

Demographic changes over >70 yr in a population of saguaro cacti (*Carnegiea gigantea*) in the northern Sonoran Desert



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ABSTRACT

We studied changes in a population of saguaro (*Carnegiea gigantea*) cacti on a 259 ha plot in the northern Sonoran Desert (Saguaro National Park) that was first surveyed in 1941. With the help of citizen scientists, we mapped and measured the height of all detected individual saguaros. The total number of detected saguaros was 13,304 in 1941 and 9023 in 2012, a 31.4% decrease. The population in 1941 consisted of mostly larger, older individuals, whereas in 2012 it was dominated by smaller, younger individuals. Based on estimated years of saguaro establishment, a period of high establishment in the mid-late 1800s was followed by many decades of poor establishment. However, establishment surged from the 1970s to early 1990s but has been very low since. Comparisons with other long-term saguaro studies suggest that the dramatic demographic changes in this area have resulted from climatic factors, most notably recent long-term drought and higher temperatures, in combination with land-use changes, especially loss of nurse trees due to wood-cutting early in the twentieth century.

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1. Introduction

The saguaro cactus (*Carnegiea gigantea* [Englm.] Britt. and Rose) is a keystone species in Sonoran Desert ecology, with >100 species of fauna utilizing the plant for survival (Drezner, 2014). Precipitation is the primary limiting factor regulating the occurrence of saguaros on the western edge of the range (Steenbergh and Lowe, 1977) and saguaro populations at the eastern and northern extent of the range are limited by the occurrence of >24 consecutive hrs of subfreezing winter temperatures (Hastings, 1963; Steenbergh and Lowe, 1976). Saguaro initiate growth after the start of the summer monsoon and growth rate across the range is strongly correlated with summer precipitation (Drezner, 2005).

The Sonoran Desert has both winter and summer rainy seasons caused by different atmospheric phenomena. Winter precipitation occurs when frontal systems originating from the Pacific Ocean follow a southern path across Arizona. Summer precipitation is

caused by the North American Monsoon, which occurs when intense solar heating causes a shift in the pattern of high and low pressure systems in the Southwest and draws moisture northward from the Gulf of California, the Gulf of Mexico, and the eastern tropical Pacific Ocean (Sheppard et al., 2002). A period of hot, dry weather, often referred to as the foreshummer, occurs between these two rainy seasons, but a precipitation shortfall in either season can lead to drought (Weiss et al., 2009). Rising average summer temperatures result in more arid conditions and increase the rate of evapotranspiration (Weiss et al., 2009). The Cactaceae family is one of the most threatened taxonomic groups worldwide (Goettsch et al., 2015) and, as one of the most studied members of its family, the saguaro provides one of only a few examples of biotic and abiotic impacts on cacti demographics (Drezner and Lazarus, 2008). Thus, a fine-tuned understanding of saguaro demographics and climatic influences on this species can greatly enhance predictions of Cactaceae dynamics under climate change scenarios (Téllez-Valdés and Dávila-Aranda, 2003).

Saguaro National Park (SNP), located near the eastern limit of the saguaro population (Fig. 1), was originally established as a national monument in 1933 to protect an area known as the “Cactus Forest,” which was considered to contain the finest stand of the giant saguaro cactus in the U.S. (Steenbergh and Lowe, 1983). In

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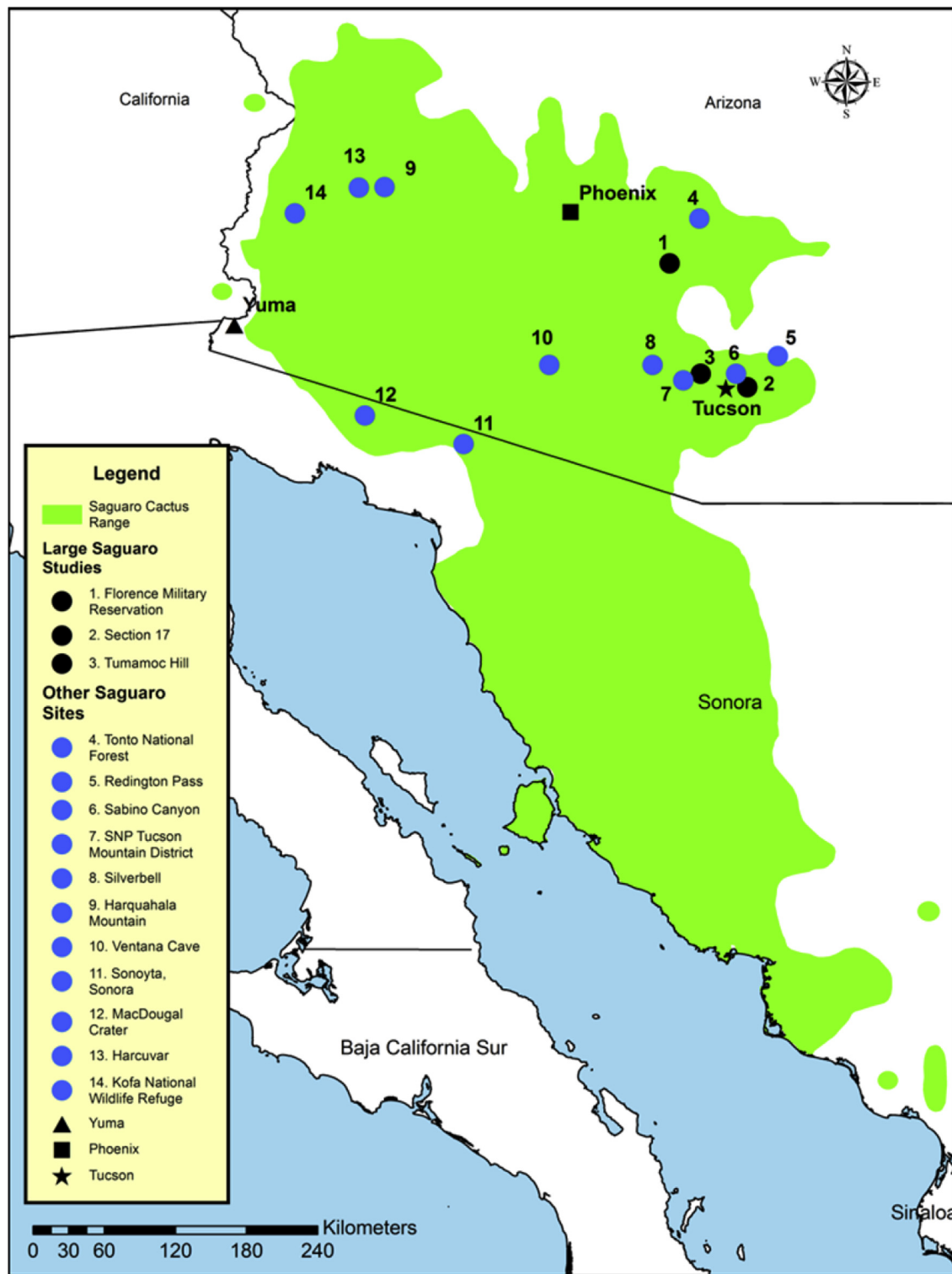


Fig. 1. The location of saguaro studies in the northern Sonoran Desert. 1. Florence Military Range (Danzer and Drezner, 2010); 2. Section 17 (this study); 3. Tumamoc Hill (Pierson and Turner, 1998); 4. Tonto National Forest (Campbell et al., 2011); 5 through 12 (Pierson et al., 2013); 13. Harcuvar (Drezner, 2006b); 14. Kofa National Wildlife Refuge (Drezner and Balling, 2008). The range of the saguaro cactus was obtained from the United States Geological Survey (Little, 1976).

1939, National Park Service (NPS) staff were alarmed by a highly visible die-off of saguaros in the Cactus Forest. Some researchers hypothesized that the widespread mortality was the result of a contagious bacterial disease (Gill, 1942). To determine if removing diseased saguaros would improve survival of healthy individuals,

researchers divided a 259 ha area (1 mi²) of the Cactus Forest (Section 17 of Range 16E and Township 14S; referred to as “Section 17” in this study), into 64, 4.05 ha plots (Appendix 1, electronic version only). All saguaros showing signs of bacterial infection were removed mechanically from the 32 southern plots of Section 17,

while the cacti in the northern half remained mostly untreated (Gill, 1942). A yearly census of Section 17 in its entirety was conducted from 1941 to 1946, and then, when it was determined that there was no difference between treatment and control halves of Section 17, a subset of plots were monitored annually through 1950 (Gill, 1951).

Most saguaro researchers now believe that the causes of mortality in the late 1930s were extreme freeze events in 1937 and 1939 (Steenbergh, 1970; Steenbergh and Lowe, 1983). The widespread mortality of mature saguaros in Section 17 was coupled with a lack of establishment and age structure analyses from the early studies showed an inverted population pyramid with far fewer juvenile saguaros than older, mature saguaros (Alcorn and May, 1962). The unbalanced population age distribution indicated that the establishment rate of new saguaros in the Cactus Forest had been low for decades before 1940. Repeat photography of the Cactus Forest from 1935 and 1998 visually documented the sharp decline in the number of visible saguaros (Fig. 2; Turner et al., 2003).

Poor establishment in the early 20th century has been

attributed to many factors including severe freezes (Steenbergh and Lowe, 1977), cattle grazing (Niering et al., 1963), and woodcutting that fed lime kilns in the late 1800s and early 1900s. As a result of human activity, many “nurse plants,” especially *Prosopis velutina* (velvet mesquite) and *Parkinsonia microphylla* (foothill palo verde), were removed from the landscape. Nurse plants are essential for the survival of young saguaros in non-rocky habitats (McAuliffe, 1996) because they protect them from crushing or herbivory by animals (Niering et al., 1963) and they create microhabitats that moderate summer maximum edaphic and ambient temperature (Franco and Nobel, 1989) and winter minimum temperature (Turner et al., 1966) in the area under the subcanopy.

Some of the land use pressures were removed throughout the 20th century. Woodcutting on federal land around the Rincon Mountains was banned by court order in 1920, although it continued at a smaller scale on private inholdings within the Cactus Forest until the NPS acquired all the land within the boundary (McAuliffe, 1996), and grazing ceased in the area in 1958 (Pinto, 2014). The cessation of these activities allowed the nurse plants

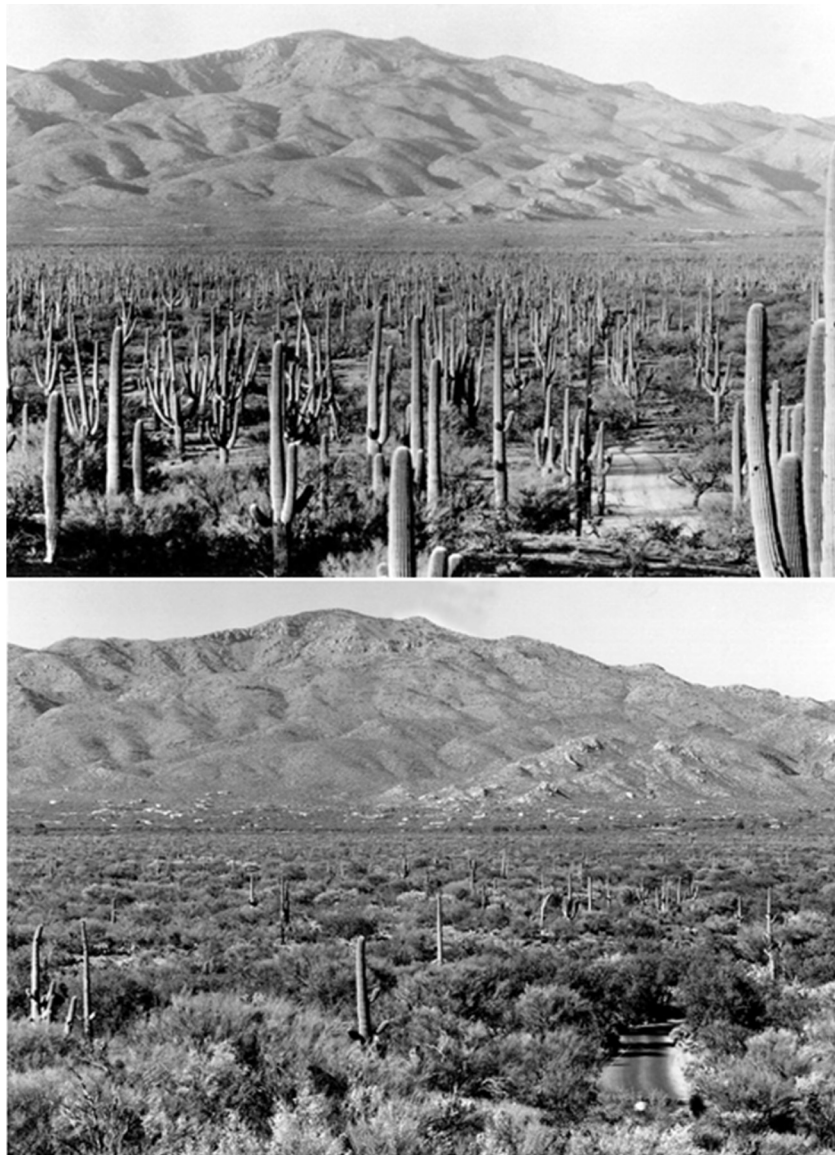


Fig. 2. 1935 (top) and 1998 (bottom) repeat photographs of the Cactus Forest. Note not only the dramatic loss of large saguaros by 1998, but also the increase in nurse trees during the period; young saguaros are currently growing beneath many of these trees (1935 photographer unknown; 1998 photo by Raymond Turner).

to regenerate and resume their normal function in the ecology of the saguaro (Fig. 2).

Age structure data are important to ecologists and resource managers because they provide an estimate of overall population health and insight into past regeneration trends (Silvertown et al., 1993; Pierson and Turner, 1998; Udevitz and Gogan, 2012). Long-lived species like the saguaro require long-term site-specific monitoring in order to determine whether changes in population dynamics represent significant trends or short-term random variations (Pierson and Turner, 1998). Saguaro demographics have been well-studied throughout Arizona and northern Sonora, Mexico; however, only a few studies rely on long-term data or have large sample sizes (Table 1), and both are present in our study.

The goal of this study was to resurvey the entirety of Section 17 in order to evaluate demographic changes. Although six long-term plots in Section 17 have been monitored continuously and intensively for more than 75 years (Orum et al., 2016), the entire 259 ha area had not been resurveyed since the original 1941–1946 census.

2. Materials and methods

2.1. Site description

SNP, located near Tucson, Arizona (Fig. 1), is divided into two districts: the Tucson Mountain District borders the west side of Tucson, while the Rincon Mountain District is located on the east side of the city. Section 17 is located within the Cactus Forest on the northwestern boundary of the Rincon Mountain District (Appendix 1, electronic version only). The area is flat with non-rocky soil, intermittent washes, and Sonoran desert scrub vegetation dominated by foothill palo verde and velvet mesquite on the higher areas and *Larrea tridentata* (creosote bush) and *Acacia greggii* (catclaw acacia) along the washes.

2.2. Acquisition of 1941–1946 saguaro census data

The original, hand-written 1941 to 1946 data and field notes of Lake Gill and Paul Lightle were carefully preserved for >5 decades by Stan Alcorn, Tom Orum, and Nancy Ferguson. We digitized the original tabular survey data into an Excel database. Gill and Lightle recorded the health characteristics of every saguaro in Section 17 but did not record precise heights; instead, they placed saguaros into height classes with 1.8 m intervals (Table 2). Gill and Lightle assigned individual saguaros a unique number and marked them with a wooden stake, but it was not possible for us to follow up on individuals that may have been present in 1941 because most of the stakes have disappeared and Gill and Lightle did not map individual saguaro locations.

We georeferenced a 1941 map of saguaro locations that was drawn from an aerial photograph taken by the U.S. Army Air Corps at an altitude of approximately 1524 m. The locations of saguaros on that map represent saguaros that were visible in the photo and not actual survey locations. We were unable to determine how many saguaros may have been omitted from the map, but it is logical to assume that the large majority of mature cacti capable of branching were drawn. For comparison, we used the georeferenced

Table 2

Height class definitions used by Gill and Lightle as described in Steenbergh and Lowe (1983).

Height class	Height (m)	Age
1	0–1.8	0–36
2	1.8–3.6	37–52
3	3.7–5.4	53–68
4	5.5–7.2	69–85
5	7.3+	85+

map as a base layer and overlaid it with the locations of saguaros >2 m that we surveyed to produce a product for visual analysis of the change in density across the study area. We selected 2 m as an arbitrary threshold with the assumption that saguaros >2 m in 1941 would have been visible in the aerial photo.

2.3. Field methods

We sampled Section 17 between October 2011 and July 2012 and followed the field methods outlined in O'Brien et al. (2011); for simplicity we refer to all results as “2012”. We re-located the corners of each plot with GPS units and used flagging to outline the sides of the plot at approximately 20-meter intervals. Teams of 3–5 individuals systematically searched the plot for saguaros. Each saguaro was marked with a numbered pin flag, measured with a folding rule to the nearest 0.01 m, and mapped using a hand-held GPS unit. We measured saguaros >4 m with a clinometer and tape measure, using two independent observers, to the nearest 0.1 m. The survey process required three “passes” through the plot: one pass to record, a second pass by a separate team to search for any missed saguaros, and a third pass to collect pin flags. Similar to previous saguaro surveys in the Park (Swann et al., 2011), data were collected by student and adult volunteer “citizen scientists”, led by trained park staff. Additional details are available in a technical report (Conver et al., 2013).

2.4. Data analysis

We used the age-height equations from Steenbergh and Lowe (1983) to determine age and, subsequently, the approximate year of germination from the height of each saguaro measured in 2012. Approximate annual establishment trends provide a finer temporal scale to support the examination of demographic composition changes. We were unable to estimate saguaro ages or the year of establishment for the 1941 data because absolute heights were not recorded.

The age-height regression equation is:

$$\log Y = -0.309 + 0.884 \log X + 0.609 (\log X)^2 \quad (1)$$

where Y equals stem height in cm and X equals age in years (Steenbergh and Lowe, 1977). This equation is only applicable for saguaro cacti less than 2.2 m, or approximately 33 years old. The height of saguaros larger than 2.2 m was determined from the age and height tables in Steenbergh and Lowe (1983). At this height, most saguaros have reached reproductive age, and growth rate

Table 1

Summary of the large scale saguaro studies, defined as having a plot size of greater than 10 ha, found in the peer-reviewed literature.

Site	Area (ha)	Saguaro Count	Reference
Florence Military Reservation	1100	12,232	Danzer and Drezner (2010)
Saguaro National Park, Section 17	259	9023	This study
Tumamoc Hill	42	2594	Pierson and Turner (1998)

becomes more variable as the saguaro diverts approximately 50% of stem growth towards reproduction (Steenbergh and Lowe, 1977).

Young saguaros are easy to overlook in a field census because they are only 2–3 mm tall one year after germination (Steenbergh and Lowe, 1983). Therefore, we applied a correction factor for detectability based on age-when-saguaro-first-found data from known saguaros on six study plots in Section 17 that are sampled annually (Orum et al., 2016). The correction added a mean of about 8 saguaros per plot to the smallest age-height class.

We binned our census data into the same height classes Gill and Lightle used in 1941 (Table 2). This allowed for a direct comparison of the total number of saguaros in each height class. We also calculated the total number of saguaros surveyed during each sampling period. We then used a χ^2 test of independence to test for changes in the number of saguaros present in Section 17 from 1941 to 2012. We also calculated the number of saguaros per plot at each time point to quantify changes in saguaro density. Last, we determined if the large scale removal of “diseased” saguaros from the southern half of Section 17 in 1941 significantly affected the distribution of saguaros surveyed in 2012. We did this by comparing the number of saguaros in the northern and southern halves of Section 17 using a χ^2 test of independence. All statistical analyses were conducted in R 3.3.1 (R Core Team, 2016).

3. Results and discussion

3.1. Saguaro demographics and establishment

The 1941 survey counted 13,304 individuals in Section 17; digitization of the 1941 raw data resulted in a count that was slightly higher than the 12,968 reported by Gill and Lightle (1942) due to mathematical errors associated with the original hand calculations. In 2012, we measured 9023 saguaro cacti, a 31.4% decrease over the 70 year period. The demographic composition of the population has flipped since 1941 (Fig. 3). In 1941, the saguaro population was dominated by older, taller individuals, whereas in

2012 the population was dominated by smaller, younger individuals. The smallest height class (<1.8 m) represented 57.1% of the total saguaro population in 2012 (Fig. 3).

We found that few saguaros established prior to the 1930s (Fig. 4). The peak year of recruitment occurred in 1984 with an estimated germination of 384 saguaros. We detected 454 saguaros (5.03%) younger than 20 years old (<0.46 m tall; Steenbergh and Lowe, 1983). This number should be considered a minimum estimate, even with our correction factor applied, because young saguaros are very small and grow slowly among the nurse tree or shrub, which makes them difficult to detect in the field. Seasonality and phenology also contributed to the limitation on detection. Periods of green-up obscure the areas around the base of nurse plants to a greater degree than periods of senescence. Our surveys spanned both periods of the phenological cycle. Despite the limitations on detectability, Orum et al. (2016) determined that field surveys in Section 17 detect approximately 40% of saguaros at 10 years old (0.052–0.064 m tall), and 95% at 20 years old.

Our results demonstrated that the demography of the saguaro population in Section 17 changed significantly in the past seven decades. The changes are the result of both mortality of larger individuals and variation in the establishment rate. The effects of grazing and removal of nurse plants severely hindered the ability of the saguaro to regenerate between 1900 and 1925 (Niering et al., 1963; Pinto, 2014) despite regional recruitment pulses linked to global volcanism (Drezner and Balling, 2008). The establishment rate increased after NPS policy eased land use pressures throughout the 1950s, and we detected the influence of volcanism in the form of the peak establishment period between 1980 and 1990 (Fig. 4) that coincided with the eruption of Mount St. Helens. Establishment rate fell sharply after 1990 due to the onset of extended drought and higher than normal temperatures (Springer et al., 2015). By 2000, the establishment rate was near zero across Section 17. This result is corroborated by the annual survey results presented in Orum et al. (2016), which found only three new saguaros on their plots since 1993.

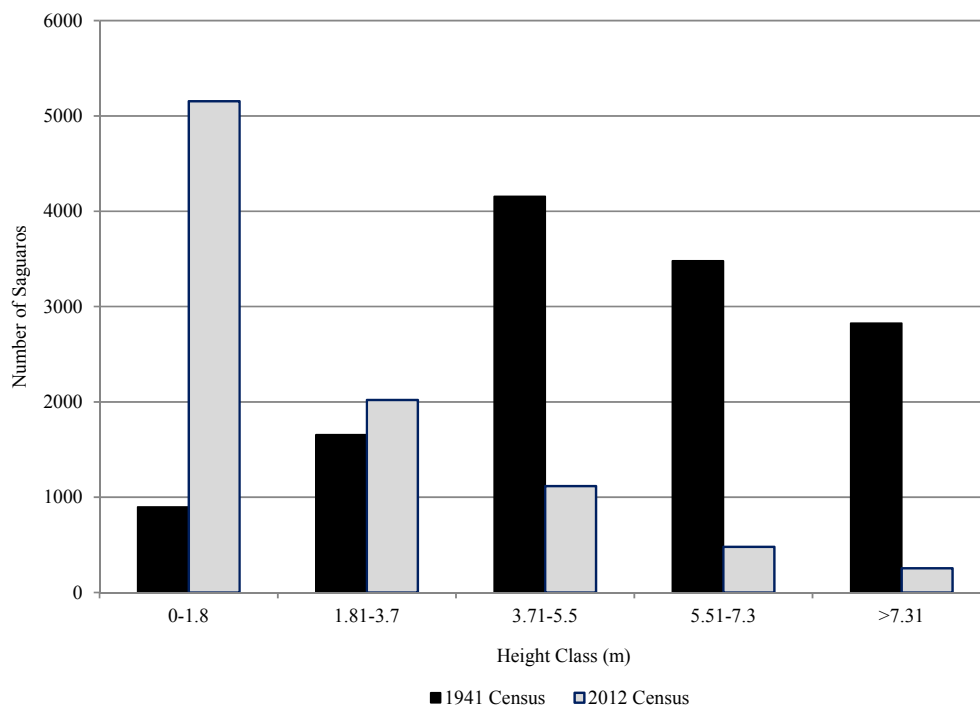


Fig. 3. Number of saguaros by height class in 2012 and 1941. See Table 2 for height class values.

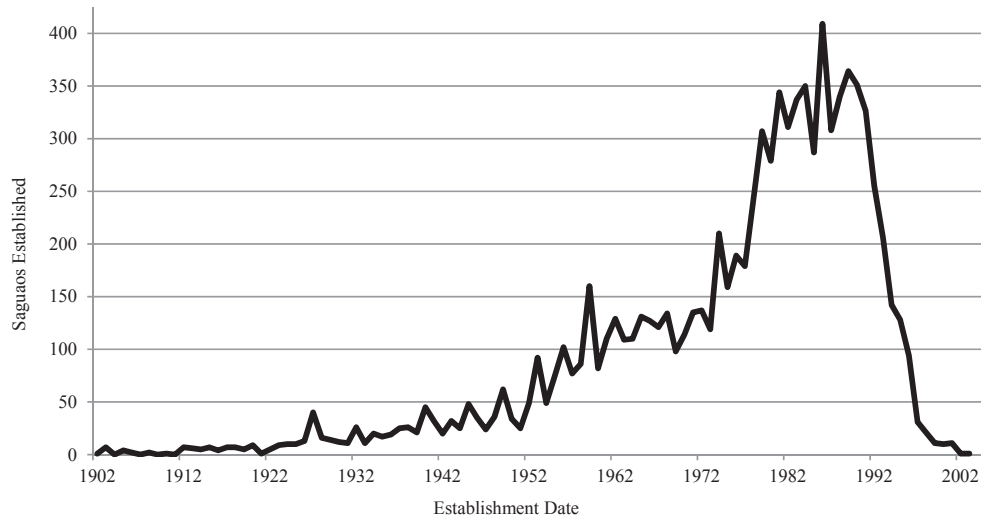


Fig. 4. Annual estimated establishment for saguaros sampled in 2012 in Section 17.

3.2. Changes in density and spatial distribution, 1941–2012

The spatial distribution of mature saguaros did not shift between 1941 and 2012 (Appendix 2, electronic version only), however we detected a significant decrease in the overall number of saguaros ($\chi^2 = 710.41$, $P < 0.001$) and a high degree of variance among plots. The mean number of saguaros per plot was 205.4 in 1941 and 144.1 in 2012. In 1941, the plots had a minimum value of 21 saguaros and a maximum of 519, and in 2012 the minimum was 20 and the maximum was 546. Six plots in the northwestern corner of Section 17 (plots H1–H3, G1, G2, F1) had a low density of saguaros in both 1941 and 2012. The density of saguaros declined by more than 50% in 14 of the 64 plots, with the greatest decreases in the center of the section (Appendix 3, electronic version only). By contrast, density increased by more than 5% on 11 of 64 plots.

With respect to the differences between the treated and untreated halves of the section, we surveyed 4895 saguaros on the northern half and 4326 saguaros on the southern half in 2012 compared to the 6423 saguaros on the northern half and 5708 saguaros on the southern half in 1941. We failed to detect a significant difference between the number of saguaros on the northern and southern halves of Section 17 ($\chi^2 = 0.04$, $P < 0.5$), potentially indicating no long-term effect of the 1941 disease removal experiment. This result is consistent with Gill (1951) who also failed to detect a significant difference between the treatment and control areas 10 years after the saguaro removal project.

3.3. Comparisons with other studies

It is important to consider changes in the demographics of the saguaro population in Section 17 in the broader geographic context. Because saguaros are long-lived and survival of young plants is known to be affected by climatic factors, especially precipitation and freeze events, a number of studies have examined their range-wide and long-term demography in relation to long-term climate change or global events that influence regional climate variability. Using long-term monitoring data from 10 populations from 1960 to 2010, Pierson et al. (2013) observed several broad peaks in saguaro establishment from 1780s to 1860s during a generally wet period. Combining results from 30 sites in Arizona, Drezner (2006a) also found that saguaro establishment rates were high range-wide in the late 1800s and early 1900s, followed by a general decline in establishment during the first half of the 20th century but recovery

after 1960.

Patterns of saguaro establishment varied across the region, however. Drezner (2006b) observed that an establishment surge during the late 1800s in western and northeastern Arizona lasted longer into the early 1900s than in southeastern Arizona. Drezner and Balling (2008) attributed the surge to an increase in the weighted historical dust veil index due to volcanic activity that resulted in warmer and wetter winters and increased pre-monsoon precipitation. With the exception of a period of greater establishment in western Arizona in the 1970s, the trend in establishment in northeastern Arizona during the 20th century was generally downward. In contrast, recruitment in southeastern Arizona was low in the late 1800s through the 1940s, but steadily increased through the middle of the 20th century with a surge of establishment after 1971 (Drezner, 2006b). The post-1970 surge was seen at most (but not all) sites in southern Arizona, including in a census of 12,232 saguaros at the restricted access Florence Military Reservation north of Tucson (Danzon and Drezner, 2010).

In Section 17, trends in saguaro establishment are consistent with regional trends in southeast Arizona for the 1800s and second half, but not the first half, of the 20th century. The 1941 age-class data confirm that establishment in the middle and late 1800s was high, and the large surge in Section 17 following 1960 is similar to (and perhaps larger than) the increase seen at other sites. However after 1900, establishment was very low for more than 50 years.

Livestock grazing, woodcutting, and herbivory by rodents in the Cactus Forest are believed to have contributed to the lack of establishment prior to the 1950s (Mielke, 1944; Pinto, 2014). Pierson et al. (2013) point out that renewed establishment on Tumamoc Hill, SNP West, and Sabino Canyon corresponded with the removal of cattle from those areas. In contrast to the Cactus Forest, the population at nearby Sabino Canyon has had a relatively stable age structure for >50 yrs.

It is noteworthy that some long-term plots within SNP but outside of Section 17 have also been relatively stable over the same period. These sites resemble the Sabino Canyon plot in that they are located on rocky slopes, in contrast with the bajada habitat of Section 17. While nearly all saguaro populations in SNP had relatively low establishment in the 20th century prior to the 1960–1980 surge, most had more consistent recruitment rates than Section 17 during that period (Turner and Funicelli, 2000; O'Brien et al., 2011). This result supports the findings from Orum et al. (2016) that suggest that establishment in the Cactus Forest may

be more episodic than in rocky areas even in the absence of anthropogenic influences.

4. Conclusion

The decline of saguaro in the Cactus Forest alarmed visitors and NPS officials for decades and spurred research to guide management actions. Niering et al. (1963) warned that, without land use changes instituted by the NPS, the Cactus Forest “may now be of value principally as a demonstration of the ruinous effects of long-continued grazing on a once-splendid saguaro forest of the upper bajada.” Our study provides insight on the negative impacts of grazing on saguaro cacti and the decades-long effects evidenced in its population demographics. This is similar to observed declines in diversity and changes in community structure in similar arid systems impacted by grazing (Valone and Kelt, 1999; Drewa and Havstad, 2001). The saguaro is a keystone species in the Sonoran Desert (Drezner, 2014) and any changes in its population structure will likely have multi-directional effects on associated species and community assemblages across the range. The current demographic pattern suggests that the population is approaching a crossroad. The age-height structure of the Section 17 population will shift over the next 15–20 years as the youngest individuals mature into reproductive age. The population would then be in an excellent position to produce a large cohort in the next favorable recruitment window. If the recruitment window opens due to favorable climate variation or a sporadic global volcanism event, it seems likely that visitors to SNP at the end of the century may witness a Cactus Forest landscape with many large saguaros similar to 1941 complemented by many juveniles under nurse trees. However, if drought persists and the recruitment window remains closed for the next several decades, the population may return to the 1941 state.

Without the pressure associated with multiple land uses, climate will regulate the frequency of future recruitment windows. Changes in temperature and precipitation are already occurring in the Sonoran Desert (Weiss and Overpeck, 2005; Weiss et al., 2009) and may affect long-term demographic patterns in unpredictable ways. Freezing temperatures are the primary limiting factor for the survival of saguaro seedlings (Steenbergh and Lowe, 1977, 1983; Nobel, 1980). Most climate models predict a three to five °C increase in average annual temperature by the year 2100 in the southwestern United States (Christensen et al., 2007; Lenart et al., 2007). Warmer temperatures may reduce the number of freeze events during winter in the Sonoran Desert (Weiss and Overpeck, 2005; Archer and Predick, 2008) that result in 100% mortality of seedlings. However, warmer temperatures also increase water demands during summer, which may result in the desiccation of saguaro seedlings that have a smaller capacity to hold water more than mature cacti (Brum, 1973; Drezner, 2004). If increases in drought frequency accompany warmer temperatures (Seager et al., 2007; Archer and Predick, 2008), water availability could become a more significant limiting factor. Nurse trees may mitigate some of the water and temperature stress associated with a changing climate (Drezner, 2006a, 2014).

This study, in a more holistic sense, demonstrates the utility of archival data and the necessity for research on an appropriate temporal scale to the life cycle of the species of interest, in this case a long-lived columnar cactus. Despite the threatened status of cacti world-wide, beyond the saguaro few detailed, long-term studies have been carried out on any cactus species (Boyle and Anderson, 2002). However, it seems likely that the species' response to both climate and land use change would be similar for many other Cactaceae in arid lands. The protections on land use afforded by the NPS have been in place for more than 70 years, or approximately

half the life span of the saguaro cactus, and allowed an environment heavily impacted by man to recover and restore itself to a more natural state. Thanks to the previous research of Gill and Lightle, and many others, this study provides context for our results beyond what we could observe. Our work will be another snapshot in time for the next generation of land managers and scientists.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2016.12.008>.

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