africanized bees (D. W. Roubik, pers. comm.).

Once established, at whatever level, Africanized honey bees will have an added impact on the floral resources and pollination within the monument. Africanized bees collect more pollen and swarm more frequently than European races. Of crucial importance, is their demonstrated acumen for harvesting immense amounts of pollen from night-blooming tropical plants normally pollinated by bats (Roubik et al. 1986; Roubik 1989). These bees are also known to heavily exploit native plants that are dioecious or have large inflorescences of small flowers. We predict that columnar cacti in Arizona and Sonora, Mexico, will be highly preferred pollen plants for Africanized honey bees, and populations of legitimate "adapted" pollinators (solitary bees and bats) may suffer from intense competition for pollen.

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Table 1. Results from Ontario Agricultural College (OAC) pollen trapping at Saguaro National Monument, 1987-1990.

Year	*n*	Precipitation (mm)	$\bar{x}$ trapped pollen (kg)	$\bar{x}$ colony harvest (kg)	grams/colony/day $\bar{x} \pm$ 95% CI (range)
1987	55	234	10.24	14.34	50.6 ± 8.7 (0-104)
1988	49	333	19.46	27.24	57.1 ± 11.8 (0-148)
1989	47	221	23.69	33.17	70.7 ± 16.4 (0-217)
1990	45	413	22.01	30.81	66.0 ± 17.6 (0-282)

[a]Based upon a 60% OAC pollen trap efficiency.

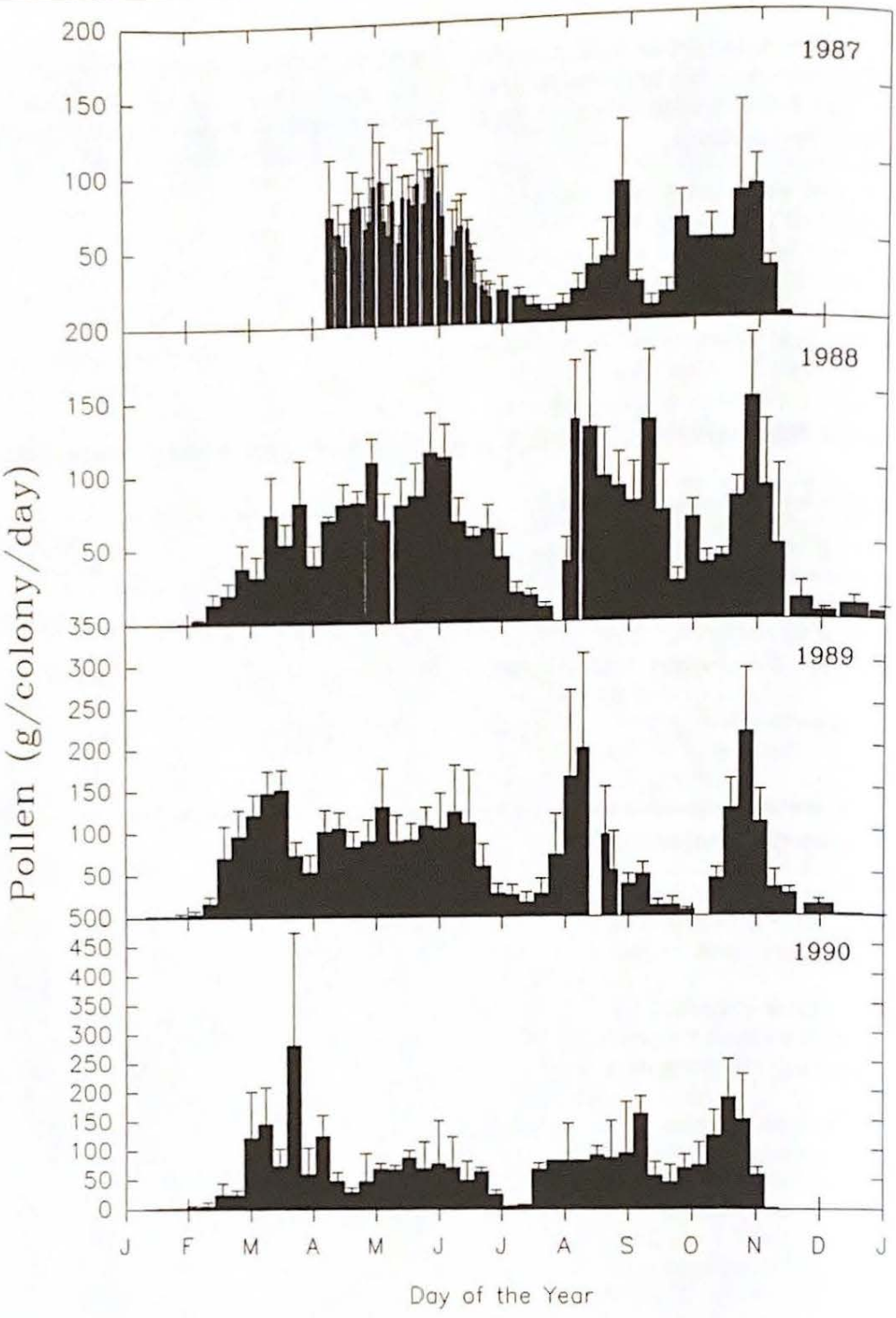


Fig. 1. Pollen harvest by honey bee colonies in Saguaro National Monument. Mean amounts of pollen trapped at weekly intervals (reported as grams/colony/day) using Ontario Agricultural College (OAC) methodology from April 1987 to December 1990. Variance between the four colonies is given as vertical error bars representing one standard deviation.

III.
Effects of Land Use on Monument Resources

The Historic Role of Fire in the Rincon Mountains

Christopher H. Baisan

ABSTRACT

Modern fire records and fire-scarred remnant material collected from logs, snags, and stumps were used to reconstruct and analyze fire history in the mixed conifer and pine forest above 2,300 m within the Rincon Mountain Wilderness of Saguaro National Monument. Cross-dating of the remnant material allowed dating of fire events to the calendar year. Estimates of seasonal occurrence were compiled for larger fires. It was determined that the fire regime was dominated by large-scale (>200 ha), early-season (May-July) surface fires. Most fires were surface burns that did little damage to the forest canopy in general, but some areas, primarily on north aspects, did experience patches of intense fire as indicated by clumps of aspen. The mean fire interval over the Mica Mountain study area for the period 1657-1893 was 6.1 years, with a range of 1-13 years for larger fires. The mean fire interval for the mixed conifer forest type (1748-1886) was 9.9 years, with a range of 3-19 years. Thirty-five major fire years between 1700 and 1900 were compared with a tree-ring reconstruction of the Palmer Drought Severity Index. The mean July index for two years prior to fires was higher (wetter) than average, while mean fire year index was near average.

INTRODUCTION

Wildfires are serious business in southern Arizona. In the summer of 1990, before the monsoon began in earnest, the Dude Fire claimed the lives of six firefighters. In early July 1989, lightning ignited the Chiva Fire on the northeastern flank of Mica Mountain. This fire burned across more than 9,000 acres in a several day period and cost nearly $1,000,000 to suppress. During June and July, wildfires ignited by both lightning and people are quite common; while loss of life is fortunately rare, controlling wildfires requires considerable expense and effort.

In the not too distant past, wildfires burned across the Arizona landscape hindered by little but wet weather. Yet, despite such fires, early European travelers were impressed by the extensive forests of ponderosa pine (*Pinus ponderosa*) and other conifers carpeting the mountain ranges of the Southwest. Lt. J. Bigelow, while scouring the Rincon Mountains for Apaches in 1886, noted an ice cold spring surrounded by "fine old pines" and looked over the "timbered declivity" stretching out from Mica Mountain (Bigelow 1968).

Lightning-caused fire is an ancient force that has been reworking landscapes and plant communities on this continent for millions of years. Plant communities have adapted to, and often benefit from, wildfire. Although flaming combustion itself is dramatic, wildfire is best understood as a component of a continual process of fuel accumulation and reduction. Fires may involve only a single tree or spread over vast areas, and the resulting changes may persist from a few months to several centuries, depending on the intensity of the fire and the type of plant community involved. The effects of the Chiva Fire on the

grassland, shrub and forest communities along Tanque Verde Ridge may be seen dramatically after a winter snowfall when the burned area appears brilliant white in contrast to the darker shrub and tree cover of the unburned area. It is clear that the signature of this fire will persist for many years to come, affecting the mosaic of plant communities and the habitat available for wildlife. The Chiva Fire has become part of the unique history of this site, incorporated in the memory of the landscape.

In the aftermath of such a fire one might ask questions such as: Were the timing, size and intensity of this event unusual for this area? How often did such events occur in the past? Were the effects of this fire beneficial or harmful? The objective of this study was to answer some of these, and other related questions.

METHODS

Records of fire occurrence obtained from Saguaro National Monument (SNM), other historical accounts, and the records contained in the rings of trees that had been scarred by fires over the past several centuries (Baisan 1990; Baisan and Swetnam 1990) were used for this study. Modern records provided a context within which to interpret information derived from trees. Fire-scarred conifers show a unique, detailed record of fire over the life of the tree. Low-intensity surface fires that pose little threat to the tree itself, may ignite flammable resins exuded around the scarred area or "cat-face". The heat kills adjacent tissue, thus leaving a permanent record of its passage. Repeated fires leave successive wounds visible as a series of ridges (Fig. 1).

Close analysis of samples allowed fire scar position to be categorized (Fig. 1). From such detailed examination of scarred sections, using dendrochronological techniques of pattern matching, it was possible to determine the year, and in many cases to estimate the season of fire occurrence. Once the year of occurrence had been established, tree-ring records were compared with historical accounts and estimates of past climate. Comparison with the climatic record can provide insight into fire-climate interactions, while historical accounts may corroborate tree-ring data. A distinct advantage of dendrochronological analysis is the ability to assign a calendar date to the formation of each tree ring, even when working with samples from dead trees where the date of death is unknown.

RESULTS AND DISCUSSION

Modern Data

Locations of over 400 lightning-caused fires that occurred in the Rincon Mountains over the past 50 years are shown in Figure 2. That such fires were common in the upper elevations, particularly around Mica Mountain, is evident. The relation of fire occurrence to elevation is also shown in Figure 3. Although more fires begin at the upper elevations, lightning may also ignite fires in the desert shrub, grassland, and pine-oak communities.

The occurrence of lightning fires is strongly seasonal, with most fires ignited between May and September. Although the peak in numbers of fires occurred during late July, the greatest area was burned in June and early July (Fig. 4).

Fire Scar Data

Collection, examination, and analysis of fire-scarred samples from more than 50 trees, snags, stumps, and logs provided information from which a 400-year record of fire occurrence was reconstructed. Sample sites and locations are shown in Figure 5, and locations of individual samples in the vicinity of Mica Mountain are shown in Figure 6. In order to construct a complete historical record, trees were sampled in groups whenever possible.

The information from samples was assembled into a fire chronology for Mica Mountain (Fig. 7). Each horizontal line represents the fire record from a tree or group of trees, and the occurrence of a fire is noted with a triangle. The occurrence of widespread fires can be seen as the vertical alignment of triangles, indicated on the margins with a calendar date. Three points may be noted about this fire chronology: (1) fires occurred throughout the period of record; (2) many were large, as indicated by the vertical alignment of the triangles; and (3) the relatively frequent occurrence of widespread fires ceased just prior to the turn of the century. In some cases, it can be seen that fires spread across the entire area sampled. In other cases, various portions burned in sequence as in 1795, 1797, and 1799. Large fires that

occurred in 1943 and 1954 were recorded by scarred trees within these burns. In addition, fires in 1879 and 1886 mentioned in the Tucson newspapers and in a published journal were recorded. Intervals between large fires varied from 3 to >10 years, nearly 20 in some cases. The mean fire interval for the Mica Mountain area was close to six years. Distribution of fire intervals for several locations and a composite for the Mica Mountain study area are presented in Figure 8.

Where seasonal position of fire scars could be identified, 99% were earlywood or dormant season scars. This indicates that spreading fires, as in the modern period, occurred prior to the onset of summer rains. Distribution of fire scar position for a number of fire years is given in Figure 9. Three types of burns may be recognized. Early season or May-June fires (e.g., 1748, 1780), mid-season or July fires (e.g., 1851, 1879), and those without a clear peak (e.g., 1768).

Comparison of the fire chronology with an estimate of past drought severity revealed a fairly consistent pattern of two wet years preceding the occurrence of large fires. It is believed that this indicates a climatic linkage between fire occurrence and the amount of grass and litter available to carry the fire. Wet years suppress fire activity and stimulate plant growth, setting the stage for spreading fires during subsequent fire seasons. The result of averaging the reconstructed July PDSI (Palmer Drought Severity Index) value for 35 fire years, seven prior years, and two following years between 1700 and 1900, is shown in Figure 10.

Fires recorded by scarred trees were low-intensity surface burns, which did little damage to the forest overstory. The frequent occurrence of these fires maintained the forest in an open condition and prevented the accumulation of fuel, which would eventually lead to intense fire. Following the decline in fire occurrence at the turn of the century, dense thickets of young trees have become established over large portions of the study area. Should a fire occur in these areas during dry, windy conditions, the entire stand might be killed, including mature trees that have survived numerous fires in the past.

A few areas on the north side of Mica Mountain and Rincon Peak showed evidence of canopy burns (e.g., patches of aspen below the North Slope Trail). However, such areas are limited in extent and the forest in general shows little evidence of this type of severe fire behavior.

MANAGEMENT IMPLICATIONS

Saguaro National Monument has an on-going prescribed burning program, initiated nearly 20 years ago. However, limitations in funding and available personnel have imposed severe constraints. The suppression costs of the Chiva Fire exceeded the yearly prescribed fire budget by more than 100 times, yet fires of this size were relatively common in the past and should not necessarily be viewed as catastrophic occurrences. The focus of fire programs nationwide should shift from crisis management to real fire management where the economic benefits of prior planning can be fully realized. Prescribed natural fire and planned ignition programs need to be funded at levels that more accurately reflect the importance of fire to the ecosystems of the Southwest. Clearly, the return to a natural fire regime with today's concerns about the urban-rural interface, smoke management, excessive fuel buildup, budget constraints, and public relations, presents a major challenge. Sound management requires scientific knowledge, good judgement, and public support. It is my hope that studies such as the one reported here will lead to increased public awareness of wildfire's necessary and positive role in natural ecosystems. This, in turn, may be translated into solid public support, both specifically for prescribed fire programs and more generally for the additional research necessary to gain fuller understanding of the complex and unique ecosystems of which we are a part.

Specific recommendations for additional research are as follows:

1. **Salvage of tree-ring material from areas to be burned with planned ignition.** This study provided a history of fire occurrence, which is fairly complete for the Mica Mountain site between 1650 and 1950. However, a number of samples contained records that extended into the 1400s. Indications of changes in fire frequency through time were noted, yet because of the limited sample size in the early portion of the record, meaningful interpretation is difficult. Concerns about

the effects of climate change on fire regimes make such information of particular interest. Old snags, logs, and remnant debris present throughout the area represent a unique and irreplaceable resource for the records of past conditions and events they contain, in addition to their strictly biological value to the ecosystem. Every effort should be made to conserve these resources by identifying and sampling (or protecting, should immediate sampling be impossible) those that might be of interest, prior to burning.

2. **Collection and analysis of additional fire scar samples to increase our understanding of ignition and fire spread patterns prior to 1900.** By building on the data already available from this study, salvage of additional fire scar samples from Rincon Peak, Heartbreak Ridge, the east slope of Mica Mountain, and Tanque Verde Ridge could provide a much clearer picture of fire behavior under conditions of unrestricted spread. This information would prove valuable to the fire management program, particularly with regard to fire sizes, intervals, and fuel relationships over a large area. The data could also be used to generate and/or test models of fire behavior.
3. **Extend the results of this study to other vegetation zones including the pine-oak forest and oak-juniper woodland.** This could be accomplished by analyzing and combining information from aerial photography with information on stand age structure and community boundaries. Knowledge about the role of wildfire in these community types, about which little is presently known, would be increased.
4. **Establish photo points in all community types in order to catalogue the changes in communities over time[1].** When large fires occur, photo points can help track recovery and change in the burned area. Photo points within the Chiva Fire, as well as an elevation transect along the Madrona-Manning Camp trail (which has not burned recently) are possible locations. Coupling of photo points with permanent vegetation plots would allow precise quantification of the exact nature and pace of change in these areas.
5. **Study the stand age structure and stand establishment patterns within the pine forest and mixed conifer forest types.** This would provide additional data about the interactions of fire and climate, and their effect on forest structure. Such information will also improve our understanding of the effects of fire interval on tree establishment.

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Bowers, J. E., and S. P. McLaughlin. 1987. Flora and vegetation of the Rincon Mountains, Pima County, Arizona. Desert Plants 8:51-94.

[1]It is recommended that black and white photos be used to document these points. The longevity of black and white negatives will allow reliable comparison for the maximum length of time.

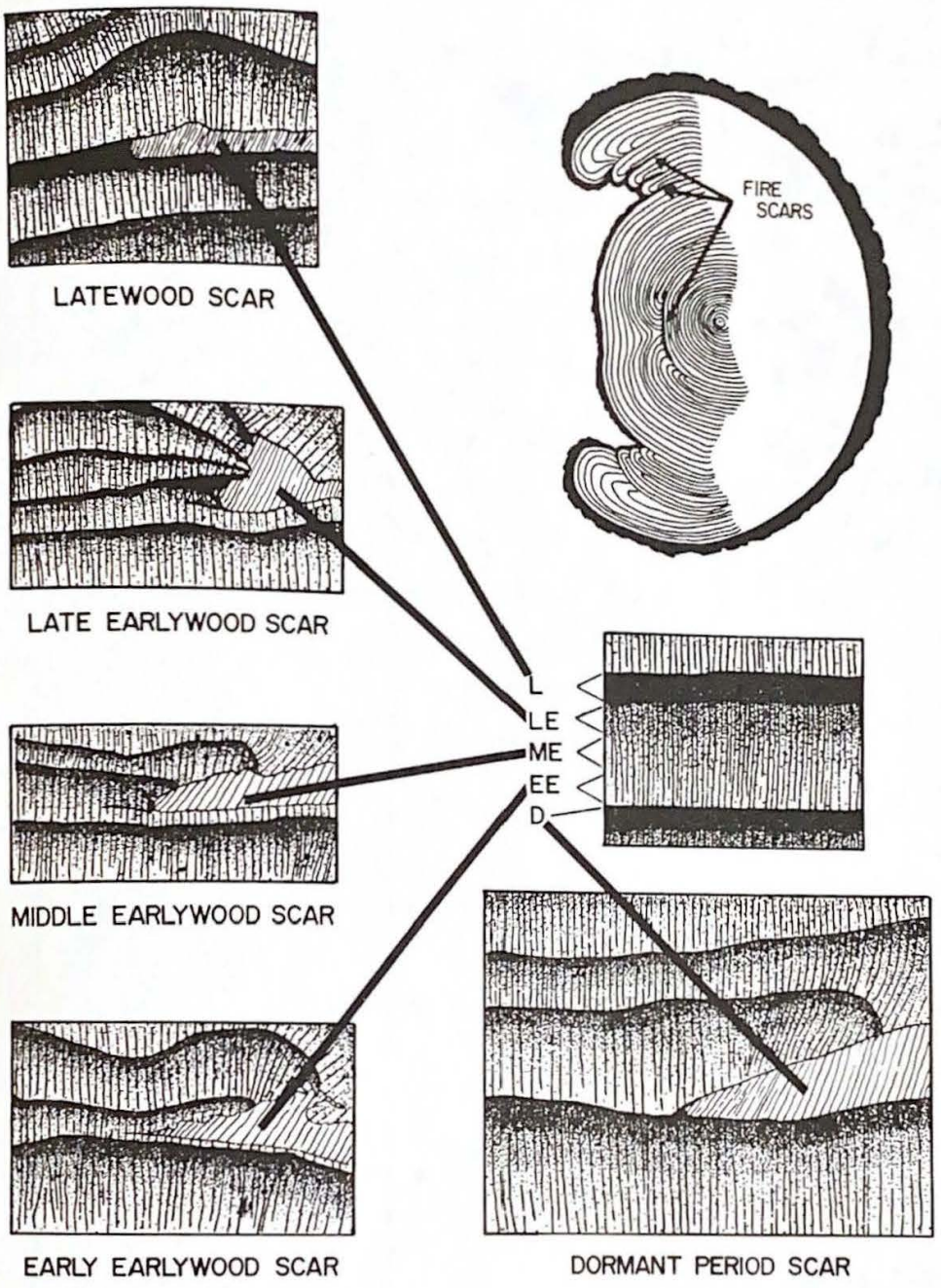


Fig. 1. Examples of the intra-annual position of fire scars and a typical fire-scarred cross section.

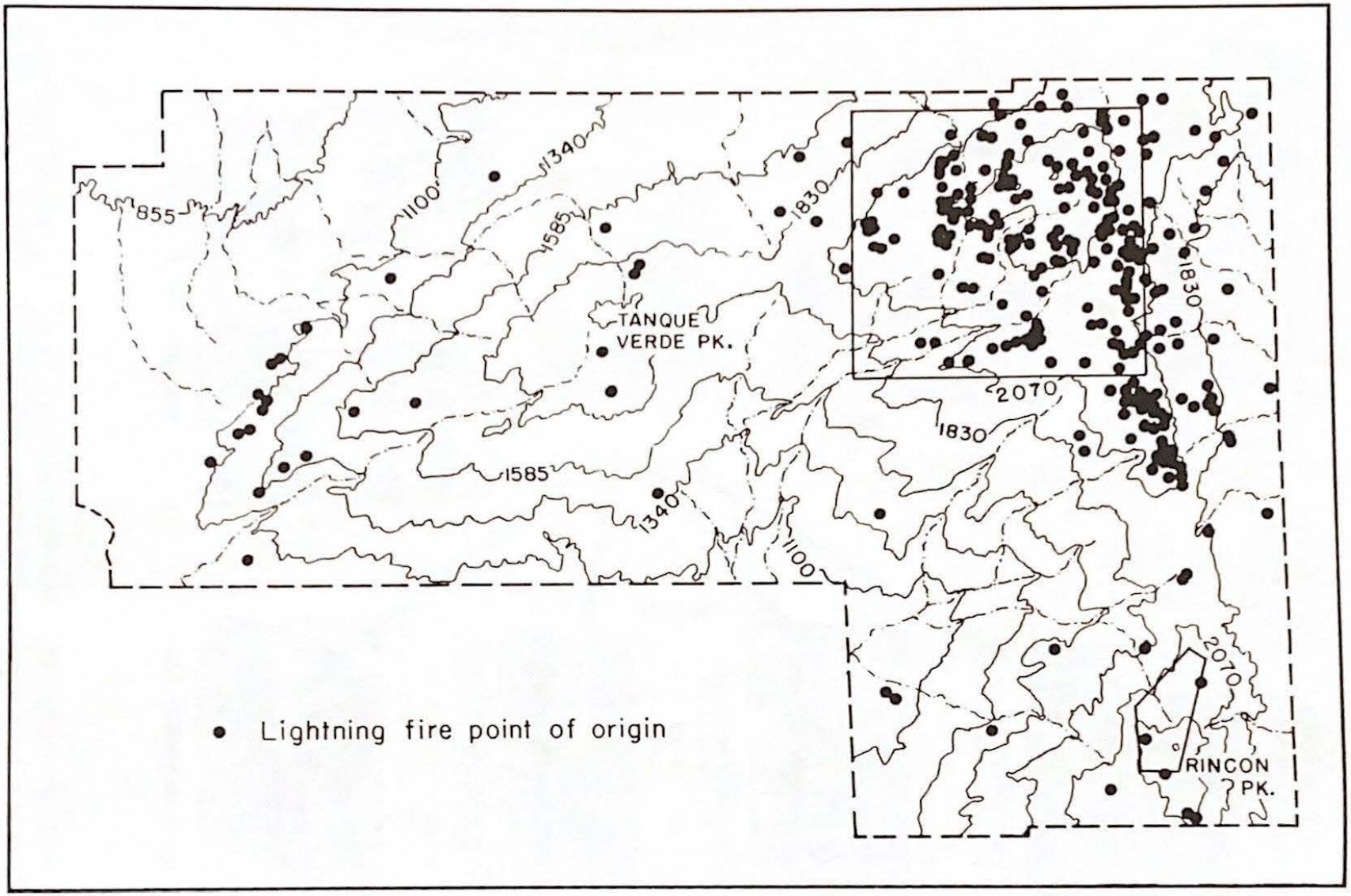


Fig. 2. Locations of lightning fire ignitions in the Rincon Mountains from 1937 to 1986.

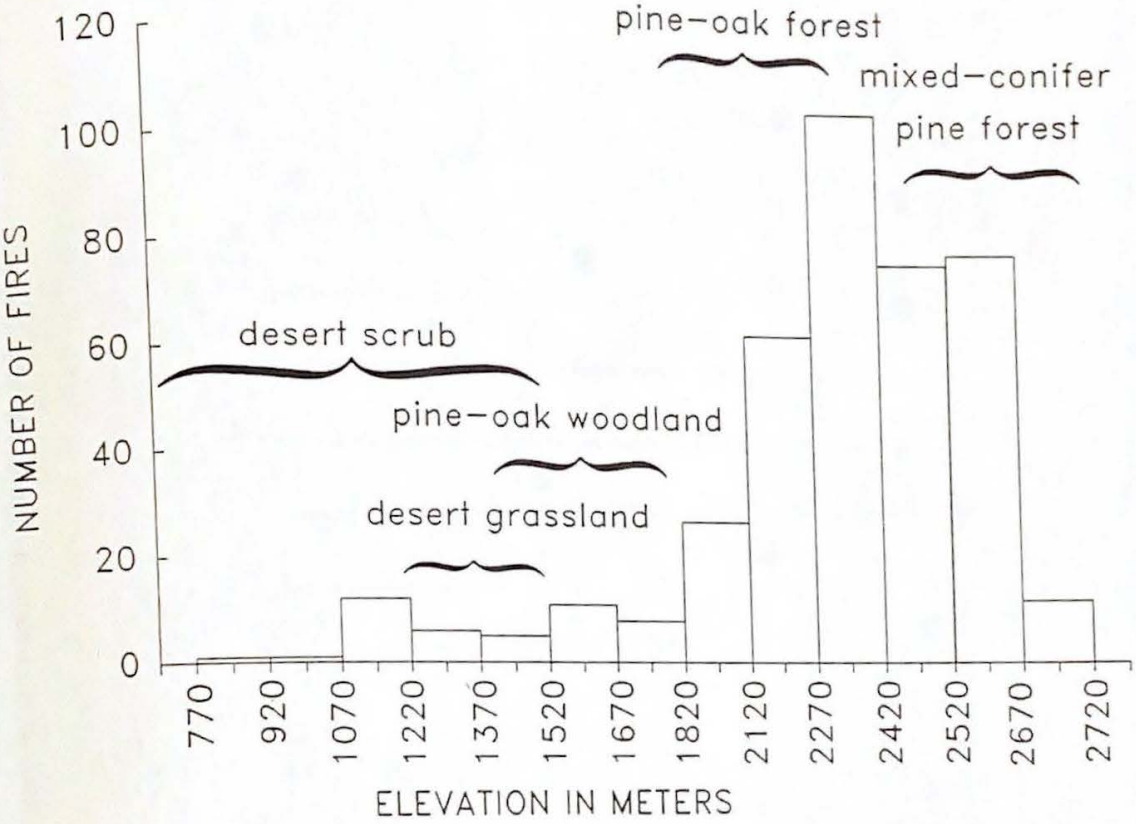


Fig. 3. Number of lightning-caused fires from 1937 to 1986 by elevation and cover type. Cover type inferred from elevation. Type designations from Bowers and McLaughlin (1987).

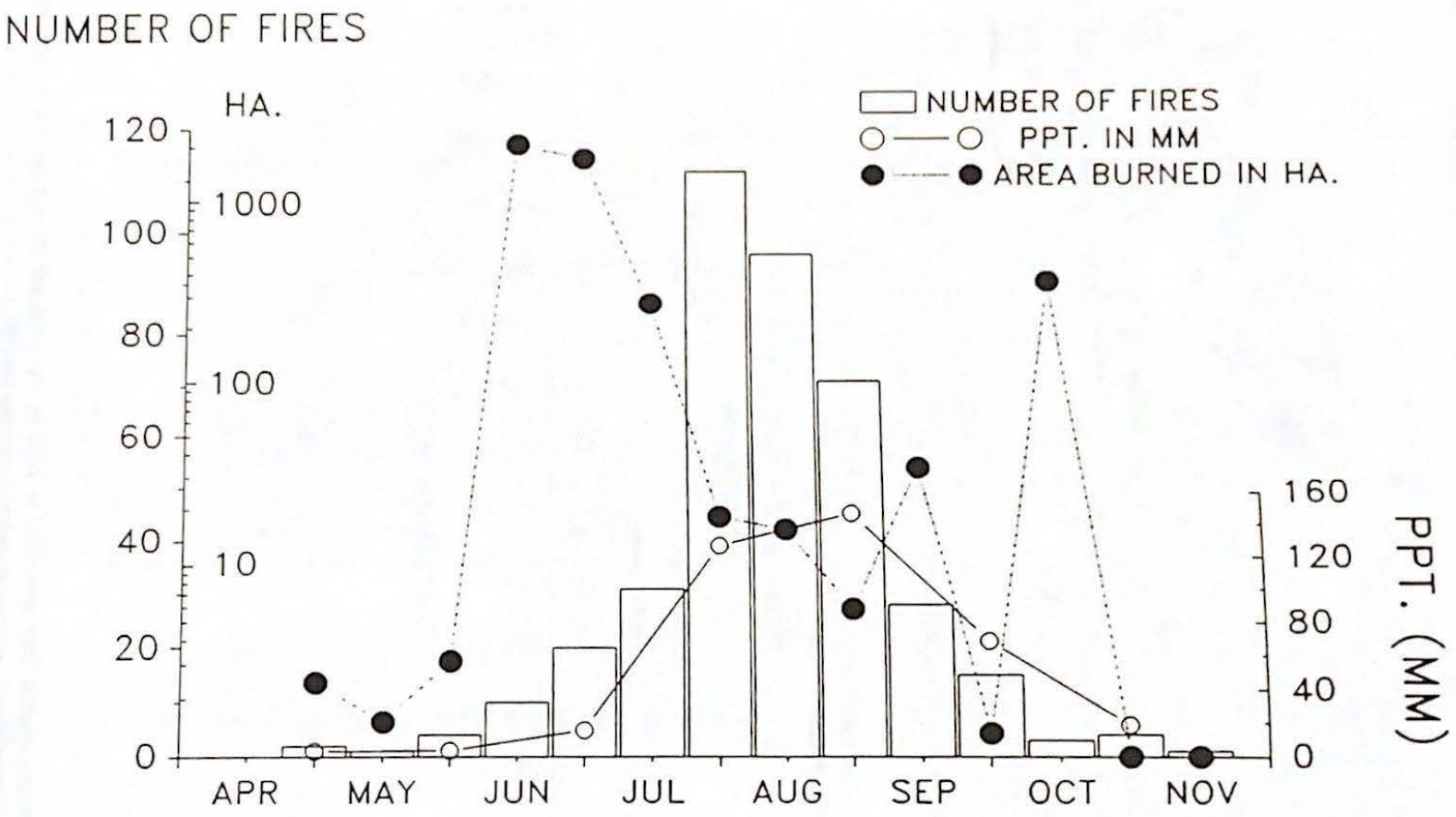


Fig. 4. Mean total monthly precipitation (mm) on Mica Mountain during the fire season versus the number of lightning fires and area burned from 1937 to 1986. Number of fires and area burned are cumulative totals by two week periods. Note log scale for area burned.

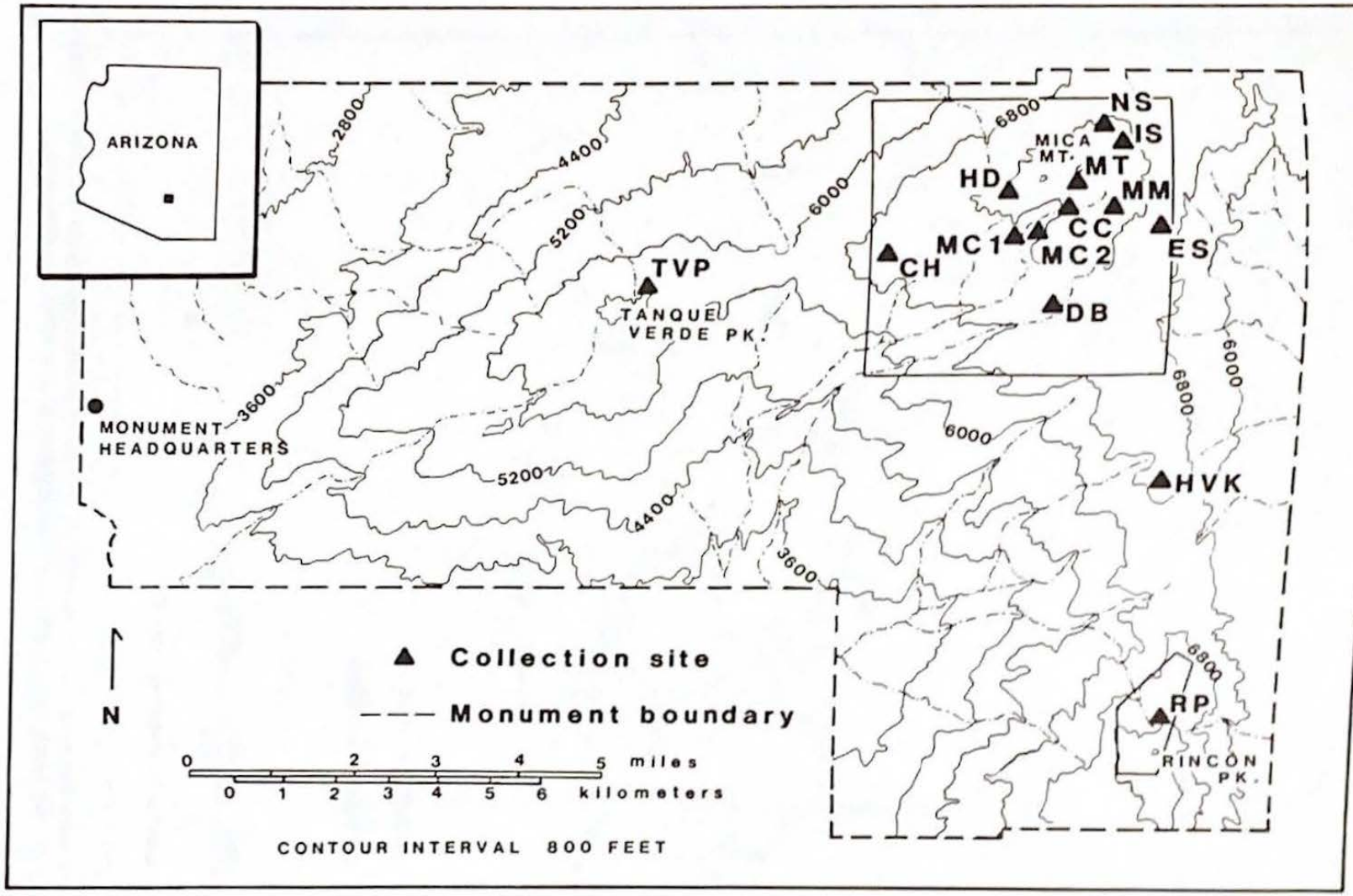


Fig. 5. Map of the Rincon Mountain District of Saguaro National Monument. Mica Mountain study area and Rincon Peak collection site outlined. Collection sites are designated by a two or three character code.

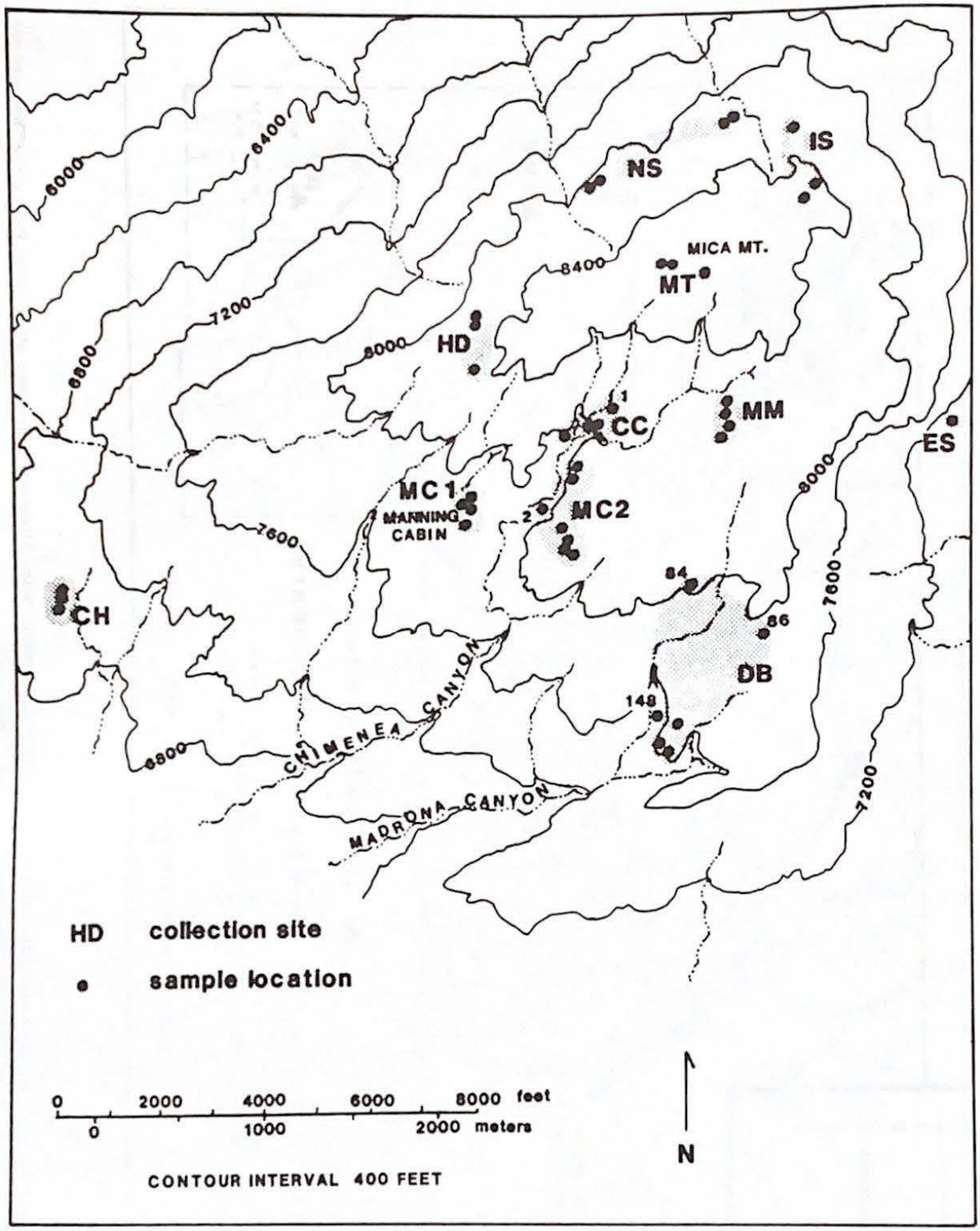


Fig. 6. Map of the Mica Mountain study area with the location of sample trees (dots) and groups (stippled). Sample trees from the 1983 study are noted by their National Park Service identification number.

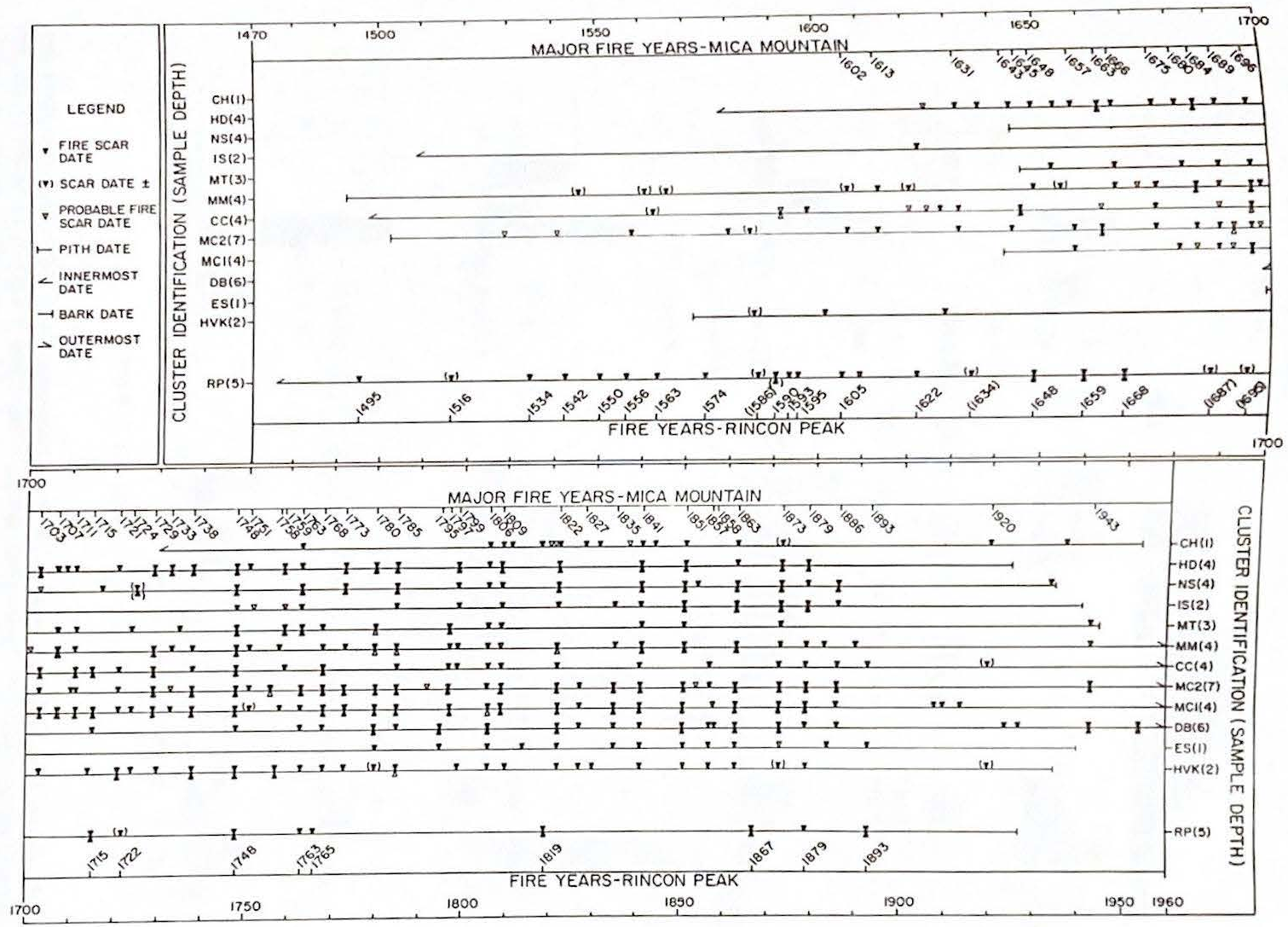


Fig. 7. Master fire chronology for the Rincon Mountains. Fire dates extend from 1495 to 1954. Major fire years are noted in margins (top for Mica Mountain study area, bottom for Rincon Peak collection site). Each line represents the fire scar information derived from all samples within a collection site. Triangles occurring both above and below the line indicate that more than one tree at the site recorded the fire. Collection site identification code and greatest sample depth (number of fire-scarred trees) are noted for each line. The regular pattern of area-wide fire occurrence is visible as the vertical alignment of triangles.

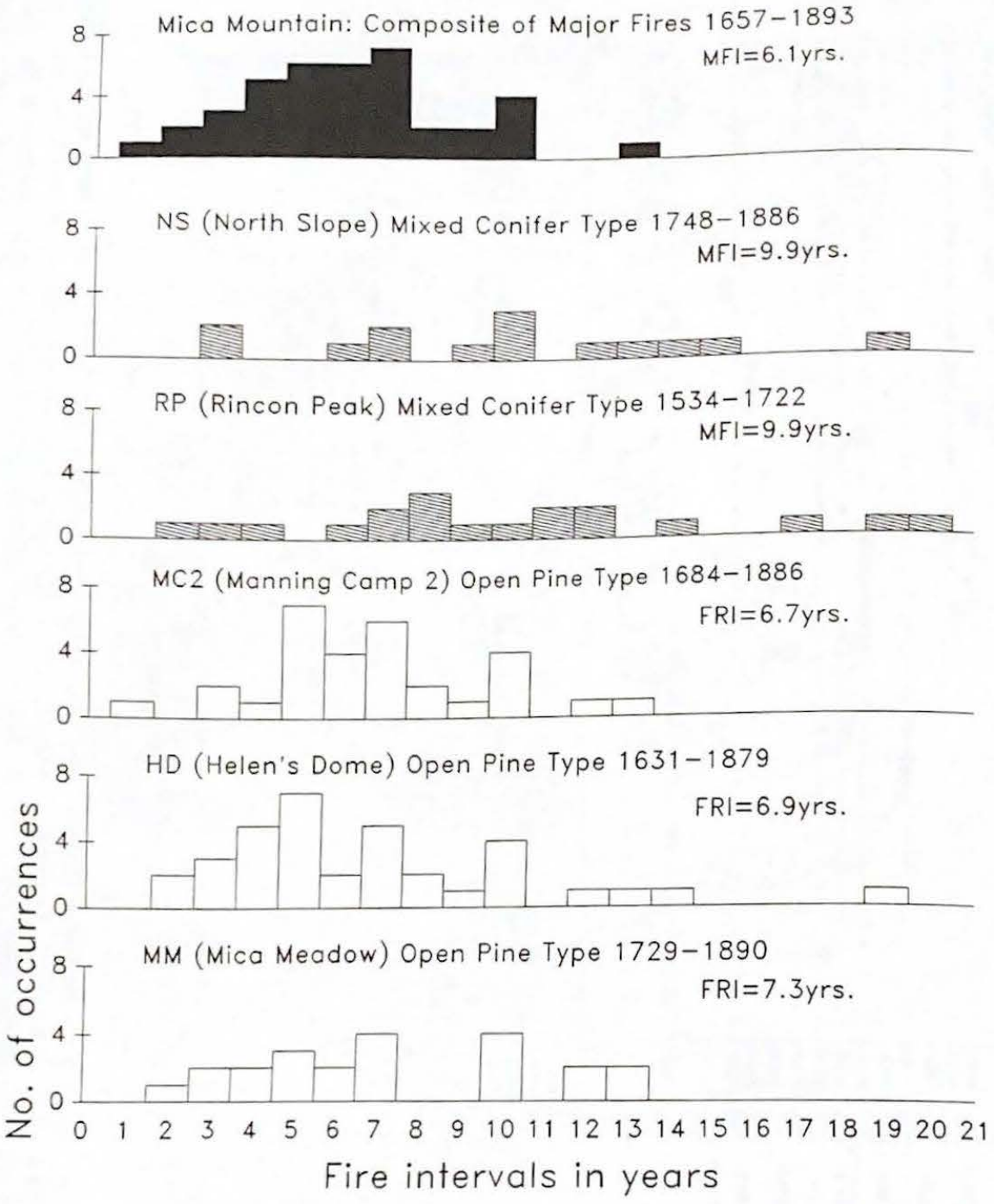


Fig. 8. Fire intervals compiled for several collection sites and a composite for the Mica Mountain study area. All sites show considerable variability. FRI (fire return interval) = the return of fire to a point. MFI (mean fire interval) = the return of fire to an area of specified size. In this case, the areas consist of collection sites or the entire study site for the composite. Refer to Figure 6.

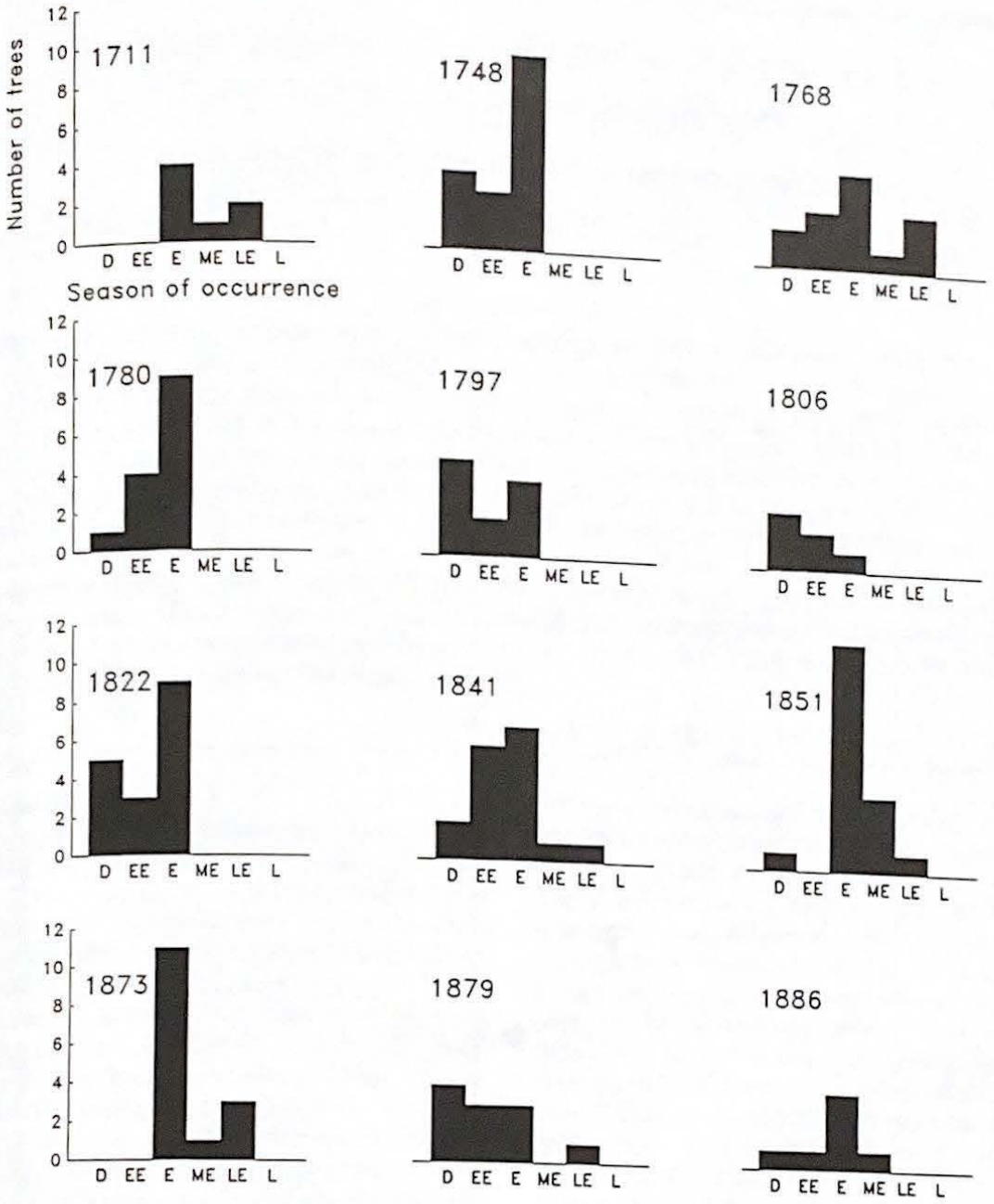


Fig. 9. The intra-ring or seasonal distribution of fire scars for 12 major fire years from 1711 to 1893. Years with a distribution weighted to the left of 'E' represent early season (May-June) burns, while those weighted to the right indicate mid-season (June-July) fires.

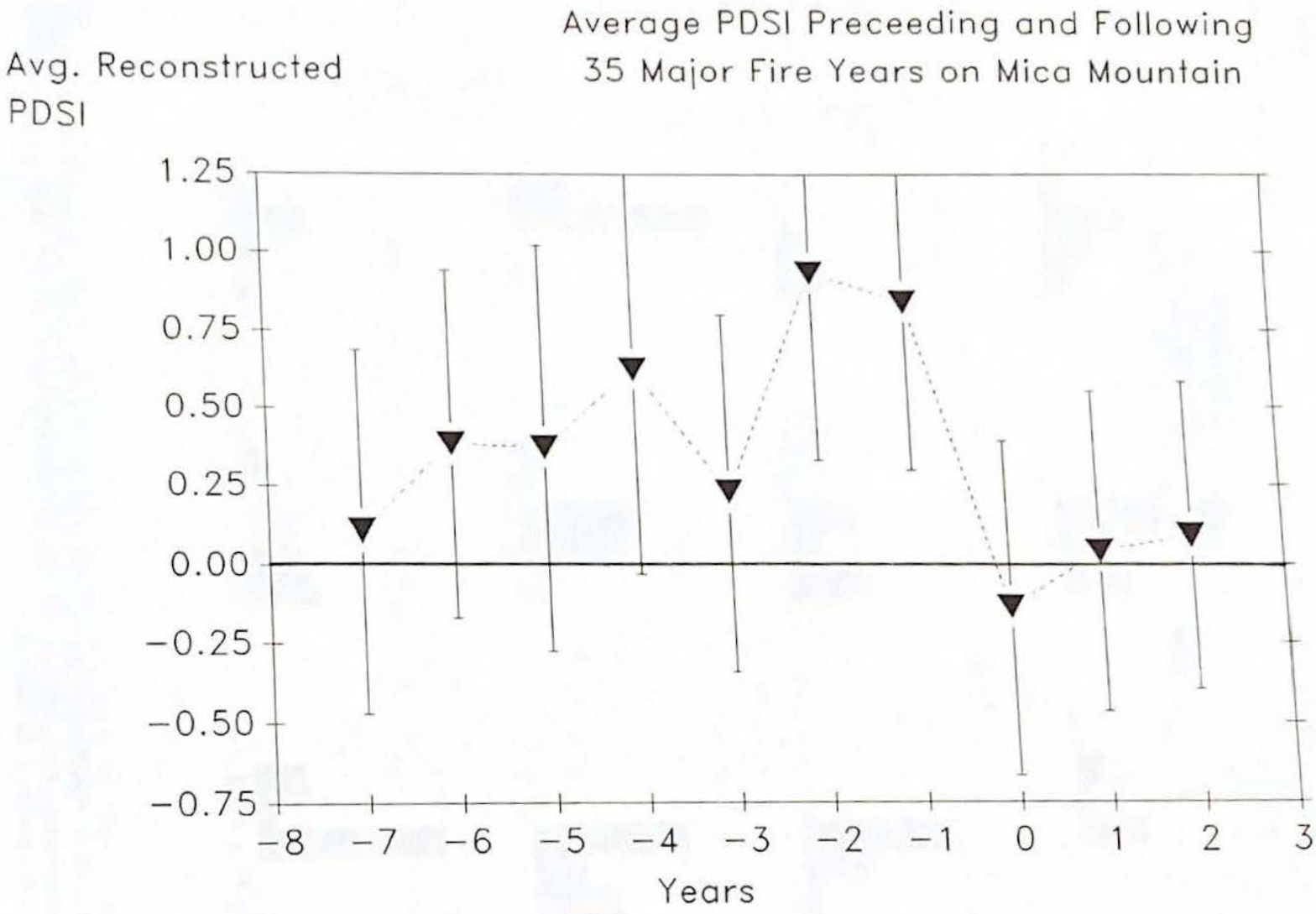


Fig. 10. Average reconstructed July PDSI (Palmer Drought Severity Index) for seven years preceding and two years following 35 major fire years for the Mica Mountain study area. Error bars represent the 99% confidence interval. Note the wet conditions prevailing for the two years prior to the fire year (lags -2 and -1).

Studies of Urbanization and the Wildlife Resources of Saguaro National Monument

William W. Shaw, Audrey Goldsmith, and John Schelhas

ABSTRACT

Studies of urbanization and the wildlife resources of Saguaro National Monument (SNM) are currently examining: movements of desert mule deer (*Ococoileus hemionus crooki*) and collared peccary (*Dicotyles tajacu*); potential displacement of native cavity-nesting birds by exotic birds; distribution, density and movements of desert tortoises (*Gopherus agassizii*); potential impacts of domestic dogs and cats; and wildlife-related attitudes, perceptions and behaviors of people who live within 1 mi of the monument. To learn more about SNM wildlife and its human neighbors, 460 households within 1 mi of its borders were surveyed. At the current low level of development, many species of animals use residential areas adjacent to the monument. Furthermore, many people encourage wildlife by providing food and water for various species. Sixty percent of the households feed wild birds and 31% feed other wildlife including deer, collared peccary, and coyotes (*Canis latrans*). As a group, monument neighbors favor low density zoning that will maintain the movement of wildlife between residential and park lands.

INTRODUCTION

Urbanization of adjacent lands is a process that is affecting many national parks and other protected areas. One survey of National Park Service (NPS) superintendents (National Parks and Conservation Association 1979) reported that two-thirds of 203 parks in the United States had problems with incompatible uses on adjacent lands. Residential and commercial uses were the first and second most frequently cited land uses creating problems.

The impacts of land use changes adjacent to natural areas do not exclusively affect natural resource managers. In addition to degrading park resources, urban expansion along park boundaries may result in losses to the adjacent community in the form of reduced scenic beauty, fewer recreational opportunities, and decreased tourism associated with the natural amenities of these areas.

In biological terms, the greatest threat of land use changes adjacent to parks is insularization. At the time most national parks were created they were simply pieces of much larger ecosystems that contained some notable features, such as the superlative examples of Sonoran Desert plants and animals found at Saguaro National Monument (SNM). As human populations have expanded, the natural ecosystems around many parks have been reduced and parks have become increasingly isolated as "islands" of nature in a human-manipulated environment. A growing body of literature in conservation biology and island biogeography has addressed the threat of insularization to preserving biodiversity (MacArthur and Wilson 1967; Miller and Harris 1979; Wilcox 1980; Soulé 1985; Newmark 1987).

Insularization is an especially relevant issue for SNM because rapid expansion of Tucson is leading to dramatic land use changes along monument borders. In 1933, when SNM was established, the population of Tucson was only 35,000 and the monument was accessible by traveling 15 mi east of town on

dirt roads. By 1986, the population of Pima County had reached 624,347; growth is expected to continue at about 3% per year and reach 940,000 by the year 2000 (Tucson Trends 1986). Major housing developments and commercial enterprises are currently proposed or under way immediately adjacent to the monument.

The potential for integrating conservation into the planning and development of cities is receiving increasing attention in Tucson (Shaw et al. 1986) and elsewhere (Leedy et al. 1978; Shaw and Mangun 1984; Stenberg and Shaw 1986). However, only limited information is available for assessing the natural resource implications of urban growth for the residents of Tucson and for the resources of the monument. This paper describes a series of recent and ongoing research projects that address these issues and presents preliminary results from one study that involved a survey of people who reside within 1 mi of SNM. The general goal of the studies is to build a foundation of knowledge that will enable the NPS and the community of Tucson to evaluate alternative patterns of urban expansion in terms of likely effects on the wildlife resources of SNM.

METHODS

Because of its diverse and productive habitats, SNM contains a large variety of wildlife. Seventy-four species of mammals and 187 species of birds are listed on SNM checklists (Southwest Parks and Monuments Association 1985; Doll et al. 1989). Herpetologists also have identified 58 species of reptiles and amphibians that are likely to be present within the monument (Lowe and Holm 1986). Faced with this diversity, an initial step in the research process was to identify several studies that would provide valuable information about urbanization and wildlife resources. Several wildlife species and related issues were identified as high priorities through use of the following criteria:

1. Scarcity and/or low reproductive capability;
2. Public interest/high visibility;
3 Easily disturbed by human activities;
4. Dependent on resources outside the park;
5. Vulnerable to predation or displacement by dogs or cats;
6. Vulnerable to displacement by exotic wildlife.

The following species or issues were identified for detailed investigations:

1. Desert mule deer (*Odocoileus hemionus crooki*) and collared peccary (*Dicotyles tajacu*) movements across monument boundaries;
2. Effects of introduced cavity-nesting birds on native bird species;
3. Distribution, density and movements of desert tortoises (*Gopherus agassizii*) at SNM;
4. Potential impacts of domestic dogs and cats on wildlife at SNM;
5. Wildlife-related attitudes, perceptions and behaviors of people who reside within 1 mi of SNM;
6. Development of a Geographic Information System database for SNM.

The deer, collared peccary, and cavity-nesting bird studies have been completed and results are presented elsewhere in this volume (Bellantoni and Krausman; Bibles and Mannan). Analyses of the other studies are under way and all research will be completed later this year. Presented below are some preliminary findings from the household survey. The objectives of this survey were to obtain information about wildlife observations, problems, and wildlife-oriented activities from SNM's neighbors.

RESULTS

Five hundred households located within 1 mi of SNM were randomly selected from Pima County property records. Following the mail survey methodology of Dillman (1978), each selected household was mailed a 12-page questionnaire covering wildlife-related attitudes, perceptions and behaviors. After deducting new arrivals, departures, and nondeliverable questionnaires, the total sample size was 460. A total of 393 households responded, yielding a response rate of 85% (Table 1). Overall, 1,877 homes and rental units are located within a mile of SNM. Thus, the 393 respondents in this study comprise about 21% of the total population of people who live within 1 mi of the monument. Absentee landowners were not included in the study.

At the current levels of development, many species of wildlife move freely between SNM and nearby private lands. The percentage of households within 1 mi of the monument that reported seeing

various species of wildlife on their property is shown in Figure 1. While observations of some species such as bobcats (*Lynx rufus*) are quite unusual, other species, including coyotes (*Canis latrans*) are seen on a regular basis.

Interactions with some kinds of wildlife are encouraged by many residents. As shown in Table 2, 60% of the respondents to this question feed wild birds and 31% feed other kinds of wildlife. Feeding large wild mammals is strongly discouraged for both biological and human safety reasons. However, substantial numbers of households feed deer, collared peccary, and coyotes (Table 3). One consequence of feeding large mammals may be an exceptionally large population of urban-adapted coyotes. Most of SNM's neighbors see coyotes on their property (Fig. 1) and over 40% believe they have lost cats to coyote predation.

The close relationships between SNM neighbors and the natural resources of the area are further reflected by responses to a question as to why people chose to live near the monument. Seventy-one percent of the respondents to this question cited proximity to the monument as either the primary or an important reason for their choice (Table 4). This positive relationship between SNM and its neighbors applies to both districts of the monument, although it is strongest at the Rincon Mountain District (SNM East).

Considerable agreement exists among SNM neighbors concerning the kinds of land uses that are appropriate adjacent to the monument (Fig. 2). When presented with seven alternatives ranging from "low density housing" (1 a or more per house) to "light industry," only "low density housing" was considered appropriate by a majority of respondents. Furthermore, although we did not offer this alternative, many people added notes to the questionnaire saying "three to four acres per house" is the only appropriate land use in their neighborhood.

MANAGEMENT IMPLICATIONS

At the current low level of development found along most of SNM's boundary, many kinds of wildlife move freely between protected and residential areas. Indeed, some species such as coyotes and collared peccary appear to thrive in neighborhoods with four or more a/house. Populations of other species are undoubtedly reduced to some extent, but it is notable that even intolerant species such as desert tortoises and gila monsters (*Heloderma suspectum*) are still observed on private property by a substantial number of SNM's neighbors.

Close association between people and wildlife is more than an incidental consequence of proximity to SNM. It is an important factor in people's decisions to live in this area and many people encourage these interactions by feeding wildlife at their homes. As a group, SNM neighbors favor land management and zoning that will maintain the interchange between the monument and adjacent lands.

The boundaries of natural areas have been characterized as semi-permeable membranes because they are imperfect barriers to the movements of humans, animals, air, and water. From a human perspective, this means that the natural amenities of parks and reserves actually reach beyond the borders of these areas and enhance the living environments of those people fortunate to live nearby. The negative implication is that the effects of human activities can penetrate boundaries and degrade the resources of protected areas.

Studies of wildlife-related boundary issues at SNM and elsewhere are gradually developing a foundation of knowledge about relationships between urbanization and protected areas. With these kinds of data, park managers and city planners can evaluate the implications of alternative land uses for the wildlife and humans that reside in and near the park.

ACKNOWLEDGMENTS

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Table 1. Sample sizes and response rates for survey of households within 1 mi of Saguaro National Monument.

Location	Original sample	Adjusted sample[a]	Number of respondents	Response rate
SNM (East)[b]	250	241	218	90.5%
SNM (West)[c]	250	219	175	79.9%
Totals	500	460	393	85.4%

[a]Adjusted sample = original sample - undeliverables, departures and recent arrivals.
[b]Saguaro National Monument, Rincon Mountain District.
[c]Saguaro National Monument, Tucson Mountain District.

Table 2. Numbers of households that feed wild birds and other wildlife.

Location	Feed wild birds	Feed other wildlife
SNM (East)[a]	134 (61.1%)	71 (34.8%)
SNM (West)[b]	93 (54.7%)	45 (27.1%)
Totals	227 (59.9%)	116 (31.4%)

[a]Saguaro National Monument, Rincon Mountain District.
[b]Saguaro National Monument, Tucson Mountain District.

Table 3. Numbers of households that feed specific types of large wild mammals.

Location	Mule Deer	Collared Peccary	Coyote
SNM (East)[a]	11 (5.0%)	39 (17.9%)	24 (11.0%)
SNM (West)[b]	3 (1.7%)	8 (4.6%)	19 (10.9%)
Totals	14 (3.6%)	47 (12.0%)	43 (10.9%)

[a]Saguaro National Monument, Rincon Mountain District.
[b]Saguaro National Monument, Tucson Mountain District.

Table 4. Importance of being close to Saguaro National Monument in decision of where to live.

Location	Primary reason	Important reason	Slightly important	Not important
SNM (East)[a]	60 (28.8%)	98 (47.1%)	17 (8.2%)	33 (15.9%)
SNM (West)[b]	33 (19.3%)	75 (43.9%)	16 (9.4%)	47 (27.5%)
Totals	93 (24.5%)	173 (45.6%)	33 (8.7%)	80 (21.1%)

[a]Saguaro National Monument, Rincon Mountain District.
[b]Saguaro National Monument, Tucson Mountain District.

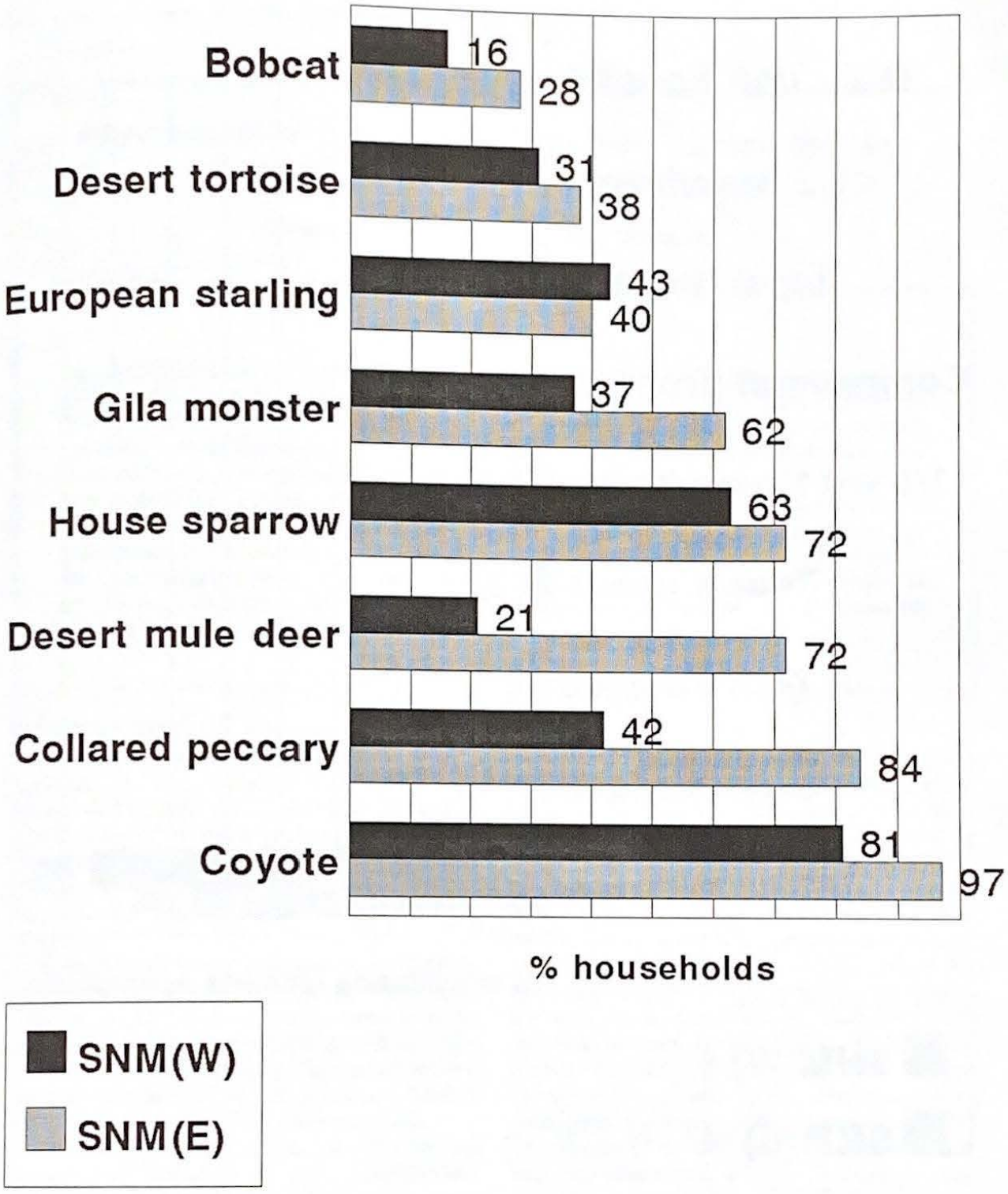


Fig. 1. Percentage of households within 1 mi of Saguaro National Monument that observe selected species on their property at least once/year.

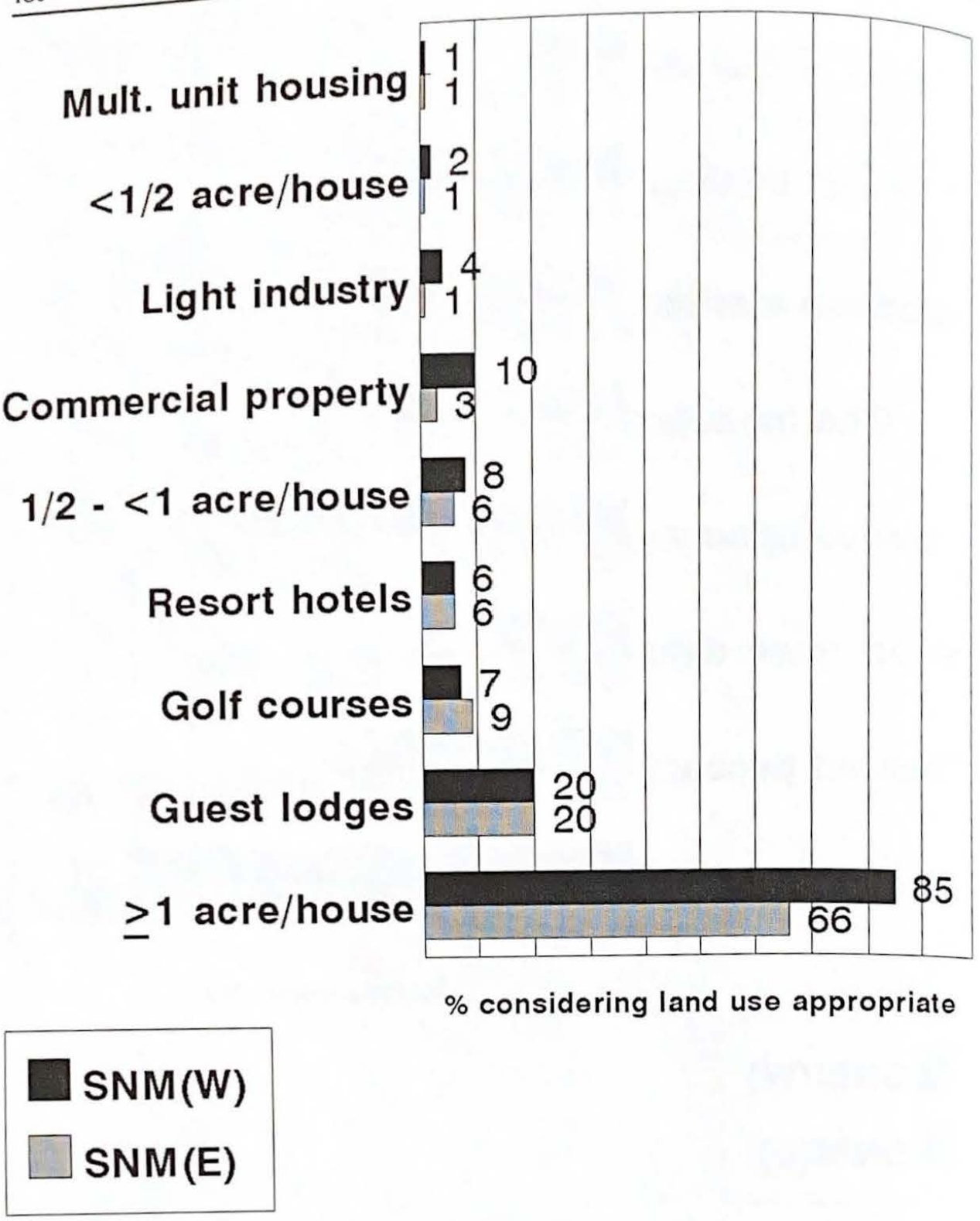


Fig. 2. Percentage of households within 1 mi of Saguaro National Monument that consider various land uses appropriate in their neighborhood.

Movements of Desert Mule Deer and Collared Peccary in Saguaro National Monument

Elizabeth S. Bellantoni and Paul R. Krausman

ABSTRACT

We studied movements of 10 desert mule deer (*Odocoileus hemionus crooki*) and five groups of collared peccary (*Dicotyles tajacu*) in the Rincon Mountain District of Saguaro National Monument (SNM) from February 1988 through December 1989. Movements of desert mule deer were closely associated with the distribution of free-standing water during the driest seasons of the year. Deer responded to losses of ephemeral water sources in SNM by leaving the monument to obtain water. Four of five collared peccary herds frequented urban areas and supplemented their natural diet by visiting some homes and/or restaurants on a daily or twice daily basis. The addition of water and supplemental food sources was a deliberate effort by homeowners to attract wildife onto their property. The current pattern of habitat islands interspersed with low density housing (<1 house/2-4 ha or <1 house/5-10 a) serves as an effective and highly desirable buffer zone between the monument and the more heavily developed urban areas 3.2 km (2 mi) to the west.

INTRODUCTION

Boundaries of national parks and protected areas are usually politically defined. In a survey conducted by the National Parks and Conservation Association (1979), urban development was cited as the primary threat facing national parks in the United States. Development on lands adjacent to national parks may irreversibly damage the natural resources of these areas.

In Arizona, the Tucson metropolitan area is developing and growing rapidly and formerly undeveloped lands are being converted to urban environments. Major changes in land use patterns occur at the edges of the city. Urban development is particularly evident along the boundaries of the Rincon Mountain District (RMD) of Saguaro National Monument (SNM).

When the RMD was established in 1933, the land adjacent to the monument was undeveloped (National Park Service 1986) and served as available wildlife habitat. As urbanization encroaches on its borders, the amount of wildlife habitat outside the monument is rapidly disappearing, travel corridors providing access to and from SNM are being eliminated, and fauna outside the monument is diminishing. Urbanization is also fragmenting the remaining wildlife habitat.

Habitat fragmentation can be a serious threat to the survival of large mammal populations because of their needs for space (e.g., isolation from humans and their pets) and habitat resources (e.g., water, forage, cover). Wildlife in isolated habitats are vulnerable for various reasons (e.g., loss of critical resources, dispersal corridors, habitat heterogeneity, genetic variability) (Wilcove et al. 1986). Wildlife movement patterns may also be affected by habitat fragmentation (Janzen 1986; Wilcove et al. 1986). Distribution of wildlife may be limited by roads, trails, and other human activity. Development occurring adjacent to SNM may cause alteration in movement and activity patterns of those animals that range along the boundaries of the monument.

The effects of urban development on desert mule deer (*Odocoileus hemionus crooki*) and collared peccary (*Dicotyles tajacu*) populations in the Southwest have not been studied in detail. Both species attract a high level of public interest and concern among sportsmen and wildlife-oriented recreationists. These animals range beyond the boundaries of SNM, where urbanization is causing loss of habitat for both species.

Our objectives in this study were to (1) describe movements of desert mule deer and collared peccary along the boundaries of the RMD of SNM and adjacent private lands; (2) determine habitat use by desert mule deer and collared peccary relative to sex, season, activity, water availability, and human disturbance; and (3) compare observations of home range and habitat use by desert mule deer and collared peccary in an urban environment to similar data reported for these species in other southwestern habitats. These data will provide information that can be used by city planners, developers and park managers to make informed decisions regarding urban growth and its effect on desert ungulates (hoofed mammals).

STUDY AREA

The study area encompassed the RMD of SNM at elevations below 1,219 m (4,000 ft) and west of Universal Transverse Mercator (UTM) latitudinal component 5,300,000 m (Fig. 1). The northern and western borders of the study area are major county roadways located 1.6 km (1 mi) north (Speedway Boulevard) and 3.2 km (2 mi) west (Houghton Road) of the northwestern and western boundaries of SNM. Rincon Mountain District is located on the eastern edge of Tucson and is bordered on the eastern and portions of the northern and southern sides by Coronado National Forest. Residential developments border sections of the western, southwestern, and northwestern boundaries of the monument.

Tucson has an arid climate with a mean annual precipitation of 28 cm (11 in.) (Sellers and Hill 1974). The majority of rainfall occurs in late summer as geographically isolated thunderstorms and in winter as widespread, regional storms. Although data for 1988 did not differ significantly from the yearly average, 1989 was the fourth driest year on record with 16.5 cm (6.5 in.) of precipitation (J. Mazur, Natl. Weather Serv., Tucson, Ariz., pers. comm.).

With the exception of a small water catchment located behind the visitor center, perennial water sources on the desert floor of SNM are limited to occasional seeps, springs, and tanks. Most ephemeral water sources disappear by late spring. The occurrence of free-standing water within SNM increases with elevation in the Rincon Mountains. Outside the monument, water is readily available year-round. The majority of water sources are located on residential property and are placed there intentionally for the benefit of wildlife.

METHODS

We captured 10 desert mule deer (5 males and 5 females) in the RMD of SNM during February and March 1988. Deer were taken with a drive net or net-gun (Krausman et al. 1985) and immobilized with xylazine hydrochloride (HCl) and ketamine HCl administered intramuscularly (DelGuidice et al. 1989). Immobilizing drugs were reversed with tolazoline HCl administered intravenously. We fitted deer with color-coded radio collars prior to release. Between February 1988 and January 1989, we captured five collared peccary (1/herd) with a net-gun or box trap. Collared peccary were handled using methods similar to those used for mule deer.

Between February 1988 and September 1989, we used radio telemetry and obtained visual observations of each collared animal every 7-10 days. We obtained additional telemetry locations every 7-14 days from fixed-wing aircraft (Cessna 182) between September and December 1989. We made observations from the ground primarily during diurnal hours, generally early morning and evening, when animals were most active. Additional data were collected by several homeowners, documenting presence and frequency of collared animals on their property.

We used the harmonic mean (Dixon and Chapman 1980) and minimum convex polygon (MCP) (Southwood 1978) methods to calculate seasonal home-range size. For the harmonic mean method, we used a 75% isopleth (that represented the area where an animal spent 75% of its time within its home range) to identify core areas of use and compared this information to similar data reported for other studies. Desert mule deer data were analyzed seasonally by sex. Only deer located ≥ 9 or more times/season were used in the analysis. Seasonal categories were based

on temperature and precipitation patterns as described by Ordway and Krausman (1986). Because preliminary data analysis indicated no seasonal differences in home-range use, we analyzed collared peccary data on an annual basis by herd. We present minimum convex polygon estimates (area defined by the outermost locations recorded for an animal within its home range) for comparison to other studies.

For mule deer data, we transformed the harmonic mean and MCP estimates to their natural logarithm and achieved homogeneity of variances. Analysis of variance was used to test for differences in these estimates between sexes and among seasons. For MCP estimates, we examined differences in home-range size among seasons using Student-Newman-Keuls (SNK) multiple range test (Norusis 1988:B-159). We tested collared peccary data for differences in home-range size between years and herd classes (i.e., herds using urban vs. non-urban environments) using the Mann-Whitney test (Norusis 1988:B-177).

RESULTS

Desert Mule Deer

We located desert mule deer 596 times during the study. Analysis of variance indicated no significant difference ($P > 0.05$) for mean home-range size between sexes and among seasons for the harmonic mean estimates (Table 1). A significant difference ($P < 0.05$) was found for MCP estimates among seasons, although the difference between sexes was not significant. Closer examination of the MCP estimates using SNK multiple range tests indicated a significant difference ($P < 0.05$) in mean home-range size during late summer for both sexes (M = 2.8 km^2, F = 4.1 km^2). During the late summer fawning period, females increased the size of their home ranges. Females moved to higher elevations during late summer, with three females using the same general fawning area. Fawning sites generally ranged between 150 and 300 m above the desert floor and were located close to perennial water. Males also enlarged their home ranges and moved to higher elevations during late summer.

Individual variation is apparent in deer use of areas outside of SNM. Although some deer (e.g., no. 442) used available habitat outside the monument all year (Fig. 2), others (e.g., no. 341) did not move out of the monument until ephemeral water sources began to disappear in late spring (Fig. 3). Other deer remained within SNM by day, often bedded in the vicinity of the boundary. Because the majority of deer sightings on residential property occurred between dusk and dawn (B. Burkholder, homeowner, unpubl. data), it is likely that some radio-collared animals moved out of SNM only during this time.

Home range increased for four of five males during the breeding season (Dec-Jan). Two males that had never been observed out of the monument previously were seen with females during this period in residential areas. Both males returned to the monument at the end of the breeding season.

Collared Peccary

We located collared peccary herds 277 times during the study. Mean home-range size between herd classes (Urban = 1.03 km^2, Non-urban = 1.00 km^2) and years for collared peccary was similar ($P > 0.05$) (Table 2).

All radio-collared urban peccaries weighed between 28-30 kg (60-65 lbs) when caught. Detailed records kept by several homeowners who provided supplemental food sources for collared peccaries indicated that these animals have become readily habituated to urban environments and have been visiting some homes and restaurants on a daily basis for years. Four herds with radio-collared animals (nos. 460, 672, 801, 921) (Fig. 4) frequented urban areas and supplemented their natural diet by visiting some homes and/or restaurants on a daily or twice daily basis. Food items most often consisted of table scraps, bird seed, bread, and dog food. A fifth herd with a radio-collared animal (no. 560), located within the interior of the Cactus Forest Loop Drive, did not use urban areas. This herd exhibited movements and habitat use typical of a free-ranging wild herd.

One urban peccary herd (no. 801) had the smallest home-range size of any herd reported in the literature (Minnamon 1962; Schweinsburg 1971; Bigler 1974; Supplee 1981; Day 1985). This herd, comprised of two animals, lived inside the SNM boundary within 200 m (650 ft) of a residential area. The radio-collared female, well-known to neighborhood residents for >4 years, had become so accustomed to humans that she could be hand fed.

Another radio-collared individual from an urban herd (no. 672) had the farthest dispersal movement

of any collared peccary reported in the literature. In early March of 1989, this adult female moved into a densely populated area (22nd Street and Prudence Road) over 8.0 km (5 mi) west of the SNM boundary. Although she and an adult male, presumably from the same herd, were later captured and returned to the monument, the radio-collared animal moved again in mid-July. She was relocated over 16.0 km (10 mi) southwest of the SNM boundary (I-10 and Valencia Road), again in the company of an adult male. In this new habitat she was repeatedly observed at a recreational vehicle campground where she was again supplementing her diet with human-provided foods.

DISCUSSION

Desert Mule Deer

Because females returned to the desert floor after their fawns were weaned or lost, it is likely that water availability was not the primary reason for the shift to higher elevations. Possible explanations for this shift in habitat use may be predator avoidance, sexual selection (Wilson 1975; King and Smith 1980), or the result of increased nutritional demands brought on by pregnancy (Short 1981; Bowyer 1991).

The larger home-range size associated with desert mule deer males during this same period corresponds to the start of the summer rains. Males that had moved out of the monument in search of water during the early summer return to the park at this time as water sources become more abundant (Fig. 3).

During the drought in 1989, deer tended to move earlier (e.g., April-May vs. June) and remain longer in habitats outside SNM, as compared to 1988 when rainfall patterns were considered normal. In most cases, deer returned to the same residential areas where they had prior knowledge of dependable water sources.

Of the 10 radio-collared deer, eight were observed out of the monument at some time during the study. A ninth animal, although not observed out of the monument, was seen on several occasions within several hundred meters of the boundary, suggesting that she may have used areas outside of the monument. We do not know if a tenth animal, which lost its collar midway through the study, used habitats outside of the monument.

Although collared peccary are capable of subsisting for long periods without water (Minnamon 1962), desert mule deer appear to be behaviorally dependent on the presence of free-standing water (Wood et al. 1970; Hervert and Krausman 1986; Rautenstrauch and Krausman 1989). The sizes of seasonal home ranges of mule deer at SNM were small compared to home-range sizes reported for desert mule deer populations in western Arizona (Krausman 1985; Rautenstrauch and Krausman 1989). Rautenstrauch and Krausman (1989) reported that desert mule deer migrated to free-standing water during the driest period of summer. Hervert and Krausman (1986) demonstrated that when denied access to water, desert mule deer females searched for it outside their known home ranges. Similar movements in response to water loss have been reported by Clark (1953), Hanson and McCulloch (1955), Johnson (1962), Wood et al. (1970), and Rogers et al. (1978). The same general movement patterns are evident among desert mule deer at SNM.

Movements of desert mule deer are closely associated with the distribution of free-standing water during the driest seasons of the year. During years of normal precipitation, these dry periods occur most notably in early summer and, to a lesser extent, winter, during the breeding season. Deer responded to losses of ephemeral water sources within their home ranges by leaving the monument to search for available water. In the majority of instances, water sources represented a deliberate effort by homeowners to attract wildlife onto their property.

Collared Peccary

Differences in habitat use between urban and non-urban peccaries illustrate the highly adaptable nature of these animals. The frequency with which urban herds supplemented their diet with human-provided foods indicates how readily these animals have habituated to urban environments. Urban herds all exhibited similar behavior patterns. During the day, these animals bedded primarily in washes within the monument. Although urban peccaries were known to forage on natural food sources, they were inclined to travel to residential areas during evening hours, frequenting locations where they knew they would be fed.

Day (1985) reported average live weights of adult peccaries on the Three Bar Wildlife Area in south-

eastern Arizona ranging from 18-27 kg (40-60 lbs). The effects of supplemental food sources provided by humans on the nutritional status or reproductive fitness of the collared peccary are unknown. However, peccaries in this study were generally heavier than those reported elsewhere (Minnamon 1962; Schweinsburg 1971; Bigler 1974; Supplee 1981; Day 1985), most likely the result of supplemental feeding.

Supplee (1981) noted that when a collared peccary herd was reduced to <4 animals, it decreased the size of its home range. At SNM, the extremely small home range exhibited by a herd comprised of two animals appears to be a function of both herd size and resource availability. This herd, perhaps more than any other in the study, developed an apparent dependence on human-provided foods. Because of the reliability and frequency with which several homeowners provided supplemental food sources, coupled with the proximity of this herd's home-range core (75% isopleth) to housing, this pair did not have to travel far to obtain human-provided foods.

Observations by Day (1977) and Supplee (1981) indicate that dispersal and formation of new herds is frequently initiated by adult females belonging to a subherd. This small herd unit also typically consists of adult males and juveniles that form the nucleus of the new herd. In our study, the extraordinary distance travelled by an adult female from an urban herd may be the result of density pressures or competition for mates (Bissonette 1976), or stimulation from the availability of suitable habitat (Supplee 1981). Because housing density increases dramatically 3.2 km (2 mi) west of the monument resulting in an associated decrease in available wildlife habitat, this animal may have been forced to search much farther than expected before finding suitable habitat to establish a territory.

MANAGEMENT IMPLICATIONS

Wildlife management agencies throughout the Southwest commonly develop water sources for wildlife. By providing deer with unlimited access to free-standing water during the driest times of the year, homeowners are, in effect, actively managing the SNM deer population. By providing deer with a resource that otherwise would be limiting during the early summer and, to a lesser extent, the winter months, homeowners encourage the high numbers of deer presently found on the desert floor during these seasons.

Hervert and Krausman (1986) demonstrated that the elimination of free-standing water within the home-range core of desert mule deer females caused these animals to seek available water in less desirable habitats. By removing water sources from outside SNM, or increasing the housing density such that the increased level of human disturbance precludes deer use of private lands, movements of monument deer to less desirable habitats (e.g., areas possessing lower-quality forage and lacking critical resources) are also likely to occur. Forcing animals to inhabit suboptimal habitats may increase their susceptibility to predation, lower their nutritional planes, and decrease their reproductive fitness.

Preserving the remaining available wildlife habitat adjacent to the boundaries of SNM will be advantageous to other desert fauna and will also aid in maintaining the integrity of SNM resources. Habitat islands in strategic locations (e.g., a 12.6 ha [31 a] travel corridor, currently for sale, located on the monument boundary between Old Spanish Trail and the southern end of Freeman Road) improve conservation and enhancement of the wildlife resources of protected areas (Harris 1984). As development continues to occur along SNM boundaries, a more pronounced interface between wildlife refuge and urban environment will result. This process will eventually lead to a reduction in the effective size of SNM as wildlife habitat.

Results of our study demonstrate the need for desert mule deer to obtain critical resources on lands outside SNM. The current pattern of habitat islands interspersed with low density housing (<1 house/2-4 ha or <1 house/5-10 a) (A. Goldsmith, pers. comm.) serves as an effective and highly desirable buffer zone between the monument and the more heavily developed urban areas 3.2 km (2 mi) west of the park. Although several radio-collared animals were observed close (<300 m or <1,000 ft) to these heavily developed areas, neither deer nor collared peccary were observed in these habitats.

Deliberate efforts to attract wildlife onto private properties indicate the high value that homeowners living adjacent to SNM place on wildlife-viewing recreation. Some residents have expended considerable effort and expense to provide elaborate watering

devices and other habitat improvements for wildlife. Increased housing densities accompanied by an associated increase in human numbers will result in a degradation of this form of recreation for homeowners. Increased wildlife depredations on vegetable gardens, flower beds, and ornamental plantings will also result. An active coordinated effort should be made by city and county planners, park managers, and developers to take actions that will enhance the congruence of the political and biological boundaries of the monument to minimize potential losses on the wildlife resources of SNM.

ACKNOWLEDGMENTS

We thank the National Park Service and the city of Tucson for funding this study. We also thank the many neighbors of Saguaro National Monument that provided information on animal movements and habitat use.

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Table 1. Harmonic mean and minimum convex polygon (MCP) estimates of mean seasonal home-range size (km^2) of desert mule deer in the Rincon Mountain District of Saguaro National Monument, Tucson, Arizona, 1988-89.

	Season[a]															
	Spring				Early summer				Late summer				Winter			
	$\bar{x}$	SE	No. deer	No. locations	$\bar{x}$	SE	No. deer	No. locations	$\bar{x}$	SE	No. deer	No. locations	$\bar{x}$	SE	No. deer	No. locations
Females																
75% isopleth[b]	0.5	0.3	3	32	0.6	0.2	7	90	0.9	0.1	7	100	0.2	0.1	3	33
MCP[c]	3.3	1.4	3	32	2.0	0.5	7	90	4.1	0.6	7	100	2.1	0.7	3	33
Males																
75% isopleth[b]	0.4	0.1	5	63	0.3	0.1	6	72	0.6	0.2	9	111	0.7	0.3	5	57
MCP[c]	2.3	0.4	5	63	1.6	0.4	6	72	2.8	0.4	9	111	3.9	1.0	5	57

[a]Spring = 1 Feb-30 Apr, early summer = 1 May-Jul 15, late summer = 16 Jul-31 Oct, and winter = 1 Nov-31 Jan.
[b]Area where an animal spent 75% of its time within its home range.
[c]Area defined by the outermost locations recorded for an animal within its home range.

Table 2. Harmonic mean and minimum convex polygon (MCP) estimates of annual home-range size (km^2) of collared peccary in the Rincon Mountain District of Saguaro National Monument, Tucson, Arizona, 1988-89.

	460[a]	No. home ranges	560[a]	No. home ranges	672[a,b]	No. home ranges	801[a]	No. home ranges	921[a,b]	No. home ranges
1988[c]										
75% isopleth[d]	0.3	30	0.3	33			0.05	39		
MCP[e]	1.0	30	0.9	33			0.5	39		
1989[c]										
75% isopleth[d]	0.2	34	0.4	39	0.7	26	0.04	53	0.3	45
					(0.2)[f]	(21)				
MCP[e]	0.8	34	1.1	39	2.3	26	0.4	53	1.2	45
					(1.3)[f]	(21)				

[a]Herd no.
[b]Radio-collared in Jan 1989.
[c]Based on seasonal year (1 Feb-31 Jan).
[d]Area where a herd spent 75% of its time within its home range.
[e]Area defined by the outermost locations recorded for a herd within its home range.
[f]Collared animal left herd in mid-July; home range calculated for collared animal after leaving herd.

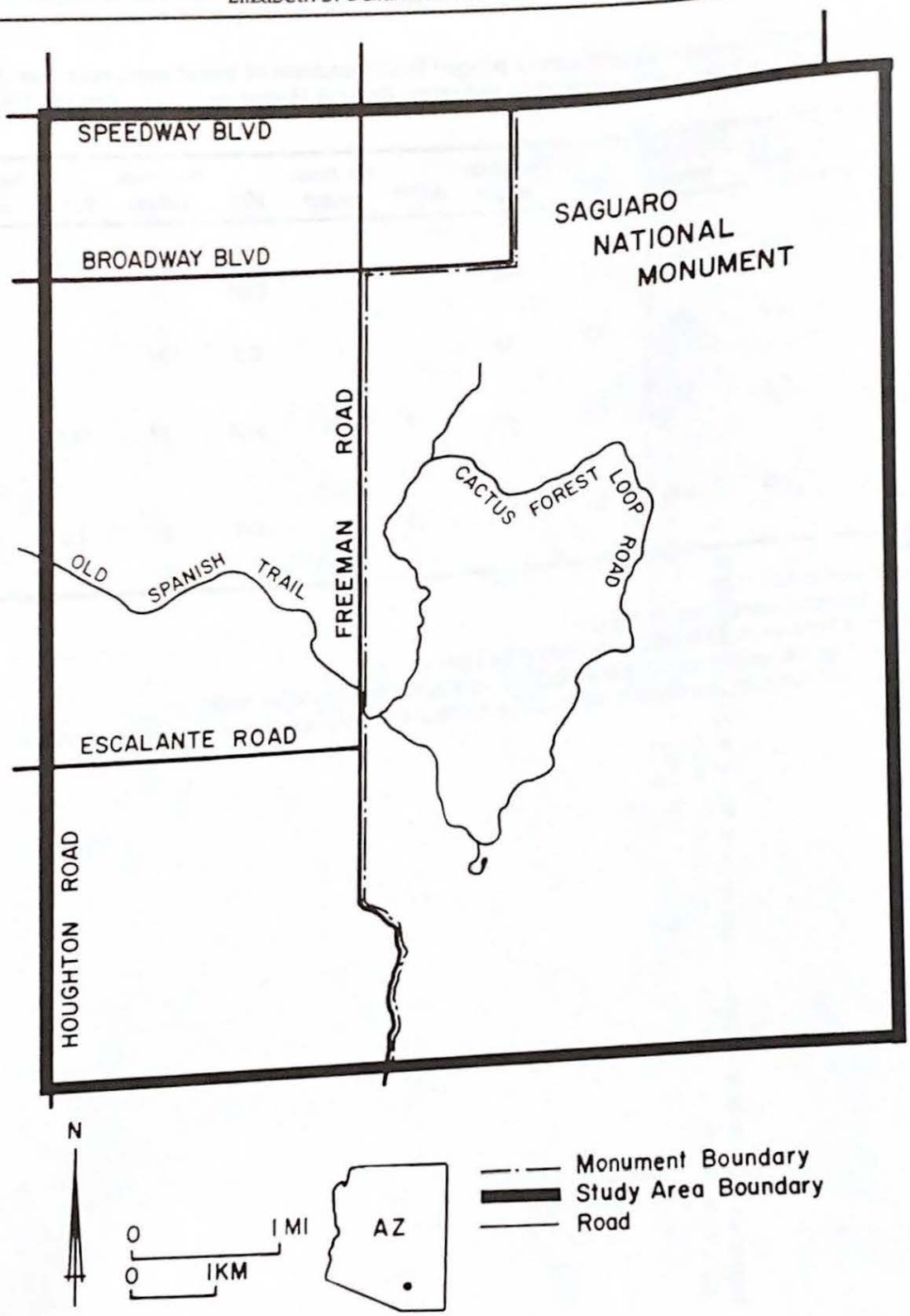


Fig. 1. Location of study area in the Rincon Mountain District, Saguaro National Monument, Tucson, Arizona.

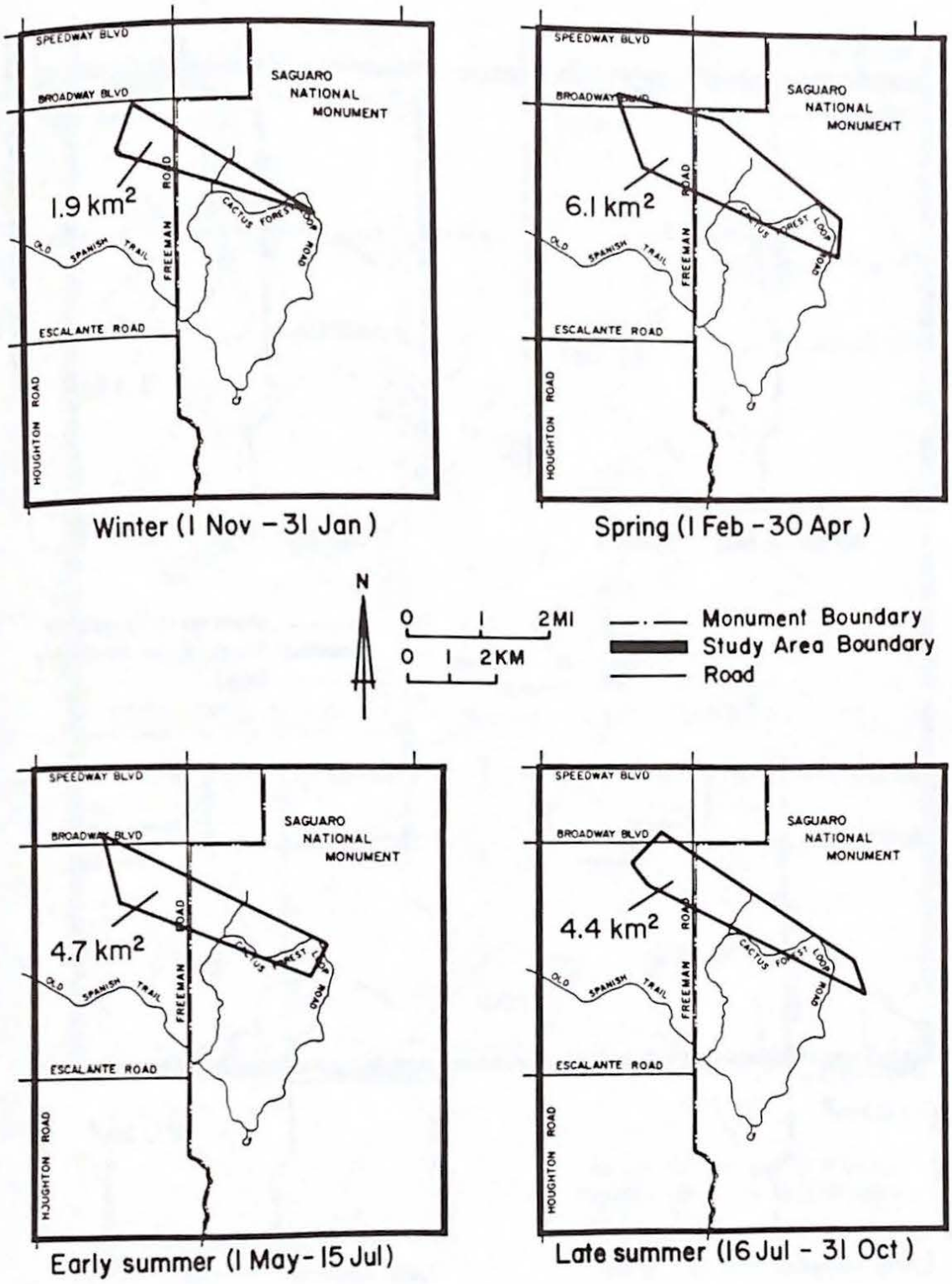


Fig. 2. Minimum convex polygon (MCP) estimates of seasonal home-range size (km^2) for a desert mule deer female (no. 442), Saguaro National Monument, Tucson, Arizona, winter 1988-late summer 1989.

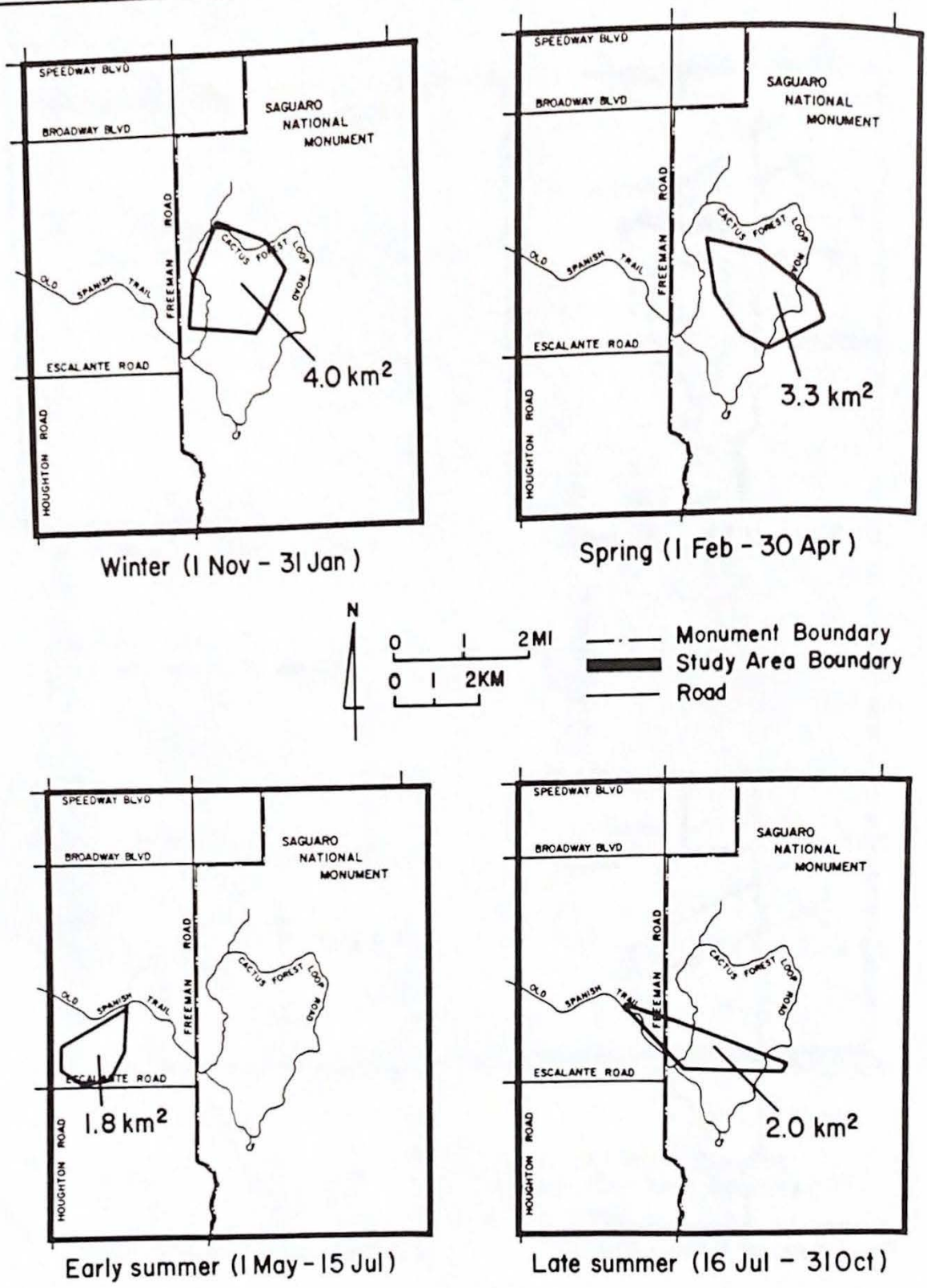


Fig. 3. Minimum convex polygon (MCP) estimates of seasonal home-range size (km^2) for a desert mule deer male (no. 341), Saguaro National Monument, Tucson, Arizona, winter 1988-late summer 1989.

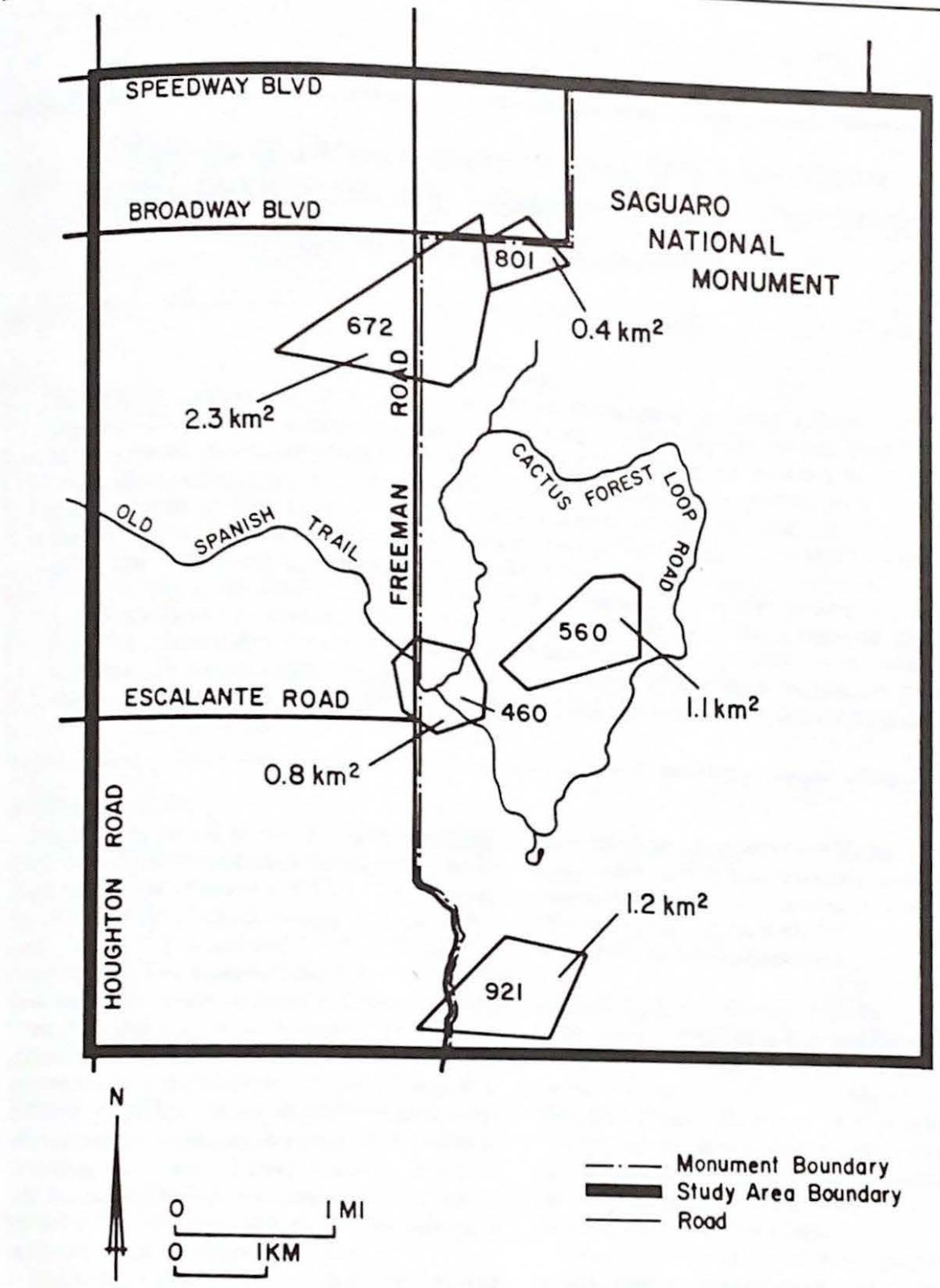


Fig. 4. Minimum convex polygon (MCP) estimates of annual home-range size (km^2) for five collared peccary herds, Saguaro National Monument, Tucson, Arizona, 1988-89.

Impacts of Exotic Cavity-Nesting Birds on Native Cavity-Nesting Birds in Saguaro National Monument

Brent D. Bibles and R. William Mannan

ABSTRACT

We surveyed cavity-nesting birds on Saguaro National Monument to determine whether a relationship existed between the abundance of native and exotic cavity-nesting birds. We also plugged cavities in saguaros (*Carnegiea gigantea*) off monument lands to examine the responses of native and exotic cavity-nesting birds to a limited number of nest sites. Exotic cavity-nesting birds were not observed on the monument. We also failed to observe competition between exotic and native cavity-nesting birds in areas where cavities were limited artificially. The abundance of cavities for nesting, and temporal differences in breeding among species, were reasons that competition for nest sites did not occur. Our results indicate that exotic cavity-nesting birds are not likely to compete with native species; therefore, the presence of exotic cavity-nesting birds on the monument is largely an aesthetic issue. The National Park Service, however, mandates that disruptive exotic species be removed from park lands. To prevent exotic cavity-nesting birds from invading the monument, housing density near the monument should be limited, and native landscaping should be required for adjacent housing.

INTRODUCTION

This study is one of several designed to identify the effects of urbanization on animal populations in Saguaro National Monument (SNM). We examined the effects of exotic cavity-nesting birds on native cavity-nesting birds in and near SNM. We focused on cavity-nesting birds for several reasons: (1) the European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*) nest in saguaro (*Carnegiea gigantea*) cavities and are common exotic species associated with development in the Tucson area (Mills et al. 1989); (2) the availability of cavities often is thought to limit the breeding density of cavity-nesting birds; and (3) competition for nest sites with European starlings has been partly responsible for the decline of native species in other regions of the United States (Yoakum et al. 1980).

We had three objectives: (1) evaluate the influence of exotic cavity-nesting birds on native cavity-nesting birds on SNM, (2) determine how the influence of exotic cavity-nesting birds changes as densities of the exotics increase, and (3) determine if European starlings are capable of excluding native cavity-nesting birds from cavities in saguaro cacti.

STUDY AREA AND METHODS

We conducted the study during 1988 and 1989 on SNM, the University of Arizona Tumamoc Hill Desert Laboratory, and an area adjacent to Arthur Pack Golf Course. All sites were in or near Tucson, Arizona, and all were areas of relatively undisturbed, desert vegetation in the paloverde (*Cercidium microphyllum*)-cacti-mixed scrub series of the Sonoran Desert (Turner and Brown 1982).

From 12 May to 12 July 1988, we surveyed cavity-nesting birds on eight transects with Emlen's (1971) line transect method. Three transects were near Avra

Valley on the Tucson Mountain District (TMD) of SNM, and three were located on the northwestern corner of the Rincon Mountain District (RMD) of SNM. The two remaining transects were located on the Tumamoc Hill Desert Laboratory. Transects began at the boundary of the monument or laboratory and extended 500 m into the interior of the properties. Transects were established to ascertain how far into the interior of the monument exotic cavity-nesting birds were nesting, and whether a relationship existed between the abundances of exotic and native cavity-nesting birds.

We also conducted an experiment to determine whether exotic cavity-nesting birds compete with native cavity-nesting birds for nest sites in an area where cavities are limited. Steps in this experiment were: (1) survey cavity-nesting birds during the 1988 breeding season in plots where both native and exotic species were nesting, (2) if necessary, reduce the availability of cavities after the breeding season to induce a shortage of nest sites the following year, and (3) resurvey the plots in 1989 to ascertain whether exotic or native species used the available cavities.

We established six 10-ha plots (316 x 316 m) in 1988. All plots were positioned to contain potential nest sites for cavity-nesting birds. Plots selected contained at least 21 saguaros with what appeared to be cavities (range = 21-37 saguaros). Two plots were adjacent to Arthur Pack Golf Course (Arthur Pack North and Arthur Pack South plots), and two were at the Tumamoc Hill Desert Laboratory (Tumamoc Hill North and Tumamoc Hill South plots). Plots not on SNM (hereafter called experimental plots) were selected because they were adjacent to potential foraging areas for European starlings and house sparrows, and thus were likely to support nests of both native and exotic cavity-nesting birds. The four experimental plots were bordered by housing subdivisions on one side. The two plots near Arthur Pack Golf Course also were bordered by the golf course. The remaining two plots (exclosure and wash plots) were in the RMD of SNM, on the north end of the Cactus Forest Loop Drive. These plots served as controls in the experiment.

We estimated the density of cavity-nesting birds on all plots with the nest location method (Enemar et al. 1976). We searched each plot until satisfied that all nests were located, usually making 4-9 diurnal visits, and 2-7 nocturnal visits. Nocturnal visits were made to locate nests of elf owls (*Micrathene whitneyi*) and screech owls (*Otus kennicottii*). Visits were made between 18 April and 14 July 1988, and 27 March and 14 July 1989. Tape-recorded calls were used to elicit territorial responses from elf owls and western screech owls on initial nocturnal visits. Nest cavities of these species were then located during mid- to late June by listening for begging calls of nestlings.

We measured the height and classified the size of the openings (see Goad and Mannan 1987) of all cavities on the experimental plots, and of nest cavities on control plots. We also measured the heights of the saguaros that supported cavities. We visually inspected all apparent cavities to distinguish real cavities from unfinished holes. An extendible ladder, 7.6 m in length, was used to climb saguaro cacti. Cavities not within reach of the ladder were "inspected" with a telescoping pole and plummet.

In 1989, we attempted to limit the availability of cavities on experimental plots by plugging those that were unused by birds or those used by exotic birds during 1988. We plugged cavities in January and February 1989 with rubber test-tube stoppers. Cavities excavated during the 1989 breeding season were not plugged.

RESULTS

We observed no European starlings or house sparrows on SNM during any of the surveys (on either transects or plots) or other field work. We did, however, see European starlings near SNM on two occasions.

Magnitude of changes in numbers of nests between years on experimental and control plots was similar for all species, and most of the differences in abundance of nests between years were relatively small (Table 1). Of the possible changes on experimental plots, 39% involved no change, 46% involved a change of ±1 nest, 11% involved ±2 nests, and 4% involved ±>2 nests. On the control plots, 20% of possible changes involved no change, 60% involved a change of ±1 nest, and 20% involved ±2 nests. The direction of changes that did occur were inconsistent within species among experimental plots. For example, five of seven species increased on some plots and decreased on others.

Species did not significantly differ in their choice of nest cavity height or height of the nest saguaro. Opening size of nest cavities used by European starlings was smaller than that used by northern flickers (*Colaptes auratus*) and ash-throated flycatchers (*Myiarchus cinerascens*) (Table 2). The size of the opening of cavities used by house sparrows did not differ from that used by native, cavity-nesting species.

DISCUSSION

Exotic cavity-nesting birds probably do not, at present, influence native cavity-nesting birds on SNM because exotics are not nesting on SNM. We were unable to evaluate how the influence of exotic cavity-nesting birds on native cavity-nesting birds changes as the density of the exotics increases, because exotics were not present on SNM.

We failed to demonstrate measurable competition between exotic and native cavity-nesting birds by plugging nest holes. We believe competition for nest sites was reduced in two ways. First, woodpeckers excavated at least 12 new cavities on the experimental plots in 1989. Second, use of cavities was being partitioned temporally by resident and migratory cavity-nesting birds, and according to opening size by northern flickers, ash-throated flycatchers, and European starlings. The woodpeckers and exotic species (i.e., resident, cavity-nesting birds) generally nested from March through May, whereas all but one of the native, secondary, cavity-nesting species (i.e., migratory cavity-nesting birds) nested from late May through July. We found six cavities (15% of those found) that were used as nests by woodpeckers or exotic species early in the breeding season, and then used again by migratory species later in the breeding season. Because European starlings and house sparrows did not evolve with native species, the "partitioning" of nest cavities through time is coincidental, and might not be effective in reducing competition under all conditions. For example, if conditions were appropriate for European starlings to produce a second brood, their breeding season would overlap that of the native, secondary, cavity-nesting birds, and competition for nest holes could increase.

The elf owl was the only native secondary cavity-nesting bird with a breeding season that overlapped those of the starling and house sparrow. Elf owls nested on only two of the experimental plots; therefore, it was difficult to evaluate how and if they competed for nest sites with exotic species. However, the abundance of elf owls where they did occur, either increased or remained the same after potential nest holes were plugged.

Our data indicated that no species was consistently lower in abundance after the holes were plugged than before. It was clear, however, that house sparrows were far less abundant on Arthur Pack South in 1989 than in 1988. All but one of the house sparrow nests on this plot ($n = 8$) in 1988 were within 50 m of a housing development. In 1989, only one of the available holes within the 50-m zone was occupied by house sparrows; other holes within this zone were used by European starlings or native cavity-nesting birds. Several holes outside the 50-m zone were available, but were not used by house sparrows. We speculate that competition prevented house sparrows from using most of the holes close to the housing development, and that empty holes farther from the development were too far from sources of food to be suitable.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

The current levels and kinds of development near SNM support relatively few exotic, cavity-nesting birds. Our data suggest that even if European starlings and house sparrows were present on SNM, they would not likely exclude native species of cavity-nesting birds. The ability of woodpeckers to excavate their own cavities and to defend them (we observed on numerous occasions that woodpeckers were dominant over starlings at nest sites) probably will allow them to coexist with exotic species of birds, assuming that an adequate number of saguaros exists to provide substrates for cavity excavation. Most native, secondary cavity-nesting species are likely to be able to coexist with European starlings and house sparrows because they nest at different times. It should be noted, however, that nesting competition could occur between these species if European starlings and house sparrows produce a second brood (Kessel 1957).

The issue of exotic species of birds on SNM is primarily an aesthetic one—is it desirable and pleasing to have exotic species of birds on SNM? The answer to this question apparently is no, based on the National Park Service mandate to remove disruptive exotic

species from park lands. We, therefore, recommend that if undisturbed land near SNM is developed, sources of food, water, and cover for European starlings and house sparrows be minimized. This is particularly important along the boundary nearest the monument headquarters because the buildings, picnic grounds, human activities, and other developments associated with the headquarters area already provide some sources of food, and potentially, nest and roost sites for exotic species of birds. We propose the following guidelines:

1. Landscape all developments near the monument with native species of plants. It is especially important to maintain saguaro cacti (as potential nest sites), and avoid planting grass lawns (e.g., golf courses) near the monument.
2. Avoid creating sources of open water near the monument.
3. Limit the property that supports horses or other livestock near the monument so that auxiliary sources of food (e.g., grain) are reduced (Feare 1984).
4. Limit the density of houses near the monument. As the density of houses increases, so does the likelihood that house sparrows will be present (Stenberg 1988; Mills et al. 1989).
5. If grass lawns, open sources of water, additional "horse property," or dense housing are developed near SNM, then house sparrows will likely nest on the monument within 50 m of housing developments, and starlings will nest on the monument within 1 to 2 km of the boundary. These "zones of occurrence" were developed on the basis of four pieces of evidence: (1) all but one of the house sparrow nests on our experimental plots were within 50 m of a housing development; (2) we documented nesting of European starlings up to 300 m from a housing subdivision on an experimental plot; (3) we observed starlings flying at least 800 m from sources of food to nests at Arthur Pack Golf Course, and from "horse property" near SNM; and (4) Kerpez (1986) found European starlings nesting up to 4 km from agriculture. The distance a bird will travel between a source of food and a nest probably depends upon the richness of the food source and on how many nest sites exist around the source. For example, some European starlings would likely nest beyond 1 km of the monument boundary if a rich foraging habitat, such as a golf course, were built next to the boundary, and if few nest sites were present in the immediate vicinity around the course.

Given these predicted "zones of occurrence," we recommend that developments that provide food, water, or cover for European starlings and house sparrows be restricted to beyond 2 km of the boundary of SNM. These restrictions are especially important near areas frequented by visitors, such as the monument headquarters and visitor center.

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Table 1. Number of nests of cavity-nesting birds on plots near Tucson, Arizona, 1988 and 1989.

Location	Species[a]						
	COAU	MEUR	MIWH	MYCI	PRSU	STVU	PADO
Tumamoc Hill							
North							
1988	3	5	0	2	2	4	0
1989	1	6	2	1	3	3	1
South							
1988	0	4	1	3	0	1	0
1989	0	3	1	3	0	1	0
Arthur Pack							
North							
1988	2	4	0	1	1	1	1
1989	2	3	0	0	0	2	1
South							
1988	1	1	0	0	2	0	8
1989	1	2	0	1	1	2	1
Saguaro National Monument							
Exclosure							
1988	1	4	3	3	1	0	0
1989	0	6	4	2	2	0	0
Wash							
1988	0	2	4	2	0	0	0
1989	0	3	6	1	0	0	0

[a]COAU = *Colaptes auratus*, northern flicker; MEUR = *Melanerpes uropygialis*, gila woodpecker; MIWH = *Micrathene whitneyi*, elf owl; MYCI = *Myiarchus cinerascens*, ash-throated flycatcher; PRSU = *Progne subis*, purple martin; STVU = *Sturnus vulgaris*, European starling; PADO = *Passer domesticus*, house sparrow.

Table 2. Characteristics of saguaro cacti and cavities used as nest sites by native and exotic species of cavity-nesting birds near Tucson, Arizona, 1988 and 1989.

	Saguaro height		Cavity height		Small cavity openings	
Species[a]	$\bar{x}$	*n*	$\bar{x}$	*n*	%	*n*
COAU	7.46	(7)	5.47	(7)	12.5	(8)
MEUR	7.87	(34)	5.39	(35)	83.3	(36)
MIWH	7.96	(25)	5.50	(25)	76.9	(26)
MYCI	7.44	(15)	6.23	(15)	42.9	(14)
PRSU	8.36	(14)	6.45	(14)	91.7	(12)
STVU	7.14	(5)	6.28	(4)	100.0	(6)
PADO	8.82	(9)	6.00	(9)	77.8	(8)

[a]COAU = *Colaptes auratus*, northern flicker; MEUR = *Melanerpes auratus*, gila woodpecker; MIWH = *Micrathene whitneyi*, elf owl; MYCI = *Myiarchus cinerascens*, ash-throated flycatcher; PRSU = *Progne subis*, purple martin; STVU = *Sturnus vulgaris*, European starling; PADO = *Passer domesticus*, house sparrow.

Saguaro National Monument: Recreational Use by Visitors, Neighbors, and Organized Groups

Terry D. Shand and A. Heaton Underhill

ABSTRACT

In this paper, we review a previously published report with the same title (Shand and Underhill 1985). Visitor activities and visitor satisfaction with monument programs and conditions, and the origin and characteristics of visitors are demographically analyzed. The opinions of neighbors living within 2 mi of monument boundaries, their impacts on the monument and its influence on them, are reviewed and analyzed as related to the situation today. In addition to summarizing results of three questionnaire surveys conducted between 1 September 1983 and 31 August 1984, we seek to relate the information found to current developments at and adjacent to Saguaro National Monument. Recommendations are made for updating information on current visitors, their satisfaction with the monument, and their impacts on its resources.

INTRODUCTION

Rapid urban development in Tucson and Pima County led Saguaro National Monument (SNM) to place the measurement of human impacts high on the priority list. In 1983, funds became available for a biological and sociological study of human impacts. We reported on the sociological portion of the study in 1985 (Shand and Underhill 1985). In that report, we pointed out that the results of the sociological study must be "closely tied to the biological study since many, perhaps most, measurements of human impacts are [involve] biological populations and associations." One of the frustrating aspects of the 1983 studies was the lack of quantitative baseline data on SNM resources or its visitors. Results of the biological phase of the human impact study have not yet been published.

The 1985 report covered three questionnaire surveys of monument users: a survey of visitors from 1 September 1983 through 31 August 1984; a survey of homeowners living within 2 mi of monument boundaries; and a survey of 13 organizations that use the monument for group activities. These surveys provided information about where visitor impacts occurred, but did not measure past impacts or how the monument may or may not have changed as a result of visitor activities. The surveys provided a baseline for future comparisons and documented who the visitor was demographically according to season, point of origin, activity participated in while at the monument, number of visits, satisfaction level, and opinions as to certain management options. The neighbor survey explored some of the same factors and measured the ways in which nearby residents related to SNM. Impacts of organized groups are small, but again, information about them was recorded. We attempted to analyze results in a manner that would make them most useful to planners and managers.

METHODS

Development of viable management plans to minimize visitor impacts while accommodating visitor demands requires accurate information beyond

monthly and seasonal visitation figures. The visitor-use surveys conducted as part of this study had the following objectives:

1. To identify the types of recreational activities most frequently participated in by visitors;
2. To determine the areas of the monument where these activities occur and the level of use;
3. To estimate the level of visitor satisfaction;
4. To determine how uses by local residents differ from those of non-local Arizona residents, out-of-state visitors, and visitors from foreign countries;
5. To identify changes, if any, that visitors would like to see in National Park Service (NPS) management and interpretive programs; and
6. To assess differences in visitor uses in different seasons and between eastern (Rincon Mountain District-RMD) and western (Tuscon Mountain District-TMD) districts of the monument.

Visitor-use, Neighborhood and Organizational Surveys

Beginning in September 1983, an "exit/mailback" survey was distributed to visitors by SNM staff and NPS volunteers. This survey was conducted through August 1984. A one-year sampling period was chosen to determine seasonal variations of recreational use and to obtain a representative sample of monument users. A total of 4,371 questionnaires was distributed at the two districts (2,518 at RMD and 1,853 at TMD). This represented 1% of the estimated total visitation for 1981, the most recent figures available when the study commenced. The number of questionnaires distributed at each district during a given season was based upon 1981 monthly visitation figures provided by monument staff.

The survey questionaires were designed in cooperation with monument staff, and patterned after the Master Park Service Visitor Survey Form approved by the Office of Management and Budget (No. 10-24-0036). Copies of these questionaires appear in Shand and Underhill (1985).

During May and early June 1984, a second survey was conducted among Tucson residents living within 2 mi of monument boundaries. In addition to meeting the objectives outlined above, this neighborhood survey was designed to (1) gain better information on equestrian use of monument lands by its neighbors, (2) determine the number of households owning pets—important because of the potential impact stray dogs and cats may have on wildlife, (3) determine if public access and use have had any adverse effects on the privacy or property of neighbors, and (4) seek opinions on how the NPS should approach local issues such as commuter traffic along Picture Rocks Road at TMD and public access to Madrona Ranger Station at RMD.

The survey questionaire for monument neighbors was patterned after the general visitor-use survey and contained many of the same questions. This was done so that comparisons could be made between visitors and neighbors. The survey was conducted using the procedures prescribed by Dillman (1978). The Pima County Assessor's Office supplied computer printouts of all owner-occupied residences within 2 mi of each district (1,910 households). A 10% random sample was drawn from each printout, which produced a list of 184 households—115 adjacent to RMD, and 69 adjacent to TMD. Seven of the 191 questionnaires mailed were returned as undeliverable. The overall response rate for this survey was 81%. The high response rate is undoubtedly due to our being able to follow-up on those who initially failed to respond by mailing out reminder cards and additional questionnaires. Copies of these questionnaires may be found in Shand and Underhill (1985).

A third visitor survey was mailed to local organized groups identified by the NPS as being regular users of the monument. A list of these groups along with the two-page questionnaire can also be found in Shand and Underhill (1985). This survey was designed to meet most of the same objectives as the other two. Of the 13 groups sent the questionnaire, 10 (77%) responded.

Data Analysis

All statistical analyses were performed with the SYSTAT program for microcomputers (Wilkinson 1984). Descriptive statistics (absolute frequencies, relative frequency percentages, means, and standard deviations) were used to summarize data and aid comparisons. Open-ended questions eliciting more than one response were analyzed manually to obtain response frequencies. Additionally, Chi-square analysis was used to determine if significant differences

existed among respondents based on season of the year and area of residence (local vs. non-local visitors).

RESULTS

Visitor-use Survey

A breakdown of visitor activities participated in at each monument district (RMD and TMD) and by season is presented in Table 1. At both districts, the most frequent activities were (1) enjoy the desert, (2) take scenic drive, (3) visit information center, (4) hike/walk, (5) study plants, and (6) observe animals. The low participation in ranger-guided walks was probably due to infrequent scheduling because of staff limitations. Joggers and bikers were not adequately sampled since they usually operated early or late in the day, when few questionnaires were distributed.

For most activities the level of satisfaction was high. The only activity showing a fairly high level of respondent dissatisfaction was viewing animals, probably because most visitors arrive after midmorning when most mammals are inactive. Only 37 of 1,029 respondents (3.6%) had this complaint.

Visitor Satisfaction.—In order to gain more insight into the level of visitor satisfaction, the visitor-use survey asked two open-ended questions. Respondents were asked to indicate "how monument facilities could be improved to increase access to and enjoyment of the monument." Respondents were also asked for "additional opinions you would like to bring to the attention of the park management. Were there aspects of your trip that were especially satisfying or disappointing which managers should be aware of?" The majority of respondents to the survey appeared to make no distinction between these two questions. Most offered the same comment or suggestion when answering both questions. Therefore, the answers to both questions have been combined, with duplicate answers from any single respondent eliminated. A total of 2,188 comments was tallied (1,381 from RMD and 807 from TMD). Of the total, 1,213 (55%) were general comments favorable to the monument, its facilities, or the NPS. Fifty-seven (3%) of the comments were generally critical. Nine hundred seventy-five (45%) of the comments offered specific suggestions on how the monument or its facilities could be improved.

The most frequent suggestions concerning improvements to facilities or interpretive programs at RMD and TMD were:

1. More information on plants and animals;
2. Better signing to and from the monument (this was the most frequent specific comment from TMD respondents);
3. More pullouts along monument roads;
4. Better marking of trails;
5. Trail maintenance needed;
6. More visitor drinking facilities;
7. More hiking trails; and
8. Road maintenance needed.

(The suggested improvements listed above were also mentioned repeatedly in earlier superintendent's or custodian's monthly reports.)

Respondents at both the RMD and TMD were asked whether horses and hikers should be allowed to use the same trails, or whether some trails should be designated for hikers only. One thousand seventy-six (1,076) RMD respondents and 779 TMD respondents answered this question. Of the 813 respondents from RMD with an opinion, 79% (644) favored designating some trails for hikers only, and 21% (169) favored allowing horses and hikers to use the same trails. Of the 546 TMD respondents with an opinion, 81% (441) favored designating some trails for hikers only and 19% (105) favored allowing horses and hikers to use the same trails.

Socio-Demographics.—Socio-demographic characteristics of visitors to both districts by season are shown in Tables 2 and 3. Party size and group affiliation are similar to most park or recreation surveys. The higher percentage of winter and spring visitors >50 years old reflects the "snowbird" population in southern Arizona, but any interpretation of age composition should recognize that visitors under 18 were not adequately sampled. Mode of arrival certainly points out America's love of the automobile.

The large percentage of visitors from the Tucson area, 45% of the RMD respondents and 32% of those at TMD, reflects SNM's proximity to a large metropolitan area. The percentage of local visitors is far higher than the percentage of local visitors at most NPS units. Approximately 60% of the visitors

surveyed were from out of state. The survey also revealed that even though the monument is adjacent to an area with >500,000 people, the vast majority of those surveyed were visiting for the first time.

Rincon Mountain District versus Tucson Mountain District.—Visitors to the two districts of the monument showed few differences. Rincon Mountain District attracted more visitors, about 58% of the total, and more of them had or would visit TMD than vice versa. This is probably because TMD is near Old Tucson, the Arizona-Sonora Desert Museum, and Tucson Mountain Park. Colossal Cave is the only attraction near RMD and it does not draw many tourists. One result of the survey is most clear: the most popular visitor activities at both districts (enjoy the desert, take scenic drive, visit information center, study plants, observe animals, and hike/walk) are in line with traditional NPS thinking as to what visitors to parks should do. The same cannot be said for all NPS units. There is a real opportunity here for the NPS to expand all interpretive programs.

Area of Visitor Origin.—Area of origin also produced some significant differences in visitor activities and attitudes. As has been pointed out, local residents are the largest single user-group. This holds true for both districts throughout the entire year. At RMD, the proportion of local use ranges from a low of 41% in spring to a high of 55% in fall. At TMD, local use ranges from a low of 26% in summer to a high of 37% in fall.

The visitor-use survey indicated some significant differences in activities by local residents as compared with other monument visitors. In terms of activities participated in, the survey showed the following differences:

1. Only 29% of local residents photograph or sketch during their visits, whereas 55 to 94% of other monument visitors participate in these activities.
2. Only 43% of local residents study plants during their visits; 59 to 81% of other visitors enjoy this activity.
3. Visiting the monument for driving/sightseeing is a popular activity among 88% of out-of-state visitors, but only 54% of local visitors come to participate in this activity.
4. As would be expected, local residents are more likely to bicycle (12%) than other monument visitors (0-5%).
5. Although picnicking is participated in more frequently by locals (21%) than by out-of-state visitors (12-18%), Arizona residents (24%), and foreign visitors (42%) participate more frequently than locals.
6. Backpackers at RMD are more likely to be Arizona residents (13%) than either local residents (9%) or out-of-state visitors (0-5%).
7. Only 45% of local residents visit the monument information centers while 62 to 94% of all other visitors use these facilities.
8. Day hiking on monument backcountry trails is more popular among locals (RMD: 43%; TMD: 47%) than among other visitors (13-40%).
9. Locals (28%) and Arizona residents (29%) are more in favor of increased backcountry access than out-of-state visitors (7-16%). Nine percent of locals had no opinion, while an average of 19% of remaining visitors had no opinion.
10. Locals (27%) are more in favor of extending monument hours than other visitors (8-16%).
11. Locals (41%) and Arizona residents (43%) are more in favor of regaining access to Madrona Ranger Station than other visitors (14-25%). This is not a well-known problem; 48% of locals had no opinion and up to 78% of non-locals were in this category.

One final note concerning the difference in use by local residents and other monument visitors. Although local residents made up the largest user-group, over half of all respondents (51-58%) indicated that this was their first visit in the last five years. This is important for NPS management to keep in mind when planning and advertising interpretive programs, and in providing adequate directions to and from both districts of the monument.

Survey of Monument Neighbors

A questionnaire was mailed to 191 randomly selected households of the 1,910 reported by the Pima County assessor to reside within 2 mi of the monument (119 for RMD and 72 for TMD). Eighty-one percent (81%) responded. Copies of the questionnaire and responses were published in Shand and Underhill (1985). About two-thirds of respondents favored maintaining current access to the monument. A much higher percentage of neighbors favored hikers and horseback riders using the same trails than did visitors

(about 45% vs. 20%). In fact, TMD neighbors were almost 2:1 in favor of combined use. Answering the question as to how the monument affected their property or their privacy, only four neighbors at RMD and two at TMD reported any problems. Ninety-six percent believed that they were not adversely affected. About 45% of neighbors reported seeing stray dogs or cats. About 85% reported having dogs or cats of their own. In preparing the questionnaire, we decided that there was little point in asking whether or not their pets were allowed to run at large.

As might be expected, neighbors biked, jogged, hiked, and rode horses on the monument more than the general public. Fairly high use of the monument by horseback-riding neighbors was reported. However, because the sample was small and covered the pleasant spring season, the level of trips reported should be used with caution in determining year-round use.

Responses from monument neighbors, Tucson residents, and other visitors were compared on certain questions. Thirty-nine percent of neighbors favored more backcountry access compared with 28% for Tucson residents and 25% for others. Among neighbors of RMD, 71% of those who had an opinion favored regaining access at Madrona Ranger Station; 80% of Tucson residents and 70% of other visitors were also in favor. On the Picture Rocks Road question, 61% of TMD's neighbors favored not widening the road, while 90% of both other groups favored leaving the road as is. The opinions of TMD's neighbors concerning access to the monument at night contrasted sharply with Tucson residents and other visitors. Sixty-nine percent of TMD neighbors favored maintaining night access while only 31% of Tucson residents and 41% of other visitors held this opinion.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In the 1985 report, we drew some conclusions and made eight recommendations that are of special interest six years later. The survey revealed that almost half of monument visitors were Tucsonans and predicted that visitation would increase as Tucson grew. That has happened. Increased conflicts between bikers, joggers, and motorists along Picture Rocks Road and Cactus Forest Loop Drive were predicted. That has also occurred, including a bike fatality on the latter. To paraphrase briefly from the 1985 conclusions:

> The visitor-use survey indicated that backcountry facilities are mostly used by local residents, and residential development adjacent to monument boundaries will produce an increase in equestrian use of backcountry trails. Higher levels of use by locals and equestrians will mean accelerated damage to trails and campsites.
>
> As monument use increases so will the demand and need for more interpretation. Over half of the visitors are first-time visitors, and interpretation is especially important to their enjoyment and understanding of monument resources. Since the majority of recreational impacts will be restricted to areas immediately adjacent to monument roads, picnic areas, campsites and trails, the single management tool that will most alleviate recreational impacts is resource interpretation. At present, many visitors do not take advantage of the information currently provided.

The eight recommendations were:

1. Close Cactus Forest Loop Drive (RMD) to motor traffic and install a tram system. This has not been implemented.
2. Construct a new commuter route to replace Picture Rocks Road (TMD) or make it a scenic parkway through the monument with a reduced speed limit. County plans call for a new road, and the SNM General Management Plan calls for closing Picture Rocks Road when that is done. Ample time is likely available to make Picture Rocks Road a scenic parkway before the new road materializes.
3. Improve the design of Mica View Picnic Area (RMD). Status is unknown.
4. Establish an aggressive trail maintenance program. This is currently being done.
5. Expand present interpretive facilities and programs. This is being done to the extent possible given budget constraints.
6. Move Tanque Verde Trail trailhead (RMD). Status is unknown.
7. Periodic surveys of monument visitors. It would appear that the time is ripe for an updated survey.

8. The NPS must take a greater part in community affairs. Present Superintendent Bill Paleck has very definitely done this.

Most of the predictions that we made six years ago were accurate. The recent developments along the southern border of SNM deserve mention. Recently, the Pima County Board of Supervisors approved a development plan for the Rocking K Ranch. The plan is a good one as far as SNM is concerned. The principal drawback is increased air pollution from automobiles. The plan calls for a 300-ft natural buffer along the SNM boundary, protection of all riparian lands along Rincon Creek and its monument tributaries, access to Madrona Ranger Station, increased visitor access to the monument, and a number of other environmental actions including a funded research and interpretive institute (Rincon Institute).

The only thing more encouraging for the monument is the recent passage of legislation that will add the Rincon Creek portion of the Rocking K property to the RMD. This bill recently passed Congress and was signed into law by the President in June 1991.

The time is ripe for a follow-up survey of visitors and neighbors to examine activities and satisfaction levels. Only then can management measure its successes and failures and develop meaningful management objectives.

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Table 1. Percent visitors participating in activities by season at each district of Saguaro National Monument. A complete listing of those activities mentioned by respondents as "other" is given by Shand and Underhill (1985).

	Rincon Mountain District					Tucson Mountain District				
	Seasons[a]					Seasons[a]				
Activity	Fall n=186	Winter n=374	Spring n=447	Summer n=168	Total n=1175	Fall n=172	Winter n=277	Spring n=317	Summer n=46	Total n=812
Photograph/sketch	46	43	49	55	47	50	53	56	63	54
Hike/walk	55	59	54	55	56	60	73	66	61	67
Study plants	51	54	54	58	54	64	64	67	72	66
Observe animals	52	47	57	64	54	45	47	52	43	48
Ranger-guided walk	2	2	4	2	3	3	3	2	0	2
Take scenic drive	53	71	76	81	71	70	73	79	78	75
Bicycle	10	6	3	8	6	1	1	0	0	1
Jog/run	4	3	2	4	3	0	1	1	0	1
Picnic	15	18	21	13	18	20	27	26	9	24
Backpack/camp	10	4	5	5	6	3	2	2	2	2
Visit info. center	55	66	69	71	66	67	72	65	96	70
Enjoy the desert	81	84	82	88	83	89	87	90	93	89
Other	6	5	7	8	6	8	4	4	4	5

[a]Fall = Sep-Nov, winter = Dec-Feb, spring = Mar-May, summer = Jun-Aug.

Table 2. Socio-demographic characteristics of visitors to the Rincon Mountain District, Saguaro National Monument.

	Season[a]				
	Fall %	Winter %	Spring %	Summer %	Total %
[b]Area of origin (n = 1170)					
Local	55	43	41	49	45
Rest of Arizona	4	2	4	4	3
California	3	7	7	7	6
Northwest	5	5	4	1	4
Southwest	5	7	5	2	5
North Central	5	13	11	7	10
Central	2	3	5	5	4
East of Mississippi	15	19	23	22	20
Foreign country	6	2	1	4	3
[b]Age in years (n = 1158)					
1-18	3	3	0	5	2
19-35	42	24	23	42	29
36-50	18	18	21	33	21
>50	37	54	56	21	48
How arrived (n = 1173)					
Walk	0	1	1	0	1
Bicycle	7	5	2	6	4
Car/truck/van	88	91	94	90	91
Motorhome	2	3	2	1	2
Other	3	1	2	3	2
Group affiliation (n = 1174)					
Came alone	20	12	11	14	13
Family	45	59	52	55	54
Friends	24	20	22	21	21
Co-workers	1	0	2	1	1
Family/co-workers	0	0	0	0	0
Friends/co-workers	1	0	0	2	1
Family/friends	6	8	10	7	8
Organized group	4	1	3	1	2
Number in party (n = 1145)					
1	17	10	11	13	12
2	43	50	46	41	46
3	11	14	14	14	14
4	15	14	18	18	16
5	5	6	5	7	6
≥6	7	7	5	8	7

[a]Fall = Sep-Nov, winter = Dec-Feb, spring = Mar-May, summer = Jun-Aug.
[b]Chi-square analysis indicates a significant difference among seasons at a 0.95 level of confidence.

Table 3. Socio-demographic characteristics of visitors to the Tucson Mountain District, Saguaro National Monument.

	Season[a]				
	Fall %	Winter %	Spring %	Summer %	Total %
[b]Area of origin (n = 807)					
Local	37	31	30	26	32
Rest of Arizona	12	6	3	7	6
California	6	10	8	2	8
Northwest	2	4	7	4	5
Southwest	5	9	6	4	7
North Central	8	12	13	20	12
Central	3	1	3	13	3
East of Mississippi	22	22	22	20	22
Foreign country	5	3	8	4	5
[b]Age in years (n = 799)					
1-18	1	0	1	2	1
19-35	39	22	27	30	28
36-50	22	23	19	37	22
>50	39	55	53	30	49
How arrived (n = 808)					
Walk	0	0	0	0	0
Bicycle	0	1	0	0	0
Car/truck/van	97	95	95	95	96
Motorhome	3	3	3	4	3
Other	1	0	1	0	1
Group affiliation (n = 810)					
Came alone	16	9	10	0	10
Family	19	23	23	11	22
Friends	52	54	57	80	56
Co-workers	3	1	0	0	1
Family/co-workers	1	0	1	0	1
Friends/co-workers	0	0	1	2	0
Family/friends	9	9	7	7	8
Organized group	1	4	1	0	2
Number in party (n = 809)					
1	16	9	7	0	9
2	54	49	49	50	51
3	11	9	13	9	11
4	12	20	18	22	18
5	4	5	4	4	5
≥6	3	8	8	6	7

[a]Fall = Sep-Nov, winter = Dec-Feb, spring = Mar-May, summer = Jun-Aug.
[b]Chi-square analysis indicates a significant difference among seasons at a 0.95 level of confidence.

IV.
Air Quality and Pollution

Regional Air Pollution Threatens Biodiversity in National Parks

David F. Karnosky, Paul C. Berrang, and James P. Bennett

ABSTRACT

Over the past 10 years, we have studied the ozone sensitivity of trembling aspen (*Populus tremuloides*) populations throughout the United States. Our results suggest a significant negative correlation between mean ozone sensitivity and ambient ozone concentrations of these populations. We have used visible foliar injury from both chamber and field trials for the ozone sensitivity determinations. We also have evidence that ozone can significantly reduce the growth and biomass accumulation for ozone-sensitive but not for ozone-tolerant genotypes. Our results suggest that an early stage of natural selection is occurring through loss of ozone-sensitive genotypes from areas with elevated ambient ozone concentrations. Thus, subtle intraspecific diversity changes may be occurring due to ozone stress.

INTRODUCTION

Ozone is one of the most important regional air pollutants in North America (Barnard et al., in press). It has been estimated to cause crop loss of about three billion dollars per year in the United States alone (Adams et al. 1988). While comparable estimates are not yet available for forest trees, it is known that ozone can reduce growth (Wang et al. 1986*a*,*b*), increase mortality (Karnosky 1980), affect reproduction (Benoit et al. 1983), and impact community structure (Miller 1973).

Approximately 10 years ago, we hypothesized that ozone was negatively affecting the gene pool of forest-tree species in some regions of the United States. To test this hypothesis, we initiated a series of studies to compare the ozone sensitivity of tree populations from National Park Service (NPS) lands across the United States, including those from Saguaro National Monument. In this paper, we review the results of this research, speculate about the implications of our findings, and discuss remaining research needs.

OVERVIEW OF NPS STUDIES

Multiple Species Studies

Berrang et al. (1986*a*) tested the relative ozone tolerances of randomly selected clones of four tree species from NPS areas in the eastern and midwestern United States[1]. Species were selected to represent a range of sensitivity to ozone. Trembling aspen (*Populus tremuloides*) was the most ozone-sensitive, followed by black cherry (*Prunus serotina* Ehrh.) and red maple (*Acer rubrum* L.). Flowering dogwood (*Cornus florida* L.) was the most tolerant. For both trembling aspen and red maple, a significant negative correlation was found between the mean population response to ozone (as determined in controlled fumigations) and the average annual ozone concentration where the populations originated. For both of these species, the percentage of leaves injured and the average leaf area injured were nearly twice as great for the most sensitive populations as for the most tolerant one. For aspen, trees from Cuyahoga Valley National Recreation Area were more tolerant than

[1]Eastern: Shenandoah (Va.), Great Smokey Mountains (N.C.–Tenn.) and Acadia (Me.) national parks; Delaware Water Gap National Recreation Area (Pa.–N.J.); Saratoga National Historical Park (N.Y.). Midwestern: Cuyahoga Valley National Recreation Area (Oh.); Voyageurs (Minn.) and Isle Royale (Mich.) national parks; Indiana Dunes (Ind.) and Sleeping Bear Dunes (Mich.) national lakeshores.

those from Voyageurs and Isle Royale national parks. For red maple, trees from Shenandoah National Park, Cuyahoga Valley National Recreation Area, and Great Smokey Mountains National Park were more tolerant than those from Acadia National Park. These results support our hypothesis that natural selection for ozone tolerance is occurring in relatively polluted parks.

Aspen Studies

Field Trials.—Our initial results with aspen (Berrang et al. 1986*b*) followed our hypothesis with regard to air pollution-induced natural selection. However, results were based on short-term fumigation to induce acute injury, and on a small number of populations that were very widely separated geographically. Therefore, we subsequently conducted additional aspen studies. First, we established field trials to compare growth and visible foliar injury by ozone in two locations (southern New York and southern Michigan) where elevated ambient ozone occurs. At least fivefold differences in visible foliar injury were measured among population means in each planting, and the means were negatively correlated with ozone concentrations for each area (Berrang et al. 1989). The relative sensitivity rankings among populations and among clones within populations agreed closely with rankings derived from the acute fumigation experiments. Unfortunately, survival in these plantations has been poor so that meaningful growth information is not available from them.

Nationwide Studies.—Berrang et al. (1991) examined the relative ozone tolerances of 15 aspen populations from NPS lands across the United States[2]. Differences among populations were statistically significant ($P = 0.05$), with the most tolerant populations from the West Coast, Northeast and industrialized portions of the Great Lakes. Populations sampled from areas that have failed to achieve the national ambient air quality standard for ozone (0.12 ppm for 1 hr) were significantly more tolerant than populations from areas that achieved the standard. As with the original study, there was a significant negative correlation between the amount of visible foliar injury and maximum daily ozone averages at localities where the populations were collected.

We detected a significant correlation between amount of injury after ozone fumigation and two climatic variables (annual precipitation and minimum temperature) on a nationwide basis. However, the relationship between visible ozone injury and ambient ozone concentration was still significant after factoring out the climatic effects. Thus, this study supported our hypothesis that ambient levels of ozone may be eliminating ozone-sensitive clones from natural populations of aspen.

Growth Studies.—Very little information exists regarding growth comparisons of ozone-sensitive and tolerant trees in clean air as compared to ozone-added air. Recently, Karnosky and Scholz (in press) compared the growth of 18 ozone-sensitive and 18 ozone-tolerant aspen clones in season-long exposures to 80 ppb ozone for six hours per day, three days per week. No significant ozone-induced growth reductions were detected for the tolerant clones. However, ozone-induced reductions of 46%, 34%, and 37% were found for stem, retained leaf, and root biomass for the sensitive clones.

In 1977, the senior author established a small field trial of ozone-sensitive and ozone-tolerant aspen clones in southern New York. After 10 years, the two ozone-sensitive clones were about one-half the height of the ozone-tolerant clone (Berrang et al. 1989). No significant differences were seen in the height growth of these clones when they were grown in charcoal-filtered (ozone-free) air (Wang et al. 1986*a*).

MANAGEMENT IMPLICATIONS

Our studies suggest that subtle population changes may be occurring in ozone-sensitive forest-tree species. These changes are not readily detectable, as stocking levels and stand appearance may be identical with or without air pollution stress (Barnard et al., in press). However, a number of implications exist. Probably the most important is that biodiversity may be reduced as sensitive genotypes are eliminated. If so, remaining populations may have a reduced potential for adapting to future changes such as global

[2]In addition to those areas mentioned previously, sites included Saguaro National Monument (Ariz.); Yosemite (Calif.), Sequoia-Kings Canyon (Calif.), Rocky Mountain (Colo.), Yellowstone (Mont.–Wyo.) and Glacier (Mont.) national parks; Mount Rushmore National Memorial (S.D.).

warming. A second important implication is that genes or alleles may be permanently eliminated as sensitive genotypes are lost. If these two phenomena are occurring, resource managers must be concerned about the conservation of adaptability in forest-tree populations under ozone stress, and strategies to facilitate this conservation effort must be developed.

Studies Needed

A number of questions remain regarding our hypothesis that ozone-induced natural selection is occurring in forest trees. To date, our research is highly correlative in nature. That is, we have correlations of ozone tolerances with ozone concentrations at various sites. However, these correlations could also result from other factors. Four types of studies to further test our hypothesis are suggested.

1. Reciprocal plantations of ozone-sensitive and tolerant aspen clones under similar climatic conditions but under high versus low ozone loading would be useful in comparing long-term effects of ozone on growth.
2. A study to compare genetic variation from high and low ambient ozone areas is needed, as our studies have not included enough individuals per population to make meaningful comparisons. If ozone is eliminating a portion of the population, one would expect variability may be decreased in the residual populations. In this regard, more intensive sampling from a small number of populations along a steep ozone gradient would enable us to compare variability in ozone responses and to minimize variability created by environmental factors.
3. Studies are needed to quantify the effects of ozone stress on competition between ozone-sensitive and tolerant genotypes. Particularly interesting would be a comparison of survival between ozone-sensitive and tolerant clones with and without ozone exposure. Also interesting would be the time course of competition events. For instance, how soon do ozone-sensitive aspen trees die out of populations as they are being outgrown by neighboring trees? Do the roots die as quickly as the tops, or do they stay alive for a long time after the stem dies back?
4. Studies are needed to see if we can detect population differences by means other than ozone fumigations. For example, isozyme or RFLP analysis could be used to examine variability in natural populations under varying ozone stress levels. Variability in populations could be examined as well as heterozygosity levels and frequency of rare alleles.

CONCLUSIONS

Our studies with trembling aspen and red maple clones collected from NPS lands suggest that ozone may be causing subtle population changes that could eventually cause reduced adaptability and/or gene loss. However, a number of research questions still remain to be addressed before policy regulators will be convinced that our hypothesis has been proven beyond a reasonable doubt.

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Air Pollution Threats to Biological Resources in Saguaro National Monument

Kenneth W. Stolte

ABSTRACT

This paper provides a cursory overview of pollutants of concern in national parks, some of the impacts to vegetation resulting from air pollution stress, and the effects of air pollution on plants found in Saguaro National Monument. There is also a discussion of the current extent of ozone problems in the monument and the concern that air pollution may be a factor in the decline of the saguaro cactus (*Carnegiea gigantea*) in the monument. Some additional air quality research issues that warrant consideration are also mentioned.

INTRODUCTION

Saguaro National Monument (SNM) is one of 158 class I areas in the United States. Federal legislation mandates that resources in class I areas (often wilderness areas) are to receive the highest protection from air pollution. It is reasonable to ask if we really need to be concerned with air quality in all class I areas or even at SNM in particular. However, it is important to note that although the entire United States was essentially wilderness less than three centuries ago, few pristine areas remain today. Consequently, it is essential to preserve class I areas to allow natural processes to proceed with as little human influence as possible.

Air pollutants that are of concern to the National Park Service (NPS) come from point sources and regional sources, and are classified by the origin of the pollutant and the nearness of the NPS unit to the pollutant source. Point sources, such as smelters, power plants, and aluminum reduction facilities, are a concern if they are located near NPS units. Point sources emit primary pollutants such as sulfur oxides (SO_x), nitrogen oxides (NO_x), toxic metals, fluorides, and a suite of organic and inorganic compounds. Areas near point sources can become contaminated for many decades with toxic metals (Lepp 1981*a*,*b*). Regional pollutants, like smog, sometimes come from sources distant from NPS units and consequently are a concern for many NPS areas. These pollutants are mostly emitted from automobiles and various urban sources but can also originate from multiple point sources. Regional air pollutant masses often contain primary pollutants such as SO_x and NO_x, and organic and inorganic compounds; they also contain secondary pollutants that are a result of chemical transformation in the atmosphere, such as ozone (O_3).

Plants are generally more sensitive to air pollution than animals (Treshow and Anderson 1989). Plants use the power of sunlight during photosynthesis to remove carbon dioxide (CO_2) from the air and make sugars, which all animals, including humans, consume. Pollutants can disrupt this basic life process by damaging cells of sensitive plant species (Smith 1990). Gaseous pollutants injure sensitive plants by entering leaves during normal gas exchange processes. If injuries to internal leaf systems are severe, they are manifested on leaf surfaces as different patterns of foliar discoloration. Specific pollutants can cause very distinctive patterns that can be used to diagnose the extent and severity of injury (Jacobsen and Hill

1970). When visible foliar injury is severe, other injuries occur such as accelerated aging of the foliage, reduced retention of needles in conifers, reduced growth of roots and shoots, reduced reproduction, altered resistance to predators and pathogens, and increased mortality (Treshow and Anderson 1989; Smith 1990). Air pollutants can also affect animals that feed on injured plants. Sugars and amino acids produced in plant leaves may be changed by pollutants, thus altering their nutritional value (Bedford 1986).

Plants in ecosystems that are in the process of successional transition may be more vulnerable to air pollution than plants in more stable life stages of the same ecosystem (Stolte 1982). For example, a chaparral plant community recovering from a fire produces many seedlings and resprouts with different leaf structure than plants in older, more decadent chaparral stands. Young, rapidly growing plants with succulent tissue appear to be more vulnerable to pollution than older plants with more sclerophyllous (tough) tissue. Air pollutants may differentially affect species of plants growing after a fire and alter the natural processes of community regeneration. Since fire is a natural component of both the montane and desert ecosystems of SNM, the potential exists for air pollutants to alter natural successional processes in the monument.

BIOLOGICAL EFFECTS OF AIR POLLUTANTS

Ozone

In the western United States, ponderosa (*Pinus ponderosa*) and Jeffrey (*P. Jeffreyi*) pines are known to be especially sensitive to O_3 (Miller et al. 1963). Ozone injures these species by destroying chlorophyll, accelerating needle aging, and causing lower retention of needle whorls. The result is death of lower tree branches and crown thinning that can lead to reduced growth or tree death. These symptoms have been documented on ponderosa pines in the Rincon Mountains (Duriscoe 1987, 1989). Some trees have little foliage remaining, while others in proximity show little damage and are apparently more tolerant because of genetics, microclimate, or both. Ozone may be upsetting the normal competitive processes of natural selection in this pine forest (Scholz et al. 1989).

Ozone damage can be geographically extensive. Pines in Yosemite, Sequoia and Kings Canyon national parks, and SNM were all surveyed for O_3 injury in 1986 (Duriscoe 1990). The survey indicated that 39% of pines in Sequoia, 29% of those in Yosemite, and 15% of SNM pines had been injured by O_3. Cumulative exposures of O_3 from 1987-1989 were very high in Sequoia as compared with Yosemite, with SNM much lower. It is reasonable to assume that if the relatively low cumulative O_3 exposures at SNM begin to increase, damage to the pines in the monument will also increase. Recent growth studies of conifers in central and southern Arizona indicate that many ponderosa pines and Douglas-firs (*Pseudotsuga menziesii*) in SNM are not growing as well as their age, climate, and previous (pre-industrial) growth rates would suggest (Graybill and Rose 1989).

Seasonal profiles of cumulative O_3 exposures in SNM are characterized by relatively high O_3 exposures occurring in spring and early summer months that may injure sensitive shrubs such as squawbush (*Rhus trilobata*) (Temple 1985). High O_3 levels in July 1990 may have been responsible for the foliar injury found on squawbush in the air pollution biomonitoring garden at SNM in August 1990 (Saguaro Natl. Monument, Div. of Sci. and Resour. Manage., unpubl. data). At SNM, high O_3 levels sometimes occur during spring months when wildflowers are completing their short growth and reproduction cycles. Some species of desert annuals have been shown to be very vulnerable to O_3 (Thompson et al. 1984).

Sulfur Dioxide

In the Southwest, relatively high levels of sulfur emissions from point sources have occurred for many decades (Wood and Nash 1976; Marsh and Nash 1979; Dawson and Nash 1980; Graybill and Rose 1989). As with O_3, SO_x enter plant leaves and cause injury to conifers, broadleaf plants, desert annuals, and shrubs (Barrett and Benedict 1979). Some plants such as lichens are very sensitive to sulfur dioxide (SO_2) (Nash 1973; Sheridan 1979). Studies conducted around major point sources such as smelters and power plants indicate that the number of lichen species decreases as one approaches the point source (McCune 1988). Vascular and non-vascular

plant species and animal species diversity (complex ecosystems) are reduced (simple ecosystems) when chronic air pollution stress is severe (Hutchinson and Whitby 1976; Freedman and Hutchinson 1980).

Nitrogen Oxides

Nitrogen oxides are a major pollutant of concern. As a gas, nitrogen dioxide (NO_2) is weakly phytotoxic, alone or when mixed with O_3 or SO_2. Nitrogen oxides are also important contaminants in polluted air as solid or liquid fertilizers. Fertilizing a lawn or garden results in the enhanced plant growth that is desired, but in natural ecosystems similar effects are rarely beneficial because natural balances are upset. If nitrogen is introduced into a saguaro (*Carnegiea gigantea*) ecosystem, all species may not respond equally. Some species, particularly grasses, may be able to use the enhanced nitrogen supply better than others (Tilman 1987). Species that are normally minor components of the plant community may be able to increase in numbers, growth rate, and reproductive success to the detriment of other species. Cacti species respond rapidly and differentially to different levels of nitrogen (Nobel 1983, 1988), but the natural structure and functioning of these desert species in relationship to nitrogen deposition is not well known. Nitrogen deposition has also been linked to alterations in winter hardening and to dehardening cycles of certain species (Freidland 1984; Freer-Smith and Mansfield 1987).

Acid Rain

When NO_x and SO_x mix with moisture, acid rain, acid fog, acid mist, or acid snow are produced. Dried acidic particles can also be produced in the atmosphere. Mixing air pollutants with normal precipitation not only adds sulfur, nitrogen, and other chemicals to the precipitation, but the pH of the precipitation is also lowered (made more acidic) in the process. In the Southwest near SNM, some summer rain events are acidic, with a pH of 3.6, which is almost as acidic as vinegar (Blanchard and Stromberg 1987). Reports from the National Atmospheric Deposition Program (1987) indicate that Arizona has some of the most acidic rain in the western United States.

If rain falling on plants is very acidic, the waxy tissue covering the leaf surface can be eaten away, but often the most serious problems to plants originate in the soil. Lowering the pH of soil can mobilize aluminum and other elements and make them available for plant uptake (Wellburn 1988). Consequently, aluminum and other undesirable elements may be taken up by plants in excess quantities instead of the calcium, magnesium, and other nutrients they really need. Desirable elements may also be less available due to soil pH changes. Mycorrhizae and soil microbes that are critical in ecosystem functioning can also be destroyed, and the whole system altered. Cactus growth rates can change markedly when pH levels in the soil drop from 6.0 to 5.0 (Berry and Nobel 1985; Nobel 1988).

Fluoride

Fluoride is a waste gas of smelters, aluminum reduction plants, and other facilities. It is very phytotoxic and can cause plant injury even at very low concentrations in the parts per billion (ppb) range (Treshow and Pack 1970; National Academy of Science 1971). Fluorides, like metals, cause injury to a wide variety of plants and are also passed along through the food chain, accumulating in animals that eat contaminated plants. Consequently, animals farther up the food chain contain more fluoride than the plants or animals they feed on. If a plant has 10 ppm fluoride, an animal that eats the plant may accumulate 100 ppm or more (Carlson and Dewey 1972; Gordon 1974).

Global Climate Change

Global climate change is a popular topic of conversation today (U.S. Forest Service 1990). To date, no consensus among scientists exists as to whether the climate is changing on a global scale. One of the causes of potential climate change is the anthropogenic (human-caused) increase in CO_2 and other gases in the atmosphere. These gases trap heat near the earth's surface and prevent it from radiating back into space. Carbon dioxide levels are definitely rising, and whether temperatures increase or not, an increase in CO_2 may favor plants that are able to make best use of an increased supply of this important compound. Shifts in plant species abundance and distribution could also occur as a result of increased levels of CO_2.

In the Tucson Basin, urbanization induces another kind of localized temperature change, with pockets

of hot and cold air altering temperature regimes in and near SNM (Kirby and Sellers 1987). Growth and competition of native plants may be changed by these localized temperature alterations.

RESEARCH EMPHASES AT SNM

Intensive research sponsored by the NPS Air Quality Division at SNM's Rincon Mountain District (RMD) has focused on pines in the mountains and cacti on the desert floor. It is generally agreed that cacti have been declining in portions of the RMD—not just saguaros, but also chain-fruit chollas (*Opuntia* spp.) and barrel cactus (*Ferocactus* spp.). Freezing has been suggested as a cause for the saguaro decline (Steenberg and Lowe 1976, 1977, 1983). However, prior to 1930 when saguaros were abundant and vigorous, many more severe freezes occurred than from 1930 to 1970, when many larger saguaros died (Steenberg and Lowe 1976). Perhaps freezing and low temperatures are not the entire answer.

Cacti may be stressed by something that makes them more susceptible to freezing, drought, windthrow, and pathogens. Researchers are now investigating whether air pollution, past or present, might be altering the natural resistance of cacti. Epidermal browning of saguaros was described long ago as a natural degradation of the epidermis of older cacti (Long 1929). Cacti are still dying and the epidermal browning syndrome associated with declining saguaros is now under serious study (Stolte 1988). Epidermal browning is strongly associated with spine loss. Spines normally fall off older cacti, but many young plants are also showing browning and spine loss. The root systems of a few brown saguaros that were toppled by wind have indicated that saguaros with epidermal browning may also have poorly developed roots. The individuals examined were 20 to 30 ft (6-9 m) tall and almost without support. Windthrow will probably claim more of these individuals with time.

What is unusual in SNM is that epidermal browning is observed on relatively young as well as old saguaros, and appears to be a process of premature aging. The long history of air pollutants within and around SNM (Wood and Nash 1976; Dawson and Nash 1980; Clemensen 1987; Graybill and Rose 1989) and the accelerated aging response frequently observed in plants exposed to toxic levels of air pollutants (Treshow and Anderson 1989; Smith 1990) suggest that air pollution should be investigated as a causal or contributing agent in the cactus decline. A system of long-term monitoring plots has been established in both districts of SNM to determine trends in epidermal browning, spine loss, age-class structure, and mortality of saguaros over time (Duriscoe and Graben, this volume).

Paloverde (*Cercidium* spp.) appear to be dying at high rates in some of the same areas as saguaros. Some trees are festooned with mistletoe (*Phoradendron californicum*), but others are not. Stems on trees with mistletoe are starting to turn black. Again, the cause is unknown, but certainly warrants further study.

Continued research and monitoring of air quality in desert and montane ecosystems of SNM is critical to understanding some of the existing and potential problems mentioned in this paper. The urban growth around this wilderness area makes SNM an unfortunate, but ideal laboratory for determining the effects of regional and local changes in air quality on native species. To protect SNM from degradation due to air pollution, we need to understand the sensitivity of SNM organisms and ecosystems to air pollutants of concern. This requires initiating and continuing short- and long-term air quality research and monitoring programs. The severity and extent of air quality degradation are not well known. However, effects on valuable natural resources at SNM are of serious concern because air pollutants are known to cause severe and, in some cases, irreversible changes in ecosystems.

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An Investigation of the Impact of Inorganic Air Pollutants on Saguaro National Monument

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ABSTRACT

Environmental data evaluating the input of inorganic air pollutants to the Saguaro National Monument ecosystem have been collected over the past four years. These data are summarized in the following discussion. The enrichment factor approach is employed to provide a framework for simplified interpretation of this large collection of data from soil, cactus, lichen, tree-ring, and air particulate samples.

INTRODUCTION

Saguaro National Monument (SNM) was created by Executive Proclamation in 1933, in response to concerns for preserving stands of saguaro cacti (*Carnegiea gigantea*) in the vicinity of Tucson, Arizona. Nearly 45 years passed before settlement of boundary disputes and land acquisition resulted in the establishment of the final monument boundaries (Clemensen 1987). In the meantime, in the early 1940s, observations were made that older saguaro cacti in the monument were dying and that reestablishment of saguaro seedlings was not occurring.

After the original observation in 1940 that saguaro cacti were dying, the so-called "saguaro decline" was initially attributed to bacterial infection. During the winter of 1941-1942, large numbers of presumably diseased cacti were removed and buried in an effort to stop the spread of the alleged infection (Clemensen 1987). Subsequently, references to saguaro decline dating as far back as 1896 were discovered, and the prevailing viewpoint of the condition changed to regard it as a naturally-occurring cyclical fluctuation resulting from general overmaturity of the saguaro population. With the change in viewpoint, the concern regarding the declining saguaro population broadened to include failure of seedling reestablishment and death of older individuals. Various factors investigated as potential influences on seedling reestablishment included cattle grazing (Clemensen 1987), nutritional deficiencies, and changes in other edaphic (soil) factors (Turner et al. 1966).

Although some effect on saguaro populations and seedling reestablishment could be linked to climatic conditions and cattle grazing, no satisfactory overall explanation of the continuing saguaro decline has been forthcoming. Studies of saguaro populations in other locations indicated that some populations are flourishing (Turner 1990), reenforcing the conclusion that the decline of the population at SNM is somewhat of a local phenomenon. The continuing decline is, however, real, and is documented in a series of photographs taken from the same vantage point in 1935, 1965, and 1985. The extreme thinning of the cactus forest is obvious and dramatic.

More recently, air pollution has become suspect as a potential causal factor in the continuing saguaro decline. Air pollution sources such as copper smelters throughout southern Arizona and also the growing Tucson metropolitan area date back to the late 19th century. Although emissions from copper

smelters have fluctuated with economic conditions, the Tucson area represents a continuously-growing source of urban air pollution. The combined emissions from these sources include particulate matter containing metals and other inorganic compounds, sulfur dioxide, and a variety of organic compounds. Aircraft application of agricultural chemicals in the vicinity of Tucson represents another airborne source of potentially toxic organic compounds.

METHODS

In 1987, a preliminary survey of soils and selected vegetation was undertaken at SNM under the auspices of an interagency agreement between the National Park Service (NPS) and the Los Alamos National Laboratory (LANL). The purpose of this survey was to identify chemical profiles that might indicate air pollution impact upon the monument. These efforts have been expanded each year, with the last sampling conducted in early 1990. Soil samples were collected inside and outside the monument (including several distances from a nearby smelter). Samples were also collected from healthy-appearing and obviously afflicted saguaro cacti, and from epiphytic lichens and tree-ring cores from four species of trees in the Catalina and Rincon Mountains along the northern and eastern boundaries of the Rincon Mountain District (RMD) of SNM. Tree-ring cores were used in an attempt to identify elemental profiles over time that might be correlated with saguaro decline and with changes in air pollution input. Control samples of soils and tree cores were collected from Walnut Canyon and Chiricahua National Monuments in Arizona, and Gila Cliff Dwellings National Monument in New Mexico.

All soil samples were air dried and sieved through a standard 20-mesh brass screen to remove organic debris and larger rock fragments. Soils from the Tucson Mountain District (TMD) of SNM were further separated into four size fractions (20, 60, 100 and <100-mesh) using stacked standard brass screens. Lichens were air dried and analyzed without further preparation. Tree cores were cut into increments representing the time periods 1800-1850, 1850-1900, 1900-1950, and 1950-present. This was accomplished by direct calibration of our cores with parallel samples taken and dated by personnel of the Laboratory of Tree-Ring Research at the University of Arizona. Tree-core segments were freeze-dried before chemical analysis. Saguaro tissue samples were cut from the "peaks" of the ribs of selected individuals on both the north and south sides of the cactus and frozen in the field. In the laboratory, samples were thawed, separated into three layers (cuticle, chlorenchyma, and parenchyma), and freeze-dried prior to chemical analysis.

To date, most elemental analysis has been conducted via instrumental neutron activation analysis at the LANL Omega West Reactor by the authors and the staff of the reactor facility. Up to 45 elements have been quantitatively determined. These methods are described in detail by Gladney et al. (1980) and Garcia et al. (1982). A small set of these samples has been analyzed for fluorine using ion selective electrode techniques. Carbonate carbon has been measured in some of the soils via acid-evolution gravimetry and both bound and unbound water have been determined by coulometry in the same subset of soils. These methods are described in detail by Gautier and Gladney (1986). All chemical analyses have been quality assured by concurrent analysis of National Institute of Standards and Technology (formerly National Bureau of Standards), U.S. Geological Survey, and Canadian Geological Survey reference materials according to our established policies (Gautier et al. 1989).

Air particulate samples have been collected since 1985 at the air quality monitoring station located south of monument headquarters in the RMD, and analyzed by proton induced X-ray fluorescence at the University of California, Davis, under a separate agreement with the NPS. Some of these data have been provided to us for comparison with our elemental measurements, and were the subject of a previous presentation describing the enrichment factor (EF) approach to air pollution impact assessment (Gladney 1991).

RESULTS

Over 825 soil samples from the various sites have been analyzed for up to 48 constituents. The EF approach detailed in Gladney (1991), has been used in an attempt to summarize this mass of data for more incisive interpretation and eventual resource management use. All EFs were computed relative to Wedepohl's average elemental abundance in the earth's crust (Wedepohl 1968). Overall means and

standard deviations of these EFs are presented in Table 1 as a function of sampling site and depth. While all elements were measured at all sites, certain constituents were consistently below our limits of detection and could not be used to calculate EFs. This is shown as "———" if all samples were below detection limits, and as a mean without a standard deviation where only one or two samples yielded EFs.

Only preliminary data are presently available on elemental concentrations in saguaro cactus tissue. We have just completed the dissection and freeze-drying of the 120 samples taken during the spring of 1990 (yielding 360 independent fractions for chemical analysis) and have not yet begun elemental measurements. Elemental concentration trends for manganese in four cacti along the northern end of the Cactus Forest Trail (RMD) are shown in Figure 1. Cacti were sampled in 1988 at different heights along the stem and divided into the previously described three tissue types. Of 13 elements thus far determined, only manganese exhibited any dramatic trends. The remainder of these data are shown in Table 2. Although these data are insufficient to implicate manganese as a causal agent, severe chlorosis (lack of chlorophyll) has been observed as a symptom of manganese toxicity in plants (Labanauskas 1966). This subject may be worthy of further investigation.

Tree-core elemental measurements via neutron activation have proven to be particularly difficult. Relatively high concentrations of manganese in the woody tissue have provided an intense analytical interference and severely hampered our ability to produce quantitative data for any other element. We are currently investigating other analytical techniques which are not so sensitive to the manganese concentrations in these samples. Similar problems have been encountered in the lichen samples and these have also failed to yield usable data at this time.

DISCUSSION

Several elements (silver [Ag], arsenic [As], bromine [Br], gallium [Ga], Indium [In], lead [Pb], antimony [Sb], selenium [Se], vanadium [V], and zinc [Zn]) have become established as indicators of various types of sources for regional inorganic air pollution (Gladney 1991). This list is worth keeping in mind during the following discussion on interpretation of the data gathered at SNM.

Soil data (Table 1) can be divided into roughly four groups for the purposes of this presentation: (1) elements that are so often at or below our limits of detection that no valid conclusions may be drawn; (2) elements that show depletions relative to Wedepohl's crustal abundances, with EFs consistently below 0.5; (3) those that exhibit EFs near 1.0 (0.5-2.5); and (4) constituents that have EFs greater than 2.5 for a significant number of sites. The last group is the arena to examine for evidence of anthropogenic air pollution input to the SNM ecosystem. The reason we chose the EF range of 0.5-2.5 to represent "no impact" for this approach is that natural variability in soils can be quite high. One must be careful not to overinterpret EF data near 1.0, but instead look for large deviations, preferably an order of magnitude or more. Even elevated levels in soils may not be biologically available, and plants growing in these soils need to be analyzed in addition to the soils to provide evidence for actual uptake.

The data in Table 1 indicate that Ag, iodine [I], In, and Se are candidates for the first group, i.e., uninterpretable because of limited data. Some data for In and Se occur with above detection limit concentrations; these will be discussed along with the other indicator elements, although any conclusions for these two elements have high levels of uncertainty. Several elements that fell into the second category (depleted), seldom exhibited this behavior elsewhere, in our experience. Calcium [Ca], chlorine [Cl], cobalt [Co], magnesium [Mg], and sometimes sodium [Na] and scandium [Sc], showed depletions over large areas of SNM and in many of the background sites as well. Although this has no air pollution implication, it seems to represent an unanticipated characteristic of southwestern soils. This also provides a counterargument to the hypothesis that saguaros are suffering from elevated levels of "salt" exposure, because these readily mobile elements seem to have been effectively leached from the soils studied. The third group (within normal natural ranges) is the largest: barium [Ba], Br, cerium [Ce], chromium [Cr], dysprosium [Dy], europium [Eu], iron [Fe], fluorine [F], Ga, potassium [K], lanthanum [La], lutetium [Lu], manganese [Mn], Na, neodymium [Nd], rubidium [Rb], Sc, silicon [Si], samarium [Sm], strontium [Sr],

tantalum [Ta], terbium [Tb], titanium [Ti], uranium [U], V, ytterbium [Yb], and Zn. We have discovered little, if any, evidence that concentrations of these elements in SNM soils are being affected by any anthropogenic source.

The fourth group, those with EFs consistently in excess of 2.5, contained some unusual members. We place As, cesium [Cs], hafnium [Hf], In, Sb, Se, thorium [Th], tungsten [W], and zirconium [Zr] in this group for which further scrutiny is required to determine possible nonnatural sources for elevated levels (relative to Wedepohl's crustal average) observed in many or most samples taken during this study. Concentrations of these elements (except Cs, In, and Se) in the TMD samples that were separated into four particle size groups, also exhibited marked preference for the smallest size fraction of soil particles. This phenomenon suggests that the enrichment of six of these elements may be related, although Hf, Th, W, and Zr are rarely found in excess concentrations in airborne emissions (except for some municipal incinerator air particulates in the eastern United States; Greenberg 1976). The four elements are associated and enriched in naturally-occurring zircons and zeolites. These minerals are highly resistant to chemical weathering, and may be ground to fine particles that are retained for extended time periods in this ecosystem, in concert with their system-wide higher EFs. We have no explanation for the unusually high EFs observed for Cs in the San Manuel Canyon and SNM Cactus Forest (Table 1). Ordinarily this element has no air pollution input or implications.

Indium, Sb, and Zn are significantly enriched in the soils from the smelter canyon, in SNM soils from the RMD, and in many of the regional "background" sites. These elements are more strongly enriched in the surface soils of the smelter canyon, and are commonly associated with the roasting process for sulfide ore oxidation and metal recovery. Regional impacts from these elements probably occur from the metal smelting industry in southern Arizona. Throughout the regional samples we examined, these elements were significantly more enriched in the surface soils relative to the subsurface soils, implying that air pollutant deposition can be a major source. Arsenic, another element commonly associated with copper ore reduction, does not yield such a clear interpretation. The problem is largely due to arsenic concentrations being near detection limits, thereby reducing our ability to make a meaningful regional assessment of distribution. Arsenic is a well known air pollutant arising from the metal smelting industry (including copper) in the Tacoma, Washington, area and we suspect that it would show a similar distribution to Sb, were our analytical method more sensitive. To date, we have observed no evidence that any airborne elements are being taken up or accumulated at elevated levels in tree rings or saguaro cactus tissue.

The preliminary saguaro tissue data provided in Figure 1 and Table 2 have some interesting implications. Cacti # 51-53 appeared to be relatively healthy individuals, while cactus 54 exhibited substantial browning on the south side coupled with general spine loss over the lower portion of the stem. Surface discoloration extended deep into the parenchyma tissue and, together with a characteristic odor of complex phenolic compounds, was observed on samples immediately after collection. Of the 13 elements thus far studied, only manganese seems to correlate with the observed external injury symptoms. To date, no direct evidence of elemental input to the SNM ecosystem has been observed in the few cactus tissue samples examined. We hope that the 1989-1990 RMD cactus samples will provide more straightforward data for these correlations, as well as for the relationship between elemental concentration and damage index.

SUMMARY AND MANAGEMENT IMPLICATIONS

Application of the EF approach to the air particulate data taken on the dichotomous sampler at the SNM air quality monitoring station clearly indicates that certain elements are currently enriched in the air particulates coming into the monument. Similarly, several trace elements in the soil samples also indicate anthropogenic impact, probably from dry deposition of air pollutant particulates. We do not yet see clear evidence that this source of trace elemental enrichment of the SNM ecosystem has had any impact on the biologial resources of the monument. We want to evaluate the relationship in detail when all analytical data on biological samples are available. Visibility impact assessments are not part of

this interagency agreement and are being studied by another group within the NPS Air Quality Division. Even though we have used some of the data from this network, our conclusions should not be interpreted in terms of visibility impact.

Clearly, saguaro cacti (and perhaps other cactus species) are undergoing a continuing decline within SNM. While our data do not implicate anthropogenic air pollution impacts for inorganic elements, atmospheric emissions related to the Tucson metropolitan area cannot yet be disregarded as a potential cause for the decline. The complex nature of anthropogenic modification of the organic compound burden of atmospheric aerosols is just beginning to be understood. Direct impact from the leeward drift of agricultural chemicals (herbicides and pesticides) from airborne spraying operations, or other organic chemical enrichment from diffuse urban sources, should be considered a high priority for investigating the mechanism underlying the observed decline in the cactus populations.

Unfortunately, organic chemical analyses in natural materials are far more difficult and expensive to conduct than inorganic determinations, and the spectrum of compounds runs into the millions. Some preliminary evidence is available from unpublished work conducted by colleagues at LANL that short-chained organic acids readily penetrate the waxy cuticles of cacti, perhaps having a heretofore unanticipated "acid-rain" effect on desert ecosystems (Gaffney 1988). Evans (1984) has also speculated on the permeability of waxy cuticles to polar versus non-polar compounds.

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Table 1. Summary of enrichment factors for soils collected at Saguaro National Monument, Catalina Mountains, Chiricahua National Monument, Walnut Canyon National Monument, and Gila Cliff Dwellings National Monument, 1987-1990.

Site	Depth (in.)	# Samples	Ag	As	Ba	Br	Ca	Ce	Cl	Co
San Manuel Smelter										
-0.5 km	0	4	—	—	1.2±0.2	—	1.1±0.7	2.2±0.4	0.2	2.0±0.2
	15	4	—	—	1.4±0.3	—	0.6±0.1	2.2±0.2	0.2	2.2±0.6
-2 km	0	3	—	—	1.2±0.1	—	0.5±0.1	2.0±0.1	0.4	1.7±0.2
	15	3	—	—	1.2±0.1	—	0.5±0.1	2.3±0.6	0.4	1.6±0.2
-5 km	0	3	—	—	1.1±0.1	—	0.4±0.1	1.3±0.3	0.1	1.1±0.2
	15	3	—	—	1.2±0.2	—	0.4±0.1	2.0±0.5	0.2	1.7±0.1
-1 mi	0	2	—	—	1.4	—	1.5	1.4	0.4	1.7
	6	2	—	—	1.2	—	2.6	1.4	0.4	1.8
Saguaro National Monument										
RMD-1	0	3	—	—	1.3±0.1	—	0.3±0.1	2.1±0.1	—	0.6±0.1
	15	3	—	—	1.3±0.1	—	0.2	2.0±0.2	—	0.7±0.1
RMD-2	0	3	—	—	1.1±0.2	—	0.3±0.1	2.4±0.8	—	0.6±0.1
	15	3	—	—	1.2±0.1	—	0.4±0.1	1.7±0.2	0.1	0.5±0.1
RMD-3	0	3	—	—	1.2±0.2	—	0.4±0.2	2.0±0.2	0.2	0.6±0.1
	15	3	—	—	1.1±0.2	—	0.3±0.2	1.8±0.4	0.2	0.6±0.1
Exclosure	0	11	—	—	1.0±0.1	—	0.2±0.1	1.4±0.2	0.5±0.3	1.0±0.2
	6	8	—	—	0.8±0.1	—	0.2±0.1	1.4±0.2	0.3±0.1	1.2±0.1
	12	8	—	—	0.8±0.1	—	0.2±0.1	1.4±0.2	0.3±0.1	1.2±0.2
Kiln Trail	0	19	—	—	1.2±0.2	—	0.4±0.2	2.0±0.5	0.2±0.1	0.6±0.2
	6	16	—	—	1.0±0.2	—	0.4±0.3	1.7±0.3	0.3±0.2	0.7±0.1
	12	4	—	—	1.1±0.1	—	0.9±0.4	2.0±0.3	0.1	0.7±0.1
RMD-CP-5	0	14	105	2.2±0.3	1.2±0.1	1.0±0.6	0.4±0.2	1.9±0.3	—	0.5±0.1
	6	14	—	2.5±0.4	1.0±0.1	2.2±0.7	0.3±0.1	1.6±0.1	—	0.7±0.1
RMD-CP-9	0	18	—	1.6±0.3	1.2±0.1	0.9±0.5	0.4±0.1	2.5±0.6	—	0.5±0.1
	6	18	—	2.0±0.5	1.0±0.1	2.6±1.1	0.6±0.5	1.8±0.2	—	0.6±0.1
RMD-CP10	0	18	—	2.5±0.4	1.2±0.4	1.0±0.6	0.5±0.3	1.8±0.2	—	0.6±0.1
	6	18	—	3.5±0.4	0.8±0.1	5.6±3.0	0.9±0.8	1.3±0.3	—	0.7±0.1
RMD-CP15	0	18	—	2.7±0.3	1.2±0.2	1.5±0.9	1.2±1.3	1.6±0.2	—	0.6±0.1
	6	19	23	3.4±0.5	1.0±0.2	4.8±1.6	1.1±1.0	1.3±0.2	—	0.8±0.1
RMD-CP17	0	18	—	2.7±0.3	1.0±0.2	0.8±0.5	0.3±0.1	1.7±0.5	—	0.6±0.1
	6	18	—	3.0±0.6	0.7±0.2	3.1±1.2	0.3±0.2	1.2±0.3	—	0.6±0.1
Limestone		4	—	—	1.7±0.8	—	340±130	1.9±1.3	0.9	0.7±0.3
Slag		3	—	—	1.1±0.1	—	0.9±0.1	1.2±0.1	0.1	0.7±0.1
TMD-1	0	7	—	2.3±0.8	1.0±0.2	—	0.3±0.1	1.5±0.1	0.3±0.1	0.4±0.2
	6	7	—	2.0	0.9±0.2	1.3	0.3±0.1	1.4	0.3±0.1	0.4
TMD-2	0	4	—	2.6±0.8	1.2±0.2	0.5	0.3±0.1	1.5±0.3	0.4	0.5±0.1
	6	2	—	3.2±0.8	1.0±0.1	0.8±0.2	0.3±0.1	1.6±0.3	0.4	0.6±0.2
TSP	0	10	—	—	0.8±0.2	—	0.4±0.1	0.8±0.2	0.4±0.2	0.4±0.2
	6	10	—	—	0.8±0.4	—	0.4±0.1	0.8±0.4	0.4±0.5	0.4±0.2
NSP	0	18	—	—	1.0±0.5	—	0.6±0.5	0.8±0.2	3±3	—
	6	18	—	—	0.6±0.1	—	0.3±0.1	0.9±0.2	0.4±0.2	0.3±0.1
	12	5	—	—	0.4±0.1	—	0.3±0.1	0.8±0.1	0.4	0.2±0.1
Regional Background										
CATAL	0	3	—	—	1.0±0.6	—	0.6±0.6	0.5±0.3	2.0	1.3
	6	3	—	—	0.5±0.2	—	0.3±0.1	0.3±0.1	0.3	0.2±0.1
	12	3	—	—	0.5±0.2	—	0.2±0.1	0.3±0.1	0.2±0.2	0.2
CHIR	0	15	—	—	0.8±0.4	—	0.4±0.3	1.4±0.3	0.4±0.2	0.3±0.2
	6	15	—	—	0.6±0.2	—	0.2±0.1	1.7±0.4	0.4±0.2	0.3±0.1
WACA	0	6	—	—	1.3±0.2	—	0.8±0.1	1.2±0.1	0.4±0.2	2.3±0.4
	6	6	—	—	1.0±0.1	—	0.4±0.1	1.1±0.1	0.2±0.1	2.0±0.2
GILA	0	6	—	—	1.0±0.2	—	0.4±0.2	1.4±0.2	0.6±0.2	0.7±0.1
	6	6	—	—	1.2±0.2	—	0.4±0.2	1.5±0.3	0.2±0.1	0.6±0.1

Table 1. Continued.

Site	Depth (in.)	# Samples	Cr	Cs	Dy	Eu	Fe	F	Ga	Hf	I
San Manuel Smelter											
-0.5 km	0	4	1.5±0.2	4.2±0.3	2.6±0.4	1.8±0.1	5.3±0.8	—	—	9.8±0.8	—
	15	4	1.6±0.2	4.9±0.2	3.0±0.4	1.9±0.4	6.7±1.6	—	—	12±3	—
-2 km	0	3	1.1±0.1	4.3±0.1	2.0	1.7±0.1	3.8±0.2	—	—	13±1	—
	15	3	0.9±0.1	4.5±0.3	2.5±0.6	1.7±0.1	3.5±0.4	—	—	11±3	—
-5 km	0	3	0.9±0.4	3.6±0.4	1.3±0.4	1.5±0.3	2.3±1.0	—	—	6±2	—
	15	3	1.2±0.1	4.3±0.2	1.9±0.4	1.6±0.1	3.2±0.4	—	—	8.5±0.3	—
-1 mi	0	2	1.0	3.6	1.6	1.4	2.6	—	—	7.6	—
	6	2	1.0	3.7	2.2	1.5	2.5	—	4.5	7.8	—
Saguaro National Monument											
RMD-1	0	3	0.7±0.2	2.7±0.1	3.4±0.6	1.6±0.1	1.3±0.3	—	—	8.3±1.5	—
	15	3	0.7±0.1	3.3±0.2	2.7±0.2	1.3±0.1	1.2±0.1	—	—	6.3±0.2	—
RMD-2	0	3	0.6±0.2	2.4±0.2	2.7±1.3	1.7±0.5	1.2±0.8	—	—	3.6	—
	15	3	0.5±0.1	3.1±0.2	2.0±0.7	1.3±0.1	0.9±0.1	—	—	3.7±0.6	—
RMD-3	0	3	0.5±0.1	2.8±0.3	2.0	1.6±0.2	1.0±0.1	—	—	5.2±1.1	—
	15	3	0.5±0.1	3.4±0.7	1.7±0.4	1.4±0.4	0.9±0.1	—	—	3.9±0.5	—
Exclosure	0	11	0.8±0.1	8.3±1.3	1.2±0.1	1.0±0.1	1.0±0.2	0.6	—	2.9±0.5	—
	6	8	0.7±0.1	9.6±0.9	1.2±0.2	1.1±0.1	1.0±0.1	0.9	—	2.2±0.4	—
	12	8	0.7±0.1	9.3±1.4	1.2±0.3	1.0±0.1	1.0±0.1	0.4	—	2.0±0.3	—
Kiln Trail	0	19	0.6±0.1	5±5	2.1±0.6	1.4±0.3	0.8±0.2	0.5±0.2	—	5.2±1.6	—
	6	16	0.6±0.1	8±9	1.7±0.4	1.3±0.2	0.8±0.1	0.6±0.1	—	3.4±0.8	—
	12	4	0.6±0.1	7±3	1.8±0.1	1.4±0.1	0.8±0.1	0.6	—	3.5±0.3	—
TMD-CP-5	0	14	0.5±0.1	2.4±0.3	2.8±0.4	1.3±0.2	1.0±0.2	—	1.0	6.4±1.4	—
	6	14	0.7±0.1	2.9±0.4	2.1±0.2	1.2±0.1	0.9±0.1	—	1.0±0.2	4.4±0.6	—
TMD-CP-9	0	18	0.4±0.1	1.9±1.0	3.0±0.8	1.7±0.3	0.9±0.2	—	1.1±0.1	6.3±1.8	—
	6	18	0.6±0.1	2.4±1.2	2.1±0.3	1.4±0.2	0.9±0.1	—	1.1±0.3	3.7±0.6	36
RMD-CP-10	0	18	0.6±0.1	2.5±0.3	2.6±0.5	1.3±0.2	1.1±0.2	—	1.1±0.2	5.9±1.2	—
	6	18	0.6±0.1	2.9±0.3	1.6±0.4	1.1±0.2	0.9±0.1	—	1.0±0.2	3.3±1.0	25±14
RMD-CP-15	0	18	0.6±0.1	3.2±0.6	1.9±0.4	1.2±0.2	1.1±0.2	—	1.0±0.2	5.0±1.0	—
	6	19	0.6±0.1	3.5±0.8	1.5±0.2	1.1±0.1	1.0±0.1	—	1.0±0.3	3.4±0.9	23±9
RMD-CP-17	0	18	0.5±0.1	6.8±4.9	2.0±0.6	1.3±0.3	1.0±0.2	—	1.0±0.2	5.5±2.0	—
	6	18	0.6±0.2	7.1±5.6	1.5±0.4	1.0±0.2	0.8±0.2	—	1.1±0.2	2.6±0.7	26±12
Limestone		4	5±3	1.4±0.9	—	1.7±1.1	1.1±0.9	3.0	—	4.1±1.3	—
Slag		3	0.6±0.1	4.6±0.3	1.2	1.1±0.1	0.8±0.1	0.1	—	2.6±0.2	—
TMD-1	0	7	0.3±0.2	2.3±0.3	0.7±0.3	0.7±0.2	0.6±0.2	—	1.1	3.4±2.0	—
	6	7	0.3	2.3	0.9±0.3	0.8±0.2	0.6	—	1.2	3.7	—
TMD-2	0	4	0.4±0.2	2.0±0.2	0.8±0.3	0.8±0.1	1.1±0.4	—	1.2±0.5	3.5±1.5	—
	6	4	0.5±0.2	2.3±0.2	0.9±0.3	0.8±0.2	1.3±0.6	—	1.0±0.2	3.8±2.1	—
TSP	0	10	2.3±2.0	1.9±0.6	1.0±0.4	0.6±0.1	0.5±0.2	0.5	—	1.8±0.6	—
	6	10	0.4±0.2	1.8±0.6	1.9±0.8	0.6±0.2	0.5±0.2	0.4	—	2.0±0.8	—
NSP	0	18	2.9±1.7	2.4±1.0	1.2±0.2	0.6±0.2	0.6±0.2	0.8	—	3.6±2.3	—
	6	18	0.3±0.1	1.5±0.4	1.5±0.5	0.6±0.1	0.4±0.1	0.8±0.6	—	1.9±0.5	—
	12	5	0.2±0.1	1.0±0.1	1.0±0.3	0.5±0.1	0.4±0.1	—	—	1.5±0.3	—
Regional Background											
CATAL	0	3	2.2±1.9	1.6±0.8	0.4	0.3±0.1	0.5±0.2	0.7	—	1.3±0.7	—
	6	3	0.2±0.1	0.8±0.2	0.4±0.2	0.2±0.1	0.3±0.1	0.7	—	0.8±0.1	—
	12	3	0.2±0.1	0.8±0.2	0.7	0.2±0.1	0.3±0.1	0.9	—	0.7±0.1	—
CHIR	0	15	0.7±0.6	3.0±0.6	1.2±0.1	0.5±0.2	0.6±0.1	0.3	—	4.6±1.1	—
	6	15	0.3±0.1	3.1±0.4	1.5±0.5	0.4±0.1	0.6±0.1	0.6	6.6	4.7±0.6	—
WACA	0	6	2.1±0.3	2.7±0.2	0.9±0.2	1.3±0.2	1.5±0.1	0.6	—	4.4±0.6	—
	6	6	1.7±0.3	3.1±0.3	0.8±0.1	1.2±0.1	1.4±0.1	0.6	4.1	3.5±0.8	—
GILA	0	6	0.7±0.2	1.6±0.3	1.9±0.4	0.8±0.1	0.8±0.1	0.4	—	4.0±0.5	—
	6	6	0.7±0.1	1.7±0.1	2.3±0.9	0.8±0.1	0.8±0.1	0.6	3.6	4.2±0.4	—

Table 1. Continued.

Site	Depth (in.)	# Samples	In	K	La	Lu	Mg	Mn	Na	Nd	Rb
San Manuel Smelter											
-0.5 km	0	4	13±8	1.3±0.2	—	—	0.7	4.6±1.4	0.7±0.2	—	2.2±0.3
	15	4	—	1.2±0.2	—	—	0.7	5.6±1.1	0.7±0.1	—	1.9±0.1
-2 km	0	3	6.0	1.3±0.1	—	—	0.6	3.3±0.4	0.8±0.1	—	2.1±0.2
	15	3	—	1.1±0.1	—	—	0.4	3.7±0.4	0.7±0.1	—	1.7±0.2
-5 km	0	3	6.2	1.3±0.1	—	—	0.4	2.4	0.7±0.1	—	2.0±0.3
	15	3	—	1.2±0.1	—	—	0.5	2.5±0.4	0.6±0.1	—	1.6±0.1
-1 mi	0	2	9.3	1.2	—	—	0.8	2.2	0.6	—	1.4
	6	2	—	1.1	—	—	0.9	2.0	0.5	—	1.2
Saguaro National Monument											
RMD-1	0	3	—	1.3±0.1	—	—	—	1.6±0.2	0.7±0.1	—	1.7±0.1
	15	3	—	1.1±0.1	—	—	0.4	1.7±0.2	0.5±0.1	—	1.3±0.1
RMD-2	0	3	—	1.2±0.2	—	—	0.4	1.3±0.6	0.8±0.1	—	1.5±0.2
	15	3	—	1.0±0.1	—	—	0.4	1.0±0.2	0.7±0.2	—	1.1±0.1
RMD-3	0	3	—	1.2±0.1	—	—	0.4	1.2±0.2	0.7±0.1	—	1.4±0.1
15	3	—	0.9±0.1	—	—	0.4±0.1	1.1±0.3	0.5±0.2	—	1.1±0.1	
Exclosure	0	11	—	1.1±0.1	—	—		0.4±0.1	0.9±0.1	0.4±0.1	—
	6	8	1.9	0.9±0.1	—	—		0.5±0.1	0.9±0.1	0.3±0.1	—
	12	8	—	0.9±0.1	—	—		0.5±0.1	0.9±0.1	0.3±0.1	—
Kiln Trail	10	19	—	1.1±0.1	—	—		0.4±0.1	1.1±0.2	0.8±0.2	—
	6	16	1.6	1.0±0.1	—	—		0.5±0.1	0.9±0.2	0.5±0.2	—
	12	4	—	1.1±0.1	—	—		0.6±0.1	1.0±0.1	0.6±0.1	—
RMD-CP-5	0	14	—	1.3±0.1	1.6±0.2	3.5±0.7		0.3±0.1	1.5±0.2	0.7±0.1	2.6±0.6
	6	14	1.1	1.1±0.1	1.3±0.1	2.6±0.3		0.3±0.1	1.1±0.1	0.6±0.1	2.2±0.2
RMD-CP-9	0	18	—	1.2±0.1	2.1±0.4	3.1±0.8		0.3±0.1	1.2±0.2	0.8±0.1	3.1±0.9
	6	18	—	1.0±0.1	1.5±0.2	2.0±0.4		0.3±0.1	1.0±0.1	0.6±0.1	2.2±0.6
RMD-CP-10	0	18	1.7	1.2±0.1	1.5±0.2	3.2±0.8		0.4±0.1	1.4±0.2	0.6±0.1	2.2±0.5
	6	18	1.6	0.9±0.1	1.2±0.2	1.8±0.5		0.4±0.1	0.8±0.2	0.4±0.1	1.6±0.4
RMD-CP-15	0	18	—	1.1±0.1	1.3±0.2	2.1±0.6		0.5±0.2	1.2±0.2	0.6±0.1	2.0±0.5
	6	19	1.6	1.0±0.1	1.1±0.1	1.6±0.3		0.4±0.1	0.9±0.1	0.5±0.1	1.8±0.5
RMD-CP-17	0	18	—	1.2±0.1	1.4±0.5	2.3±0.6		0.3±0.1	1.6±0.3	0.8±0.1	2.2±0.7
	6	18	1.4	1.0±0.2	1.0±0.3	1.7±0.6		0.3±0.1	1.3±0.5	0.6±0.1	1.5±0.6
Limestone		4	—	—	—	—		5.4±2.2	4.8±0.1	0.1	—
Slag		3	—	1.2±0.2	—	—		0.8±0.1	1.0±0.1	0.6±0.1	—
TMD-1	0	7	—	1.0±0.1	1.4±0.1	0.8±0.3		0.3±0.1	0.5±0.1	1.1±0.4	1.4±0.2
	6	7	—	1.0±0.1	1.3	0.8		0.3±0.1	0.6±0.2	1.1±0.2	1.6
TMD-2	0	4	—	1.2±0.1	1.5±0.2	0.9±0.2		0.3	0.6±0.2	1.1±0.2	1.7±0.5
	6	4	—	1.1±0.1	1.6±0.3	1.0±0.3		0.3±0.1	0.7±0.2	0.9±0.2	1.9±0.6
TSP	0	10	—	1.0±0.3	—	—		0.6	1.9±0.3	0.9±0.2	—
	6	10	—	0.8±0.2	—	—		0.6	2.4±1.1	0.9±0.3	—
NSP	0	18	5.7	1.2±0.2	—	—		0.4	2.1±1.1	0.7±0.2	—
	6	18	—	0.9±0.1	—	—		0.2±0.1	1.2±0.3	0.9±0.1	—
	12	5	—	0.9±0.1	—	—		—	1.0±0.4	0.9±0.1	—
Regional Background											
CATAL	0	3	—	0.9±0.2	—	—		—	3.0	1.0±0.2	—
	6	3	—	0.8±0.1	—	—		—	1.6±0.8	1.2±0.1	—
	12	3	—	0.8±0.1	—	—		—	2.0±0.2	1.2±0.1	—
CHIR	0	15	—	1.4±0.2	—	—		—	3.3±2.1	0.9±0.2	—
	6	15	3.2	1.4±0.2	—	—		0.4±0.1	1.1±0.3	0.9±0.2	—
WACA	0	6	—	0.8±0.1	—	—		1.1±0.2	1.4±0.1	0.3±0.1	—
	6	6	—	0.6±0.1	—	—		0.9±0.2	1.0±0.1	0.2±0.1	—
GILA	0	6	—	1.3±0.1	—	—		0.6±0.1	1.4±0.2	0.8±0.1	—
	6	6	—	1.4±0.1	—	—		0.6±0.1	1.3±0.2	0.8±0.1	—

Site	Depth (in.)	Sc	Sm	Sr	Ta	Tb	Th	U	V	Yb	Zn
San Manuel Smelter											
-0.5 km	0	1.2±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	15	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
-2 km	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	15	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
-5 km	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	15	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
-1 mi	0	1.1	0.8	110	—	—	1.2	—	10	0.6	1.2
	6	1.1	0.8	110	—	—	1.2	—	10	0.6	1.2
Saguaro National Monument											
RMD-1	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	15	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-2	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	15	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-3	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
15	3	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
Exclosure	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	12	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
Kiln Trail	10	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	12	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-CP-5	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-CP-9	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-CP-10	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-CP-15	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
RMD-CP-17	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
Limestone		1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
Slag		1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
TMD-1	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
TMD-2	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
TSP	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
NSP	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	12	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
Regional Background											
CATAL	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	12	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
CHIR	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
WACA	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
GILA	0	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2
	6	1.1±0.1	0.8±0.1	110±20	—	—	1.2±0.2	—	10±2	0.6±0.1	1.2±0.2

Table 1. Continued.

Site	Depth (in.)	# Samples	Sb	Sc	Se	Si	Sm	Sr	Ta	Tb	Th
San Manuel Smelter											
-0.5 km	0	4	34±14	1.8±0.2	—	1.2±0.1	2.4±0.1	—	1.8±0.4	—	3.2±0.6
	15	4	14±4	2.3±0.5	—	1.2±0.2	3.0±0.7	—	2.8±0.9	—	4.4±2.2
-2 km	0	3	22±4	1.6±0.1	—	1.2±0.1	2.1±0.1	—	1.7±0.2	—	3.7±1.6
	15	3	10.5±0.3	1.6±0.2	—	1.2±0.1	2.4±0.3	—	1.7±0.2	—	3.0±0.1
-5 km	0	3	20±7	1.1±0.3	—	1.3±0.1	1.6±0.4	—	1.1±0.3	—	2.2±1.5
	15	3	13.9±1.3	1.4±0.1	—	1.2±0.1	2.0±0.2	—	1.3±0.4	—	2.1±0.5
-1 mi	0	2	36	1.2	—	1.2	1.3	—	0.9	1.0	2.2
	6	2	13	1.0	—	1.1	2.2	—	1.0	1.6	1.8
Saguaro National Monument											
RMD-1	0	3	9.5±0.4	0.7±0.1	—	1.4±0.1	2.4±0.4	—	0.5±0.2	—	2.9±0.2
	15	3	8.0±1.7	0.8±0.1	—	1.1±0.1	1.9±0.3	—	1.3±1.3	—	2.4±1.3
RMD-2	0	3	6.3±1.1	0.8±0.1	—	1.2±0.1	2.0±0.7	1.0	0.4±0.1	—	2.8±1.0
	15	3	7.4±1.9	0.7±0.1	—	1.1±0.1	1.8±0.3	—	0.4	—	2.0±0.3
RMD-3	0	3	4.9±1.7	0.7±0.1	—	1.2±0.1	2.3±0.2	—	0.4±0.1	—	2.4±0.4
	15	3	4.3±1.3	0.7±0.1	—	0.9±0.1	2.1±0.3	—	0.4±0.1	—	2.0±0.3
Exclosure	0	11	8.0±1.1	0.8±0.1	—	0.9±0.1	1.2±0.2	—	0.4±0.1	0.7±0.1	1.6±0.2
	6	8	6.3±1.2	0.8±0.1	—	0.8±0.1	1.3±0.2	—	0.4±0.1	0.7±0.1	1.5±0.2
	12	8	5.8±1.2	0.8±0.1	—	0.7±0.1	1.2±0.2	—	0.3±0.1	0.7±0.2	1.4±0.2
Kiln Trail	0	19	7.7±2.9	0.7±0.1	—	1.1±0.1	1.9±0.5	2.1	0.4±0.1	1.4±0.5	2.3±0.7
	6	16	6.7±1.8	0.8±0.1	—	0.9±0.2	1.6±0.2	—	0.3±0.1	1.2±0.2	1.9±0.2
	12	4	7.0±1.8	0.8±0.1	—	1.0±0.1	1.8±0.3	—	0.3±0.1	1.2±0.1	1.9±0.1
RMD-CP-5	0	14	7.5±0.7	0.6±0.1	9.8	—	2.1±0.3	—	0.4±0.1	1.6±0.2	2.4±0.4
	6	14	6.0±0.7	0.7±0.1	7.7	—	1.6±0.1	—	0.4±0.1	1.4±0.1	2.0±0.2
RMD-CP-9	0	18	4.1±2.0	0.7±0.1	—	—	2.7±0.6	0.9	0.4±0.1	2.0±0.5	3.0±0.8
	6	18	4.3±2.1	0.7±0.1	—	—	1.9±0.3	1.0	0.3±0.1	1.4±0.2	2.1±0.3
RMD-CP-10	0	18	6.9±0.7	0.7±0.1	—	—	1.9±0.2	1.4	0.5±0.1	1.6±0.3	2.3±0.3
	6	18	5.9±1.0	0.7±0.1	—	—	1.4±0.3	—	0.3±0.1	1.1±0.2	1.7±0.3
RMD-CP-15	0	18	7.8±1.0	0.7±0.1	—	—	1.6±0.2	1.8±1.0	0.5±0.1	1.2±0.2	1.9±0.3
	6	19	6.8±1.2	0.7±0.1	—	—	1.4±0.2	1.0±0.3	0.4±0.1	1.0±0.2	1.7±0.2
RMD-CP-17	0	18	5.8±0.9	0.7±0.1	8.8	—	1.8±0.6	—	0.8±0.3	1.3±0.4	2.1±0.7
	6	18	4.7±1.6	0.7±0.1	—	—	1.4±0.4	—	0.6±0.3	0.9±0.2	1.5±0.4
Limestone		4	40±40	0.6±0.2	—	1.7±1.0	4.1±1.8	33±5	0.6±0.2	1.7±0.7	0.8±0.2
Slag		3	7.3±0.9	0.7±0.1	—	1.0±0.1	1.2±0.1	—	0.3±0.1	0.9±0.2	1.4±0.1
TMD-1	0	7	5.8±2.4	0.4±0.2	7.3	—	1.0±0.2	1.3±0.3	0.6±0.1	0.5±0.2	2.9±1.4
	6	7	5.6	0.4	—	—	0.9	1.1±0.2	0.6	0.4	3.0
TMD-2	0	4	6.6±2.5	0.4±0.2	200	—	1.1±0.3	0.7	0.6±0.1	0.6±0.2	3.4±2.3
	6	4	6.7±1.9	0.4±0.2	280	—	1.1±0.4	—	0.6±0.2	0.6±0.2	3.6±1.8
TSP	0	10	6.8±2.7	0.6±0.2	—	1.0±0.1	1.2±0.5	—	1.0±0.7	1.1±0.5	1.1±0.4
	6	10	2.4±0.7	0.6±0.2	—	0.9±0.2	1.1±0.5	—	0.5±0.1	1.1±0.4	1.0±0.5
NSP	0	18	12±10	0.6±0.1	—	1.1±0.3	0.8±0.2	—	1.3±0.8	—	1.1±0.3
	6	18	2.6±0.9	0.7±0.1	—	0.8±0.1	0.8±0.2	—	0.4±0.2	—	1.3±0.3
	12	5	2.4±1.0	0.7±0.1	—	0.7±0.1	0.8±0.2	—	0.5±0.2	—	1.2±0.2
Regional Background											
CATAL	0	3	9±5	0.4±0.2	—	1.0±0.1	0.7±0.4	—	0.9±0.5	—	0.6±0.3
	6	3	2.5±0.4	0.3±0.1	—	0.9±0.1	0.4±0.1	—	0.5±0.1	—	0.4±0.1
	12	3	1.8±0.6	0.3±0.1	—	0.9±0.1	0.4±0.1	—	0.5±0.1	—	0.5±0.1
CHIR	0	15	8±4	0.4±0.1	—	1.2±0.2	1.5±0.4	—	1.0±0.2	—	2.4±0.6
	6	15	4.7±1.8	0.3±0.1	—	1.3±0.2	1.2±0.4	—	1.1±0.2	—	3.0±0.4
WACA	0	6	9±3	1.2±0.1	—	1.3±0.2	1.2±0.1	1.8	0.5±0.1	—	1.1±0.1
	6	6	5.5±1.3	1.2±0.1	—	1.0±0.1	1.2±0.1	—	0.5±0.1	—	1.0±0.1
GILA	0	6	5.0±1.3	0.4±0.1	—	1.0±0.1	1.9±0.2	—	0.5±0.1	—	1.6±0.2
	6	6	4.2±1.1	0.5±0.1	—	1.1±0.1	1.7±0.2	1.7	0.5±0.1	—	1.8±0.1

Table 1. Continued.

Site	Depth (in.)	# Samples	Ti	U	V	W	Yb	Zn	Zr
San Manuel Smelter									
-0.5 km	0	4	5.2±1.6	1.7±0.1	4.6±1.1	—	3.2±0.6	6.3±2.7	—
	15	4	6.1±1.6	2.5±0.4	5.8±1.4	—	4.0±0.8	4.1±1.1	—
-2 km	0	3	3.7±0.6	1.7±0.1	3.3±0.2	—	3.0±0.2	4.1±0.3	—
	15	3	3.7±0.3	1.5±0.2	2.8±0.2	—	2.9±0.6	2.4±0.2	—
-5 km	0	3	3.4±1.0	1.3±0.3	2.2±1.0	—	1.8±0.6	2.2±0.6	—
	15	3	4.0±0.5	1.3±0.2	2.7±0.3	—	2.0±0.1	2.4±0.4	—
-1 mi	0	2	2.8	1.3	2.0	—	2.0	5.2	—
	6	2	2.8	1.4	2.2	—	1.8	2.6	—
Saguaro National Monument									
RMD-1	0	3	1.2±0.2	1.6±0.2	0.9±0.1	—	4.8±1.0	1.4±0.1	—
	15	3	1.1±0.1	1.2±0.2	0.7±0.1	—	3.4±0.2	1.4±0.1	—
RMD-2	0	3	1.0±0.5	1.2±0.3	0.7±0.3	—	2.0	1.3±0.2	—
	15	3	0.8±0.1	0.9±0.1	0.6±0.1	—	2.0±0.7	1.3±0.1	—
RMD-3	0	3	0.9±0.1	1.3±0.2	0.7±0.1	—	2.5±0.1	1.3±0.1	—
	15	3	0.8±0.2	0.9±0.1	0.7±0.1	—	1.9±0.4	1.5±0.1	—
Exclosure	0	11	0.8±0.1	1.2±0.1	0.7±0.1	—	1.3±0.2	1.6±0.5	—
	6	8	0.7±0.1	1.1±0.2	0.7±0.1	—	1.2±0.2	1.4±0.1	—
	12	8	0.6±0.1	1.0±0.1	0.6±0.1	—	1.2±0.2	1.4±0.2	—
Kiln Trail	0	19	0.8±0.2	1.4±0.3	0.6±0.1	—	2.2±0.7	1.4±0.2	—
	6	16	0.7±0.1	1.1±0.2	0.6±0.1	—	1.8±0.4	1.3±0.2	—
	12	4	0.8±0.1	1.2±0.2	0.6±0.1	—	1.6±0.1	1.2±0.1	—
RMD-CP-5	0	14	1.0±0.1	1.4±0.2	0.7±0.1	2.4±0.7	4.6±0.7	1.0±0.2	3.8±0.8
	6	14	0.8±0.1	1.0±0.1	0.6±0.1	2.1±0.3	3.2±0.4	1.1±0.1	4.9±0.9
RMD-CP-9	0	18	0.9±0.2	1.4±0.4	0.6±0.1	2.1±0.9	4.0±1.1	1.0±0.1	4.5±1.4
	6	18	0.7±0.1	1.0±0.1	0.6±0.1	2.0±0.5	2.7±0.6	1.1±0.1	3.0±0.8
RMD-CP10	0	18	1.0±0.1	1.3±0.2	0.7±0.1	2.2±0.2	4.1±1.0	1.2±0.2	4.1±1.0
	6	18	0.7±0.1	0.9±0.2	0.7±0.1	2.1±0.4	2.4±0.7	1.1±0.1	2.6±1.1
RMD-CP15	0	18	1.0±0.1	1.2±0.1	0.7±0.1	2.4±0.4	2.8±0.7	1.2±0.2	3.6±0.9
	6	19	0.8±0.1	1.0±0.1	0.7±0.1	2.3±0.4	2.1±0.3	1.1±0.1	3.1±1.2
RMD-CP17	0	18	0.9±0.2	1.4±0.2	0.6±0.2	2.8±1.1	2.9±0.8	1.1±0.1	5.2±2.0
	6	18	0.6±0.1	1.0±0.3	0.6±0.1	2.8±1.3	2.2±0.8	1.0±0.2	1.7±0.6
TMD-1	0	7	0.6±0.3	1.9±0.8	0.5±0.2	3.0±0.8	—	0.8±0.4	3.3±0.4
	6	7	0.6±0.2	2.7±0.4	0.7±0.4	3.2	—	0.8	3.8
TMD-2	0	4	0.6±0.2	2.7±0.6	0.7±0.3	3.0±0.5	—	0.8±0.2	3.1±2.2
	6	4	0.7±0.2	2.8±0.7	0.8±0.4	3.0±0.8	—	0.8±0.2	2.9±1.4
TSP	0	10	0.5±0.2	1.2±0.4	0.4±0.2	—	2.2±0.6	1.6±0.5	—
	6	10	0.4±0.2	1.2±0.7	0.4±0.2	—	2.9±1.2	0.8±0.2	—
NSP	0	18	0.6±0.2	1.0±0.2	0.4±0.2	—	1.7±0.5	3.1±0.4	—
	6	18	0.4±0.1	1.2±0.4	0.3±0.1	—	2.3±0.4	1.2±0.3	—
	12	5	0.3±0.1	0.9±0.1	0.2±0.1	—	2.6±0.9	1.7±0.2	—
Regional Background									
CATAL	0	3	0.4±0.2	0.7±0.2	0.3±0.2	—	0.8±0.2	2.8±2.1	—
	6	3	0.4	0.6±0.1	0.1±0.1	—	0.6±0.2	0.8±0.1	—
	12	3	0.2	0.6±0.1	0.1	—	0.9±0.2	0.8±0.2	—
CHIR	0	15	0.7±0.2	2.0±0.4	0.4±0.1	—	1.5±0.3	2.2±0.8	—
	6	15	0.6±0.2	2.3±0.3	0.3±0.1	—	1.7±0.3	1.6±0.2	—
WACA	0	6	1.5±0.2	0.9±0.1	1.3±0.1	—	1.1±0.2	2.6±1.0	—
	6	6	1.2±0.1	0.8±0.1	1.3±0.1	—	0.9±0.1	1.6±0.2	—
GILA	0	6	0.9±0.2	1.1±0.2	0.6±0.1	—	1.8±0.3	1.8±0.2	—
	6	6	1.0±0.1	1.2±0.1	0.7±0.1	—	1.8±0.4	1.5±0.2	—

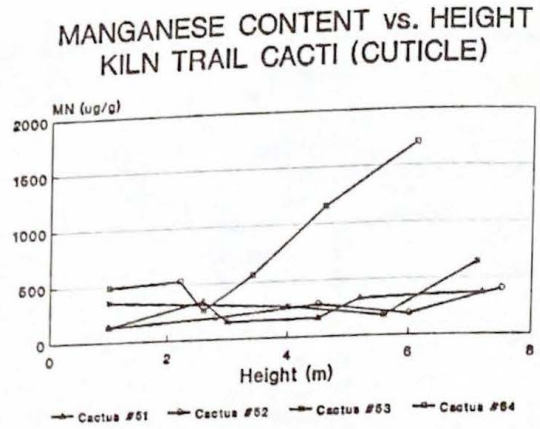
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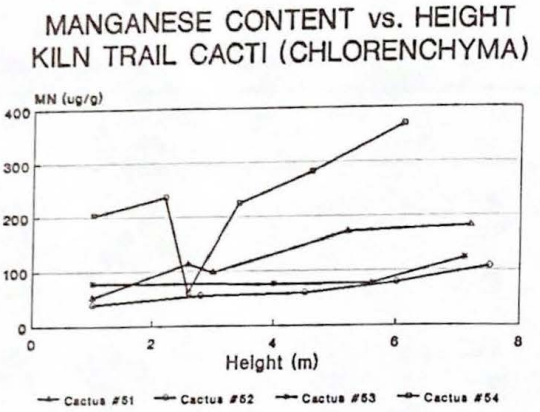
Ag - silver
Al - aluminum
As - arsenic
Ba - barium
Br - bromine
Ca - calcium
Ce - cerium
Cl - chlorine
Co - cobalt
Cr - chromium
Cs - cesium
Cu - copper
Dy - dysprosium
Eu - europium
F - flourine
Fe - iron
Ga - gallum
Hf - hafnium
I - iodine
In - indium
K - potassium
La - lanthanium
Lu - lutetium
Mg - magnesium
Mn - manganese
Na - sodium
Nd - neodymium
Pb - lead
Rb - rubidium
S - sulfur
Sb - antimony
Sc - scandium
Se - selenium
Si - silicon
Sm - samarium
Sr - strontium
Ta - tantalum
Tb - terbium
Th - thorium
Ti - titanium
U - uranium
V - vanadium
W - tungsten
Yb - ytterbium
Zn - zinc
Zr - zirconium

Table 2. Whole cactus mean elemental concentration in saguaro tissue (µg/g unless otherwise stated).

	Al	Ba	Br	Ca (%)	Cl	Cu	In (ng/g)	Mg (%)	Mn	Na	S (%)	Sr	V (ng/g)
Cuticle													
Cactus # 51	127	219	47	4.3	1650	8.7	26	0.68	260	187	0.42	272	168
Cactus # 52	76	184	16	4.7	980	6.6	27	0.65	239	179	0.44	216	81
Cactus # 53	103	256	31	5.7	1090	9.8	24	1.03	360	209	0.66	510	143
Cactus # 54	114	322	47	3.6	1270	16	35	1.14	920	250	0.68	350	200
Chlorenchyma													
Cactus # 51	47	164	77	8.6	3330	11	47	1.59	131	800	1.22	490	88
Cactus # 52	62	125	100	7.1	8100	12	51	0.99	67	770	1.20	240	79
Cactus # 53	126	186	31	10.9	2160	8.4	22	1.32	88	360	0.59	980	106
Cactus # 54	205	209	154	7.4	6400	13	50	2.02	257	650	1.20	560	160
Parenchyma													
Cactus # 51	97	153	45	5.4	1900	11	50	3.1	125	1000	1.07	370	96
Cactus # 52	75	130	86	4.4	7900	12	40	1.9	55	820	1.34	170	120
Cactus # 53	222	208	18	4.7	1400	14	36	3.0	119	930	0.65	540	102
Cactus # 54	246	290	102	8.3	5300	13	54	2.7	203	1850	1.05	606	108

Al - aluminum
Ba - barium
Br - bromine
Ca - calcium
Cl - chlorine
Cu - copper
In - indium
Mg - magnesium
Mn - manganese
Na - sodium
S - sulfur
Sr - strontium
V - vanadium





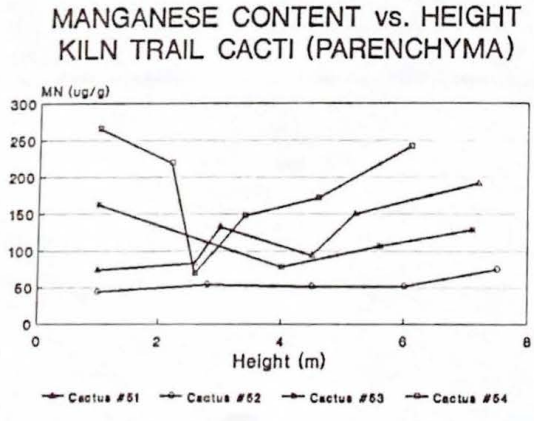


Fig. 1. Elemental concentration trends for manganese in four cacti along the northern end of the Cactus Forest Trail, Rincon Mountain District, Saguaro National Monument.

V.
Long-Term Monitoring

Epidermal Browning and Population Dynamics of Giant Saguaros in Long-Term Monitoring Plots

Dan M. Duriscoe and Sandra L. Graban

ABSTRACT

Forty-five permanent vegetation plots each comprising an area of 4 ha were established throughout both districts of Saguaro National Monument. The purpose was to identify the extent and severity of epidermal browning on giant saguaro cacti (*Carnegiea gigantea*) and to initiate long-term studies of vegetation dynamics. Results of the study indicated that epidermal browning is a widespread condition. Little geographic pattern to the condition was found, although several plots in the western portion of the Cactus Forest area (Rincon Mountain District) exhibit severe browning. Browning was much more severe on the south side of plants than the north side, was positively correlated with height (and presumably age), and was negatively correlated with spine retention. An increase in young saguaros (<0.5 m) in the Cactus Forest population over the past 10-20 years was documented

INTRODUCTION

In November 1987, the National Park Service (NPS) Air Quality Division filed a report on observations of the decline of giant saguaro cacti (*Carnegiea gigantea*) in the Rincon Mountain District (RMD) of Saguaro National Monument (SNM). Severe browning of the epidermis was reported coincident with areas of numerous dead and dying cacti, and healthier (greener) cacti were observed near and in washes, coexisting with mesquite (*Prosopis velutina*) trees. Observations of healthy saguaro stands in areas adjacent to the RMD, particularly the San Pedro Valley, led to the conclusion that the severe browning and decline of the Cactus Forest may be a localized phenomenon, possibly related to airborne contaminants (Stolte 1988). The NPS Air Quality Division sought to establish a systematic network of plots for long-term monitoring of cactus throughout both the RMD (SNM-East) and the Tuscon Mountain District (TMD; SNM-West) of SNM. According to Stolte (1988):

The sprawling urban development of the Tucson area threatens to degrade both these units. Establishment of long-term plots will enable the National Park Service to monitor the stability of this species relevant to increasing levels of urban pollutants.

OBJECTIVES

The objectives of the study were to (1) determine whether the existing cacti in the RMD of SNM are still declining and (2) develop a mechanistic understanding of the nature of the decline. Of particular interest was the characterization of the development of the epidermal browning symptom and the relationship of that symptom to susceptibility of the cacti to freeze injury (National Park Service 1988). We believed that the cacti selected within plots should

represent an unbiased sample of the entire population of saguaros within the boundaries of the monument.

METHODS

Sampling Design

The study area was defined by the political boundaries of the monument. Within these boundaries, the extent of a target population of saguaros was identified with the aid of vegetation maps. Budgetary considerations determined that a maximum of 45 plots could be established. With this in mind, we set out to devise a sampling design that would give good geographic coverage of the sample area while maintaining independence of sample points and remaining unbiased. We chose a stratified random approach to locating plot sites, as described by Taylor (1977).

The area defining the saguaro type in the RMD was divided into 25 equal portions with horizontal (east-west) and vertical (north-south) lines on the map. First, five east-west trending belts of equal area were defined, then each of these was divided into rectangular areas that included approximately 1.5 km^2 of cactus type. Thus, 25 subpopulations were defined throughout the monument (Fig. 1). This approach was taken to prevent clumping the plots, a potential result of simple random sampling. Because each of the subpopulations consisted of an equal area, each site had an equal chance of being selected if one site per subpopulation was chosen. A 100 x 100 m grid was placed over the map, defining 1-ha areas. In each of the 25 units, a grid cell was selected at random. We then attempted to establish a plot at each of these randomly chosen sites. Of the 25 random points first chosen, only one had to be rejected after field checking, after which a successful second try was made. A similar technique was employed for TMD, except that the total number of plot sites selected there was 20. Figures 2a-b identify the location of each plot as actually established; plot boundaries are shown to scale.

Plot Design

The use of permanent quadrats is appropriate for studies of vegetation dynamics (Austin 1981). A fixed area for all plots allows easy comparison of the relative importance of many plant species over time. We chose an area of 4 ha (10 a) for each plot, based on observations of the relative densities of saguaros within the sampled area. We set a minimum number for saguaros ≥2 m in height at 30 per plot, and we projected that the use of 4 ha would insure finding 30 in all areas mapped as saguaro type.

Every saguaro of a height ≥10 cm was tallied in each plot. Plants ≥2 m were then selected for detailed measurement and long-term monitoring. Thirty such plants within each plot were randomly picked from all those found. These 30 saguaros were considered to represent the 4-ha plot, and the subpopulation in which the plot was located. The total number of cacti ≥2 m found in each plot ranged from 32 to 400 (Table 1).

Within each plot, a much smaller "ecological plot" of 100 m^2 (10 x 10 m) was established for the purpose of monitoring small perennial plant species, including grasses. The methods used for these plots followed those applied by researchers at Tumamoc Hill in Tucson (Goldberg and Turner 1986). Within each ecological plot, the stem(s) and canopies of each individual plant were mapped and the species identified. Ecological plots were established with boundaries aligned with major compass directions; one of the selected saguaro cacti was in the center of each plot (Fig. 3).

Data Collection

The location of each plot was mapped on 7.5 minute topographic maps to within 30 m of the actual location. The 4-ha area was surveyed as a square 200 m on each side, accurate to about 2%. Each of the 30 saguaros selected for long-term monitoring was mapped in relation to plot boundaries and topography. Rebar stakes with yellow plastic caps were placed at each of the plot corners. A stake was placed just north of each of the selected cacti and affixed with a numbered aluminum tag for future identification. Each cactus was also photographed in color from the south side of the plant, and the maps and photographs were archived for future reference.

Variables measured at each saguaro included:

1. The height of the main stem (within ± 0.5 m);
2. A visual estimate of the percentage of the stem and arms covered with epidermal browning on both the north and south sides of the plant;
3. A visual estimate of the percentage of spines retained on the main stem and arms on both the north and south sides;

4. The number and estimated total length of arms to the nearest meter;
5. The microsite characteristics as one of six classes as an indication of moisture availability;
6. A count of squares on a 225-square grid (made of 0.5 in. hardware cloth in a wooden frame) that contained areas of epidermal browning, scarring, and undamaged tissue (the grid was placed 1.3 m above ground level on both the north and south sides of the plant);
7. The presence or absence of scars from mechanical damage, nesting birds, freezing, and discoloration caused by the presence of betacyanin. Percent visual estimates were made in classes following the Horsfall-Barrett system of plant disease measurement (Horsfall and Cowling 1978). Associated trees, shrubs, and succulent species in the immediate vicinity of each cactus were recorded.

Maps of ecological plots were digitized and a count and total canopy area for each species in each plot were obtained using a customized computer program. The total area covered by perennial grass species in each plot was estimated in the field as a percentage of the plot area and noted on each map; individual grass plants were not mapped.

RESULTS AND DISCUSSION

Epidermal Browning

Two obvious patterns emerged from the epidermal browning data: (1) taller cacti are browner and (2) the south sides of plants are browner than the north sides. The first relationship is illustrated in Figures 4a-b. Figure 4a is a plot of the mean percentage of epidermal browning on the south stem as the dependent variable (y-axis) and height in meters on the x-axis. The heights of individual plants have been "binned" into 0.25 m classes up to 7.5 m, and 0.5 m classes between 7.5 and 10 m; the relatively small number of cacti observed with heights >10 m were placed in two classes, 11-12 m and 12-14 m. The mean and standard error bars of percent browning on the south stem were plotted at the center point of each "bin". The plotted points describe a curve that may be interpreted either as a power function passing through the origin, or as two linear functions with an inflection point of about 4 m in height. The inflection point may be called a "threshold height" above which the browning follows a steeper linear model. Figure 4b appears to support the power function model by revealing a linear relationship when the points are plotted on logarithmically-scaled axes.

When results from individual plots are considered separately, departures from the model for the entire population may be interpreted as representing the severity of the "disease" in a given area. Figure 5 illustrates this idea with data from two plots, 9 and 41. Plot 9 contained a large proportion of green cacti, as evidenced by the clustering of points along the x-axis until about the 7 m height level, beyond which a steep upward trend is defined by three points. By contrast, data from plot 41 define a threshold of about 4.5 m, beyond which the scatter of points indicates a similar steep upward trend.

At first glance, the data may infer that plot 41 experienced a more severe attack of the browning disease. However, it is reasonable to conclude that the severity of browning is not so much a function of height as age. The power function model would fit this concept, for the age versus height curve for saguaro cactus has been shown to approximate a power function (Steenberg and Lowe 1983). Also, saguaros grow at widely differing rates depending on their environment, which may be determined by differences in elevation, topography, and/or soil structure over relatively short distances (Steenberg and Lowe 1977). Plants 5 m in height may be the same age as 8 m tall plants growing in a more favorable environment. Plot 9 is a relatively well-watered, flat area with good soil development. Plot 41 is a steep, severe southwest-facing rocky slope where moisture availability may be more limited. Thus, the "threshold" heights of 7.0 and 4.5 m may, in fact, represent plants of the same age.

An ideal "index" of the severity of epidermal browning would account for the age of the plant. It is not possible to determine the age of each saguaro investigated merely from its height, or any other direct means. We used a simple method of quantifying the severity of browning on a particular cactus using the following formula:

$$\text{browning index} = \frac{\text{visual estimate of browning on south stem (\%)}}{\text{height (m)}}$$

Since we sampled cacti ≥2 m in height, the maximum index value in our sample would be 50 (100%/2 m) and the minimum 0 (for cacti of any height with no browning). This linear model of browning may be considered a rough approximation, ignoring the effects of threshold heights, different age-height functions for different areas, and possible nonlinear response relationships. It is, however, much preferred to comparing percentages of browning directly regardless of the height (and associated relative age) of the plants. When index values are averaged over all 30 cacti within a plot, a "plot index" that may be compared geographically is obtained. A summary of the following data is presented in Table 1: mean browning index values for all 45 plots along with mean heights of cacti, numbers of saguaros counted in each of five height classes, percent brown observed on the south stem, percent spines retained on the south stem, elevation, general aspect, and topographic position. Means are also presented for each district of the monument and for the entire population sampled. The mean browning index for TMD is greater than the mean for RMD (2.36 vs. 2.08). Mean index data by plot are shown in Figures 6a-b. No apparent pattern is evident for TMD, while RMD reveals some zones of similar browning severity. An area of relatively green cacti appears to occur in a general northeast-southwest line in the center of the bajada area north of Tanque Verde Ridge, defined by six plots with relatively low browning indices. Three plots near the western boundary of the RMD indicate an area of greater browning, while plots in the foothills and on the slopes of Tanque Verde Ridge are generally intermediate in severity.

The statistical significance of the apparent differences among plot means may be estimated by comparing the means and 95% confidence intervals for browning index of all 45 plots (Fig. 7). Further statistical testing was not conducted because of severe departures from normality and non-homogeneity of variance observed in the data. The within-plot variability increased with increasing values for the mean, as revealed by wider 95% confidence intervals. We conclude that plots with means of 3.0 or greater are significantly different from plots with means of 1.0 or less, and that plots lying between these values are different from only a few plots (15, 16, and 18) with extreme values. Plots in the RMD appear to exhibit a wider range of browning indices than TMD plots. Of particular interest are plots 8, 9, 11, and 18, which have mean index values below 0.7 and narrow confidence intervals indicating the majority of sampled cacti have little or no browning. Plots 8, 9, and 18 are all near major washes. Plots 15 and 16 had the highest browning indices (4.99 and 4.06) of all plots.

The severity of browning was greater on the south side of all plants investigated than on the north side. This phenomenon is apparent to even the casual observer. Numerical results (Table 2) imply that light and/or heat from the sun has a definite role in the formation of epidermal browning (south sides averaged 13.4% browning, while north sides exhibited only 3.0%). Yet in many instances, severely brown cacti were seen growing next to green, healthy cacti of the same height, suggesting some sort of plant-specific process.

The effects of microhabitats on the severity of epidermal browning were investigated by describing site factors at each cactus as one of six classes: (1) flat rock, (2) sloping rock, (3) flat soil, (4) sloping soil, (5) ridge, and (6) basin. Comparisons of the mean browning index for each of these six groups indicated no statistical significance between sites and no definite trends.

The microhabitat in which a particular cactus grows may also be characterized by plant species associated with it. We looked for differences in mean values of browning index, percent browning on the south stem, and height among groups of cacti associated with selected individual species and groups in which these species were not present. The following associated species were investigated: mesquite (*Prosopis velutina*), paloverde (*Cercidium microphyllum*), teddy-bear cholla (*Opuntia bigelovii*), ocotillo (*Fouquieria splendens*), and brittlebush (*Encelia farinosa*). The means for each group were compared by an independent sample t-test (Table 3). Cacti associated with mesquite yielded the lowest mean browning index (1.31), which was significantly lower than cacti which are not associated with mesquite (2.32). Saguaros growing in association with foothill paloverde had a significantly higher browning index (2.36) than those not in association with paloverde (1.60), as well as a higher index than the mesquite-associated cacti. This difference may be a reflection of the different soil

moisture regimes where the trees often grow; mesquite commonly occurs along washes and paloverde above washes and on drier bajadas (Larson and Larson 1977). A comparison of index averages with the average for all cacti sampled (2.07) suggests that cacti associated with mesquite are greener than average and that cacti associated with foothill paloverde are browner than average. Two other dry-environment species, ocotillo and brittlebush, also appear to be associated with browner cacti (Table 3). A comparison of mean browning index of saguaros growing in the presence and absence of teddy-bear cholla revealed no significant differences. This species grows primarily in the thermal belt of the mountain slopes.

Spine retention was negatively correlated with the severity of browning. Plot-level means of percent visual estimates of spines retained on the south stem compared with mean percent brown grid squares counted on the south stem are shown in Figure 8. A fairly good linear relationship is evident, with a correlation coefficient of -0.85 and a slope near -1 (-0.90). This, in itself, is not enough to imply cause and effect. Spine retention and browning both vary with height, which is related to age. Decreased spine retention may be a normal part of the aging process.

A correlation matrix of many of the variables measured, summarized to the plot level by averaging, is given in Table 4 (n = 45 for comparisons). Many of these data are not normally distributed, so the matrix should be used only as a guide for further investigation of processes that may be involved, not as a definitive analysis of such processes. Noticeably absent is any distinct linear correlation between any variable and elevation except average cactus height (r = -0.57). This indicates that plots located on steep, rocky slopes (which, in this area, occur almost exclusively in the higher elevations) contain a smaller proportion of tall cacti than plots on the bajadas.

Population Density and Structure

The data collected allow a plot to plot comparision of numbers of saguaros of various height classes and the total number of cacti. Density values (plants/ha) may be obtained by dividing plot numbers by 4, for comparison with previous work (Table 5). A histogram of saguaro height structure for each plot is shown at respective plot locations in Figures 9 and 10. Since all cacti ≥2 m were not measured, data for the height range 2-13 m were extrapolated from the random sample of 30 that were measured. No test of the precision at which these values represent the true values was made for any of the plots.

It is evident from Figures 9 and 10 that a different population structure exists for bajada areas than for mountain slope areas. This is consistent with the studies of Steenberg and Lowe (1983). Rocky slopes generally possess a so-called "stable" population with many more smaller cacti than tall ones. The bajada areas, particularly northeast of Tanque Verde Ridge in the RMD (Fig. 9) display a distinct peak in saguaro distribution at about 6 or 7 m. The density of cacti of all heights is also much lower in bajada areas. In TMD (Fig. 10), many plants in the 0.1-1.0 m height class are seen in the high mountain plots. At plot 45, elevation 4,200 ft, density reaches 128 plants/ha, highest of any in our sample. Of interest in the bajada plots of both districts is the existence of a sharp peak in the 0.1-1.0 m class, consistent with the work of Turner (this volume) in that it documents possible recovery of the Cactus Forest population in years to come. Potential recovery is not evident in every plot, however. Plots 1, 2, 8, 9, and 10 do not exhibit an increase in recruitment over the past decade or two. Our data indicate that the population of saguaros is still in decline in these areas.

CONCLUSIONS

Epidermal browning of saguaro cacti is a widespread condition; no area within the monument may be said to be free of it. Browning appears to begin in the presence of sunlight, but very green cacti up to 8 m tall (at least 70 years old) with good spine retention and many arms may be found without a trace of it. Therefore, some plant-specific factor must be involved in the process. Browning appears to be well correlated with age, suggesting it may be part of a normal aging process. However, in some plants this appears to be accelerated. The reasons for this are presently unknown. A decrease in spine retention is correlated with increased epidermal browning. Since the browning often begins at the areoles of the cacti, this result may indicate a cause and effect relationship between the incidence of browning and spine loss at a given areole; this bears investigating.

The saguaro population appears to be stable in most foothill and mountain environments sampled.

In the bajadas, a large anomaly in the population structure exists in that a peak in density of cacti at 6 to 8 m in height occurs. A number of young plants in the 0.1-1.0 m height class were observed in many of the bajada plots, indicating some recruitment has taken place after many decades of steady population decline. Recruitment was not seen in all plots, however, and cactus numbers in some areas are still declining.

The data set amassed in this research project will serve as a base for future monitoring of the individuals studied. Long-term monitoring will provide greater insight into the cause of epidermal browning and document the ever-changing distribution of plants in this area of the Sonoran Desert.

ACKNOWLEDGMENTS

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Table 1. Means of selected variables by monument district and by plot.

Plot No.	Height (m)	Percent brown	Percent spines	Browning index	No. of plants by height class (m) .1-.5	.5-1	1-1.5	1.5-2	>2.0	TOTAL	Elevation	Aspect	Topographic position
Entire population													
	5.02	13.43	68.43	2.08	58	38	24	14	142	276	911	243	
Rincon Mountain District													
All	4.79	11.25	70.03	1.86	31	35	25	15	123	228	969	261	
1	5.09	20.67	59.07	3.37	4	0	1	3	32	40	904	310	Bajada
2	5.98	14.00	50.40	1.99	4	0	0	2	105	111	875	340	Bajada
3	4.19	12.10	69.67	2.30	15	25	16	4	73	133	975	280	Foothills
4	3.69	13.03	66.33	2.89	13	15	20	13	60	121	1000	300	Foothills
5	6.00	25.00	41.83	3.53	28	24	29	15	57	153	867	350	Bajada
6	4.42	8.23	74.07	1.27	19	22	28	17	109	195	975	290	Foothills
7	4.23	12.50	64.27	1.96	30	55	42	27	167	321	1000	250	Foothills
8	6.91	4.70	56.73	.64	6	1	0	2	56	65	818	0	Bajada
9	5.72	5.20	69.45	.67	5	2	3	2	43	55	890	350	Bajada
10	5.75	5.83	69.53	.84	1	4	1	3	75	84	872	999	Bajada
11	4.40	2.40	84.03	.42	13	13	11	6	100	143	860	330	Bajada
12	4.62	18.43	50.83	3.35	56	50	36	25	188	355	1113	190	Slopes
13	4.55	9.90	70.27	1.50	28	22	19	12	176	257	902	260	Foothills
14	4.29	6.80	79.30	1.22	4	8	7	4	37	60	1052	300	Foothills
15	6.62	38.07	32.80	4.99	30	41	36	7	94	208	844	30	Bajada
16	3.96	19.00	62.43	4.06	58	58	41	22	196	375	1024	210	Slopes
17	5.11	6.27	70.07	1.04	40	23	7	3	95	168	843	340	Bajada
18	4.63	1.27	93.77	.28	8	17	16	7	63	111	920	180	Bajada
19	4.43	5.13	84.53	.76	59	49	35	12	127	282	844	290	Bajada
20	4.34	5.03	91.40	.99	27	21	13	9	113	183	1042	90	Foothills
21	5.20	13.23	77.50	1.90	35	54	28	17	220	354	1128	200	Slopes
22	3.81	6.37	88.59	1.39	17	35	18	19	200	289	1067	190	Slopes
23	4.46	6.20	88.30	.80	12	5	3	0	68	88	1231	80	Slopes
24	3.63	10.37	83.87	1.87	75	83	64	37	207	466	1052	200	Slopes
25	3.84	11.63	71.60	2.44	183	239	159	99	409	1089	1119	170	Slopes

Table 1. Continued.

Plot No.	Height (m)	Percent brown	Percent spines	Browning index	No. of plants by height class (m) .1-.5	.5-1	1-1.5	1.5-2	>2.0	TOTAL	Elevation	Aspect	Topographic position
					Tucson Mountain District								
All	5.29	16.15	66.44	2.36	93	43	22	13	165	336	839	220	
26	5.93	29.37	49.00	3.95	37	36	26	28	235	362	747	30	Foothills
27	5.02	6.13	76.67	.97	30	21	10	6	52	119	847	0	Bajada
28	5.56	13.80	71.60	2.06	49	29	25	8	282	393	805	250	Foothills
29	5.19	15.67	70.97	1.70	8	6	4	1	66	85	689	280	Bajada
30	6.83	24.93	50.97	3.00	19	31	18	5	194	267	869	340	Foothills
31	5.38	11.63	55.60	1.60	49	26	5	5	98	183	732	330	Bajada
32	4.86	7.20	74.07	1.33	7	5	3	3	77	95	777	350	Bajada
33	4.93	7.83	79.53	1.02	28	7	10	7	57	109	686	310	Bajada
34	5.33	14.30	68.43	2.45	24	26	11	8	133	202	899	80	Slopes
35	5.74	13.93	71.87	2.02	100	22	4	4	64	194	680	280	Bajada
36	4.66	21.70	70.40	3.71	306	122	48	14	156	646	1061	200	Slopes
37	6.15	14.13	68.43	1.79	149	89	45	15	227	525	786	170	Foothills
38	4.79	20.93	61.67	3.45	176	75	50	44	400	745	823	160	Foothills
39	4.57	8.60	80.00	1.35	91	38	27	11	250	417	780	330	Foothills
40	6.54	25.27	43.13	3.06	51	13	9	7	344	424	738	270	Bajada
41	5.19	28.53	52.17	4.00	196	86	41	22	178	523	1091	240	Slopes
42	4.97	14.77	67.07	2.31	37	26	24	25	144	256	792	80	Slopes
43	4.36	13.87	77.03	2.37	120	33	20	12	81	266	960	180	Foothills
44	5.69	20.17	59.77	3.11	22	11	3	8	89	133	747	330	Bajada
45	4.20	10.27	80.50	1.94	362	151	57	26	176	772	1280	190	Slopes

Table 2. Comparison of the appearance of north and south sides of cactus stems.

Stem surface	$\bar{x}$	SD	n
	Epidermal browning on main stem		
South	13.431	20.480	1350
North	2.999	6.754	1347
	Epidermal browning on grid		
South	23.581	36.586	1334
North	5.251	15.441	1339

Table 3. Comparison of means for selected factors among groups of saguaro cacti growing in the presence or absence of various other plant species.

Species:	Present		Absent		Independent t-test	
Factor	$\bar{x}$	n	$\bar{x}$	n	t	P
Prosopis velutina:						
% Browning south stem	8.32	336	15.12	1014	5.32	<0.001
% Browning south grid	15.46	331	26.25	1003	4.69	<0.001
Browning index	1.31	332	2.32	1003	5.40	<0.001
% Spines south stem	71.85	335	67.31	1012	-1.98	0.047
Height (m)	5.12	332	4.97	1003	-1.15	0.249
Cercidium microphyllum:						
% Browning south stem	15.71	836	9.73	514	-5.26	<0.001
% Browning south grid	27.29	827	17.51	507	-4.77	<0.001
Browning index	2.36	827	1.60	508	-4.57	<0.001
% Spines south stem	65.39	834	73.39	513	3.94	<0.001
Height (m)	5.12	827	4.82	508	-2.67	0.008
Opuntia bigelovii:						
% Browning south stem	13.40	72	13.43	1278	0.01	0.990
% Browning south grid	25.73	72	23.45	1262	-0.51	0.608
Browning index	2.31	72	2.05	1263	-0.71	0.479
% Spines south stem	65.38	72	68.61	1275	0.73	0.463
Height (m)	4.59	72	5.03	1263	1.83	0.067
Fouquieria splendens:						
% Browning south stem	14.70	457	12.78	893	-1.63	0.104
% Browning south grid	25.09	451	22.81	883	-1.08	0.281
Browning index	2.44	453	1.88	882	-3.32	0.001
% Spines south stem	69.37	456	67.96	891	-0.68	0.498
Height (m)	4.65	453	5.19	882	4.79	<0.001
Encelia farinosa:						
% Browning south stem	15.92	316	12.67	1034	-2.47	0.014
% Browning south grid	28.47	313	22.08	1021	-2.71	0.007
Browning index	2.71	313	1.87	1022	-4.41	<0.001
% Spines south stem	66.71	316	68.97	1031	0.97	0.335
Height (m)	4.61	313	5.13	1022	4.03	<0.001
Entire population						
% Browning south stem	13.43	1350				
% Browning south grid	23.58	1334				
Browning index	2.07	1335				
% Spines south stem	68.44	1347				
Height (m)	5.01	1335				

Table 4. Correlation matrix of selected variables using plot-level means.

Pearson's *r* (N) 2-tailed prob.		Height	Browning index	Percent brown visual estimate		Percent brown grid count		Percent spines visual estimate		Elevation
				S stem	N stem	South	North	S stem	N stem	
Height		1.0000 (45) *P* = .2010	.2010 (45) *P* = .186	.4405 (45) *P* = .002	.4771 (45) *P* = .001	.4302 (45) *P* = .003	.3675 (45) *P* = .013	-.6547 (45) *P* = .000	-.5617 (45) *P* = .000	-.5657 (45) *P* = .000
Browning index		.2010 (45) *P* = .186	1.0000 (45) *P* = .000	.9431 (45) *P* = .000	.7385 (45) *P* = .000	.9141 (45) *P* = .000	.6922 (45) *P* = .000	-.7298 (45) *P* = .000	-.7886 (45) *P* = .000	.0485 (45) *P* = .752
Percent brown visual estimate	South stem	.4405 (45) *P* = .002	.9431 (45) *P* = .000	1.000 (45) *P* = .000	.8448 (45) *P* = .000	.9629 (45) *P* = .000	.7710 (45) *P* = .000	.9629 (45) *P* = .000	.7710 (45) *P* = .000	-.1193 (45) *P* = .435
	North stem	.4771 (45) *P* = .001	.7385 (45) *P* = .000	.8448 (45) *P* = .000	1.0000 (45) *P* = .000	.7825 (45) *P* = .000	.8094 (45) *P* = .000	-.6762 (45) *P* = .000	-.7071 (45) *P* = .000	-.1941 (45) *P* = .201
Percent brown grid count	South	.4302 (45) *P* = .003	.9141 (45) *P* = .000	.9629 (45) *P* = .000	.7825 (45) *P* = .000	1.0000 (45) *P* = .000	.7628 (45) *P* = .000	-.8513 (45) *P* = .000	-.8855 (45) *P* = .000	-.1357 (45) *P* = 374
	North	.3675 (45) *P* = .013	.6922 (54) *P* = .000	.7710 (45) *P* = .000	.8094 (45) *P* = .000	.7628 (45) *P* = .000	1.0000 (45) *P* = .000	-.6158 (45) *P* = .000	-.7004 (45) *P* = .000	-.1351 (45) *P* = .376
Percent spines visual estimate	South stem	-.6547 (45) *P* = .000	-.7298 (45) *P* = .000	-.8124 (45) *P* = .000	-.6762 (45) *P* = .000	-.8513 (45) *P* = .000	-.6158 (45) *P* = .000	1.0000 (45) *P* = .000	.9506 (45) *P* = .000	.2950 (45) *P* = .049
	North stem	-.5617 (45) *P* = .000	-.7886 (45) *P* = .000	-.8568 (45) *P* = .000	-.7071 (45) *P* = .000	-.8855 (45) *P* = .000	-.7004 (45) *P* = .000	.9506 (45) *P* = .000	1.0000 (45) *P* = .000	.1885 (45) *P* = .215
Elevation		-.5457 (45) *P* = .000	.0485 (45) *P* = .752	-.1193 (45) *P* = .435	-.1941 (45) *P* =.201	-.1357 (45) *P* = .374	-.1351 (45) *P* = .376	.2950 (45) *P* = .049	.1885 (45) *P* = .215	1.0000 (45) *P* = .000

Table 5. Density of saguaro cacti found in plots in 1-meter size classes and total density.

	Density in plants/ha by height class														
Plot	.1-1	1-2	2-3[a]	3-4[a]	4-5[a]	5-6[a]	6-7[a]	7-8[a]	8-9[a]	9-10[a]	10-11[a]	11-12[a]	12-13[a]	13-14[a]	Total density
1	1.00	1.00	0.80	1.60	2.40	1.33	0.80	0.00	0.27	0.53	0.27	0.00	0.00	0.00	10.00
2	1.00	0.50	0.88	3.50	1.75	4.38	11.37	1.75	1.75	0.88	0.00	0.00	0.00	0.00	27.75
3	10.00	5.00	6.69	4.26	1.22	3.65	0.61	1.22	0.61	0.00	0.00	0.00	0.00	0.00	33.25
4	7.00	8.25	4.00	6.00	2.00	2.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.25
5	13.00	11.00	0.47	2.37	2.37	2.37	1.90	1.90	1.90	0.95	0.00	0.00	0.00	0.00	38.25
6	10.25	11.25	7.27	3.63	8.18	4.54	0.91	0.00	2.73	0.00	0.00	0.00	0.00	0.00	48.75
7	21.25	17.25	13.92	6.96	4.17	9.74	5.57	1.39	0.00	0.00	0.00	0.00	0.00	0.00	80.25
8	1.75	0.50	0.00	0.47	0.93	0.93	4.67	4.67	1.40	0.93	0.00	0.00	0.00	0.00	16.25
9	1.75	1.25	1.07	0.72	1.43	2.51	3.94	0.00	0.36	0.36	0.36	0.00	0.00	0.00	13.75
10	1.25	1.00	0.63	1.25	3.13	4.38	6.25	1.88	0.63	0.63	0.00	0.00	0.00	0.00	21.00
11	6.50	4.25	4.17	5.00	10.00	4.17	0.83	0.00	0.00	0.83	0.00	0.00	0.00	0.00	35.75
12	26.50	15.25	12.53	9.40	9.40	1.57	4.70	7.83	1.57	0.00	0.00	0.00	0.00	0.00	88.75
13	12.50	7.75	5.87	14.67	10.27	2.93	5.87	2.93	0.00	0.00	1.47	0.00	0.00	0.00	64.25
14	3.00	2.75	0.93	4.01	1.23	1.85	0.93	0.31	0.00	0.00	0.00	0.00	0.00	0.00	15.00
15	17.75	8.25	3.13	3.13	1.57	4.70	3.92	2.35	1.57	0.78	0.78	0.00	1.57	0.00	52.00
16	29.00	15.75	16.33	9.80	8.17	9.80	3.27	1.63	0.00	0.00	0.00	0.00	0.00	0.00	93.75
17	15.75	2.50	2.37	2.37	3.17	8.71	5.54	1.58	0.00	0.00	0.00	0.00	0.00	0.00	42.00
18	6.25	5.75	2.10	2.62	5.25	2.10	2.62	1.05	0.00	0.00	0.00	0.00	0.00	0.00	27.75
19	27.00	11.75	7.41	7.41	5.29	5.29	4.23	0.00	1.06	1.06	0.00	0.00	0.00	0.00	70.50
20	12.00	5.50	5.65	7.53	7.53	3.77	0.94	2.83	0.00	0.00	0.00	0.00	0.00	0.00	45.75
21	22.25	11.25	3.67	12.83	12.83	7.33	12.83	1.83	0.00	0.00	3.67	0.00	0.00	0.00	88.50
22	13.00	9.25	11.67	16.67	16.67	3.33	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	72.25
23	4.25	0.75	4.53	2.27	5.10	3.40	0.57	0.57	0.00	0.00	0.00	0.00	0.00	0.57	22.00
24	39.50	25.25	24.15	12.07	5.17	3.45	3.45	1.73	1.73	0.00	0.00	0.00	0.00	0.00	116.50
25	105.50	64.50	34.08	34.08	10.22	10.22	10.22	0.00	3.41	0.00	0.00	0.00	0.00	0.00	272.25
26	18.25	13.50	9.79	9.79	3.92	3.92	9.79	1.96	11.75	5.87	1.96	0.00	0.00	0.00	90.50
27	12.75	4.00	2.17	2.60	2.17	1.73	1.73	1.73	0.43	0.43	0.00	0.00	0.00	0.00	29.75
28	19.50	8.25	4.70	7.05	23.50	7.05	9.40	11.75	4.70	0.00	2.35	0.00	0.00	0.00	98.25
29	3.50	1.25	2.20	3.85	2.75	1.10	3.30	1.65	1.10	0.55	0.00	0.00	0.00	0.00	21.25
30	12.50	5.75	0.00	3.23	8.08	8.08	4.85	6.47	8.08	6.47	3.23	0.00	0.00	0.00	66.75
31	18.75	2.50	4.08	3.27	3.27	6.53	1.63	2.45	0.82	0.82	0.82	0.82	0.00	0.00	45.75
32	3.00	1.50	0.64	5.13	5.13	5.13	1.93	0.00	1.28	0.00	0.00	0.00	0.00	0.00	23.75
33	8.75	4.25	1.90	3.80	2.37	2.37	0.95	0.95	1.43	0.47	0.00	0.00	0.00	0.00	27.25
34	12.50	4.75	3.33	5.54	4.43	3.33	12.19	3.33	0.00	1.11	0.00	0.00	0.00	0.00	50.50
35	30.50	2.00	2.13	1.07	2.67	1.60	5.87	1.07	0.00	0.00	1.07	0.53	0.00	0.00	48.50
36	107.00	15.50	7.80	7.80	9.10	5.20	6.50	1.30	1.30	0.00	0.00	0.00	0.00	0.00	161.50
37	59.50	15.00	7.57	5.67	5.67	7.57	3.78	15.13	3.78	3.78	3.78	0.00	0.00	0.00	131.25
38	62.75	23.50	16.67	13.33	33.33	13.33	6.67	10.00	3.33	3.33	0.00	0.00	0.00	0.00	186.25
39	32.25	9.50	8.33	22.92	6.25	12.50	4.17	2.08	4.17	2.08	0.00	0.00	0.00	0.00	104.25
40	16.00	4.00	2.87	11.47	8.60	11.47	14.33	20.07	8.60	2.87	2.87	0.00	2.87	0.00	106.00
41	70.50	15.75	8.90	4.45	10.38	4.45	8.90	4.45	1.48	0.00	1.48	0.00	0.00	0.00	130.75
42	15.75	12.25	7.20	6.00	6.00	6.00	1.20	4.80	4.80	0.00	0.00	0.00	0.00	0.00	64.00
43	38.25	8.00	7.42	2.70	3.38	2.02	2.03	2.03	0.00	0.68	0.00	0.00	0.00	0.00	66.50
44	8.25	2.75	2.23	0.00	4.45	5.19	5.19	4.45	0.74	0.00	0.00	0.00	0.00	0.00	33.25
45	128.25	20.75	8.80	11.73	13.20	4.40	1.47	4.40	0.00	0.00	0.00	0.00	0.00	0.00	193.00

[a]Density values for these height classes were extrapolated from a random sample of 30 cacti with heights ≥2 m within the 4-ha plot.

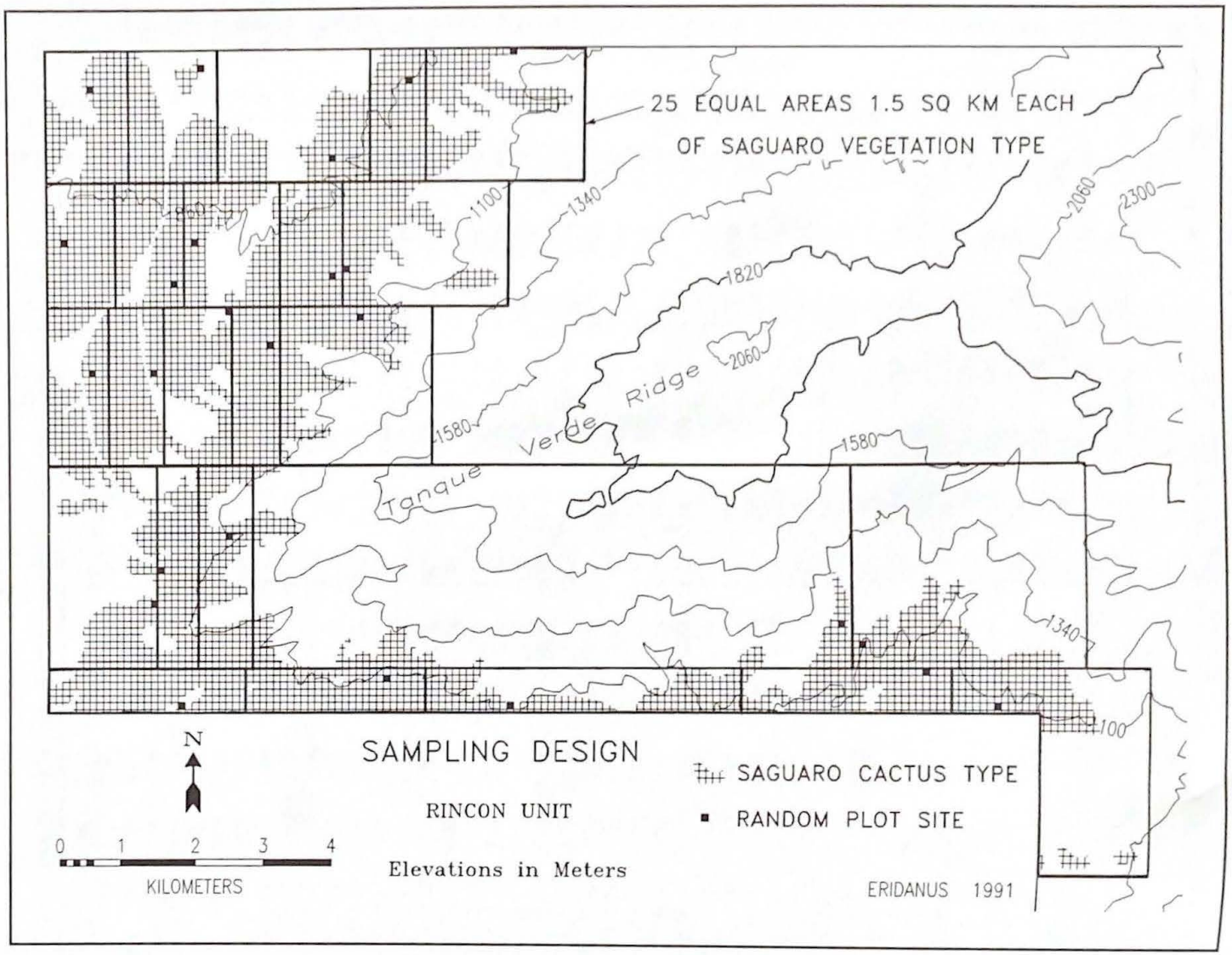
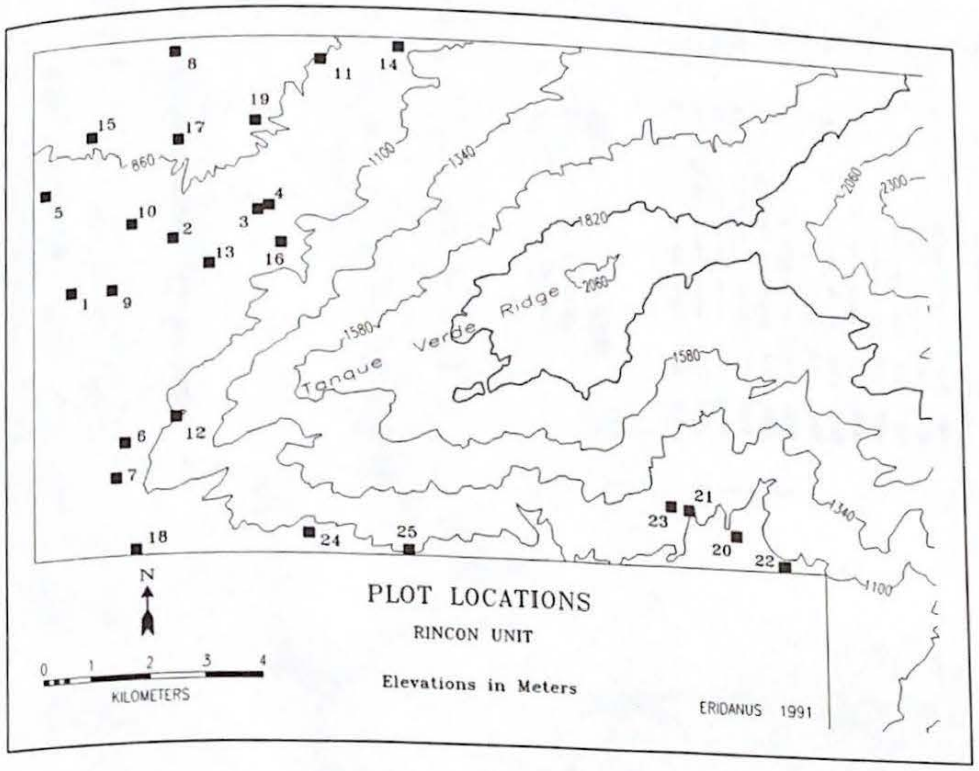


Fig. 1. Map of the Rincon Mountain District showing the sampling design.



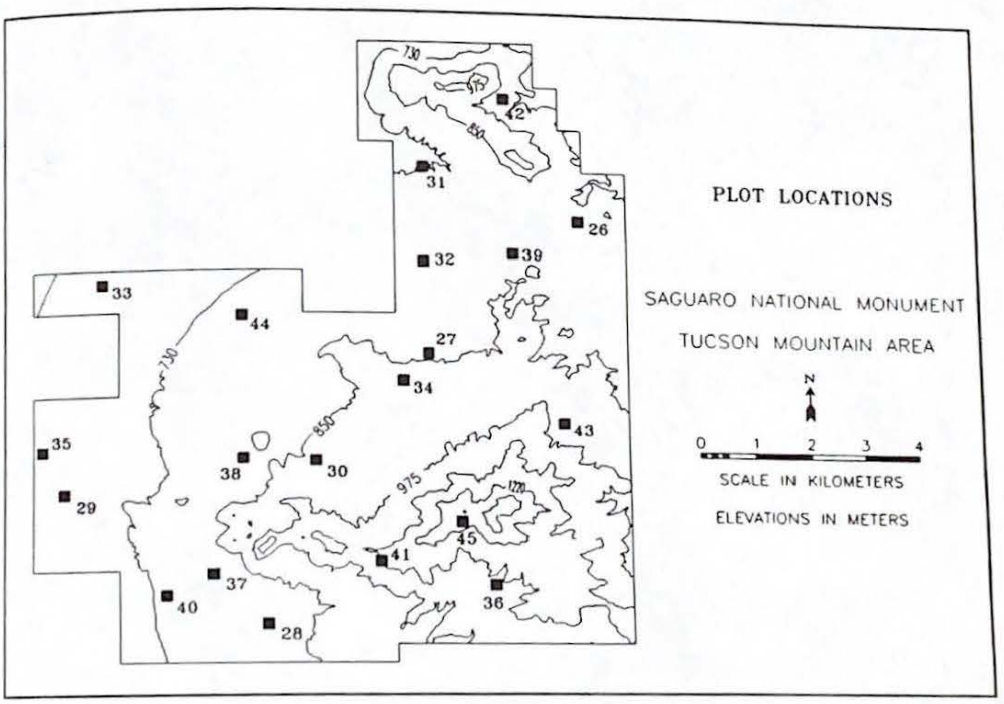


Fig. 2. Maps of (a) the Rincon Mountain District, and (b) the Tucson Mountain District showing plot locations.



COLOR	LABEL	SPECIES	COUNT	AREA (sq m)
	ACCO	Acacia constricta	3	5.886
	AMDE	Ambrosia deltoidea	7	1.355
	AYCO	Ayenia compacta	56	2.637
	CAER	Calliandra eriophylla	37	7.064
	CAGI	Carnegiea gigantea	2	0.573
	CEMI	Cercidium microphyllum	7	10.973
	ENFA	Encelia farinosa	3	1.246
	EPNE	Ephedra nevadensis	10	5.928
	ERLA	Ericameria laricifolia	1	0.228
	JAGR	Janusia gracilis	29	4.720
	KRGR	Krameria grayii	1	0.794
	LYBE	Lycium berlandieri	8	1.608
	MAMI	Mammillaria microcarpa	1	0.005
	OPAC	Opuntia acanthocarpa	10	1.636
	POGR	Porophyllum gracile	1	0.163
	SILO	Siphonoglossa longiflora	1	0.130
	SPSP	Sphaeralcea sp.	3	0.176

GRASSES	% COVER
Aristida purpurea	<1 %
Hilaria belangeri	2 %

ECOLOGICAL PLOT MAP

PLOT 42

SAGUARO NATIONAL MONUMENT, ARIZONA

February 16, 1990

N

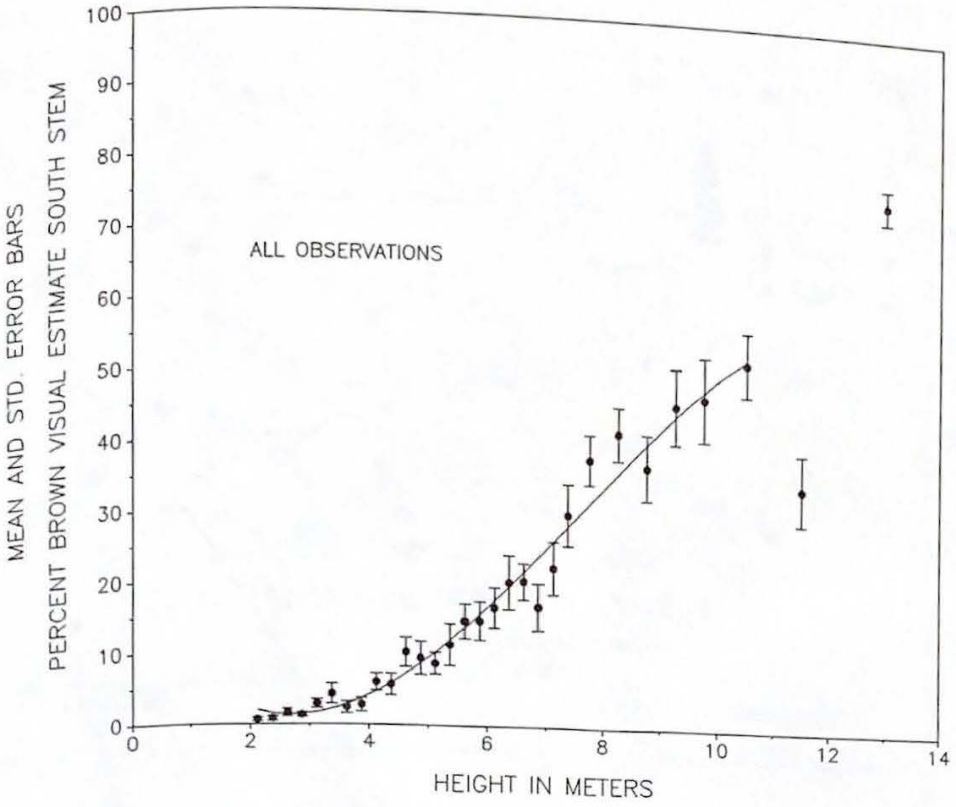
SCALE IN METERS

0 1 2 3 4

Canopies and stems of perennial plants found within the plot mapped at an accuracy of plus or minus 10 cm by plane table.

MAPPED BY ERIDANUS RESEARCH ASSOCIATES
THREE RIVERS, CALIFORNIA
D. M. Duriscoe, D. Milholland & S. L. Graban

Fig. 3. Ecological plot map for plot 42 in the Tucson Mountain District.



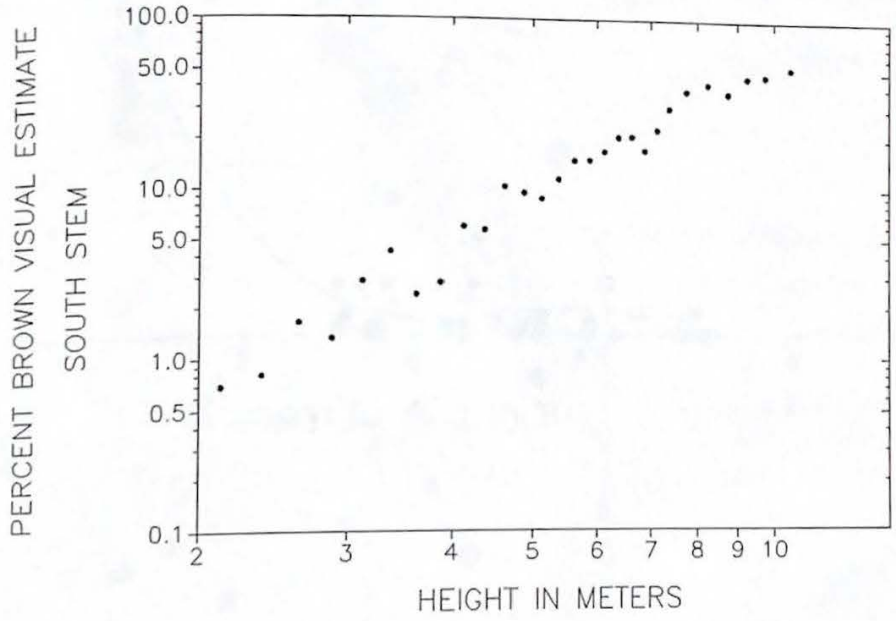


Fig. 4. Graphical representation of the relationship of severity of epidermal browning with height of saguaro cacti.

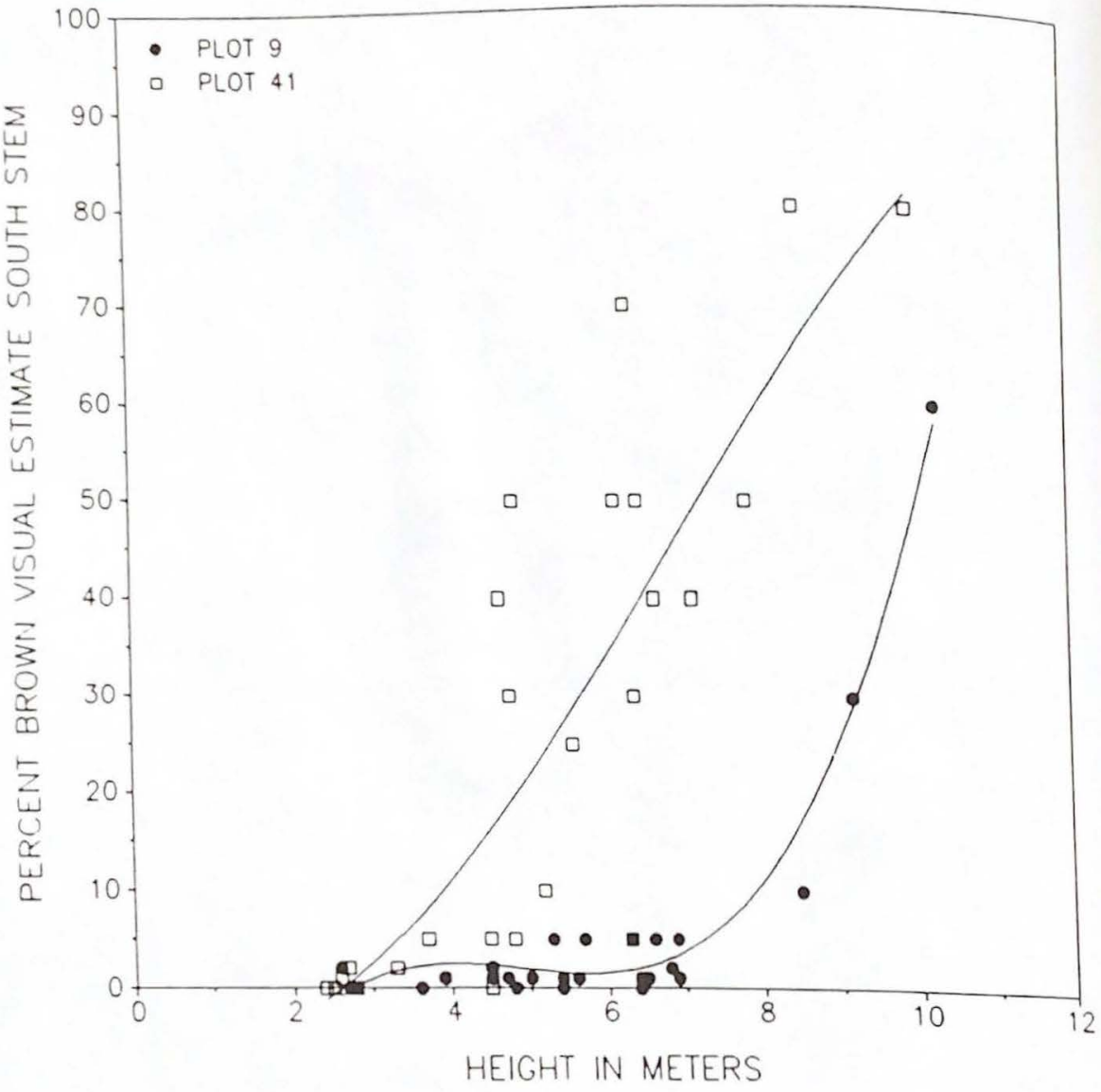
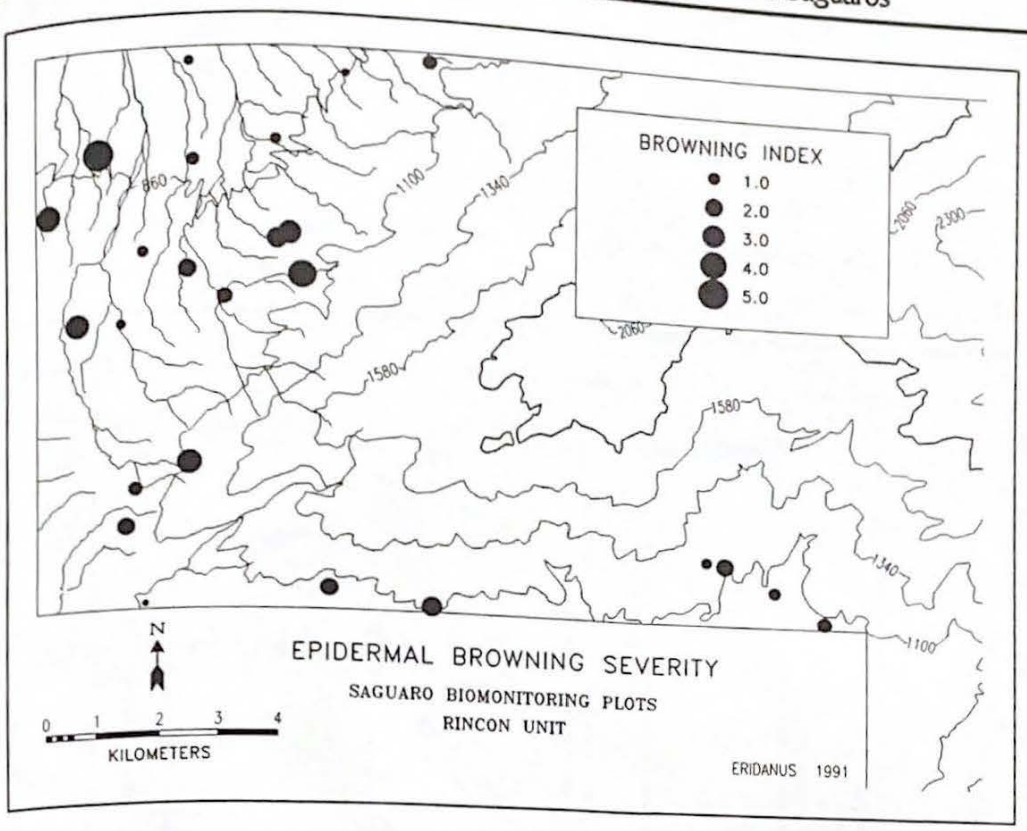


Fig. 5. Comparison of epidermal browning-height relationship for cacti in two different plots.



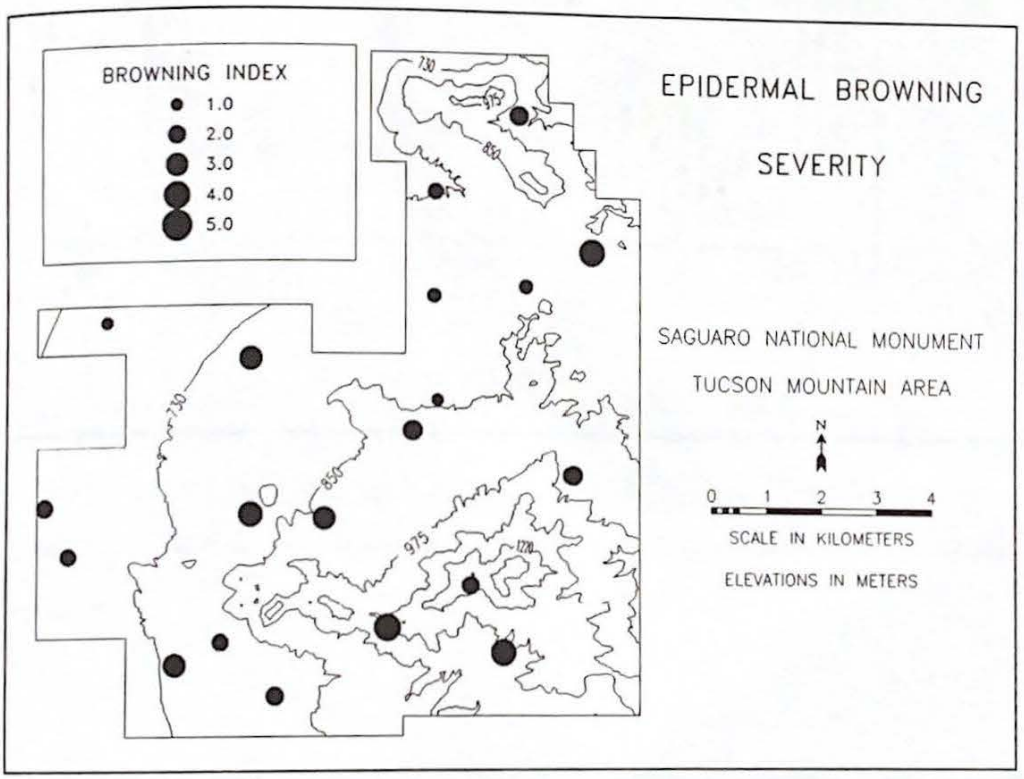


Fig. 6. Graduated circle maps of (a) the Rincon Mountain District, and (b) the Tucson Mountain District showing the severity of epidermal browning observed at each plot.

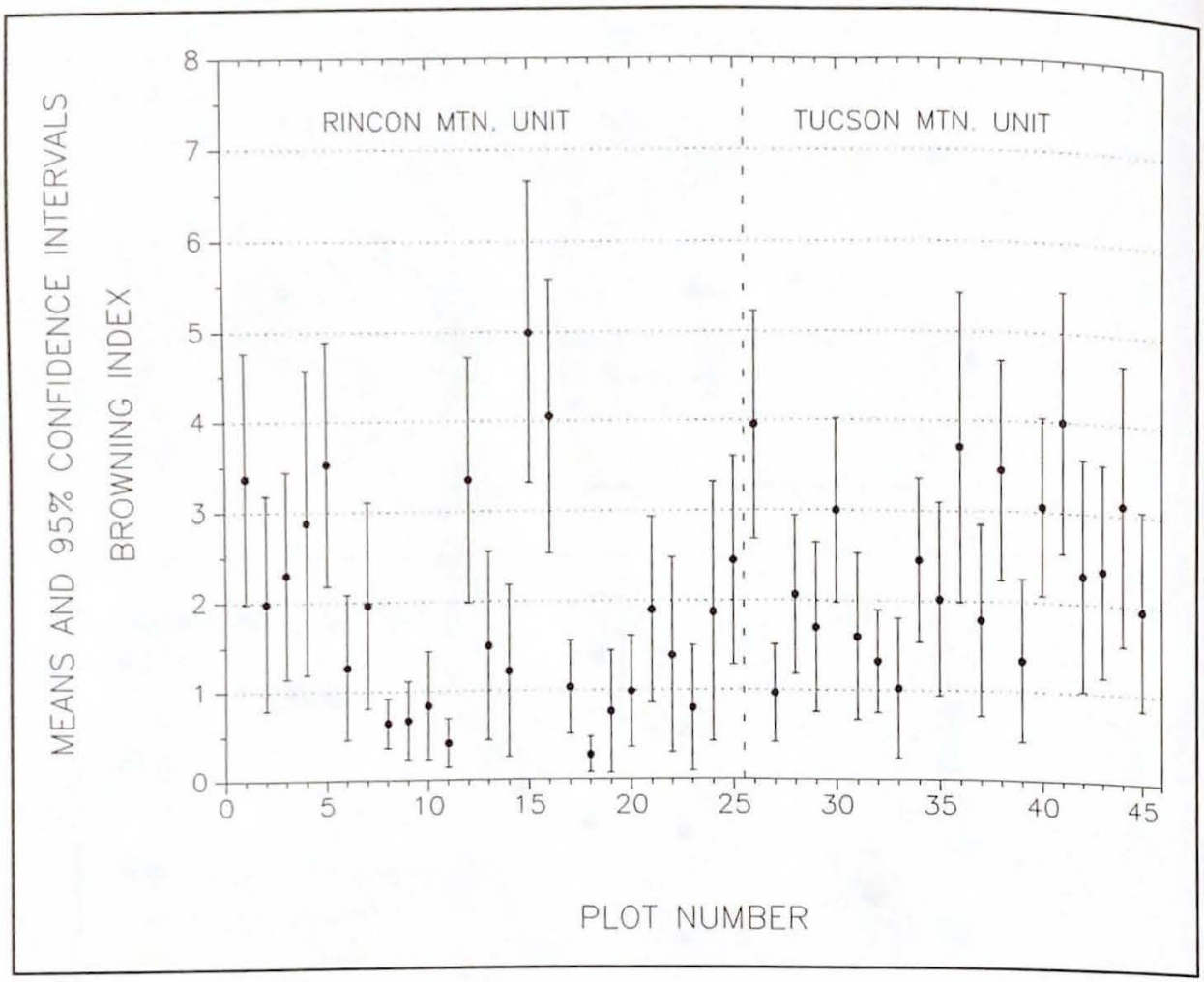


Fig. 7. Mean and 95% confidence intervals of the percentage of epidermal browning observed on the south stems of cacti in each of the 45 plots.

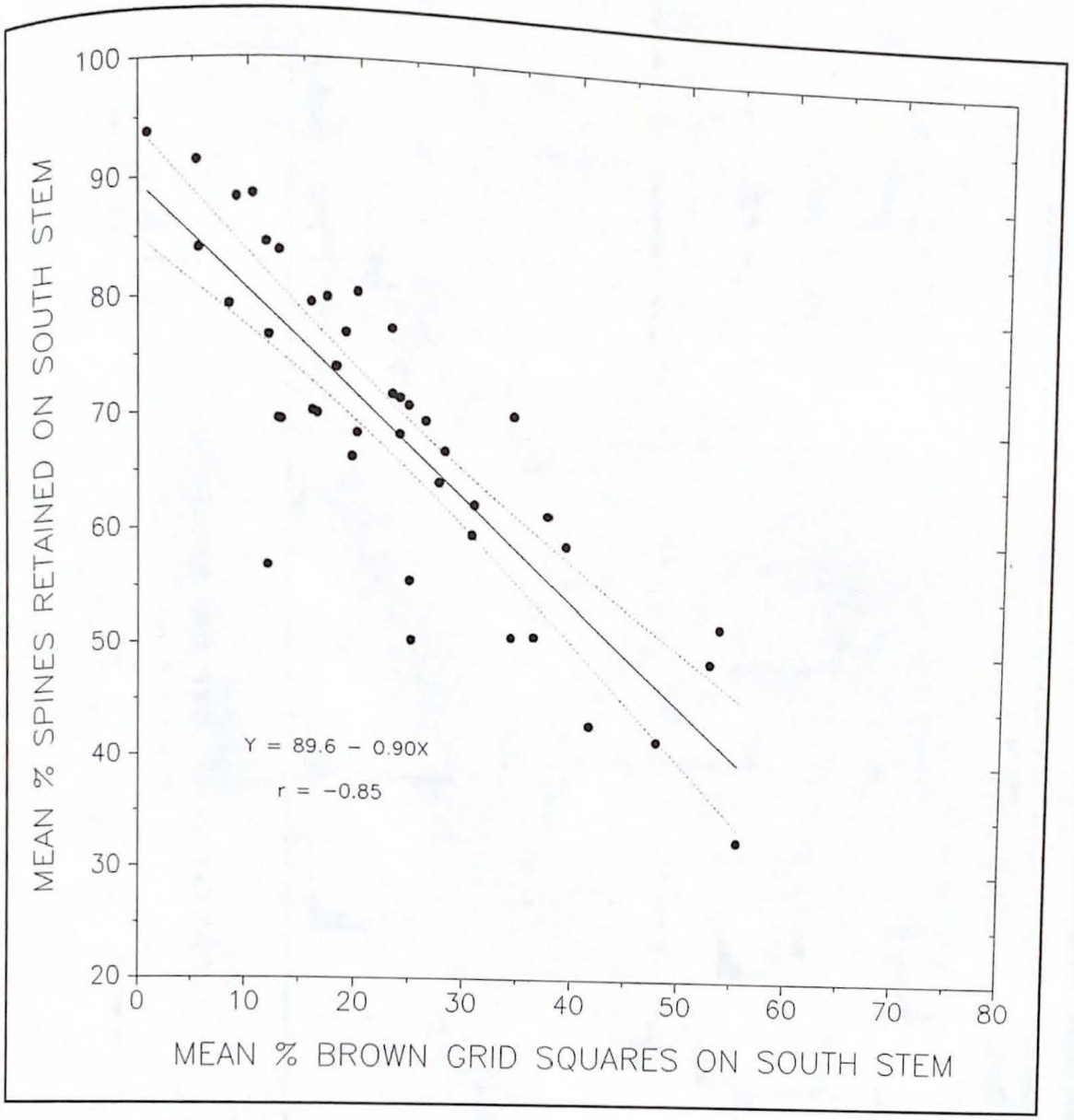


Fig. 8. Scatter plot of percent spines retained with percent epidermal browning on the south stem of cacti using plot-level means.

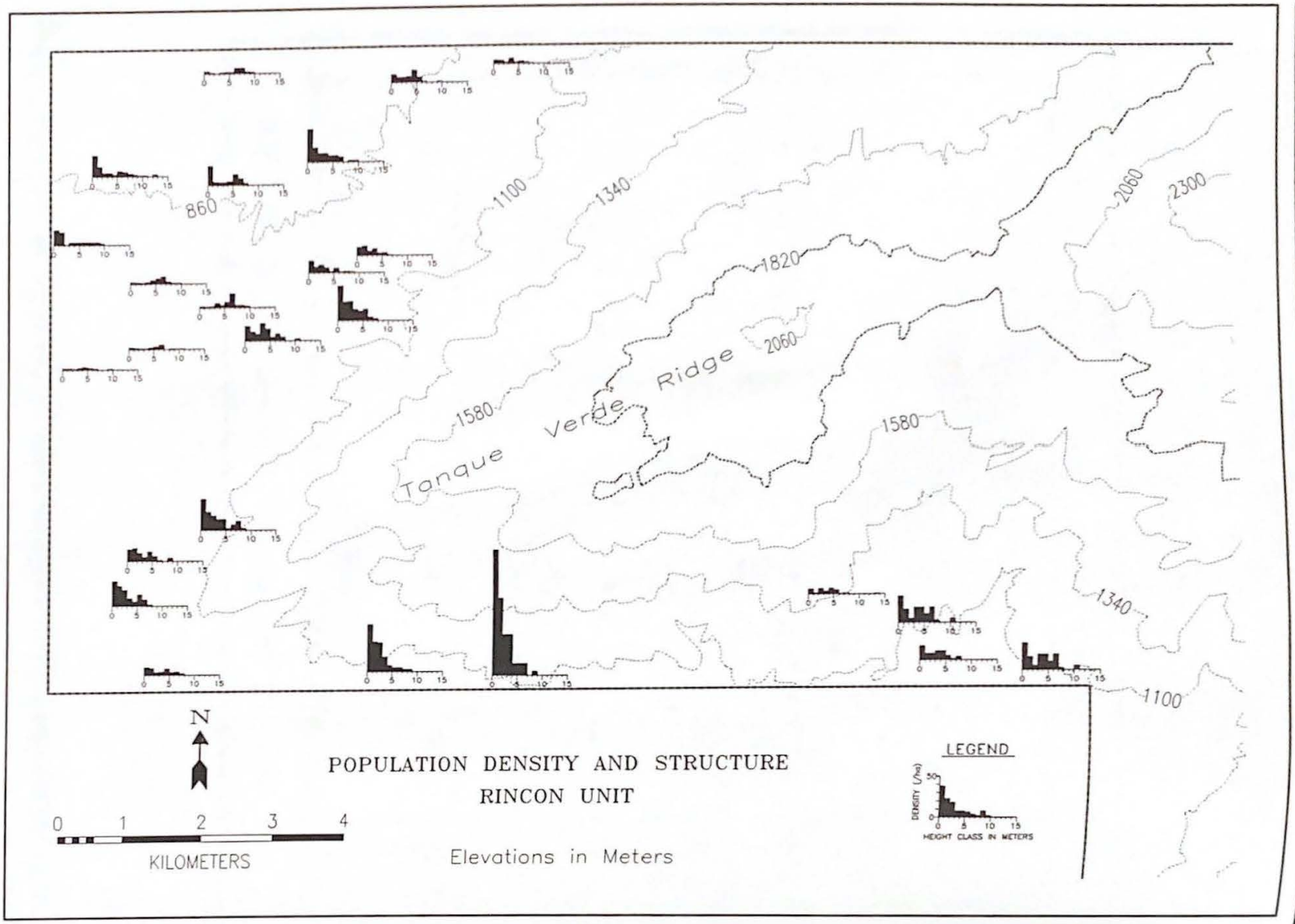


Fig. 9. Map of the Rincon Mountain District showing histograms of saguaro population structure and density at each plot location.

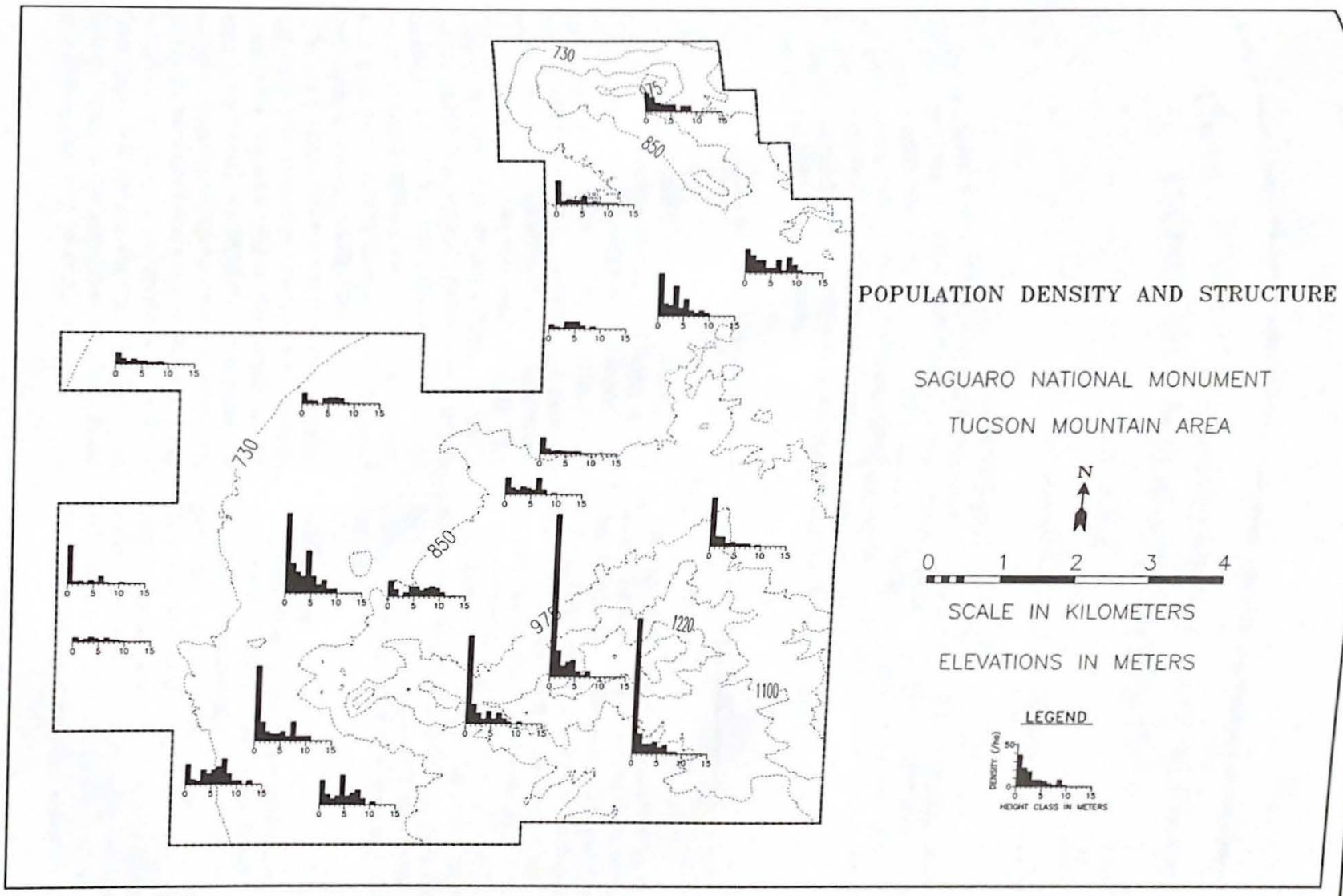


Fig. 10. Map of the Tucson Mountain District showing histograms of saguaro population structure and density at each plot location.

Characteristics of Cyanobacterial-Lichen Soil Crusts in Long-Term Saguaro Monitoring Plots

Jayne Belnap

ABSTRACT

Cyanobacterial-lichen soil crusts were surveyed in plots established for monitoring epidermal browning of saguaro cacti (*Carnegiea gigantea*). Percent cover, composition, chlorophyll *a*/phaeophytin *a* ratios and nitrogenase activity were measured. No correlation was found between the amount of soil crusts present or its composition and saguaro cactus damage. Significant correlations were found between increased chlorophyll *a*/phaeophytin *a* ratios and nitrogenase activity and saguaro cactus epidermal browning. It is suggested that non-nitrogenous, acidic air pollutants could explain the observed phenomena.

INTRODUCTION

Cyanobacterial-lichen soil crusts, an important component of many ecosystems, are found in arid and semi-arid regions throughout the world. These crusts play a vital role in reducing soil loss from wind and water erosion by binding soil particles together. They contribute nitrogen and organic matter to systems that often have low levels of both. They also increase availability of other nutrients for nearby vascular plants (Harper and Marble 1990; Belnap and Harper, unpubl. data). In addition, many air pollutants significantly affect the physiological functioning of these crusts, making them useful as indicators of the presence of pollutants (Belnap 1990).

The major constituents of cyanobacterial-lichen soil crusts are several species of filamentous cyanobacteria. Although very resilient when wet, filaments are extremely susceptible to compressional damage such as trampling by livestock when dry. Since crusts are metabolically active only when wet, dry filaments that are crushed are easily blown away. When large areas are destabilized, sediment that blows or washes in can bury the crusts, often resulting in death of portions or all of it.

A significant decline has occurred in the saguaro cactus (*Carnegiea gigantea*) population found within the boundaries of Saguaro National Monument (SNM). Since the monument has been subjected to heavy livestock grazing in the past, as well as heavy air pollution at present, adverse impacts to the soil crusts would be anticipated. Crust damage or loss may in turn affect cactus health and/or survival. This study was designed to ascertain possible correlations between the present status of the cyanobacterial-lichen crusts in SNM and the observed cactus decline.

METHODS

All sampling was conducted in long-term monitoring plots established as part of the ongoing study of the saguaro cactus decline. All saguaro cacti in each plot were examined for external signs of injury (epidermal browning); the number of lesions present on each cactus was used to construct a relative injury value. Injury values for each cactus were then pooled and averaged to arrive at an injury index for each plot (Duriscoe and Graben, this volume).

Within each plot, transects were established to estimate cover values for plants, rock, gravel, litter, bare ground and soil crusts. The relative composition of the crusts (cyanobacteria, lichens and moss) was also measured. Samples were collected for chlorophyll concentration and nitrogenase activity analyses.

For chlorophyll analyses, samples were extracted immediately with dimethylsulfoxide (DMSO). Samples were analyzed with a Beckman spectrophotometer at optical densities of 398 and 362 nm, following the methods of Ronen and Galun (1984). The wavelengths used had been previously determined to represent chlorophyll *a* and phaeophytin *a* in the crusts by spectrophotometric scans of extracts before and after acidification with 1N HCl (hydrochloric acid). Using these two values, the ratio of chlorophyll *a* to its degradation product, phaeophytin *a*, was obtained. This ratio is an indication of the status of chlorophyll concentrations in the crusts.

Nitrogenase activity in the soil lichen *Collema tenax* was measured with the acetylene-reduction technique. Circular samples of the lichen, 3 cm in diameter, were collected when dry. The entire surface was then moistened with 1.5 ml water and placed in gas-tight, translucent tubes. Sufficient acetylene was injected into the tubes to make a 10% acetylene atmosphere. Tubes were then incubated for four hours in a growth chamber illuminated with full spectrum lights. Measurements were made on a flame ionization detection gas chromatograph, using an 8-ft, 8% NaCl (sodium chloride) on alumina column.

Results for the transects were analyzed with analysis of variance and multiple range tests. Results comparing the presence of crust, chlorophyll ratios and nitrogenase activity with the saguaro damage index were analyzed with regression models.

RESULTS

Statistically significant correlations were found between increased chlorophyll *a*/phaeophytin *a* ratios and the saguaro injury index (Fig. 1), as well as between increased nitrogenase activity and the saguaro injury index (Fig. 2). No significant correlations were found between the amount of soil crust present and cover values for vascular plants, bare ground, litter, rock or gravel. No significant correlation existed between the saguaro damage index and the total amount of crust present, or the amount of cyanobacteria, lichen or moss present.

DISCUSSION

Increased chlorophyll *a*/phaeophytin *a* ratios have been found in crusts on four substrates (gypsum-, limestone-, quartz monzonite-, and sandstone-derived soils) exposed to simulated acid precipitation. Crusts on sandstone-derived soils showed the same effect where exposed to effluents from a coal-fired power plant containing large amounts of sulfur dioxide and nitrogen oxides (NO_x) (Belnap 1990). Decreased ratios have also been found in crusts and rock lichens exposed to urban pollutants (Belnap 1990; Garty et al. 1985) and rock lichens exposed to coal-fired power plant effluents (Belnap and Harper 1990). It is postulated that substrate buffering might account for different responses to the power plant effluents: cyanobacteria embedded in highly alkaline substrates probably receive a much greater amount of buffering from acidic compounds than rock lichens that are only attached to the surface of the substrate. If protected from acidic effects, the cyanobacteria would be able to take advantage of the incoming buffered nitrates and sulfates as fertilizers. Urban pollutants from the Los Angeles, California Basin (dominated by automobile exhaust), however, had the opposite effect on crusts from these same substrates. Chlorophyll degradation was significantly higher in crusts exposed to those pollutants than those in clean air (Belnap 1990). This would indicate that at least some compounds in urban pollutants cannot be buffered to prevent injury to chlorophyll in the crust.

In light of the above evidence, it is possible that the increased chlorophyll *a*/phaeophytin *a* ratio seen in plots with higher saguaro cactus injury indices may indicate that the crusts are receiving greater input of some fertilizing, buffered compound when compared to crusts found in plots with less damage. These compounds are probably different than those most commonly found in air pollutants dominated by automobile exhaust, since those have been found to degrade chlorophyll *a*. Addition of acidic compounds to the alkaline soils would make positively-charged nutrients more available to organisms, thus enhancing the fertilizing effect.

As with chlorophyll *a*/phaeophytin *a* ratios, nitrogenase activity increased in plots with greater saguaro cactus injury indices. Maximum rates of nitrogenase activity in soil-dwelling cyanobacteria usually occur at or near pH 7.0 (Stewart 1969; Granhall 1970).

Phosphate, molybdenum, iron, and sulfur can be limiting, so additions of these may stimulate nitrogenase activity (Henriksson and Pearson 1981; Gallon and Chaplin 1987). Decreased nitrogenase activity with the addition of nitrogen-based compounds (ammonium, nitrate, or nitrite) has been reported in both the laboratory and the field (Gallon and Chaplin 1987). Effluents from a coal-fired power plant, with high NO_x concentrations, have also been shown to decrease nitrogenase activity (Belnap 1990).

Several possible scenarios would explain the increased nitrogenase activity in plots at SNM. First, deposition of any acidic compounds would tend to lower the pH of the soil surface, thereby possibly increasing nitrogenase activity due to the pH effect. Secondly, addition of any acids would make positively-charged nutrients more available to organisms, and could act as a fertilizer. Thirdly, addition of compounds such as sulfur or phosphates, excluding those that are nitrogen-based, could act as fertilizers and stimulate nitrogenase activity.

The combined evidence makes it plausible to suggest that some non-nitrogenous, acidic compounds in the air may be responsible for increasing both nitrogenase activity and chlorophyll *a*/phaeophytin *a* ratios of the cyanobacterial-lichen soil crusts. These compounds may also be affecting the cactus. Non-nitrogenous compounds, buffered by surface soils, could increase nitrogenase activity by reducing the pH of the surface soil and either adding nutrients and/or releasing nutrients to act as fertilizers. This would also stimulate chlorophyll production and/or reduce chlorophyll degradation. Sulfur dioxide is the most common pollutant to fit this description, although many others would fit as well.

SUMMARY AND MANAGEMENT IMPLICATIONS

Further work needs to be done on the relationships between air pollutants present in SNM, saguaro cactus, and the cyanobacterial-lichen soil crusts. The research summarized here gives direction to future investigations. Acidic air pollutants found in SNM should be identified. Laboratory and field tests should then be conducted with these compounds to elucidate their effects on saguaros and soil crusts.

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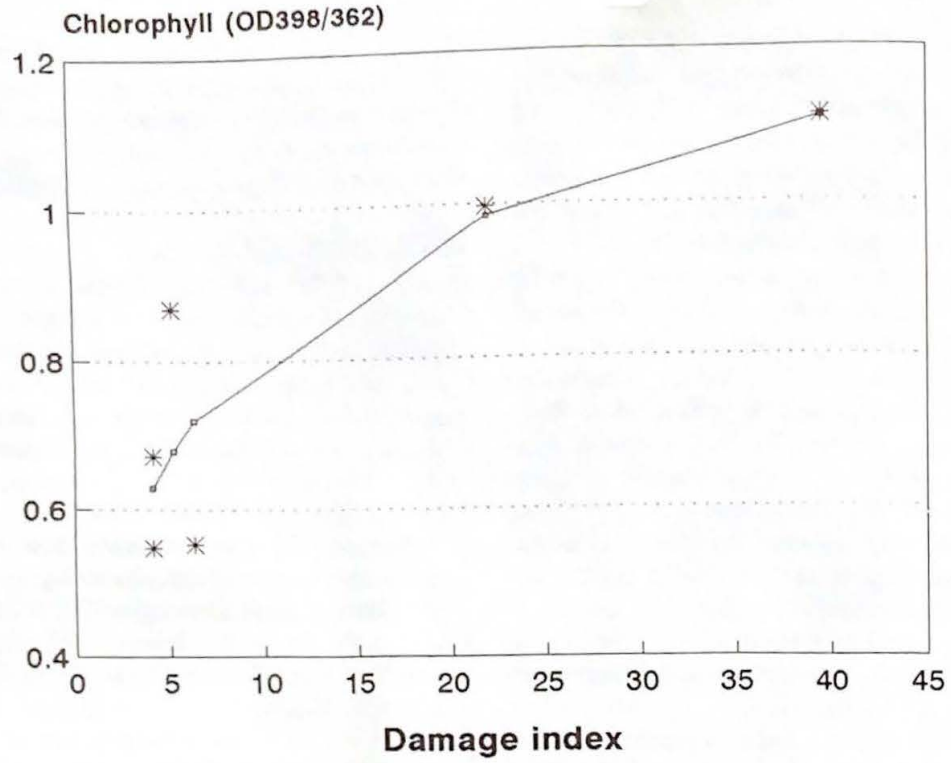


Fig. 1. Regression of chlorophyll *a*/phaeophytin *a* ratio on saguaro cactus damage index ($P < 0.02$).

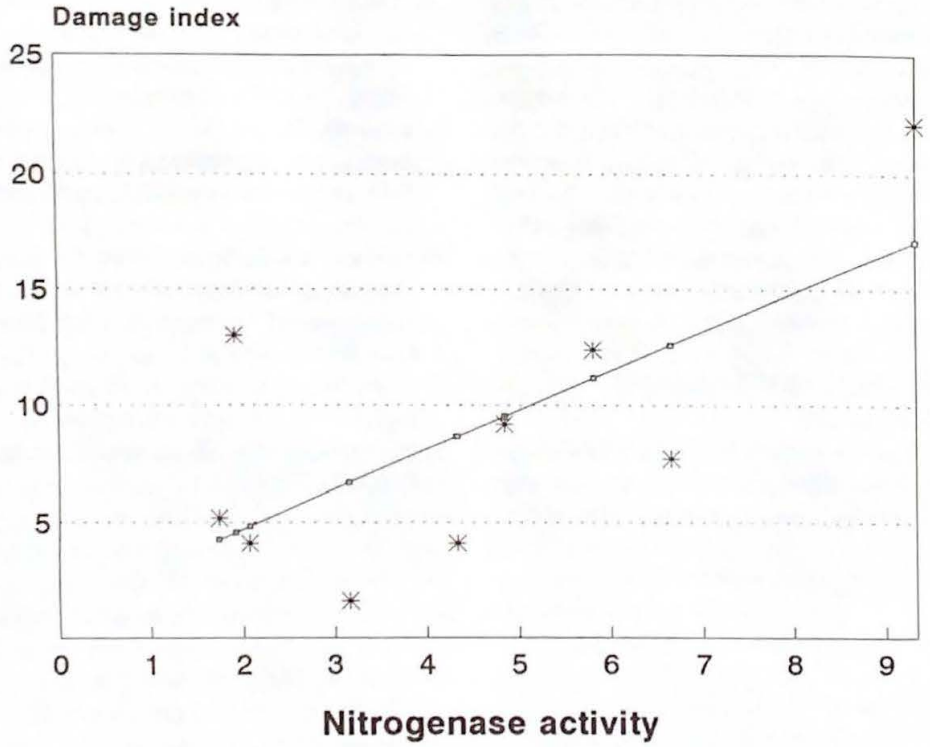


Fig. 2. Regression of nitrogenase activity on saguaro cactus damage index ($P < 0.05$).

Dendrometer, Dendrograph, and Phytogram Measurements on Douglas-fir and Southwestern White Pine in the Rincon Mountains

William Gensler

ABSTRACT

Main stem diameters and respiration of the main stem cambial region were simultaneously measured for a stand of Douglas-fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*) on the north slope of the Rincon Mountains. The immediate objective of the study was to establish baseline values of stem expansion and contraction and concomitant stem respiration. The long-range objective is to use this sensor complex to determine the influence of natural and anthropogenic stresses. Results indicate that stem diameter change is dominated by expansion and contraction due to water status. Contraction caused by drought occurs over time scales of many months and appears to carry over from season to season. Water status changes supercede any change related to biomass production. Short- and long-term weather patterns cause simultaneous changes in stem diameters and respiration. Age of the plant and water status are strong influences in the magnitude of responses to weather patterns.

INTRODUCTION

In recent years a substantial decline has occurred in the forests of western Europe and North America. The problem is very complex and involves the interaction of chemical, physical and biological factors in the soil-atmosphere continuum. Anthropogenic impacts are believed to be the cause of this forest decline and changes in the health of trees visibly change in response to such impacts. One technique widely employed in forest science to detect change is the measurement of tree circumference by manual means with dendrometers, or automatically with dendrographs. Circumference measurements are employed because they provide an integrated measurement of the change in the radius of the tree main stem without the necessity of extrapolating from a measurement at a single point on the perimeter.

In a previous study, the PHYTOGRAM technique was tested to determine whether it can be used as a quantitative scale of health (Gensler 1990). The technique is based on the use of invasive electrochemical sensors placed in the tree tissue for indefinite periods. The potential patterns derived from these sensing electrodes, termed PHYTOGRAMS, are a measure of respiration of the tissue (Gensler 1980, 1990). The objective of this project was to determine the correlation between the PHYTOGRAM respiration patterns and main stem circumference patterns on daily, seasonal, and annual time scales.

METHODS

The study site, shown schematically in Figure 1, is divided into four quadrants with data acquisition PODs (Potential Observing Device) at the center of the diagram. The basic approach was to install manual dendrometers and PHYTOGRAM electrodes on 21 Douglas-fir (*Psuedotsuga menziesii*) and 21

southwestern white pine (*Pinus strobiformis*). In addition, 12 automatic dendrographs were installed on each species, permitting the simultaneous measurement of the two species by three techniques under the same ecological conditions. Tree selection for sampling was guided by an attempt to obtain a wide variety of ages from each species.

Circumferential Dendrometers and Dendrographs

Each of the 44 manual dendrometers consisted of a 3.17 mm wide, 0.051 mm thick band made of Hastalloy C276, and wrapped around the main stem at breast height. The two ends of each band were attached to a well-type readout. The well depth read with a digital micrometer was accurate to within ± 6 μm (micrometers).

The 24 automatic dendrographs employed linear variable differential transformers (LVDT) as displacement sensors. An invar band was attached to the core of the LVDT and served to convert the stem diameter changes to changes in core position. Resolution of the sensor was 4 μm with an unadjusted range of 16,000 μm and a total adjusted range of 45,000 μm.

PHYTOGRAMS

Each of the 44 electrodes was placed in the region of the cambium, following bark removal. Tar was used to seal the entry points and at the same time insulate the electrodes. A reference electrode buried in the ground, completed the electrochemical circuit. The potential was measured between the electrode in the tree and the reference electrode. Automatic dendrographs and the electrodes were measured every 15 minutes, with data stored as one hour averages.

RESULTS

Long- and Short-term Radius Changes

The change in stem radius for the period October 1989 to June 1990 is shown in Figure 2. Overall, only four of the 40 trees, all of them young, had a positive change in radius. Fourteen of the 17 trees showing a positive increase in stem diameter from February to June 1990 were Douglas-fir.

A comparison of young (31 years) versus old (224 years) Douglas-fir showed similar overall contractions from day 285 to day 365. For the old tree, the contraction was 278 μm over 76 days (3.65 μm/day), and for the young tree the contraction was 378 μm over 76 days (4.2 μm/day). The change in radius is similar in spite of the wide difference in age.

A comparison of the response of a young (31 years) versus an old (224 years) tree to individual weather disturbances, indicates that the younger tree is much more volatile. Both trees responded to weather disturbances on days 292 and 322. However, the younger tree initially contracted, then expanded back to the pre-disturbance radius and overshot the steady state level. The older tree made a very slow and muted expression in the period following day 331, whereas the younger tree showed a very strong contraction and then a recovery to a level well below the day 331 level. The same response was observed for several of the young trees (e.g., tree 7.2, 21 years old and tree 42, 42 years old) during this time interval. In like manner, a second old Douglas-fir (tree 84, 199 years old) manifested the same behavior as the 224-year-old tree. The generalization suggested is that older trees are better able to withstand short-term adverse disturbances.

The comparative radius response beginning on day 292, 1989, is illustrated in Figure 3. Both radii followed the same pattern until an erratic temperature change on day 293 and a generally lower temperature caused a strong difference in response. The younger tree expanded with the lower temperature, while the older tree contracted.

Correlation Between Electrical Potential and Radius Change

The response of the electrode and the automatic dendrograph on the same tree to a short-term cold front is presented in Figure 4. The radius before and after the response is in a relatively straight line. This suggests that the response was in a sense superimposed on a steady increase in the radius. The electrochemical and physical responses are definitely similar.

CONCLUSIONS

A number of definite conclusions can be drawn from the analysis of data from the three types of sensors. First, the manual dendrometers indicated quite clearly that the magnitude of the hydration/dehydration cycle is great enough to obscure the determination of the biomass increment during the time interval under analysis. The contraction due to water

loss in the fall of 1989 was not compensated for by the snowmelt in the spring of 1990. The part of the seasonal hydration cycle observed in this data set, commonly had amplitudes in the order of 300 to 400 µm and reached as high as 1,100 µm.

Second, the responses of tree radius to daily hydration cycles are relatively small compared with the response to individual weather disturbances over a seasonal cycle. Daily peak to peak amplitudes in the order of 10 to 20 µm in radius were observed, compared to a seasonal amplitude of 225 µm. Weather disturbances have such a major influence on tree radii that the reading of the manual dendrometer on a particular day must take into account the weather several days before that day. It appears that weather disturbances can cause changes in tree radius as high as 225 µm.

Third, very little pattern in change in radius was evident as measured with the manual dendrometers. This means that the trees must be analyzed on an individual basis until a pattern is determined that can lead to a generalization about age-specific responses. Microsite variations and/or intrinsic genetic variations are likely quite strong.

Resolution of circumference at the 4 µm level in dendrographs is necessary to discern the magnitude and form of the diurnal radius cycle. The range of the automatic dendrographs at this resolution is 2,500 µm in radius. If the seasonal diurnal radius cycle is in the order of 1,000 µm or more, it will be necessary to set the initial value of the dendrograph with some care. This has already been found to be true.

The question of species differences was only briefly examined. A computation of the average PG11 index of the Douglas-fir had a relatively steady level of 400. The southwestern white pine had a PG11 magnitude of 285, with a substantial increase in magnitude between day 69 to 75. Because Douglas-fir were generally older than southwestern white pine, it is probably premature to place too much emphasis on the difference in index. However, the fact that 14 of 17 trees experienced a positive increase in radius in the spring, during a time period that corresponded to this index computation, suggests a significant difference between the two species may exist. The higher index values are a sign of more vigorous trees. Douglas-fir may have been able to sustain the rigors of the north slope climate better than the southwestern white pine during the time interval under consideration. However, this is not in keeping with the common observation that southwestern white pines are able to grow in drier climates than Douglas-fir.

The potential-radius plots indicate a very definite correlation between changes in the radius and changes in the potential. Potential and radius respond almost simultaneously. In other words, the correlation with regard to the question of "when" is excellent. This coincidence was also found in 1982, in cotton (*Gossypium hirsutum* L.), a woody perennial (Gensler and Dias-Munoz 1983). The sudden drop in potential was accompanied by an increase in the radius of the main stem.

The correlation with regard to "how much" and "in what direction" in the case of the trees in this project must be further investigated. Examples in the tree population were observed wherein the potential rose in the morning and fell in the afternoon. This has been shown for various species in numerous data sets and in various parts of the continent, to be concomitant with healthy, well-watered trees. By contrast, in this project, potential fell in the morning and rose in the afternoon for some trees. This indicates relatively extreme drought stress. In other words, conditions of the trees at the site do not appear to be uniform.

MANAGEMENT IMPLICATIONS

Two definite management implications follow from these results. Drought effects appear to carry over from year to year so that any testing or research effort during a particular year must take into account the extended precondition of the forest. The influence of suspected pollutants must be examined with great caution, since natural environmental disturbances have great magnitude and extended duration. This necessitates a very complete and extended data set on forest performance before conclusions about anthropogenic influence can be assessed.

ACKNOWLEDGMENTS

The author would like to thank Robert Hall, Patricia Haddad and Michael Danisiewicz of Saguaro National Monument for their splendid cooperation. In matters as varied as diameter tapes, mule trains, helicopter schedules and fireproof boots they contributed to the success of this project. My colleague, Frank Telewski, was a very active participant in the

project formation and installation of the equipment. He selected the trees under investigation and has provided insight into all aspects of this work. The genesis and purpose of the project are the work of Walter Franke. He recognized the strength of interdisciplinary scientific analysis and constantly kept sight of the objective. He supplied the funding and also a detailed understanding of the measurement systems.

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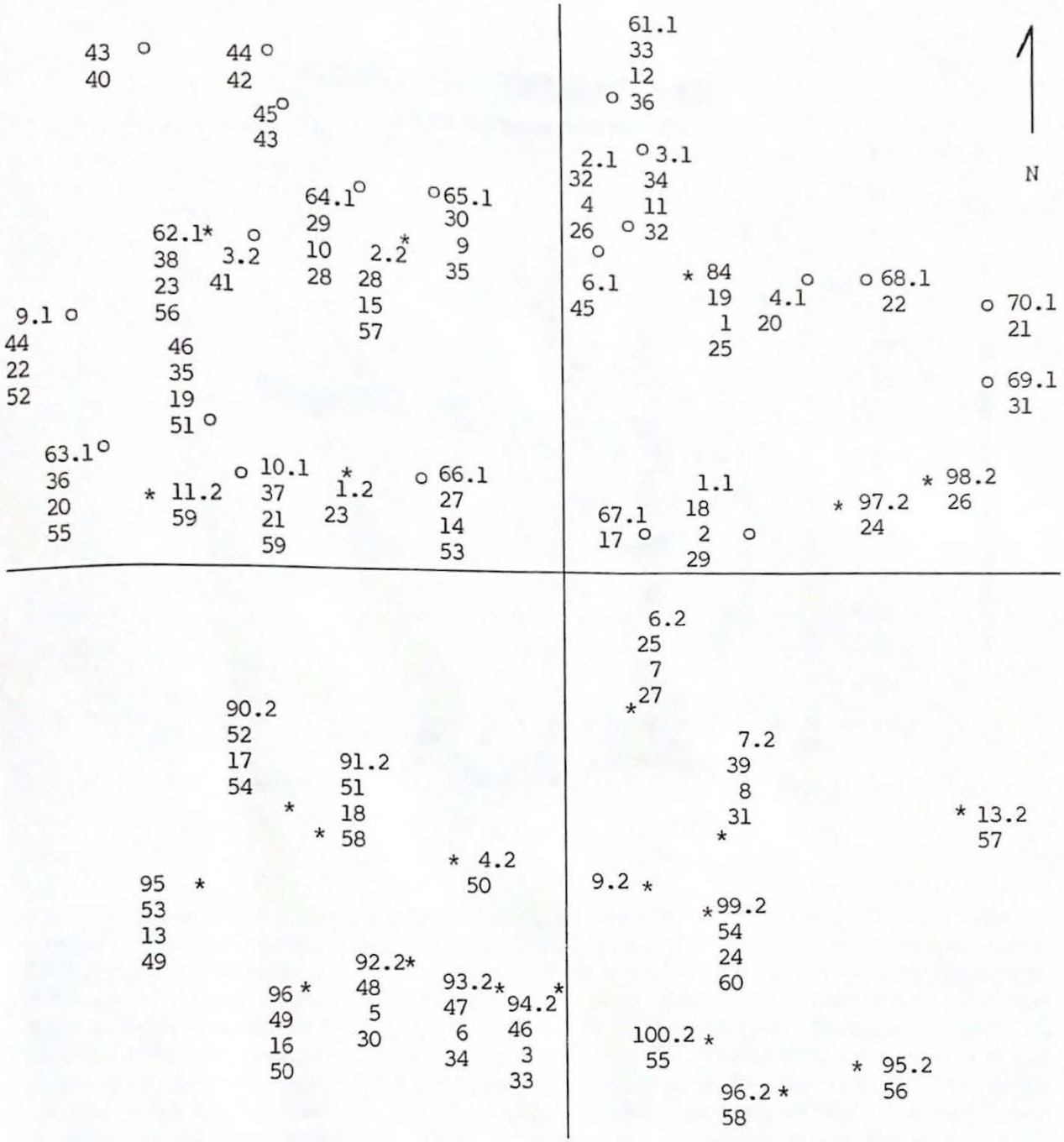


Fig. 1. Schematic layout of the site. The dendrograph and PHYTOGRAM PODs (Potential Observing Devices) are located at the center of the diagram. The slope of the hill is from the south to the north. A shallow wash is located just east of the POD. The scale of distance is approximately 40 m from the PODs to the outermost tree. Asterisks represent Douglas-fir; open circles represent southwestern white pine. (Example of code: 61.1 = tree number, 33 = electrode wire number, 12 = LVDT channel number, 36 = LVDT wire number.)

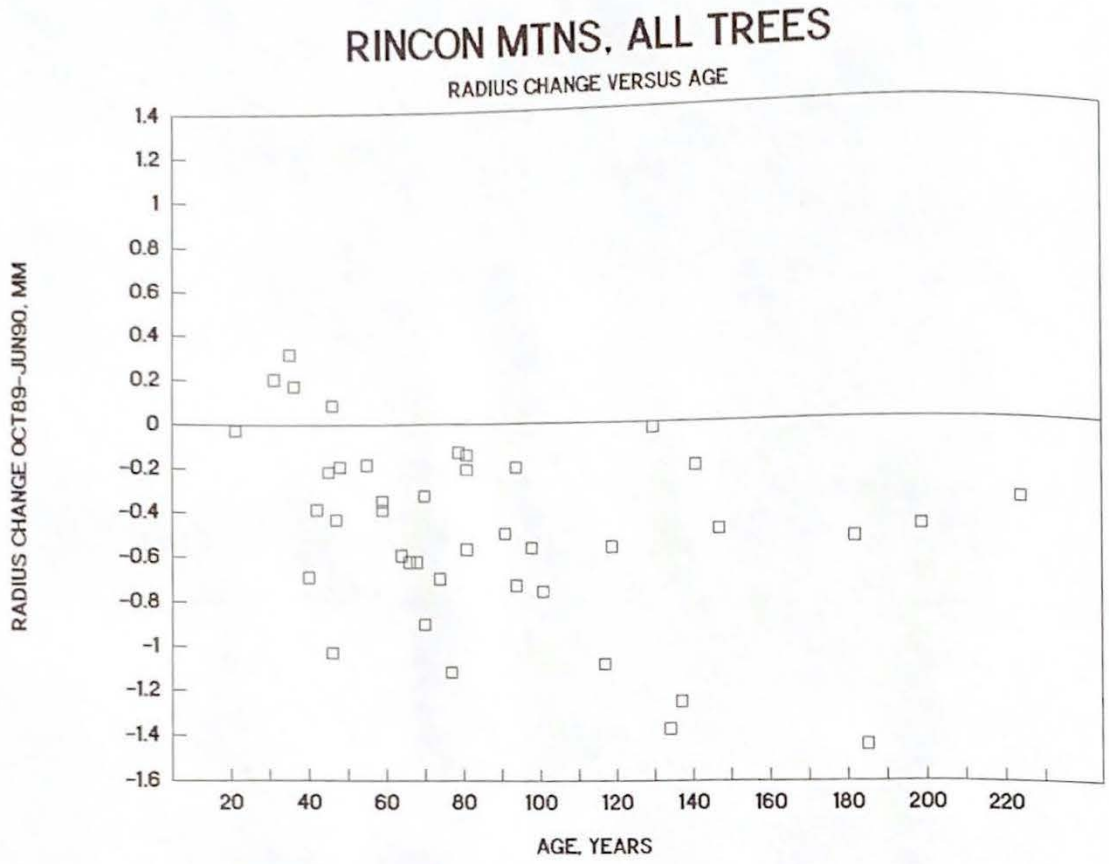


Fig. 2. Radius change (mm) versus age between October 1989 and June 1990. Between October 1989 and February 1990, every tree in the sample contracted. Between February 1990 and June 1990, 17 of the trees expanded. This curve gives the overall result for the complete time period. Fourteen of the 17 trees which expanded between February and June were Douglas-fir.

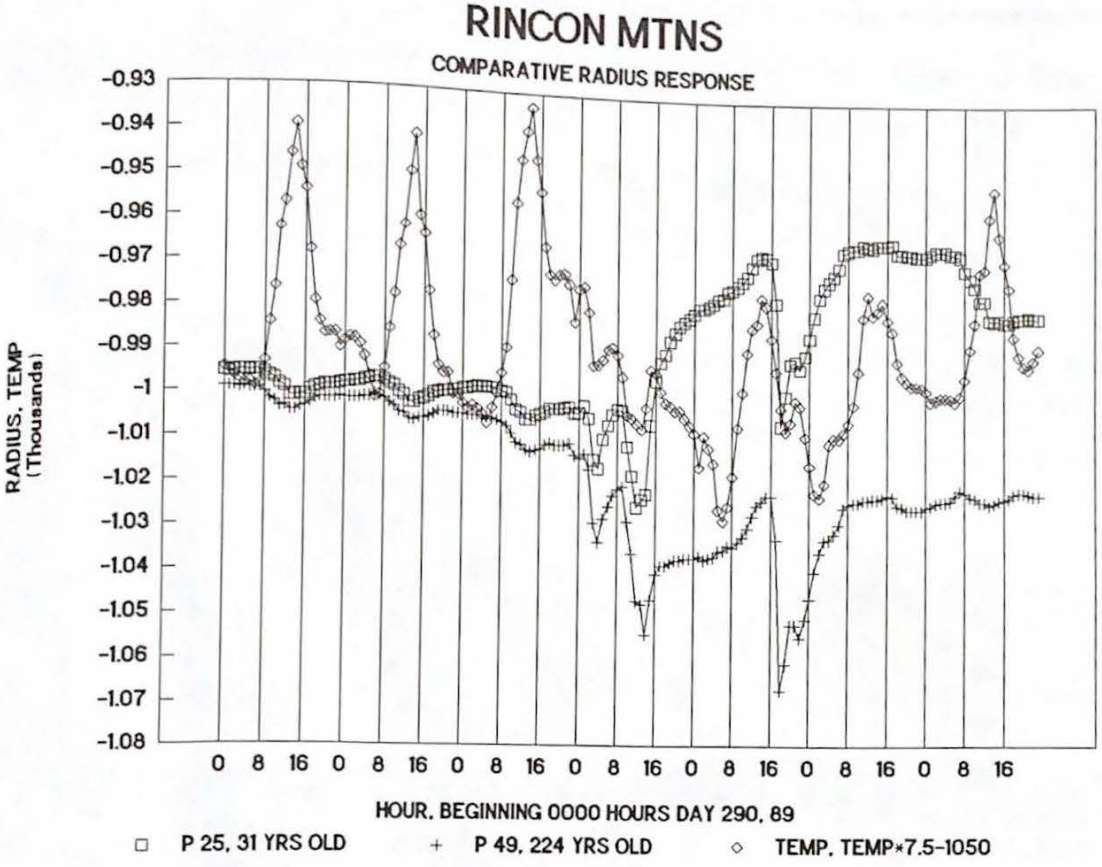


Fig. 3. Comparative radius response between a young (31 years old) and an old tree (244 years old). The response of both trees appeared to be caused by the erratic temperature cycle on day 293. The temperature at 0200 hours on day 293 began to rise. This rise lasted until about 0730 hours whereupon the temperature began to fall until 1400 hours. At this time the temperature began to rise again. At 0200 hours on day 293 the radii responded in the same manner. Both reversed their contraction and began to expand. The expansion lasted until 0800 hours when the temperature decline was already underway. The two trees responded with even greater magnitude this time until 1500 hours when they once again both began to rise. The expansion of the old tree was substantially different insofar as it did not rise past its pre-disturbance level. By contrast, the younger tree expanded well past its pre-disturbance level. Both trees responded very strongly to what appears to be a normally occurring temperature drop in the afternoon. The only difference in this temperature drop compared to others which provoked very little response was the temperature level. The temperature level this time was substantially lower than before. The radius scale is arbitrary on this graph, but the change in radius is absolute. The temperature scale is absolute.

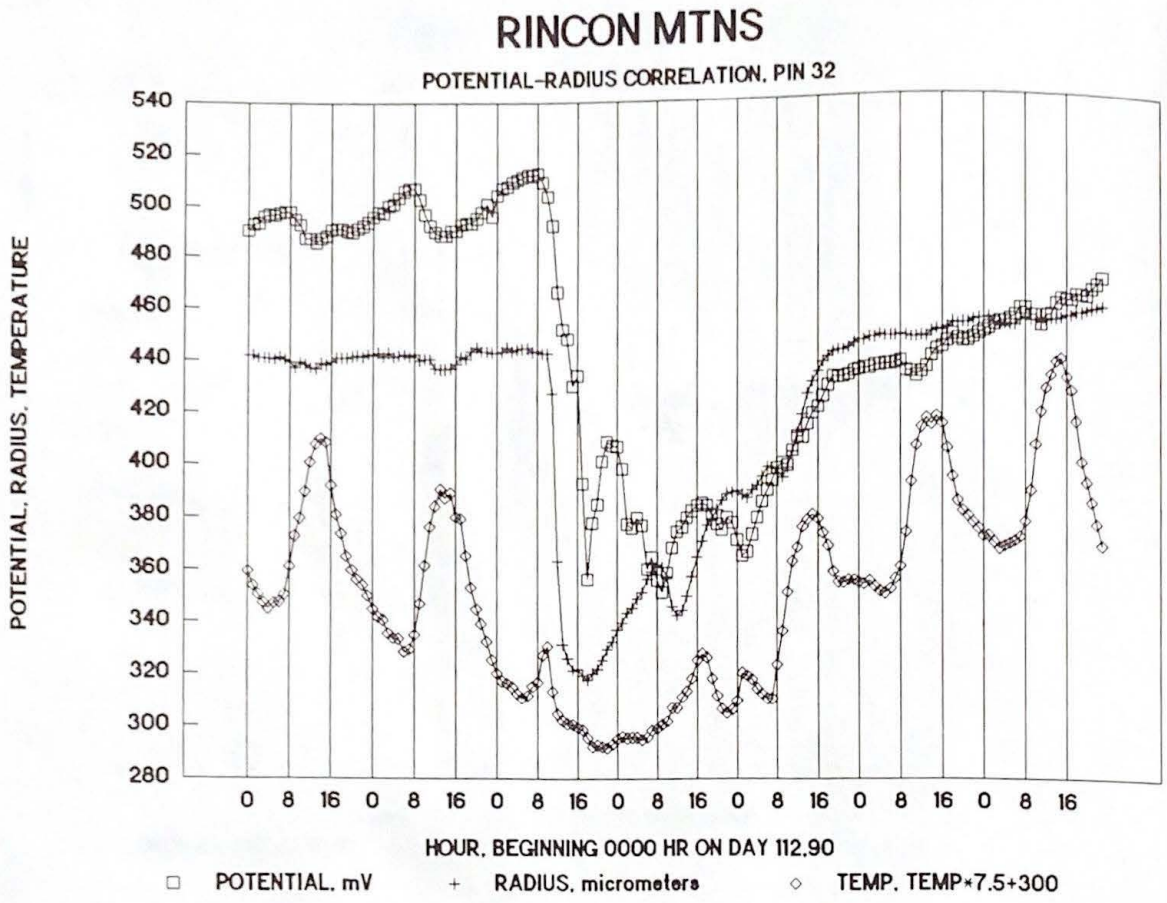


Fig. 4. Example of the potential-radius correlation, tree 2.1, 45 years old. The diurnal cycle of the radius is almost indiscernible. The diurnal cycle of the potential has a peak at 0800 hours and a minimum at 1400 hours. Both the potential and radius responded sharply at 0900 hours on day 114. The low temperature on day 112 was about 5.3°C and the high was 14.6°C. The radius and potential drop began when the temperature was above freezing. Potential scale is valid but the radius scale is arbitrary. Changes in radius are according to the scale. The actual temperature value can be obtained from the formula given.

Monitoring the Ecosystem and Its Impact on Honey Bee Reproduction: A Valuable Tool for National Parks

Steven C. Thoenes, Stephen L. Buchmann, and Justin O. Schmidt

ABSTRACT

Two systems of monitoring an ecosystem with honey bees (*Apis mellifera*) are presented. The first involves honey bee colonies equipped with pollen traps that are placed on scales in natural areas. This system yields data on pollen and nectar quantity collected by bees throughout the year. Further analysis of the pollen samples yields quality estimates and species diversity indices. The second monitoring system uses swarm traps to monitor periods of swarm movement and numbers of swarms. This provides a database in which changes in the bee population (such as an invasion by Africanized honey bees [*Apis mellifera scutellata*]) can be recognized and investigated. Overall, natural areas can benefit by the many ways honey bees can be used as biomonitors to aid in understanding important aspects of particular ecosystems.

INTRODUCTION

The Tucson Basin is a highly varied and complex ecosystem, including areas of vast urbanization with little native flora, rural areas of low human habitation with much of the native flora intact, and natural areas including national and state parks, monuments, and forests. Honey bees (*Apis mellifera*) can be used as a work force to monitor blooming periodicity for the majority of plant species in these areas, both native and exotic (O'Neal and Waller 1984). This information when combined with climatological data can be used to monitor quality (protein content) and quantity (amount available) aspects of pollen in ecosystems.

The Africanized honey bee or so called "killer" bee (*Apis mellifera scutellata*) is now present in the United States. This bee is characterized by highly defensive behavior, high reproductive rates, and long distance swarm movements. The various agencies dealing with natural areas, especially those located near urban centers, are faced with possible invasions by these bees posing human health and public relations problems. Understanding the current relationships among bees, plants, and climate within the ecosystem would provide baseline data to allow significant changes in honey bee populations (such as an invasion by Africanized bees) to be detected, characterized, and handled in an appropriate manner. In this paper, we explain how honey bees can be used as effective monitors of ecosystems, how the ecosystem affects honey bee reproduction, and how honey bee swarms can be monitored with traps, leading to possible future control methods.

METHODS

Honey bee colonies were placed in various locations across the Tucson Basin, including both units of Saguaro National Monument (SNM). Modified Ontario Agricultural College (OAC) pollen traps (Waller 1980) placed on standard honey bee colonies were used to collect pollen samples, usually on a weekly basis. Quantity of pollen collected was obtained by weighing each sample. Subsamples were

analyzed for plant species diversity with a microscope. A subsample was also analyzed for percent nitrogen, using micro-Kjeldahl digestions, and was subsequently converted to percent protein (Milton and Dintzis 1981). Selected bee colonies were placed on either platform or electronic scales to monitor weight changes (Moffett et al. 1981; Buchmann and Thoenes 1990). Data compiled by University of Arizona weather stations were used for temperature calculations and rainfall data were obtained from the Pima County Department of Transportation and Flood Control District. Timing and locations of honey bee swarms were obtained mainly from records of telephone calls to various private and government agencies when a swarm landed in a person's yard, tree, or house. Swarm traps were placed across the Tucson Basin as extra monitors of swarm movement (Schmidt and Thoenes 1987, 1989, 1990). National swarming patterns were developed from literature references for each state (mainly Jones 1918) and fine-tuned with the few swarm patterns available for specific cities.

RESULTS

Pollen trap records from any one site showed high variability on both a weekly and yearly basis. Weekly collections for urban areas ranged from 0.0 to 2,317.0 g ($\bar{x}$ = 846.0 g) and yearly values ranged from 13.5 to 37.9 kg ($\bar{x}$ = 26.5 kg). Natural areas yielded weekly values of 0.0 to 1,974.0 g ($\bar{x}$ = 427.7 g) and yearly values of 19.5 to 23.7 kg ($\bar{x}$ = 22.7 kg). Species diversity in the pollen samples revealed that honey bees collected pollen mainly from species of zoophilous (animal-pollinated) plants, but also from species of anemophilous (wind-pollinated) plants (5-28% of diet per year). Honey bees collected pollen from 20 to 25% of the flora within flight range, and 10 to 24% of this was pollen from exotic flora such as ornamentals. Percent protein calculations (crude nitrogen x 5.6) yielded a range of 12.6 to 28.5% ($\bar{x}$ = 21.5%). Weights of colonies showed the largest gains in colony mass during April and May, peaking in late May. Modest gains were also recorded in mid-August.

A total of 3,069 swarms was recorded. Swarms occurred from late January to mid-November, but the majority of swarms occurred from March through May. Captures of swarms with swarm traps closely mimicked the corresponding yearly pattern of reported swarm occurrence. Variation in swarm occurrence was somewhat correlated with climatic factors such as temperature and rainfall, but was highly correlated with various plant bloom factors, such as peak spring pollen quantity, spring rise in pollen quality (% protein), and negatively related to nectar flows.

DISCUSSION

The National Park Service has many parks, monuments, and historic areas, which include unique or significant undisturbed ecosystems. Results of this study show that honey bees can be used as a work force of data collectors, and this information can be used to quantify important bee/plant/climate interactions to build databases in natural areas. The entire data-collecting device includes a single colony of honey bees equipped with a pollen trap and placed on a scale (preferably an electronic scale interfaced to a portable data-collecting device). Data collection by park or other personnel requires only weekly records of pollen and colony weight. This system is already in place and functioning well in Organ Pipe Cactus National Monument. Trend analysis of the weekly colony weights and a more in-depth analysis of the pollen can be accomplished through a cooperative program with research personnel from the Carl Hayden Bee Research Center in Tucson.

Schmidt/Thoenes swarm traps provide artificial cavities for swarms of honey bees to set up new colonies. The tremendous advantage of these traps is that they can be easily deployed in any ecosystem of interest. Usually, only the "most fit" colonies reproduce by swarming, and do so at the time of year most advantageous for survival. Successful captures in swarm traps can be noted by park personnel and baseline data gathered that give information on the floral health of the ecosystem, population density of honey bees and periods of normal swarm movement for that area. National swarming patterns yield basic knowledge as to when swarms should be moving in a particular area of the country. This broad spectrum view can be used to determine the best periodicity of trap inspection (i.e., once or twice a week during the peak and monthly otherwise).

Besides gathering data to reveal significant aspects of honey bee reproduction, swarm trap information is very important in what it reveals about honey bee populations and movement. This information has an extremely important application in detecting the process of "Africanization" in the bee population. Africanized bees are of tropical origin and have high rates of reproductive swarming and swarm movement throughout the year. Thus, the pattern of swarm capture will be dramatically different than that of honey bees adapted to temperate climates. Many natural areas across the country are already viewed as "repositories" of a variety of exotic, or unwanted species, but few if any of these species are viewed as life-threatening. The public outcry against "killer" bees in natural areas could be potentially devastating to public perceptions and use of parks. We believe that a well designed series of swarm trap "lines" can yield information that will either detect Africanization of local honey bees as it occurs, or show that Africanization has not yet occurred. A basis for possible control and elimination of honey bee populations through swarm control may also be provided.

SUMMARY AND MANAGEMENT IMPLICATIONS

Honey bees can be used as biomonitoring devices to more completely understand the unique or significant ecosystems of many natural areas. Important information such as floral bloom phenologies, presence or absence of particular flora, and honey bee diet preferences can be easily collected. Such efforts would take little time and could easily be integrated into existing bee research programs. Valuable insights about overall interrelationships of bees, plants and climate would be obtained.

Baseline data showing periodicity and quantity of honey bee swarm movement in natural areas is essential. Programs using swarm traps as monitors can yield the needed information. Databases showing national swarming patterns can aid in minimizing time spent by park personnel in monitoring. Without proper data, invasions by Africanized bees can go unnoticed until a serious stinging event occurs. Maintenance of swarm trap monitoring programs may also provide future control for honey bee populations, but this particular aspect is still under investigation by the authors.

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