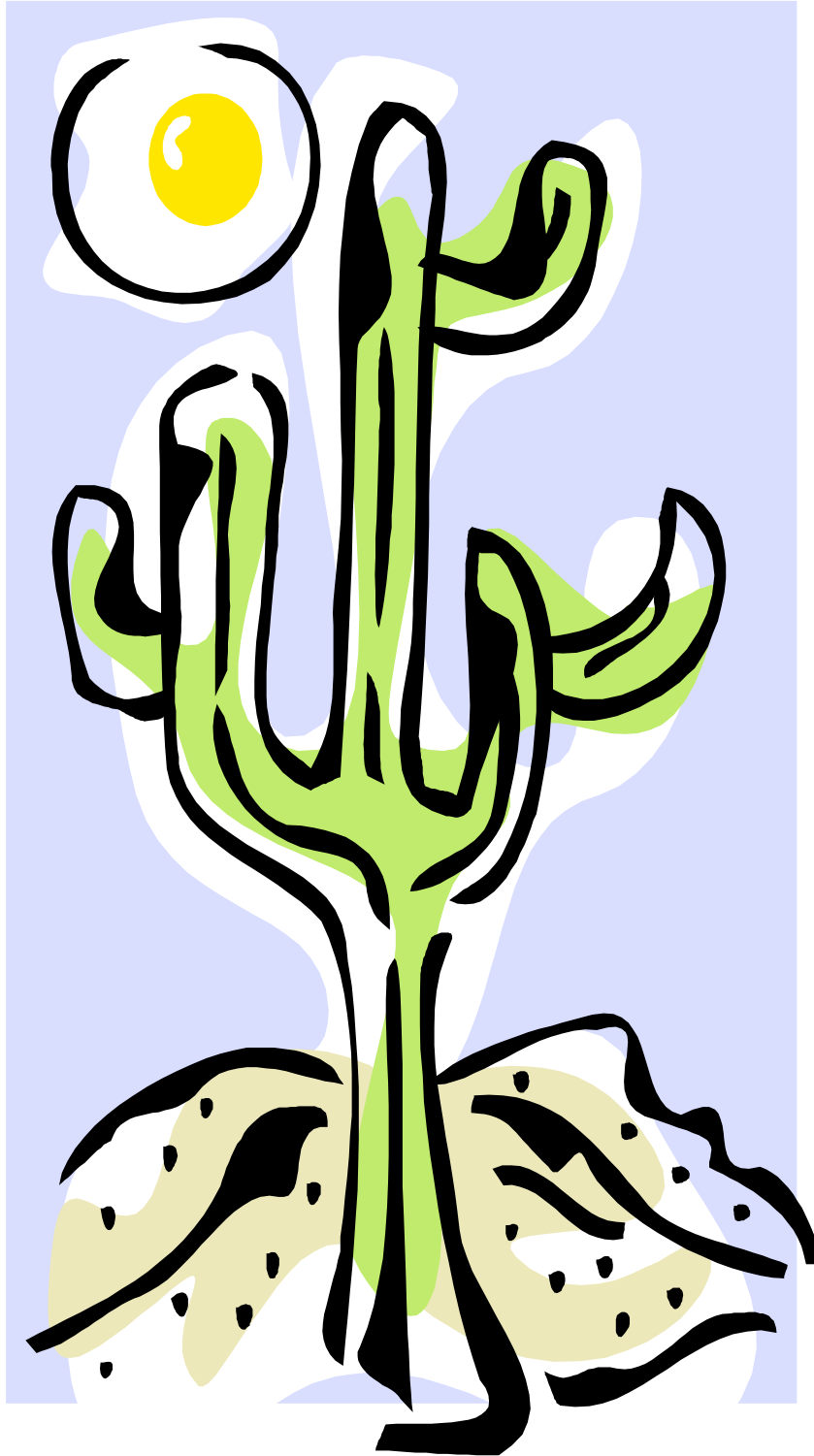


**LIFETIMES OF RESEARCH,
BUT STILL INTRIGUING:**
The Saguaro Saga of the 20th Century
and Beyond



FINAL REPORT

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I. HISTORICAL PERSPECTIVE

Saguaro National Monument was established in 1933 to preserve and protect one of the southwestern United States' unequivocal natural treasures: an impressive "old-growth" stand of giant saguaros (*Carnegiea gigantea*). The grandiose population located at the base of the Rincon Mountains near Tucson, Arizona has been affectionately dubbed "the Cactus Forest." In 1961 the National Park Service added a new district to the monument, west of Tucson in the Tucson Mountains. Congress raised the status of the monument to a national park in 1994 (**slides 2, 13, 14, 24, 65**).

Saguaros are limited in distribution to the Sonoran Desert, which spans southern Arizona, southeastern California, and much of Sonora, Mexico. It is the largest species of columnar cacti native to the United States, although the cardon cactus of Baja California can be taller. The saguaro is a tropically-derived species that is limited in the northern portion of its range by frost (**slides 66, 29**), and limited in the western portion by low rainfall (Shreve 1951). At the southern limits of its range, the saguaro is limited by high rainfall and the increased competitive pressure from other plant species.

Much of what we know about this special cactus species has been revealed over decades of study. Ideas regarding the biology and ecology of saguaros have evolved over the past century. Especially impressive has been the variety of forecasts regarding the long-term health of the saguaro populations at Saguaro National Park, which have ranged from utterly dire to strongly optimistic. Because the National Park Service mission commands park personnel "to preserve and protect" natural resources for future generations of visitors, long-term biological monitoring of this plant is necessary. However, it takes many decades to unravel the mysteries of saguaro population dynamics, especially because these giants easily outlive the people who study them. McAuliffe (1993) identified three principle areas of saguaro interest and funding that have driven saguaro research and monitoring over the past century: the saguaro disease

investigations of the 1940's to the 1960's, the ecological investigations of the 1960's to the present, and the Air Quality Division investigations of the late 1980's and early 1990's.

During the early 1940's, Saguaro National Monument personnel and the scientific community became increasingly aware of a dramatic change in the character of the Cactus Forest. The once dense forest of robust and grandiose saguaros appeared to be in serious trouble (**slides 49, 50, 51**). Suddenly, venerable old cacti were dying in droves, seemingly the victims of a mortally-wounding disease that caused them to ooze black liquid and topple to the ground (**slides 16, 17**). Alarm over the large-scale mortality was amplified by the fact that few if any young saguaros were growing up to replace the dying. This was a predicament for park managers: what is to be done when the very namesake of your park appears to be in the process of major devastation, with no apparent regeneration?

Plant ecologists in various parts of the United States had, in recent years, seen the ravages of chestnut blight, Dutch elm disease, and white pine blister rust, so it is no surprise that this saguaro “epidemic” was taken very seriously. Gill (1951) warned that *“there are notable examples where similar forests have degenerated completely within the memory of men living today. The causes are obscure in all cases and the possibility must be recognized that if nature is allowed to take its course, the spectacular groves of saguaro may in time become sparse and mediocre.”*

Plant pathologists from the University of Arizona were quick to respond, and permanent monitoring plots were established in 1939 and 1940 to study this unidentified disease. Soon, the bacterium *Erwinia carnegiea* (**slide 81**) was identified as the “cause” of the saguaro’s “bacterial necrosis disease” (Lightle et al. 1942). These events were the subject of much sensationalized reporting, and soon the public was experiencing a “saguaro hysteria”— with many fearing the unrecoverable loss of our southwestern plant mascot.

Initial studies focused on isolation of bacterial necrosis to prevent its spread. In 1942 the US Department of Agriculture's Bureau of Plant Industry (BPI) initiated "disease suppression" experiments. A war-like approach involving the removal of several hundred diseased plants was intended to prevent the spread of the bacterial necrosis to healthy plants (**slides 70, 71**). The entire Cactus Forest area comprises 8 to 10 sections; all infected plants (313 plus 12 incidental healthy plants) were removed from a half section (320 acres, or 1.3 square kilometers). This was an extraordinarily aggressive action — it encompassed a very large proportion of the Cactus Forest, and required heavy machinery to remove and transport saguaros to 4 large burial pits, where the carcasses were fumigated with pesticides, burned, and then buried. In the end, it was found that these ecologically invasive actions had no effect on the condition of bacterial necrosis in the Cactus Forest (Gill 1951).

Subsequent studies were aimed at understanding the nature of bacterial necrosis and effecting a "cure". An important step forward was the identification of the principal vector (how *E. carnegiea* is transferred from one plant to another): a moth whose larva tunnel through live cactus tissue (Boyle 1949). Some researchers had success in treating saguaros with antibiotics, although the cost of treating large areas would be prohibitive (Boyle 1949, Bardsley 1957).

Several proposed and severely misguided responses to the saguaro epidemic were avoided due to a fortunate combination of extenuating circumstances and reasonable decision-making. Some suggested controlling the spread of bacterial necrosis by killing the moth vector with the aerial application of pesticides such as DDT (Bardsley 1957, McAuliffe 1993). Fortunately, that approach was not employed as we have since learned of the deleterious biomagnification effects of DDT. There also was a saguaro "reforestation" effort planned that was narrowly avoided due to a lath house fire in the early 1960s (McAuliffe 1993) (**slides 77-79**). A surprising recommendation was made by the regional Park Service Director in 1945 that Saguaro National Monument be abolished altogether due to

the decline of the Cactus Forest (McAuliffe 1993). The National Director prudently rejected this notion.

Alcorn and May (1962) extrapolated the losses from bacterial necrosis in the Cactus Forest and wrote: *“Assuming no changes in the rate of decline in the future, this plant population will theoretically (at the 95% level of confidence) cease to exist between 1995 and 1998.”* We know now, with many saguaros populating the Cactus Forest, that such doomsday predictions were not correct. Several ecologists in the early 1960’s began to assert different opinions regarding the bacterial necrosis epidemic, citing reasons other than a disease epidemic for the die-off in the Cactus Forest. First, the pathogenic capability of *E. carnegiea* was questioned in healthy saguaros (Niering et al. 1963), then both Lowe (1966) and Steenbergh (1970, 1972) outwardly rejected the notion that bacterial necrosis was a disease at all. *“This flamboyant misnomer ‘bacterial necrosis disease’ is not a control and not a disease—it is the important natural process of tissue decomposition (Lowe 1966).”*

Saguaro research then took a shift in direction. Ecologists were beginning to believe that bacterial necrosis was merely a symptom, not the cause, of decline in the Cactus Forest. Furthermore, scientists began to recognize that such a decline was occurring not only because many of the saguaros were quite old, but because there were no young saguaros growing to replace them. Prior to this time, most research was addressing mortality but ignoring the issue of depressed seedling establishment and recruitment. It was clear that in order to understand the decline of the Cactus Forest, much research was needed on the basic ecology of the saguaro. McAuliffe (1993) identified six major lines of ecological investigation aimed to better understand saguaro biology: climate variability (e.g. precipitation patterns), catastrophic freezing, pollination and seed dispersal studies, requirements for seedling establishment, impacts of livestock grazing, and permanent plot studies of demographic patterns. This diverse suite of studies comprises the bulk of saguaro research from the 1950’s to the present,

and has highlighted the complex ecological interrelationships that govern the health and character of saguaro stands.

CLIMATE VARIABILITY

In the Sonoran Desert, precipitation occurs during 2 distinct seasons: summer and winter. The summer “monsoon” usually arrives during the month of July, and heavy rains can last until September (**slide 67**). Winter rains are less predictable, and generally occur during the months of December and January. Saguaros and other Sonoran Desert species have evolved under the constraints of these precipitation patterns (as well as other abiotic factors).

Hastings and Turner (1965) reviewed precipitation patterns since 1898, and concluded that winter rainfall has progressively dropped and winter temperatures have risen since that time, making the Sonoran Desert a warmer and drier place than it had been in the previous century. Turner et al. (1966) suggested that such climate trends (in concert with grazing pressures) could be responsible for a decline in many Sonoran Desert plant species, including saguaros, which would decline in a delayed fashion in response to fewer available nurse-plants. Steenbergh and Lowe (1977) argue that there is not enough evidence to support such claims, and instead favored catastrophic freeze events as the explanation for saguaro decline.

CATASTROPHIC FREEZING

Steenbergh and Lowe (1976, 1977) were the major proponents of the idea that the decline of the Cactus Forest was due to repeated catastrophic freezing during the 20th century. Saguaros in the Tucson area are near the northern and eastern limits of the species’ distributional range; further, the species boundary actually slices through the Rincon Mountain District of Saguaro National Park. Saguaros at the eastern and northern limits of the species range are limited by recurrent sub-freezing events that control density and distribution. In this portion of the

range, saguaros frequently freeze to death, and saguaros are most successful in winter-warm microenvironments such as south-facing slopes and rocky slopes. Freezing temperatures selectively kill the oldest and youngest individuals in saguaro populations and favor intermediate age classes.

In the Tucson area, it is not uncommon for winter low temperatures to dip below 32 degrees Fahrenheit, but in general these periods are brief and mild. When freezing is more intense, however, it also tends to last longer. Freezing in the Sonoran Desert is defined as catastrophic when it is cold enough and lasts long enough to kill or severely damage a wide variety of plants over a vast area. During the 20th century, there were several catastrophic freezing events (1913, 1937, 1949, 1962, 1971, and 1978) that contributed to the decline of older saguaros and prevented the establishment of young plants (Bowers 1981). After each severe freeze, a slow process of decay in the freeze-damaged plants resulted in a wave of saguaro deaths (**slides 18, 29**).

POLLINATION AND SEED DISPERSAL

Saguaros bloom mostly during the period of late April to June, although anomalous plants can be observed blooming any month of the year (**slides 3, 4**). Saguaro flowers open shortly after dusk and remain open until late afternoon the next day, when they close permanently. During periods of unusually low temperatures, however, they have been observed to remain open for up to 3 days (McGregor et al. 1962). Schmidt and Buchmann (1986) observed 295 flowers per plant over the course of a single season, with each plant producing close to 150 fruits. Flowering is highly variable within a population; this insures pollination success, because pollinator populations vary. There is also geographic variation in flowering dates—flowers open progressively later as one travels south to north and from low to higher elevations (Steenbergh and Lowe 1977). This causes the 1 – 2 week lag in flowering between the Tucson Mountain District and the Rincon Mountain District of Saguaro National Park.

In the late 1950's and early 1960's, several researchers became interested in the pollination ecology of saguaros and other columnar cacti, and a suite of studies were initiated (**slides 68, 75**). McGregor et al. (1962) found that saguaro flowers are self-sterile and there is little cross-fertility between flowers on different arms of the same plant. Ultimately, saguaros must be cross-pollinated to set fruit. Saguaro flowers are available to both day and night pollinators. The main pollinators are honeybees, which were introduced about 100 years ago; prior to that, the primary pollinators were bats, native bees, and white-winged doves (Alcorn et al. 1961, Schmidt and Buchmann 1986) (**slides 15, 27, 28**). Flowers fall from the plant 3 days after opening (McGregor et al 1962). It takes 31 to 45 days for fruit to become mature, and there are approximately 2250 seeds per fruit (Steenbergh and Lowe 1977).

The saguaro fruit crop is a dependable hot-summer food source for desert wildlife, as it is insured every year regardless of rainfall (Steenbergh and Lowe 1977) (**slide 5**). Saguaros utilize stockpiled stem moisture for the reproductive effort, and the fruit crop emerges at the hottest and driest part of the year, during the late spring and early summer. This timing guarantees that seeds will mature with impeccable timing, just before the summer monsoon. Steenbergh and Lowe (1977) noted that although the reproductive effort occurs annually regardless of rainfall, catastrophic freezing events will negatively impact fruit-set.

Seeds are dispersed to appropriate germination sites by both early summer rains and the many animals that feed on the ripe fruits. These include: white-winged doves, mourning doves, harvester ants, round-tailed ground squirrels, Harris' antelope ground squirrels, Gambel's quail, curve-billed thrashers, cactus wrens, Gila woodpeckers, gilded flickers, brown towhees, kangaroo rats, pocket mice, white-throated woodrats, cactus mice, long-nosed bats, coyote, and javelina (Steenbergh and Lowe 1977). In general, the larger the animal, the more viable seeds are likely to be recovered from the feces (except in the case of primary seed-consumers). Steenbergh and Lowe (1977) found viable saguaro seeds in the scat of the following animals, making them potentially important seed-dispersers:

coyote, javelina, curve-billed thrashers, cactus wrens, Gila woodpeckers, and gilded flickers.

Until recently, seed-eating birds such as white-winged doves were not considered effective dispersers of viable saguaro seeds (Steenbergh and Lowe 1977) (**slide 9**). However, Olin et al. (1989) reported an interesting symbiosis between these birds and effective saguaro germination and establishment. White-winged doves are saguaro flower pollinators (McGregor et al. 1966) and fruit-eaters that nest preferentially in palo verde and mesquite trees. Olin et al. (1966) examined fecal matter underneath palo verde and mesquite trees, and found extremely low seed viability. A more significant contribution of viable saguaro seeds under the trees, however, came as a by-product of the feeding behavior of the birds. White-winged doves regurgitate food (including saguaro fruit) to their young, and drop much regurgitate in the process. This results in the dispersal of viable saguaro seeds directly to favorable establishment sites beneath desert trees. Interestingly, white-winged dove distribution (Cottam and Trefethen 1968) in Arizona matches that of the saguaro (Shreve 1951). Wolf and Martinez del Rio (2000) used stable isotope and crop content analysis to demonstrate that saguaro fruit is the most important component of desert-dwelling white-winged doves. This symbiotic relationship also helps to explain the location of seemingly anomalous saguaros that are remote from any others.

REQUIREMENTS FOR SEEDLING ESTABLISHMENT

Like many long-lived woody plants of the Sonoran Desert [the saguaro] reproduces episodically when a series of climatic and microhabitat conditions are met...(Pierson and Turner 1998)

Saguaro seed germination requires a complex interaction of separate optimum conditions of light, imbibation period, temperature, and other variables. Alcorn and Kurtz (1959) found that saguaro seeds will not germinate at low or high temperatures, but will germinate under alternating high and low temperatures

and also that seeds require repeated exposure to red light (daylight). Because of these requirements, saguaro seeds planted in the conventional manner (seeds buried to a depth at least equal to their thickness) do not germinate readily, whereas seeds placed on soil surface do.

There is a measurable difference in seedling survival patterns in rocky habitats versus flat habitats (Steenbergh and Lowe 1969). Rocky habitats are comprised of coarse soils that support poor tree and shrub cover; this provides fewer suitable germination sites, but a better chance of seedling survival. Rocks concentrate moisture in the soil for deeper water penetration and less evaporation, while providing shade that offers protection from the elements and predation (Turner et al. 1966) (**slide 23**). Flat habitats, on the other hand, are comprised of finer soils that support many shade sources and lots of suitable germination microhabitats. However, the survival rate in flatlands is much lower because of the poor soil drainage characteristics (**slide 62**). These pressures assure that in rocky habitats there are more seedlings from fewer germinations. In the flats, there are fewer seedlings from many more germinations.

A very small percentage of the seed crop remains on the ground until suitable germination conditions may or may not present themselves with the summer monsoon. Most of the seeds are removed through the actions of birds, insects, and small mammals. Seedlings (**slide 63**) emerge when 2 or more rain events occur within a 5 day time-span during the summer monsoon. Of those that germinate, most will die within the first year, as a result of such factors as predation (by rodents, insects, birds, ground squirrels, and granulate cutworm), drought, erosion, and frost (Steenbergh and Lowe 1969). The most critical period during the first year of seedling life for survival is the dry hot period (May and June) before the monsoon (Turner et al. 1966). The high level of mortality within the first year of life drops off sharply thereafter; as seedlings become older and larger, they can more successfully resist predation and are less vulnerable to climate extremes (Steenbergh and Lowe 1969).

At the earliest stages of life, saguaro seedling stems occupy the lowest 1 cm of atmosphere, and their roots are in the top 1 – 2 cm of soil; this situation amplifies the effects of extreme temperature and drought (Steenbergh and Lowe 1969). Add to this the fact that seedlings have a low water storage capacity and a large surface area to volume ratio, attributes that exacerbate the threat of dehydration. The average life expectancy of a newly emerged saguaro seedling is less than 6 weeks (Steenbergh and Lowe 1977). In order to maximize the chance of survival, seedlings need protection from the elements and predators. Saguaro seedling success increases with distance from the parent plant, due to the intensive wildlife foraging that occurs in the area immediately below a saguaro, which is heavily concentrated with fruit litter (Steenbergh and Lowe 1977). This is especially true in flat habitats that lack protected rocky areas for seedling establishment. Shade and cover are essential to seedling survival (Turner et al. 1966).

This protection often manifests in a “nurse plant” association (**slide 62**). Seedlings are successful when they germinate in close proximity to another plant (or other shade-producing object). The nurse plant scenario offers many advantages in the struggle for seedling survival and establishment: reduction of high soil surface temperatures, extended periods of soil moisture, concealment and protection from predators, and protection from frost injury. Seedlings are not associated with particular species, but plants with certain structural and life history characteristics may be better nurse plants. Successful nurse plants are always perennial, as they must offer several years of protection for the saguaro to survive. Turner et al. (1966) summarized the phenomenon: *“Woody perennials produce localized patches within the desert environment where saguaro seedlings can survive.”*

During the early twentieth century, the Rincon Mountains were heavily affected by wood-cutting activities associated with lime kilns, mining operations, and ranching (Clemenson 1987). Paloverde wood was used to fire lime kilns for the construction of the Ft. Lowell military reservation, and mesquite was intensively

cut for firewood. The widespread removal of suitable nurse trees may have had considerable deleterious effects on saguaro establishment and recruitment. Young saguaros would have been trampled directly through the wood cutting; further, without the protection of nurse tree cover, young saguaros would be exposed to the full unmitigated effects of biotic and abiotic forces.

During this same timeframe, untold numbers of young saguaros were poached from the Cactus Forest area by cactus merchants for sale to landscapers and cactus fanciers (Steenbergh and Lowe 1977) (**slide 47**). There are no data available on how many cacti may have been removed. However, the cacti chosen were almost certainly in the easily-transplantable age range of 10 – 30 years old. Large-scale removal of this age cohort helps to explain the paucity of intermediate-age saguaros today in the Cactus Forest landscape.

LIVESTOCK GRAZING

In 1890, there were 114,000 head of cattle in Pima County (Niering et al. 1963) (**slide 80**). A severe drought from 1891 – 1893 coupled with overgrazing led to a severe decline in the number of cattle. However, much of the damage was already done; increased run-off and floods of new intensity gouged new arroyos. Niering and Whittaker (1965) described an interaction between grazing and rodent populations that present a young saguaro with a *combination of adversities*. Grazing directly decreases the cover of nurse plants, and encourages the growth of other unsuitable nurse-plant species such as prickly pear and cholla that promote an increase in rodent density. Rodents feed with increased intensity on young saguaros left exposed by the lack of nurse-plant cover. In the Cactus Forest area, the combination of sandy soils and grazing history have promoted rodent populations detrimental to saguaro establishment.

Cattle seek shelter under the very same desert trees that are required for saguaro seedling establishment; extensive grazing, therefore, allows trampling of crucial saguaro microhabitat. Grazing has the most impact on saguaro populations in

flat lands, where germination, establishment, and survival are most dependent upon vegetative cover (Steenbergh and Lowe 1977).

Subsequent studies corroborate the negative impacts of grazing on seedling establishment, and underscore that saguaro populations require decades of time to recover from such events (Helbsing and Fisher 1997, Abouhaidar 1997). Although most cattle were removed from Saguaro National Park much earlier, some illegal grazing occurred until 1979 (**slide 80**).

PERMANENT PLOT STUDIES

...Substantial fluctuations in population size and age structure may occur on decadal or longer scales (Goldberg and Turner 1986, Turner 1990, 1992, Parker 1993). Distinguishing long-term population trends from erratic, short-term dynamics requires observations spanning several decade (Pierson and Turner 1998).

One of the most fascinating aspects of the saguaro's life is its long lifespan. Determining the age of many plant species (temperate woody plants) is straightforward, as they acquire discrete annual growth rings that can be counted. Cactus species, however, do not grow in the same manner, and other methods must be employed to determine or estimate age (**slide 69**). Saguaro biologists have used patterns in height and growth rates to estimate age. Shreve (1910) was the first to point out that careful height measurements of saguaro or other columnar cacti repeated at intervals over significant periods of time could be used to estimate growth rates for the purpose of estimating the age of plants (**slide 74**). Saguaro growth rates have commanded significant long-term research attention, and age prediction models have been developed for several populations (Hastings and Alcorn 1961, Steenbergh and Lowe 1983, Parker 1988, 1993, Turner 1990, Bowers 1997). Because there are so many factors that affect how saguaros grow, these predictive models are highly location-specific; a model

developed for one location may not accurately describe a population in a different area.

Saguaro population structures fluctuate substantially over time, as do our perspectives of their health. Pierson and Turner (1988) pointed out the importance of re-measuring saguaros at intervals, because age structures from a single point in time can lead to erroneous conclusions that do not reflect long-term trends. The oldest long-term monitoring plots at Saguaro National Park were established in the Cactus Forest in 1941 as part of the bacterial necrosis investigations. Six of these 10-acre plots have been monitored *every year* since 1955 (Tom Orum, personal communication). The only data set that is longer comes from plots on Tumamoc Hill in the Tucson Mountains, which have been measured at irregular intervals for 85 years (Pierson and Turner 1998). This degree of study requires not only the dedication of a researcher's lifetime, but also the inheritance of the project by new researchers. Steenbergh and Lowe (1977) revisited the 1941 plots in 1976, and much of our current insight into saguaro population dynamics resulted from this work. Those plots are currently in the process of being revisited, and will yield a 60-year glimpse into saguaro ecology of the Cactus Forest. In addition, a set of 45 permanent monitoring plots were established by Duriscoe and Graban (1992) in 1990 and revisited a decade later by Turner and Funicelli (2000). These plots are unique because they are distributed randomly throughout different areas of Saguaro National Park – not just concentrated in areas of short-term interest. The Division of Resource Management intends for these plots to be revisited every decade. See Section II for more discussion of how our current understanding of saguaro biology and ecology has benefited from ongoing long-term studies.

II. CURRENT UNDERSTANDING

In the 1980's, a new potential threat to saguaro health began to receive a lot of public attention, the phenomenon of epidermal browning. This is a condition in which the outer skin (epidermis) of the saguaro changes from normal healthy green to brown in color. This is a progressive condition which begins with discoloration at the base of spine clusters (areoles), spreads along the pleat ridges, then into the pleats between ridges, to eventually form continuous sheets across the saguaro's skin surface. Eventually, the epidermal surface becomes completely covered by scar tissue (bark) (McAuliffe 1993) (**slides 52, 86, 87**).

Epidermal browning progresses from the base of the plant on the southern exposure, up the plant, and eventually to the northern exposure. In addition, taller (older) plants tend to show more epidermal browning than shorter (younger) ones (Duriscoe and Graban 1992, Evans et al. 1992b, Turner and Funicelli 2000). Turner and Funicelli (2000) showed a significant correlation between epidermal browning and loss of spines.

Epicuticular wax (the substance which prevents evaporative water loss) builds up as tissues turn from green to brown. This build-up obscures the underlying stomata, preventing normal gas exchange and leading to a decrease in number of chloroplasts per cell and photosynthetic activity (Long 1929, Evans et al. 1992a). The deeper tissues cannot take in as much carbon dioxide (Lajtha and Kolberg 1992, Lajtha et al. 1997), and thus photosynthesize. Therefore, an extensively browned saguaro becomes energetically starved, handicapped in its ability to pump water from its roots and to perform normal growth and reproductive functions.

Epidermal browning is a poorly understood phenomenon, and suggested explanations for it have varied from natural freeze damage (Steenbergh and Lowe 1977), high soil temperatures (Nobel et al. 1986, Jordan and Nobel 1984) air

pollution (Stolte 1988, Duriscoe and Graban 1992, Gladney et al. 1992, Lajtha and Kolberg 1992), excessive ultraviolet-B radiation (Evans et al. 1992b), photoinhibition (Adams et al. 1987) and thermal loading (Lajtha et al. 1997). Several other cacti species exhibit this phenomenon—it is not limited to saguaros (**slide 85**); nor is it a new phenomenon, as it is documented in historic photographs as early as 1947 (**slide 73**). Studies that were designed to answer questions about the cause of this condition were either inconclusive or abandoned due to design weakness (McAuliffe 1993).

Recent research indicates heat loading as the proximate cause of epidermal browning (Lajtha et al. 1997, Turner and Funicelli 2000). In this hypothesis, high surface temperatures on the affected parts of the epidermis cause localized tissue damage that induce epidermal browning. All suggestions regarding the cause of epidermal browning should be approached cautiously as more research is required.

Turner and Funicelli (2000) repeated the epidermal browning and population structure study of Duriscoe and Graban (1992). This study confirmed that epidermal browning is a progressive condition, that is, individual saguaros get browner as time passes. The data also showed an overall increase in the occurrence of epidermal browning on the population level from the previous decade. The authors caution that more study is needed to confirm this trend and to determine if it is cause for alarm.

An exciting by-product of the Duriscoe and Graban (1992) and Turner and Funicelli (2000) studies has been the insight into changes in the population structure of saguaros at Saguaro National Park. The demographic comparison showed that the saguaro population has increased dramatically over the past two decades throughout the Saguaro National Park, resulting from a large pulse in the establishment of young saguaros. The permanent study plots associated with these studies are distributed in both districts of Saguaro National Park, and will allow park managers to track saguaro population dynamics through time.

Turner and Funicelli (2000) corroborated the findings of Orum et al. (1998), who tracked saguaro population dynamics over a much more extensive time-span (57 years) at one location in the Cactus Forest area. The reversal of the declining trend in the number of saguaros at that location began in the early 1970s, and continues through the present. This recruitment pulse is most likely the synergistic result of several consecutive years of high rainfall in the early 1980s, lack of catastrophic winter freezing, and the removal and recovery from historic limiting factors such as grazing, wood-cutting, and cactus harvesting.

The recent demographic insights underscore the importance of long-term/repeated study in understanding saguaro population dynamics. Earlier researchers made dire predictions about the future of saguaros at Saguaro National Park based on short-term “snapshots in time.” Niering et al. (1963) stated that: *“The vegetation at low elevations in the Rincon Mountains section of Saguaro National Monument represents an advanced stage of the degradation process in a vulnerable community. On the lower flats and adjacent parts of the study area there is no reproduction of saguaro, while the older saguaros are dying at a rate (about 2 percent per year) which implies that the last individuals will disappear from this part of the Monument between 1990 and 2000.”* This prediction was accurate based upon the information that was available to the researchers at the time. Due to the lack of long-term data, researchers were not able to consider their data within the framework of a natural fluctuating environment, nor were they able to predict how Saguaro National Park would recuperate from historic disturbances.

III. LOOKING AHEAD: NEW QUESTIONS FOR SAGUARO BIOLOGISTS

Despite decades of research, there are still many unanswered questions regarding saguaros. These long-lived giants have evaded many questions about basic biology and ecology, and the Sonoran Desert ecosystem itself is an ever-changing environment. Clear-cut answers regarding the driving forces behind saguaro population dynamics have never been possible, given the myriad of interrelated effects of climate and land use, and many new complicating factors are arising in the 21st century. Researchers are just beginning to address the direct and indirect effects of changes in regional land use, such as urban sprawl in Phoenix and Tucson, and the expansion of grazing in Sonora, Mexico. Continued long-term monitoring projects will be necessary to provide insight into saguaro population dynamics, and perhaps into how influences such as land use, climate change, shifting nurse-plant associations, epidermal browning, and saguaro cactus virus (Appendix C) may affect saguaro populations in the coming decades.

Much of the information we have today is a result of work associated with Saguaro National Park and Organ Pipe Cactus National Monument—both areas that are near the northern limits of saguaro distribution. Saguaro biologists would like to know how representative this information is of populations in other parts of the range. There is a surprising lack of information about saguaros in Sonora, despite the fact that Sonora contains the majority of their range. It would also be very informative to have a map depicting the density of saguaros throughout their range, so that large-scale population shifts can be tracked.

One newly important phenomenon for researchers to address is how land use, especially urban development and grazing, directly and indirectly affect saguaro populations (**slides 39 – 46, 88, 89**). It has recently become apparent that these land uses are altering the natural fire regime with which Sonoran Desert organisms have evolved. Concomitant with increased human population is

increased incidence of human-caused fire. Although fire is a natural part of the ecology in many areas of the American West, the Sonoran Desert is poorly equipped to cope with such disturbances. Historically, the occurrence of natural fires in this ecosystem has been infrequent. Many ecologists agree that the relatively rare natural fire events in the Sonoran Desert are spurred by unusually high production of winter annuals that build up as a result of successive wet winters (Rogers and Vint 1987, McLaughlin and Bowers 1982). Many factors have coalesced in the Sonoran Desert to increase the frequency and intensity of fire, including urbanization and invasion of exotic plant species.

A major challenge in southern Arizona is the invasion of buffelgrass (*Pennisetum ciliare*), an exotic grass from Africa which encourages fire in the Sonoran Desert. This species, and its relative, fountain grass (*Pennisetum setaceum*), are rapidly and vigorously establishing in both urban and wilderness environments. Both are used as ornamentals in landscape plantings, and buffelgrass is planted extensively (especially in Sonora) for livestock grazing.

Many Sonoran Desert plants are ill-adapted to cope with fire disturbance. For many, such events are utterly catastrophic (**slides 21, 22**). The low height of most desert species is within the reaches of even the lowest intensity fires. In fire-adapted communities, many plants regenerate by re-sprouting. However, in the Sonoran Desert, most plants do not have this ability. Saguaros do not re-sprout or maintain seed reserves in the soil. Recovery of saguaros depends upon the survival of large individuals and seedling re-establishment via seed dispersal from unburned plants (Rogers 1985). It is plausible that if a saguaro population is subject to repeat fires within a 30-year timeframe, they could be exterminated from a site. It takes saguaros at least 30 years to attain reproductive maturity (Rogers 1985).

Quantifying fire effects on saguaro mortality has been difficult (**slides 91, 92**). If surveys are initiated too quickly after a fire, then mortality is vastly underestimated because saguaros can remain alive for several years following a mortal

injury. Steenbergh and Lowe (1977) observed plants flowering and producing seed for 9 years and longer after the being mortally wounded by a freeze event. On the other hand, if too much time passes between the fire event and the survey effort, then researchers miss the mortality of saguaros in the youngest age classes (Rogers 1985).

Perhaps the most compelling new question for saguaro biologists is the issue of global climate change. Scientists estimate that by about the year 2050, the level of carbon dioxide in the atmosphere will be double the level at the beginning of the industrial revolution. This will almost certainly have dramatic effects on the distributions of plants worldwide. The potential range of the saguaro is projected to move southeastward into the Chihuahuan Desert (Ray Turner, personal communication). What will become of the westernmost populations of saguaros?

Some other topics that need further research:

- Germination requirements for the *very* small plants—1 to 3 cm tall. Biologists would be able to make direct statements about conditions during the exact year of germination.
- Details on physiology and cause(s) of epidermal browning.
- Distribution and effects of saguaro cactus virus.

There will be no shortage of research questions for biologists of the 21st century to address; to the contrary, there are many more biologists' lifetimes worth of data to collect and analyze. Our perceptions of saguaro biology and ecology will certainly continue to evolve as we address these and other questions in the coming decades.

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APPENDIX A: SAGUARO FACTS

- The saguaro is the second-tallest cactus in the world, behind the cardon cactus of Baja California, Mexico.
- A 6 meter (20 ft) tall saguaro can weigh about 1600 pounds. Up to 85% of this weight is water.
- Saguaros grow faster in a nursery setting than in their natural environment.
- Saguaros are dormant in the winter and grow most rapidly during the summer monsoon season.
- Maximum saguaro lifespan is estimated at over 200 years (**slides 72, 54, 55**).
- The spines of the saguaro are an adaptation that both deters predation by herbivorous animals and insulates the plant from temperature extremes. Spines trap and hold air at the surface of the plant, allowing it to stay 2 – 3 degrees F warmer in cold weather and 2 – 3 degrees cooler in hot weather.
- The spines of young saguaros are deflexed (point downward); scientists hypothesize that this might benefit the plant by directing water to the base of the plant and by deterring rodents from climbing up the plant to eat the growing tip.
- Contrary to popular assumption, saguaros do not have massive taproots. Instead, they have an extensive network of radial roots that lie mostly within a few inches of the soil surface. These roots can extend 20 meters (65 feet) in all directions from the plant, and can soak up as much as 750 liters (200 gallons) of water in the days following a major rain event, enough to last an entire year.
- In the Tucson area, saguaros generally begin to flower when they are about 2 meters tall (about 30 years old).
- Once a plant becomes reproductive, the number of fruits per year increases rapidly.
- Saguaros bloom mostly during the months of April, May, and June, although aberrant individuals can be observed flowering during any month. Each flower opens only once, around midnight, and closes mid-afternoon the next day. The flowers on a particular plant do not open all at once, however, they open continuously throughout the flowering period in order to insure pollination by different animals, such as lesser long-nosed bats, white-winged doves, and honeybees (**slides 27, 60, 76**).

- Saguaros at the Tucson Mountain District begin to flower 1 – 2 weeks sooner than those at the higher-elevation Rincon Mountain District.
- The addition of arms to a saguaro stem increases the reproductive potential of the plant. Flowers occur at the tips of stems and branches; therefore, the more branches a saguaro has, the more opportunities for seed production. New arms can produce flowers and fruits as early as 3 years after budding, quickly adding to the plant's reproductive potential (**slides 1, 61**).
- Saguaro stems completely severed from their roots can continue to produce flowers for at least 2 years (**slide 90**).
- Fruits are ripe in June and July. Each fruit contains about 2250 reddish-black seeds. A large saguaro can produce hundreds of flowers in a single season, which in turn can produce up to 40 million viable seeds over 100 years of reproduction effort. However, due to predation and germination/seedling establishment requirements, it is likely that very few or only one seed from all of those produced in a saguaro's lifetime produce a plant that lives to reproductive maturity. Saguaro fruits are vastly important in the Sonoran Desert ecosystem. Fruits are eaten by: javelina, coyote, gray fox, kit fox, ground squirrels, harvester ants, and many bird species. (**slides 5, 9**).
- If proper conditions exist, germination happens in early July, before the dry fall season.
- Saguaro cavities are excavated by Gila woodpeckers and northern flickers each spring for nesting. Other species use abandoned cavities, such as: American kestrel, Lucy's warbler, cactus wren, western kingbird, phainopepla, elf owl, screech owl, the endangered cactus ferruginous pygmy-owl, purple martin, European starling, honeybee, and white-footed mouse. The excavation of stem tissue for cavities does not generally harm the saguaro in a long-term way; the wound becomes hard and callused so that it does not spread or invite bacterial or insect infestation. The callused wounds are the "boots" that are observed in some saguaro skeletons (**slides 6, 10, 12, 59**).
- Saguaro arms also provide important nesting sites for the red-tailed hawk, Harris hawk, mourning dove, white-winged dove, and great-horned owl (**slide 11**).
- Woodrats tunnel through and jackrabbits will girdle saguaro stems near the base to get moisture from the succulent stem. This causes unsightly damage to the saguaro, but it will not kill the plant. These injuries do, however, leave the saguaro more susceptible to wind and freeze damage (**slide 57**).

- Saguaros are very sensitive to cold, and cannot grow in places where overnight freezes are a common occurrence. Tucson is in the northern portion of the species' range. Saguaros here tend to have more spines, especially at the sensitive growing tip to help insulate against the cold. Despite this, the saguaro is more cold tolerant than other species of large columnar cactus. It is found farther north than any of the other species (**slides 29, 66**).
- Saguaros can expand to accommodate water opportunistically. The accordion-like pleats and ridges spread apart and shrink depending upon how much water is in the plant (**slide 20**).
- A saguaro can lose up to 82% of its tissue water before it will dehydrate completely and die.
- A lightning strike is always fatal to a saguaro (**slides 14, 64**).
- There are a few saguaros in California—along the Colorado River from the Whipple Mountains of San Bernardino County to the Laguna Dam in Imperial County. Saguaros do not grow extensively there because California does not consistently experience the summer monsoon rain which the saguaro is so dependent upon, especially for seedling establishment.
- Saguaros grow best on soils with rocky or gravelly textures, because they are low in salts and offer good drainage. This is why saguaros are often observed on sloping bajada areas as opposed to flat areas—sloped terrain has generally coarser texture than the fine soils of flatlands.
- Saguaros are generally found below 3500 feet elevation, although at least one plant has been found at an astonishing 5100 feet elevation.
- Extrapolation from census data taken in 2000 (Turner and Funicelli 2000) estimates that there are between 1.3 and 1.9 million saguaros within the current boundaries of Saguaro National Park.
- No one knows exactly what causes the cristate formation (**slides 7, 8, 56**).

Appendix B: Interview with Ray Turner

August 27, 2001

At his home in Tucson, Arizona

Questions asked by Carianne Funicelli

**When and where was your personal interest in saguaros sparked?
Why have you remained dedicated to their study for so many years?**

My interest was sparked when I was teaching botany at the University of Arizona. As a class project I had the students go out in the field and measure saguaros at the same place every year—we'd go back and some of these plots then became ultimately these permanent study plots that I now go back to. It would have been sometime between 1956 and 1962—probably most of that once a year when I was teaching.

What grabbed you about saguaros?

The thing that struck me was that they provide a means of assigning an age to a plant that is not too unlike that of trees that present annual rings that you can count. In the case of the saguaro it is the annual height growth that once the plant has accumulated that height it doesn't lose it. The stature of palo verde and creosote bush, or other woody plants can shrink and they undergo drought pruning under serious drought conditions. And the saguaro doesn't do that—once it puts on a certain amount of height growth it keeps it.

How has our understanding of saguaro biology and ecology evolved over the past century?

That emphasis [bacterial necrosis] came about at a time after pathologists had done a lot of work. [Here Ray was trying to remember the name of Alice Boyle]. And then Stan [Alcorn] came along, and he was with the Agricultural Research Service at first. A certain amount of money was directed toward the study of diseases in the saguaro—it just happened. Three or four decades later, the National Park Service Research Laboratory had a lot of money to study the effects of air pollution on plants, and that's where the Duriscoe plots [and Lance Evans] came from. I think they were off on the wrong track. We have the same sort of old-age phenomenon at MacDougal Crater miles from any source of pollution. They might have better spent their money on distribution of the [epidermal browning] throughout the saguaro's range before they started concentrating on populations close to Tucson where there was pollution. I think part of the reason for the changes in emphasis of research is the change in the source of funding.

What do you think are the most common public misconceptions about saguaro biology?

They're always wanting to know the age, of course, and always want to know how many arms...They never seem to ask about flowers, except in flowering season. They're always interested in maximum age, maximum height...

Do people seem to still buy into “saguaro-extinction hysteria”?

Yeah, you know we have a state law that protects desert plants, such as the palo verde. When a developer goes into an area, they have to box the roots to transplant it. It's nonsense! And they do that to saguaros! And often a saguaro will be moved into an urban area—and this is another thing that ought to be studied—I think once it's moved onto an urban area it is more prone to attack by woodpeckers. Before when we bought this house, it was a lot smaller, and we put on an addition, and we had two or three saguaros growing out there. And they had woodpecker holes. One day we watched a woodpecker being evicted from the hole by a group of starlings. So it gave up—it couldn't fight three of them. So it had to work to make another hole in the same saguaro. I think this happens all the time, and I don't know whether it's starlings or non-native sparrows or maybe native birds that like to live where humans are. I think this has an effect on saguaros, and it's silly to put those transplanted saguaros close to humans. And the other thing is I think once they have reached the height where they are reproductively mature, the chances of them surviving more than 3, 4, 5 years as transplants is very small. I think certain people are happy to make it tough for developers, (and I am one of them!)

*see Joe McAuliffe paper on flickers/Gila woodpeckers

Alcorn and May (1962) listed only 3 means for saguaro death: wind, “bacterial necrosis”, and human eradication. What are other causes of individual demise (lightning, fire, rodent damage....)?

Well, certainly rodent damage [for seedling mortality]—a paper that Stan and I published showed that. We had caged and uncaged plants (although the cages had flaws—animals crawled under them). But I have no doubt that the rodents have an impact on the very small [saguaros]. And lightning...somebody's writing a paper on that—I think someone with the Arizona-Sonora Desert Museum, but I'm not sure.

Can we equate bacterial necrosis with natural senescence—do saguaros die of “old age”?

As saguaros get older, they get taller, and I think the energy that is required to move nutrients from the ground up is exhausting. I think that the reason that the growth rate diminishes, and they get smaller around and all of this is because water and nutrients are having a harder time getting up there. So, *maybe* [they die of old age].

Can wood rat tunnels kill saguaro?

Just as bird holes can cause a saguaro to die when we have unusually severe cold winters, I think packrat tunnels could too. But typically, I don't think they do. The population at Silverbell [with all of the rat tunnels] has not gone down more steeply than any of the others. The small plants may be killed outright, because too much of the epidermis is gone, but saguaros can be completely girdled—clear in to the woody stele [and remain alive]. Most of the packrat damage doesn't go past the ribcage, and it's not a lethal thing.

How accurate are the height-age relationships?

The Steenbergh and Lowe prediction is very good; but I don't use their [for my plots] predictions for the sites they studied. I had to determine a different height versus age relationship for every site. And what Betsy Pierson and I did at Tumamoc Hill where we studied the saguaros on large plots on the four slopes at Tumamoc Hill to determine a height versus age relationship—a separate one for each of the plots. And you test this—you test how good a job you're doing by if you have a long period of record, and we did, the first measurements were made in 1964, a second set of measurements in 1970, of each marked saguaro. Then we measured them again in the 1990s and we said 'ok, we'll use the 1964 – 1970 data to establish a model.' And then using that information, we'll say 'ok, if our model is correct, we should be able to anticipate how tall a saguaro is going to be after x number of years.' And so we went through this little exercise, and plotted the actual height of the saguaro against its predicted height, and if you got a nice straight line at a 45 degree angle, then you're right on. Well, we had a scatter, but not a very wide scatter around that. And so we can answer your question on how off we were, because the mathematics are right there.

Is it ok to use the Steenbergh and Lowe age estimate tables in the Rincons or the Tucson Mountains, provided that you stay in areas similar to their plots?

I think it's probably safe if you were on the flats out at Saguaro National Park East, and anywhere in that flat, lowland country I think it would work. But as soon as you got up on the mountain slopes, I think you'd have to use another model. And I wouldn't carry the model for the rolling slopes at saguaro east over to Saguaro west—there's 400 ft at least in elevation difference. But I think you're ok.

Betsy Pierson and I have another study in progress, and we have quite a bit of information on it and a model estimated for each of these sites. We have nine saguaro sites scattered across the northern part of the saguaro's range from Redington on the San Pedro River to Saguaro National Park East, Sabino Canyon, Saguaro West, Silverbell, and we have one on the Papago Indian Reservation, Ventana cave, and another in the Harquahala Mountains, west of Phoenix almost to the Colorado River, and a couple down in northern Mexico—one in the

Pinacate (MacDougall Crater) and one east-southeast of the town of Sonoyta, Sonora. So using these 9 permanent plots, all of which were established around 1960 (so we have close to 40 years of records). We've gone back to these 3, 4, 5, 6 times and have re-measured saguaros to see how much they've grown and how many have died and how many new ones have come in, and we have a model for each one. So we can probably see from these models how well one would fit the other place.

Is there a clear-cut gradient from east to west in the growth rates?

That is a good question, something we ought to include in our final report.

What have your nine permanent plots shown you?

This [chart] just shows the number of plants per plot, plots are different sizes, so these numbers are converted to number of plants per unit area. The intriguing thing to me is that the terminal point in all cases is lower than the beginning point. We went back to Saguaro East last year, and look what has happened there—[increase]—prior to that it dropped way down and had not come up to the level of the initial point, but now it's way up. I think that's what you and Dale had found, too. Now the thing that intrigues me though is that we have a 1935 photograph of the same area [cactus forest] and the population, if we had a count would be clear up here. So it still hasn't attained what it was in the 30's, but it is increasing.

Why the decline?

Part of those plots are grazed, and part are not grazed. Some have never been grazed, and they went down anyway. So you can't just say grazing, although at Saguaro East grazing may be an important ingredient. But in other areas where perhaps it didn't get grazed as heavily it probably isn't as important.

The thing that has intrigued us is that we started looking at the "weak links" in the saguaro's life history, and it seems to us that one of them is that its seeds are very short-lived—they only live a few weeks after they're on the ground—maybe a few months—but they certainly don't over-winter. So when the seeds are produced in July and fall to the ground, they must receive an appropriate amount of moisture within the next few weeks, or it's over, for that year, as far as the plant is concerned, as far as the population is concerned. We looked at the long-term rainfall record for Tucson, and it goes back to 1867, and we determined the amount of rain that is provided by July – August rainfall—that's the critical period, (actually it can go into September.) We found that typically, over the long term, that accounts for 40% of the long-term average annual rainfall. So we said, 'ok, let's now find out how many years July – August rainfall exceeded 70% (an arbitrary large value) of the long term.' We found that on average, between about 1867 and 1895, it happened about on the average of every third year. Since that time, it has been every 11th year. There is something going on here....And if

you look at the annual rainfall and ignore the seasonality you don't come out with anything like that. This little important issue is hidden in the annual values—you have to dissect the annual values and look at the seasonal values. I think one would have to go even farther than that—I think you'd have to find out when we had good summer rains followed by good winter rains, too. That would be the next step.

With, maybe a successive set of warm winter years, with not a lot of freeze?

Right, although I think in most cases the saguaros probably are not heavily influenced by temperature. And that is becoming more and more insignificant with time in the range of the saguaro. We have recently had occasion to plot the occurrence of catastrophic freezes and they used to occur around the turn of the century just every few years, and recently, [they] have been separated by a decade or more. The last really cold spell we had was in 1978; prior to that there was one in 1962. So we're not having cold winters like we used to.

I'm not saying that low temperatures aren't important in some places (especially at higher elevation) in the saguaro's range, but most of the places where they are found it is probably not having much of an impact. One of the saguaro plots—the one we have over here at Redington, that's our coldest, farthest north plot, and right after we set the plot up in 1960–1961, we had a very strong freeze. Fortunately, we'd taken pictures of the plants just before, as well as a count. And we went back after the freeze and photographed them. They are part of a book called *The Changing Mile* that we've revised. The photographs show the injuries, the scars, that came from the freeze. Then, it got hit again in 1978, and we took additional photographs. And so some of the saguaros now have injuries from 2 freezes. A good many of them, a lot of the big ones, were killed. And in the 1978 freeze especially. The very small ones did a pretty good job of surviving as long as they were under a shrub. Interestingly, the shrubs that were most successful in keeping them from getting killed were not little bursages, but were taller shrubs. If the plant had started under the bursage, and exceeded the height of the bursage, it got zapped—still too small under those circumstances. But if it was under an acacia, or something of a larger plant, then it survived. And once it got a meter and a half or so tall and started going above the nurse plant, then it survived.

Where is that data presented?

That will be in the paper that Betsy and I are working on. We had gotten a paper together that was 80% done based on those sites. But I looked at it and I said, 'Boy, some of those haven't been visited for ten years!' And I want to know what has happened in the ten years—partly because of the work you and Dale did. So we halted everything. Jean and I went out and did this one [RMD] last year, and now I'm going to get volunteers together.

How long does it take to read a plot?

A couple of days. We also measure the coverage of the associated woody plants with a Bitterlich stick. We have two stations at the center of each plot, and we do this each time we go out. We get two readings for each plot, then average them. Also for plants that do not lend themselves to this sort of analysis (hedgehog cactus, etc.) we count the # in a 50 m circle, around the same point.

The Bitterlich stick was designed for estimating the amount of wood in a stand of trees. And they would just half the diameter—use this to measure the diameter of all the tree stumps. Charles Cooper modified the forester's instrument for use in measuring coverage of desert perennials. What you do is you stand in one spot and aim at each plant using either this [spacing at end of stick] to determine an angle or this [wider spacing at the end of the stick]. If its palo verde or a large plant, then you use the larger angle (I forget what angle this is) and if it's bursage you'd use the smaller one. You look through this and you count every bursage (in this case) that the crown width of which equals or exceeds this angle—as far as you can see. Soon, they are so far away and relatively small, that you don't count them. The ones that are close, of course, all get counted. The small ones will cease being counted before the larger ones. I use a little hand counter and saguaro ribs on the ground to define pie sections. I think it's fairly accurate. Then you divide the count of the small one by four and the big one by 2, and it converts right to percent. The mathematics behind this is described in that paper.

We measure the height of all the saguaros, and determine whether they've died or lived. We've always depended upon a lot of volunteers.

Have you ever used annual constrictions to age saguaros?

We have been aware of that, but the problem is that there is a certain amount of secondary thickening that goes on at the base of the saguaro as it ages and it obliterates these constrictions. Hastings and I used to call that the "Mae West effect." Another example would be used today, I'm sure! One of the things that we highlight in one of *The Changing Mile* photos – I have photograph in Sabino Canyon—that shows a saguaro in 1962, and it had just been hit six months earlier with that freeze, and it was showing no signs of injury—it has the constrictions. And then when we matched it again in the 90's, it had grown more, with additional constrictions, plus a scar from that [1962] freeze. It only went up so far and then stopped. So in the caption we asked the reader to count the constrictions and see if they agree with us that it comes out roughly to have been 30-odd years earlier. I think it works in certain saguaros. But once you get near the base there are no more constrictions to be seen so you really can't use it for each plant.

Why is it impossible to make assumptions about the age of a saguaro based upon the number/height of origin of its arms?

First of all, isn't it interesting the emphasis that people place on branches, or arms of a saguaro? They don't do that for woody plants. And I think it's a sort of anthropomorphism that they are assigning to the plants—humanoid characteristics. And in fact, the very use of the word “arm” instead of “branch” suggests that. There is a real hang-up on arms, and they're interesting—well, they're very interesting to me, because the annual height growth curve for the saguaro—if you plot against age, the amount of growth that a saguaro plant attains each year, you find that when they are small, there is a very slight amount of growth that gets bigger and bigger until they are a couple of meters tall, maybe 2 1/2 meters tall. Then they are growing maybe 3, 4, 5, inches a year. And then it slows down again; Steenbergh and Lowe show it—the point where the inflection occurs (and it slows down) is when they start reproducing. So when they become sexually mature, and they are expending a lot of energy on...flowering and fruiting. After that peak, the amount of annual growth increment declines year by year. Until, there is another inflection point, after which it doesn't decline quite so much per year, and this extends out almost flat, but not quite—a slight downward slope for the rest of the plant's life. And that second inflection point is when the branches are produced. They erupt through the surface of the plant, through the epidermis probably somewhere around 20 years after the plant becomes sexually mature. Although it took perhaps 50 years for the tip of the main axis of the plant to start producing flowers, it only takes 2 or 3 years for that branch to start producing. So very suddenly that plant's reproductive potential shoots way up. We play games with that—we count the arms anytime we make a survey. So you can talk about reproductive potential of each one of these plots. And even though the Saguaro National Park East plot now has a lot more plants than before, the reproductive potential is still going down. [Until maybe 30 years from now] when suddenly it will go up pretty fast; and then in 20 more years, when the arms start coming on, it will go up even faster.

We've got data that show the number of arms in each one of our populations, and I think that very suddenly, when the plant is 70 years old (or whatever it is) it will start producing arms. If you look at a saguaro from the side, it is spindle-shaped—fairly narrow at the bottom, and its diameter increases until you get to a height where it first starts producing flowers—and that is its greatest diameter. Then it gets smaller again. The first arms that are produced are just above that maximum diameter spot, and usually there is a whorl of stems there. And then, it may produce more up higher. I haven't seen any indication that they're timed in any way. In the drier habitats, like the MacDougall Crater plot, most of the arms are very high on the plant.....

I have noticed an incredible gradient of architecture in plants in the northwestern (ORPI, west of Phoenix) part of the range versus plants in the Tucson area. The western plants are thinner, taller, branch higher on the stem, and there seems to be a higher occurrence of the “double whorl.” Has this been quantified? What are some possible

explanations? How is architecture affected in different parts of its range?

If you go over as far east as the San Pedro River Valley, where our Redington plot is, you find that those plants have many branches, and they seem to hug the stem almost. Many stems and massive diameters of the stems are all much larger than they are farther to the west. I have noticed that, and I do not know the explanation. I have an idea, and I wish somebody would test it, on why the branches occur down by that maximum diameter. I think that growth hormones probably control that, growth hormones that are produced at the apex of the plant when new growth spurts occur. Those hormones circulate through the plant, moving downward, and suppress arm growth. This is a well-known phenomenon. If you prune a woody plant, the pruning eliminates a source of the growth hormone, and in the absence of that growth-suppressing hormone, side branches then can erupt. I think that maybe somewhat the same thing is going on in saguaros. It flows down the plant, and as it comes to this part of the plant that has a larger diameter, it becomes diluted, and its effectiveness to suppress growth is diminished. That may explain what is going on at that point of the plant, but what is going on farther up, I do not know.

How might abiotic influences across the range of the saguaro affect the architecture of the plant?

I think probably, you would find fewer ribs in the individuals that are to the west, in the drier part of the plant's range. [The plants] are actually making a surface to volume ratio that could be a disadvantage—more dehydration. I think that it probably doesn't get much bigger than this because of lack of moisture—lack of growth.

One other thing that has struck me is the work that—I forget his name...A study out in western Arizona, and he [looked at] flowering in the saguaros in dry years. The saguaros that occurred in the runnels in the landscape, where there is more water because of run-off, would produce flowers, and those on the interflues, the slightly elevated ridges would have no flowers. The person who did that was out of Riverside, California...[Brum 1973]

Another thing I've noticed, along I-8, is that all of the saguaros are chewed up with woodrat tunnels. I wonder if you move farther away from the interstate if that lessens, because of a higher density of rodent-eating snakes (that are becoming roadkill near the interstate)?

Tony Burgess and I were out [at the Silverbell plot], and we noticed that saguaros young and old had been chewed on by rodents, and we think it is by packrats, not by ground squirrels. In fact we have a table here somewhere that indicates the percentage of plants that have some sort of injury. 'What's going on here?' We'd never seen that at any of the other [plots]. Tony looked around, and he said 'you know what's missing? No *Opuntias*—no prickly pears, no chollas.' And the

packrat is a unique desert rodent in that it can't manufacture water—it has got to have that source. It goes to prickly pears and chollas by preference. In their absence, it goes to something it may not like as well: the saguaro. I've seen that on Interstate 8 many times, and I get excited every time I see it! One of the things that we've started to do is to map packrat dens on the permanent plots. In the desert they just make mounds of plant debris. It would be quite easy to test. We will describe that in this paper.

What are your impressions about cristate saguaros?

A lot of plants do this—not just the saguaro. I don't know what causes it—probably a genetic mistake of some sort. The plant morphologists call it “faciation”.

What do you see as the most eminent questions for modern saguaro biologists?

I'd sure like to know the extent to which those curves [of the nine permanent plots] are an expression of what is going on throughout the saguaro's area. Some of my friends have said they know areas where saguaros are really reproducing heavily, and I'm sure that's the case. We selected these nine sites because they had fairly dense saguaro stands, so that we could establish a rectangular plot with quite a few plants in it. I don't think there was any real bias other than that. My idea is to get random sampling of habitat. But I don't know what is going on down south.

I'd like to have a better idea of how prominent that phenomenon of die-off is. My feeling is that the saguaro decline that is shown on that chart will level off. I don't think there is any danger that the saguaro is going to disappear.

[In reference to USGS report “Strategy for assessing potential future changes in climate, hydrology, and vegetation in the western US”] I don't know if you've seen this—it shows what we expect climate to be like when the date comes—probably 2050—when the amount of carbon dioxide in the air is twice that of its level at the time of the beginning of the industrial revolution. It [the report] estimates what effect this is going to have on different species. What they show is [the] saguaro's range extending southward into Chihuahua. It shows creosote bush going the other direction—it's going to go north. Saguaro is going to head southeast. The saguaro dies out in certain places (they show where they expect them to die out)—the whole range shifts. A lot of people don't place much confidence in these general simulation models—a lot of assumptions. What they show is not a sudden expansion of its range—it's a *potential* range. Just as potential range today is shown to be Baja California, and it's [the saguaro] not there. If someone were to take [saguaro] plants down to potential habitat sites in Baja California, they'd do very well. This is one of the things that biologists should be addressing—“Are we actually going to lose some populations?” Will some of plots that we've been studying—the westernmost plots—start falling off more rapidly

than the ones to the east? It would be important to me to get these plot data to someone or some organization that will be sure to continue interest in them.

Appendix C: Interview with Tom Orum and Nancy Ferguson

September 18, 2001

At their home in Tucson, Arizona

Questions asked by Carianne Funicelli

**When and where was your personal interest in saguaros sparked?
Why have you remained dedicated to their study for so many years?**

In the fall of 1977 I began working with Stan Alcorn in the Department of Plant Pathology at the University of Arizona. Dr. Alcorn had been working on the saguaro since 1955, and his emphasis was on the bacterial necrosis disease. So for the first 2 years (Fall 77 – Spring 79) I was working entirely in the lab and in the greenhouse with the bacterium (that was associated with the bacterial necrosis disease). Then in 1979 I began doing the field surveys of the saguaro plots that Dr. Alcorn had been working on since 1955. These are the 6 ten acre plots that are in section 17 in Saguaro National Park East that were set out in 1941. We would spend 2 or 3 days surveying those 6 10 acre plots each spring. And I have been doing that since then [either with Dr. Alcorn or with Nancy], without missing a year. In the intervening period I was also doing labwork related to bacterial necrosis and also saguaro cactus virus.

How do these plots relate to the Gill and Lightle plots that were established in that same year?

Those are the same plots. Gill and Lightle set out in 1941 – 1945 and mapped, surveyed, identified and counted every single saguaro in that section. And there were ten to fifteen thousand. We have the original notebooks of Gill and Lightle that go back to 1941. They divided the section into half. Their concern was that the bacterial necrosis that they were observing—that is the decomposition of the saguaros with the black ooze—was a rampant newly introduced disease, and spreading rapidly. And so they designated that section as a research area—I don't think it was even a part of the park at that point. One of the standard techniques in forestry was to remove the infected individuals. And in their panic that's what they chose to do. In retrospect, it was not so much a treatment, as a research, in my interpretation. The idea was would removal reduce the incidence of what they were seeing. They had to do it over a large enough area to have an effect. That's why they were looking at that large half section. They did it for 5 years, I think—went back and evaluated the condition of every single plant. But by 1946/1946 they had concluded that it wasn't working—that there really was no difference between treatments. So they abandoned that, but it was about in 1945 that they said ok we can't afford to look at all of these every year. So they selected pairs of plots in each half [the treated half and the untreated half] based on density. So they selected a number of pairs that were low density, a number of pairs that were middle density, and a number of pairs that were high density.

And then at random, they selected one low-density pair, one medium-density pair, and one high-density pair for ongoing study. This was a study by the USDA—the Forest Service. Now, in background, there was very early on disagreement between the Department of Pathology and the Forest Service on how to manage those plots. When Stan came in 1955, he was working for the USDA Forest Service, not the Department of Pathology. At that time only the Plant Pathology Department was doing isolations—the Forest Service was doing inoculations. So there was confusion very early on in terms of the disease and how to manage it and interpret it, and who's turf it would be on and so on. Stan's predecessor, who was Craig Brian, (who succeeded Gill, I think—I'm not sure how that chain of events worked) left in 1953. Stan came on in 1955, so there was a one year gap in the surveying of those six plots.

Nancy: And then at some point, Stan went from working from the USDA to the Plant Pathology Department....

Right—in 1962 there was an opening in the Plant Pathology Department. What happened was that Carl Hayden died. Carl Hayden was a powerful senator in Arizona and he had the line-item (this of course is just background—nothing you'd want to put in a slide show) for some one to study saguaros, and particularly the decline of saguaros in the USDA budget. When Hayden died, they took out that line item, and the job disappeared. Stan then transferred the work to the Department of Plant Pathology. But of course he was no longer completely focused on the saguaros. The big question that Stan worked on early was not really the question of bacterial necrosis so much, although that was a major interest, but it was why there wasn't any recruitment. When he started in 1955, there hadn't been recruitment for a number of years. And between 1955 and 1962/63 when he went to work with the Plant pathology Department, there was no recruitment going on. So he did a lot of really good work on pollination. One of the questions was were the seeds viable—were they being pollinated, and so forth...was there an absence of a source of pollinators. He worked with George Olin.

[Now, there's a person you should interview....He's still alive—he's in his 90's, and he's up in the Scottsdale area. We visited with him at Stan's memorial service, and he is still sharp. He put in some of the fences for the cattle exclusion, actually did some of the work and definitely some of the supervising for it. From a historical perspective, and of course, great photography—George Olin would be a great one.]

Stan and George and others were working on pollination. And what they discovered was that there were LOTS of pollinators. Not just bats, but doves and bees, and many different kinds of pollinators. So that's not the problem. So, then they worked on seed germination. One of the things that was happening in agriculture was the red shift associated with lettuce. And, you need exposure to certain wavelengths of light to trigger a switch as far as seed germination. Stan discovered that a similar thing occurred in saguaro seeds. So he did a lot of

germination studies and light wavelength studies, and found that there was plenty of seed germination. So, basically, the conclusion was: not a pollination problem, not a germination problem...So, maybe it's an establishment problem...Then Stan and Ray Turner did a few transplant studies. And what they discovered was that rodents just decimated [the transplants] unless they had cages. They did their transplant work in one of our plots—which is actually one of the plots that you guys [Dale Turner and Carianne Funicelli] studied. It's quite a challenge to know which ones are transplants and which ones aren't. Ray [Turner] went out 2 or 3 years ago and re-measured the transplants. So they were keenly aware of the rodent component as far as the establishment issue.

I am a little bit confused, because the “Steenbergh and Lowe” plots that I’ve been referring to—5 of them at RMD are along the Cactus Forest Loop Drive—were established by Gill in 1941....

So they must have had other plots as well...I didn't realize that they were predecessors to the Lowe plots as well...

What grabbed you about saguaros?

My interest grew over the years as I realized we were going back and watching these plants. What happened was just about the time I started working, we started finding little ones! Here we had since 1955—Stan working on these plots every single year—to 1977, finding 3 or 4 [new] plants on the entire 60 acres. So suddenly we were finding 10 or 12, then by 1980/1981, we were finding 40 or 50 new plants a year. Then some years we'd [only] find 10 or 12. We'd get embarrassments some years where we'd find 12 inchers that we'd missed. So that suddenly changed the whole picture, from one of population decline and mortality to recruitment. That made it really interesting.

Tell me about *Erwinia carnegieana*...

In the lab there was a rampant confusion related to the bacterium that is associated with the rot. The *Erwinia carnegieana* bacterium that was sent to me by the Type Culture Commission was not *Erwinia* at all---it was a contaminant. It didn't have flagella, and it didn't produce pectolytic enzymes and it wasn't pathogenic. And it wasn't the original bacterium that was isolated in the 1940's. That was quite confusing. Furthermore, the original authors associated the bacterium only with saguaro, and [they] said that the bacterium rotted only saguaro. All of the isolates that Stan collected over the years—well, first of all he collected from 7 or 8 different species of cacti—and the bacterium rotted all different sorts of species of cactus, as well as peaches, vegetables, and so forth—so it had a wide host range. Most importantly, it was present in the desert across a wide range of cacti, and it was present in the soil. So, it was not specific to the saguaro, and there was no relationship between the original type culture and the isolates that were described originally or the ones that Stan worked on. So, that was confusing. But finally in 1991 we published 2 papers relating that—rejecting

the name *Erwinia carnegieana*. We were trying to clear up the fact that the *carnegieana* type culture wasn't an *Erwinia*, and also to show that the host range of this bacterium was very broad.

One of the things Stan wanted to do is look at lots and lots of isolates. So we did a lot of isolation. But there has been a lot of confusion on the disease and there really isn't agreement even still. What I think everybody agrees, I'm sure, is that everything going on in Saguaro National Park is a natural process—there's nothing exotic in terms of the bacterium or in terms of the mortality. The biggest concern is that the public not be unduly alarmed. Certainly since the 1950's that has been a great concern. I've got a whole folder of sensational articles in the newspapers. What is interesting and what makes it sort of different is that now we know that there is recruitment out there, whereas in the 50's and 60's they did not know that.

**Is “bacterial necrosis” a term that should be thrown out the window?
I notice that you still use it....**

I still use it...I think Joe McAuliffe doesn't want to use it. It depends on how it is used. It seems to me that if one uses it referring to the gooey collapse of saguaro stems, then that is an absolutely appropriate term. You have to call it something. There is the whole catastrophic freeze situation, and each researcher is influenced by the events that they experience. Lowe and Steenbergh were doing their work between 1960 – 1975, and there were 2 or 3 big freezes in that time. And that was their big message. I started in '79, which was the date of the last big freeze. So we've had 20 years without a big freeze, and the decline has continued. So it is hard for me to accept [catastrophic freeze as the sole cause].

What do you mean by “decline”?

What I mean is that the original population of 1942, if you just start with those, and you look at age-related decline in that population, it just continues on—they just keep dying.

But that's because they're getting old—they're not dying younger now, are they?

No [they're not dying younger]—what I'm saying is that if you look at that same population, more or less, I think bacterial necrosis is a condition of older plants. Although it can occur following insect infestations in younger plants. Basically it is bacterial rot associated with a weakened, old plant. And just like pneumonia kills older people, pneumonia kills people with immune suppression, that's the thing. You have a microbe that, when a plant's defenses drop, can explode. Where my experience is different from a lot of people is that the bacterium that I associate with the rot, I know produces enzymes that allow it to move from a rot pocket into healthier tissues—producing enzymes that cause decomposition. So that's why I still think it is a disease situation. But it is a disease of aging and

weakened plants. So it is not a highly infectious disease that moves from plant to plant attacking healthy plants. Then it becomes a question of how to effectively communicate that to the public. Some folks think that if you say “disease” to the public that they get highly emotional about it and so forth.

I tend to think of disease as part of the natural system. My perspective is one of the plant-disease triangle, where you have the interactions of the host (which is the saguaro), the environment, and the pathogen. It is the interaction of all of these factors. Again, this is just one perspective. Under environment, you have freezing—no doubt—and drought, injury by insects and birds, lightening, and other environmental factors that influence the host. How the host reacts to those environmental factors depends upon its genetics. One of the differences between natural populations and agricultural populations is that in agriculture you are usually dealing with monoculture—a single genetic type, whereas in a natural there are wide differences in genetic resistance. Difference in age makes a big difference in host susceptibility. And epidermal browning, is one of those—the amount of photosynthesis, and plant density. And then the pathogen—*Erwinia cacticida*, and the main thing about it is that it is not host-specific, and it produces pectolytic enzymes which allow it to move beyond a particular rot pocket in a weakened plant. I think there are ecologists who would look at this same thing and want not to call it a disease triangle, but a natural population decline or senescence triangle, or something like that. But to me, it seems silly to attach the label “freeze-damage” to every rotting saguaro, because I know that there are saguaros that are healthy one year, that go through 2 or 3 years where there is absolutely no freeze, and you can see a flicker hole, or a woodpecker hole where the rot has started, and it extends up and down the aging saguaro. I tend to think that freeze is only one environmental factor that influences an older plant (or a younger plant). In '83, '84, '85, there was a larva of a beetle called *Metamaceous* sp. that we took to Floyd Warner and he identified. Little plants that were 12 – 18 inches were getting eaten by these beetle larvae, and were rotting associated with it. And in some cases the plant was small enough that the larva itself was eating the whole plant. But in other cases it would get started, dirt would get in, the bacteria would get started, and you would get rot. That's an example of a young plant-insect-bacterium connection causing mortality. We recorded a lot of mortality in '83, '84, '85, for some reason, there was a major burst of this insect, which is usually on *Opuntia* sp., Floyd thought it was a couple of mild winters.

Do saguaros die of “old age”?

Good question. They certainly get weakened—you'd almost have to say yes, that there is a period where they get pretty old; there are a variety of factors....

Alice Boyle was the first woman to get her Ph.D. in Plant Pathology [at the University of Arizona] in 1949. She was quite a character—she went on to be on the faculty. She did her Ph.D. on *Erwinia carnegieana*. In those days, they could cut up saguaros, and she'd get these beautiful long sections. She was looking at

the relationship between the cactobrosis moth and the bacterial necrosis—she thought there was one. Stan, following up on that, really studied it hard, and he trapped moths up by the flowers. The moths lay their eggs up at the base of the flowers buds, then they crawl down and enter the saguaro at that point. He collected hundred of cactobrosis larvae, ground them up, and put them out on plates, looking for *Erwinia carnegiana/cacticida*—and never found it. However, in any plant that is flowering age (or younger, even) you can see the little exit holes of the cactobrosis moth. And if you look carefully sometimes, in the flute, in the center, you'll see a little black (3 – 4 mm) circle, and you can sometimes see the pupa coming down from it. We've seen them in as small as 2 or 3 foot saguaros. Usually you first see them when they are 6 or 8 feet. The point being, that that is the first major exposure to the elements. As the plant gets larger, it accumulates cactobrosis injury holes. So, in terms of 'do plants die of old age?' well you've got the epidermal browning, you've got the insect larvae ongoing, you've got birds making holes, and rats tunneling through...So then, if they were pristine, would they ever age? Who knows? They probably would anyway—just the physiology.

The other thing is that you get the population dynamics—lightening is a factor, and we can't judge it in our plots, really. We can't really distinguish in our plots between a lightening strike that kills a plant dead and rots, and a lightening strike that causes injury and then the bacterium comes in...What occurs to me is that when the stand was really large, there were so many targets...Back in the 40's and 50's you had thousands of saguaros—the number of saguaros would outnumber the lightening strikes. But, as the population declined, you had, now, very few of these sentinels up there, so that the probability of a saguaro getting hit...increases. Because, if there were 10 big ones and only 1 lightening strike, then it was only 1 in 10; but now, if there is just one big one and a lightening strike, there is a higher probability that that big one is going to get zapped. I think lightening is a big factor in mortality, but it is hard to measure. My impression is that it is a bigger factor in [more recent] years than in the earlier years, because of this density effect.

Now, for windthrow there is also a plant pathology perspective. There is a fungus that is frequently isolated from the roots of saguaros that are thrown over with the ball up. We used to call it *Poreia carnegiana*, but it has another name now. Basically, it is a wood-rotting fungus that weakens the root system, so you get again the disease triangle. You have the host, the environment (in this case heavy rain and wind) and the pathogen (the fungus that is capable of rotting the roots). In our plots, when we define *Poreia*/wind, when you can actually see the root ball, as a cause of mortality, it is pretty small—it is like 3 – 5% of the mortality (as opposed to the standing-stem rot). The other thing that I like about the idea of rot and the saguaro is whole community of organisms that follows the rot. The whole rotting system is part of the natural ecosystem. You have the *Drosophila* fruit fly related to the yeast—and the association of the yeast with the fruit fly larvae with the nematodes and protozoans and the whole community. Dr. Heed in the Ecology Department has, (with his graduate students Tom Starmer and

Jim Fogelman) looked at the association between species of fruit fly and different species of cactus rot, and in many cases there was a specific species of fruit fly associated with a specific species of cactus rot. Cactus species have specific [associations with] species of yeasts. It seems to me, though, that the saguaro fruit fly was one of the generalists. They were looking at a whole range of rotting columnar cacti and found these associations—there is a whole series of papers that Dr. Heed and his students wrote. Dr. Heed is still alive—he would be a great person to interview. I really like that perspective—of the long-term—that shows that it is really part of a system. The take for the public is that this is a natural system. And I've always been attracted to the fruit fly-yeast approach as emphasizing the naturalness of that system because the co-evolution that has occurred there shows that we are dealing with a system that is very old. And the bacterium is a part of that, because you don't get the rot with out the bacterium. There was an 1899 paper by a guy named Humbolt, I believe, that describes insect species associated with rotting.

Can you tell me about saguaro cactus virus?

A little bit...It was discovered by accident. Merritt Nelson was the virologist in the Plant Pathology Department. He was a good buddy with Stan Alcorn. One of Merritt's students, Gene (?), was doing a survey of viruses of cacti. Stan kept bugging Gene to inoculate some with these saguaros. Stan was collecting flower buds, it would have been in the late 60's, early 70's. He took some pollen from a saguaro flower, and rubbed it on a *Chenopodium amaranticolor* in the greenhouse—which is an indicator plant for viruses. Low and behold, a number of small yellow lesions appeared on the leaves of the *Chenopodium*, indicating the presence of a virus. So, there was something there, and they isolated it and they could inoculate it into the little [saguaros]. They started figuring it out—they filtered out the nectar from the pollen and traced it to the pollen. Then they ground up tissue and they inoculated it and found it. So it was discovered by accident, and it was discovered based on inoculation in a greenhouse indicator plant from material that was collected at Saguaro National Park East. Interestingly enough, there are no symptoms associated with the plant. So you can't go out to a saguaro cactus and look at it and know that it has saguaro cactus virus. There are absolutely no symptoms. The only way that you can tell is to collect flower buds and grind them up—try to get them before they open—and inoculate them onto this *Chenopodium* plant. If you see the lesions, then you know that you have the virus. Dr. Nelson and Gene (?) did some of the early work in isolating the virus and characterizing it. It turned out that it is closely related to carnation mottle virus. Later, Dr. Xioung, who was in the Plant Pathology Department, a virologist that came in 1994 – 1995, took a molecular approach, and he was able to sequence the virus. He again showed that it was closely related to the carnation mottle virus, but not the same—they are two different viruses. Just 2 or 3 years ago a graduate student who worked with Dr. Nelson and myself undertook a project to look at the spatial distribution across the whole saguaro habitat. We collected samples from Saguaro East, Saguaro West, Organ

Pipe, Kofa, Mexico, and 5 or 6 of the parks up in the Phoenix area to try to get a map of the distribution.

What did you find?

Only in the eastern part of the distribution—none at Organ Pipe, we didn't find any in Mexico (although we only had about 20 samples there), none in Yuma County up at Kofa—only 2 out of a couple hundred in the Phoenix area. Saguaro National Park East—lots, some at Saguaro West, a lot in Catalina State Park, 1 out of 20 at Picacho, we found one single plant up in the San Tan Mountain Park (which in Pinal County, but it is part of the Maricopa County Park System), one near Winkelman, and 4 or 5 positives over in the San Pedro Valley. So, it's in the eastern part. Betsy [Pierson] is going to write up a paper. It's a mystery, and it's ongoing, because Xiung is doing some additional molecular work. Another classic case—who knows what it does? The population there by the Mica Mountain picnic area was 60 or 70% of the older plants. The best guess is that it is pollen-transmitted. There are [other] pollen-transmitted viruses. The tighter end pollen is very high and it has not been isolated from plants before they start to flower. That's only the hypothesis. Where we have taken collections from plants that have *just* began to flower, they have all been negative—so they need to be flowering for some years before [infection]. One of the interesting questions, in my mind, is it is strong in Saguaro National Park East, but you have this generation of flowering plants dying out, and this whole new generation coming on that isn't flowering very much yet. We haven't seen any of it in the new generation—so will it disappear in that little part of the world? We now know that there is a lot of it at Catalina State Park, so it is not going to disappear from the whole population. We don't know whether it is recent, introduced, or it has co-evolved with the saguaro...it is a fascinating question to me, because if it co-evolved with the saguaro, why isn't it throughout the saguaro distribution? Is it the heat? One of the speculations is that you get sort of a heat-cure at the very hot temperatures in the low lands where we haven't found it. Is it important? We don't know. We [plant pathologists] think it is interesting—it is biologically interesting, but it is certainly not something that we want to be like the epidermal browning or the bacterial necrosis. We don't want headlines across the paper: "Virus striking saguaros, da-da da-da..." It's not that kind of thing, but it is an interesting biological phenomenon.

What do you see as the most eminent questions for modern saguaro biologists?

Well, I'm still caught up on the question of what causes recruitment and what doesn't...But long-term, an important question is what is global warming going to do? We know that there is going to be hotter summers...And then, from my perspective, following the saguaro cactus virus—how much genetic diversity is there in the saguaro cactus virus...I think the bacterial necrosis question is answered to my satisfaction, but I think it will need to be fine-tuned over the years. People will come to different understandings. We talked about all kinds of

inoculation experiments that could be done, but I'm pretty happy with my interpretation of it.

I think it will be interesting to see what happens in terms of nurse tree associations. We've seen a lot of different nurse-trees other than paloverde and mesquite. We've seen a lot of *Haplopappus* [*Isocoma tenuisecta*, burrowweed] serving as nurse plants, and they're pretty small. Most of the saguaros that we have [on our plots] have not yet outgrown it—and so it will be interesting to see what happens when this generation of 6 or 8 inchers gets up to 2 – 3 feet and are no longer [protected].

Do you think the young saguaros are using these smaller sub-shrubs due to a paucity of suitable tree microhabitats?

Ray [Turner] and Jan [Bowers] have a paper about that. That's an interesting question—Mary Olsen and I have been talking about what on earth is going on with the paloverdes. Mary is—she's a pathologist at the University [of Arizona]—she thinks that there is a strong drought or water component with the decline of the paloverde. We've been seeing it for 20 years. What is going on with the paloverdes? Is it just an aging thing, is it a decline that will recycle? Are we going to see them come back? Stan [Alcorn] and George Olin thought that the saguaros were often under the paloverdes because that's where the white-winged doves were nesting. And they did some experiments where they put drop cloths underneath it, and what they found was, that in the defecation, that the seeds were pretty well mashed up, and there wasn't much germination. But, they were sloppy feeders, so in their regurgitation, there were a lot of viable seeds. So thought that the reason you get such good numbers [of saguaro seedlings] under the paloverde was because that was a choice nesting site for the white-winged dove. It led to this sort of distribution away from those trees and the question of their survival. That's a good question that should be known in the next decade. I think they'll be alright—that's my bet.

Nancy: Well, they already don't grow as fast as the ones under the paloverdes.

Tom: Well—that's true, they are exposed longer.

Nancy: I guess one of the games that I want to play, that we haven't played yet is—this dataset that we have inherited—it follows individuals. So you could go out to a particular individual, and know its life history. Some years there's not much action—but you could know when scars are first produced, when it first gets its arms...and that makes it a very individual kind of thing. You know how fast it is growing, and how many other saguaros are right there in the neighborhood with it...I think that sort of individual approach is something that we as humans would like to log—it makes it easy to relate to saguaros.

Tom: Here's a hard question, though, that I think would be interesting for a researcher with a lot of time. Find them 1/2 inch to 1 inch tall...I don't have a clue

how old a 1/2 inch saguaro is. Because you can get them that big in a year or two, watering them in the greenhouse. But in the field...And I know that Steenbergh and Lowe did some work in a particular year, crawling around and finding them—and a lot of theirs, they lost. To follow them *up to that stage*. Most all of the work is projections. Can you imagine the task? First of all, the first year you'd look, you might not find any, because it might not be a good germination year.

They might be there, but they would be *so hard* to find.

Yes—find a little cotyledon in July or August. And then *hope* that 1 or 2 of the ones that you had put a little metal pin by would survive until the next year. We are guessing between 3 and 6 years for those small ones, but we really don't know. There is really a gap in the database. Future work to complete the saguaro picture.

Nancy: A gap that if it were then closed, you could then really associate the year of germination with the environmental conditions.

Of course all of our studies have just been in this one plot. Looking across the broad scale is really important—that will help us understand the different environmental factors.

The other thing that would have been helpful in our virus report was a density map of saguaros across their distribution. It's a huge job. We were thinking it would be good to sample different densities. It's clear that there are huge differences in densities—Organ Pipe is very dense. But, of course, densities shift over time, which makes it harder. If you go to the Kofa, there is much lower density, except in a few places. Up around Lake Pleasant—very high densities. There are some really interesting areas around Wickenburg, where the densities are high. But then you can go for miles and miles and only see 1 or 2 saguaros. In terms of understanding something like the saguaro cactus virus, having a baseline of density information would be very useful. And how would one approach it in such a way that it is do-able. We have some aerial photos that Cooper took, very early in the morning. You can actually count the saguaros by the shadows.

Nancy: Once they're 6 feet tall.

Nevertheless, that would be a potential way to survey for density of reproductive individuals. And that would be very expensive! Cooper flies low, and to fly low over such a broad area....

I have noticed an incredible gradient of architecture in plants in the northwestern (ORPI, west of Phoenix) part of the range versus plants in the Tucson area. The western plants are thinner, taller, branch higher on the stem, and there seems to be a higher occurrence of the “double whorl.” Has this been quantified? What are some possible

explanations? How is architecture affected in different parts of its range?

Nancy: Are you familiar with the San Pedro population? You should drive from Benson to San Manuel. People that know the saguaros there say that they are so different. Bulky-armed devils over there.

You could choose the plants that had the most arms—and, note how many arms—even choosing the plants with the most arms, generally, you can see that...I think rainfall, maybe genetics.

What are your impressions about cristate saguaros?

The thing about the cristate is that it is not just the saguaro that has the cristate [formation]. If I were to study it—and I've talked to Xioung about it—he thinks he couldn't necessarily rule out a virus, but most people think of it as a genetic condition. I think I'd actually study the *Opuntia*, because it is much easier to destroy. If you could transfer it...people speculate on some sort of genetic mutation that goes haywire on the growing tip. But what kinds of things also could do that—nematodes, galls, arthropods. Then you might think that you'd find it in clusters, which you usually don't.

To my knowledge there is no pathogen that has been associated with it. But you could begin to research it with *Opuntia*, because it is fast-growing. Then you could do some sort of manipulations. If it's a virus, it's not been found yet...

Appendix D: Slide Inventory

ID #	SOURCE	PHOTOGRAPHER	DESCRIPTION
1	Michael Chamberland	Michael Chamberland	saguaro with many arms
2	Michael Chamberland	Michael Chamberland	saguaro silhouette
3	Michael Chamberland	Michael Chamberland	saguaro flower buds
4	Michael Chamberland	Michael Chamberland	saguaro flowers
5	Michael Chamberland	Michael Chamberland	saguaro fruits
6	Michael Chamberland	Michael Chamberland	saguaro hole
7	Michael Chamberland	Michael Chamberland	cristate saguaro
8	Michael Chamberland	Michael Chamberland	cristate saguaro
9	TMD	C. Allan Morgan	white-winged doves with saguaro fruit
10	TMD	C. Allan Morgan	screech owls in saguaro hole
11	TMD	Paul and Shirley Berquist	great-horned owl nest
12	TMD		gilded flicker
13	TMD		clouds and saguaro silhouette
14	TMD		young saguaros with mexican poppies
15	TMD		bat in saguaro flower
16	TMD	S. Moser	bacterial necrosis-black ooze
17	TMD	S. Moser	bacterial necrosis-"bleeding saguaro"
18	TMD	S. Moser	bowled dead saguaro
19	TMD		lightening
20	TMD		cross section
21	TMD		fire (young saguaro)
22	TMD		fire (older saguaros)
23	TMD		young saguaro growing in rock crevice
24	TMD		nice saguaro shot
25	Bill Peachy	Bill Peachy	dead saguaro
26	Bill Peachy	Bill Peachy	dead saguaro
27	Bill Peachy	Bill Peachy	honey bees at saguaro flower
28	Bill Peachy	Bill Peachy	split open fruits
29	Bill Peachy	Bill Peachy	saguaros in snow
30	Bill Peachy	Bill Peachy	graph
31	Bill Peachy	Bill Peachy	bat at feeder

32	Bill Peachy	Bill Peachy	Mexican long-nosed bat
33	Bill Peachy	Bill Peachy	bat at feeder
34	Bill Peachy	Bill Peachy	flower up close
35	Bill Peachy	Bill Peachy	flower diagram
36	Bill Peachy	Bill Peachy	bat guano (orange = saguaro pollen)
37	Bill Peachy	Bill Peachy	bat guano
38	Bill Peachy	Bill Peachy	bat guano with saguaro seeds
39	RMD	J. Pickus	road foundations
40	RMD		bulldozer and saguaros
41	RMD	Scott Croll	tract housing and Mica Mountain
42	RMD		downtown Tucson
43	RMD		smog over Tucson
44	RMD		Twin Peaks cement plant
45	RMD		rural development
46	RMD	H. Coss	air pollution NW of RMD
47	RMD		cactus rustling article
48	RMD		saguaro vandalism
49	RMD		cactus forest 19935
50	RMD		cactus forest 1960
51	RMD		cactus forest 1985
52	RMD	R. Casey	epidermal browning
53	RMD		saguaro skeleton
54	RMD	B. Bodiger	Granddaddy saguaro dead
55	RMD		Granddaddy saguaro alive
56	RMD	L. Cannataro	cristate saguaro
57	RMD		saguaro vandalism
58	RMD		saguaro cross-section
59	RMD		saguaro "boot"
60	RMD		lesser-long-nosed bat
61	RMD	H. Coss	saguaro flowers
62	RMD		cluster of young saguaros
63	RMD		seedling saguaro
64	RMD	C. Allan Morgan	summer lightning
65	RMD	H. Coss	saguaro sunset
66	RMD		mountains with snow
67	RMD		winter rainstorm

68	Tom Orum (collection of Stan Alcorn)	George Olin	ORPI; May 1961; pollination experiment cage
69	Tom Orum (collection of Stan Alcorn)	George Olin	Dr. Ives Ferguson attempting to core saguaro with dendrometer March 1962
70	Tom Orum (collection of Stan Alcorn)	George Olin	RMD eradication program
71	Tom Orum (collection of Stan Alcorn)	George Olin	RMD eradication program
72	Tom Orum (collection of Stan Alcorn)	George Olin	Granddaddy saguaro December 3, 1951
73	Tom Orum (collection of Stan Alcorn)	George Olin	epidermal browning May 13, 1949
74	Tom Orum (collection of Stan Alcorn)	George Olin	Stan Alcorn measuring saguaros early 1950's
75	Tom Orum (collection of Stan Alcorn)	George Olin	Alcorn and Olin pollination study
76	Tom Orum (collection of Stan Alcorn)	George Olin	honeybees pollinating saguaro flower
77	Tom Orum (collection of Stan Alcorn)	George Olin	water truck for transplant study
78	Tom Orum (collection of Stan Alcorn)	George Olin	transplant study
79	Tom Orum (collection of Stan Alcorn)	George Olin	transplant study
80	Tom Orum (collection of Stan Alcorn)	George Olin	cow at RMD 1950's
81	Tom Orum (collection of Stan Alcorn)	Stan Alcorn	<i>Erwinia cacticida</i>
82	Tom Orum (collection of Stan Alcorn)	Tom Orum	Stan Alcorn late 1990's
83	Dale Turner	Dale Turner	betacyanin
84	Dale Turner	Dale Turner	saguaro volunteers Spring Break 2000
85	Dale Turner	Dale Turner	epidermal browning on prickly pear
86	Dale Turner	Dale Turner	epidermal browning
87	Dale Turner	Dale Turner	epidermal browning
88	Dale Turner	Dale Turner	field work

89	Dale Turner	Dale Turner	field work
90	Dale Turner	Dale Turner	dead saguaro with live arms
91	Dale Turner	Dale Turner	Golden Gate burn
92	Dale Turner	Dale Turner	Golden Gate burn

Appendix 5: Slides