Resurvey of Saguaro Monitoring Plots in Saguaro National Park Following the 2011 Freeze Event

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ABSTRACT

After many decades of decline, the saguaro cactus (*Carnegiea gigantea*) population in Saguaro National Park (SNP) began to rebound in the 1960s, and recruitment surged in both the eastern Rincon Mountain District (RMD) and western Tucson Mountain District (TMD) through a wet period that ended in the early 1990s. Since then, surveys on long-term plots in the northwestern "Cactus Forest" area of RMD have detected very few young saguaros, suggesting that recruitment has again declined. Changes in recruitment and survival may be related to environmental factors, including higher temperatures, drought, and freeze events, the latest occurring in 2011. We monitored saguaros in both park districts in 2010 and 2014 to better understand recent changes in saguaro demographics across all habitats. We used two sets of data; 1) 45 randomly-located plots established in 1990 and last surveyed in 2010, and 2) 11 plots representative of typical saguaro habitat established in 1941 and 1975 and last surveyed in 2014. We categorized these plots by district and habitat related to the geographic setting (bajada, foothill, and slope) and used generalized growth models based on data from each district to estimate year of germination. Our results indicate that saguaro recruitment has slowed dramatically throughout Saguaro National Park since the early- to mid- 1990s. Establishment has been very low in bajada and foothill areas, and there has been only limited recruitment on slopes. In addition, mortality of older saguaros was very high throughout the park during 2010-2014, suggesting that the 2011 freeze had a widespread effect.[1]

INTRODUCTION

The saguaro cactus (*Carnegiea gigantea*) is a long-lived, iconic Sonoran Desert species that has been the subject of biological research for more than 100 years. In 1933, Saguaro National Monument was established by President Herbert Hoover (Congress elevated Saguaro to National Park status in 1994), due to an impressive stand of very tall saguaros in an area known as the "Cactus Forest" in the foothills of the Rincon Mountains. University of Arizona President and plant scientist Homer Shantz was an advocate for the monument as "a great natural area for maintaining the botanical and zoological forms of the Southwest under natural conditions" (Clemensen 1987). Shantz wanted to utilize the landscape as an outdoor laboratory where researchers and students could study the multitude of species and ecosystems, especially the saguaro cactus. Biological research, especially on saguaros in the Cactus Forest, has been a core function of Saguaro National Park (SNP) since its establishment (McAuliffe 1993, 1996; Ahnmark and Swann 2009).

Given the park's primary purpose, multiple generations of scientists have been interested in the status of the saguaro population at SNP. Even prior to the park's establishment, researchers had

[1] This technical report represents a preliminary analysis and its distribution is made available to the public through the NPS Integrated Resource Management Applications (IRMA) portal. Some material may be published separately through peer-reviewed journals and/or other NPS reports.

observed that age-structure demographics in what is now the Rincon Mountain District were skewed towards older cacti (Shreve 1910), which gave them concern about the long-term viability of the species (Wilder and Wilder 1939; Niering et al. 1963). In addition, large-scale mortality of cacti was observed in the late 1930's in the Cactus Forest. While initially disease was implicated in the decline of the saguaro population (Gill 1942; Gill and Lightle 1946; Gill 1951) further studies attributed the lack of younger saguaros to land use activities, most notably grazing and woodcutting that caused near complete mortality of seedlings and juveniles (Alcorn and May 1962; McAuliffe 1993). The land use hypothesis seemed to be confirmed when the land use pressures were released in the 1960s and 1970s, as saguaro establishment throughout the park increased dramatically for the next three decades (Steenbergh and Lowe 1983; Duriscoe and Graban 1991; Turner and Funicelli 2000, O'Brien et al. 2011).

However, recent studies of saguaros in the Cactus Forest suggest that establishment (recruitment, or survival of young saguaros) peaked in the early 1990s and has been very low since then. Land use cannot explain this recent decline, but 2000 to 2009 was the hottest decade on record for the Tucson area (NOAA 2010), and climate models predict increasing temperatures for the Southwest (Christensen et al. 2007; Lenart et al. 2007) and an increasing frequency of drought (Seager et al. 2007; Archer and Predick 2008). In addition to drought, saguaros are known to be impacted by freeze events, where temperature remains below freezing for more than 24 hours (Hastings 1963, Bowers 1980). After several freeze events in the 1970s that were intensively studied by Steenbergh and Lowe (1976, 1977, 1983), the park experienced a long period without such events until February 2011, when temperatures dropped to historic low for two consecutive nights (O'Brien et al. 2011). Some climatologists have hypothesized that hard freeze events may occur more frequently in the southwestern United States as a result of increased global temperatures that change the pressure systems associated with the Arctic Oscillation, but this link is complex and underdeveloped (Guido 2011).

The major goal of this study was to determine whether recent declines in establishment observed in the Cactus Forest are occurring throughout the park, and how establishment may vary among different habitat types. We examined the effect of climate on the age-height distribution of juvenile cacti on 45 randomly-located "saguaro census" (SC) plots that were established in 1990 and last surveyed in 2010, as well as on 11 additional "historic monitoring" (HM) plots established in 1941 and 1975 and last surveyed in 2014. A secondary goal was to investigate the response of the saguaro population to the 2011 hard freeze on the 11 HM plots that were surveyed before (2010) and after (2014) the freeze event. We hypothesized that slopes would have the highest rates of establishment and survivorship due to the increased availability of rocky microclimates that shelter juveniles from environmental extremes, while foothills and bajadas will have lower rates of establishment and survivorship due to finer soil types, cold air drainage, and an isomorphic landscape.

STUDY AREA

Saguaro National Park contains two districts located on either side of the city of Tucson, Arizona (Figure 1); the western district, named the Tucson Mountain District (TMD), and the eastern district, known as Rincon Mountain District (RMD). Although saguaros occur in both districts, the habitats are quite different. TMD is a low desert mountain range, with elevations ranging from 670-1,429m, while RMD ranges in elevation from 816 to > 2,633 m. Saguaros occur through the TMD, and up to 1,550 m on south-facing slopes at RMD.

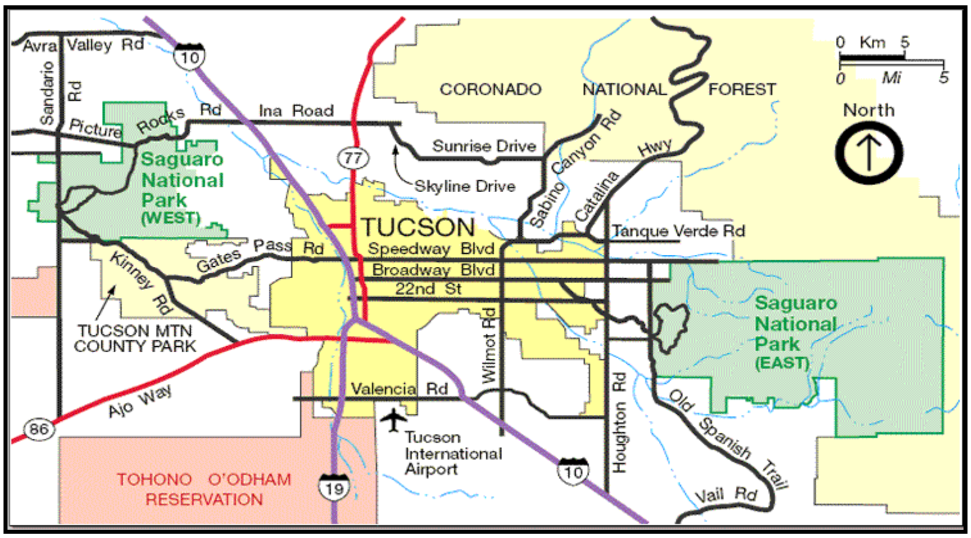
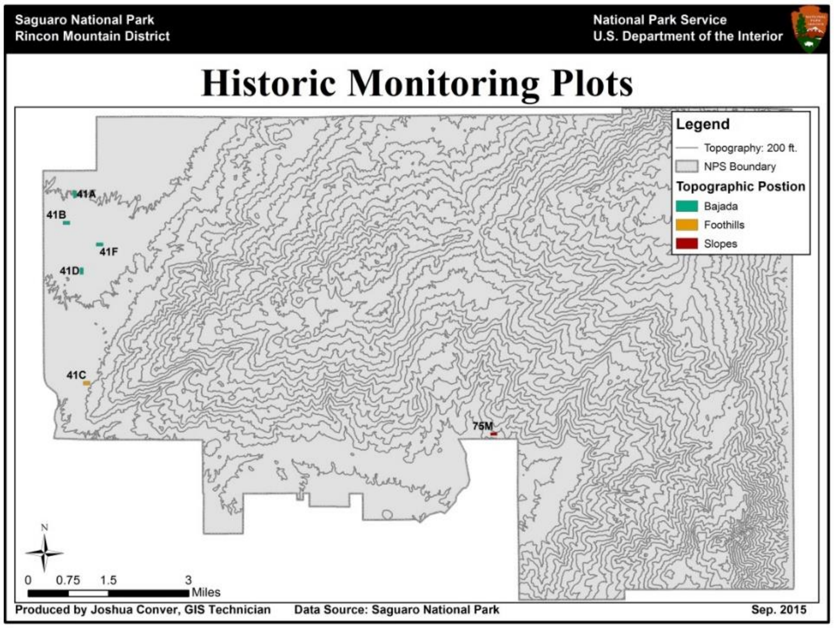


Figure 1 – Location of RMD (East district) and TMD (West district) relative to the City of Tucson.

The HM plots, each 100 x 200 meters, were used by Warren Steenbergh and Charles Lowe to support their research for the Ecology of the Saguaro series (Steenbergh and Lowe 1976, 1977, 1983). Steenbergh and Lowe (1983) re-located five existing plots in RMD that had been originally established in 1941 by Lake Gill and Paul Lightle. They established six additional plots, including several plots at TMD (Figure 2), with the goal that the 11 plots would represent the full range of saguaro habitat in the park. After Steenbergh and Lowe completed their studies, the plots went unmonitored for 27 years until Carianne Funicelli and Dale Turner (2002) re-surveyed them in 2001. SNP Resource Management crews and citizen scientists surveyed the HM plots again in 2010 (O'Brien et al. 2011) and in 2014 for this study.

The forty-five SC plots (25 plots in the RMD and 20 in the TMD; Figure 3) were established in 1990 by Dan Duriscoe and Sandra Graban in a project sponsored by the National Park Service with long-term monitoring as one goal (a second goal was to study epidermal browning). The plots, each 200 x 200 meters, were distributed randomly throughout the TMD. However, RMD contains considerable area where saguaros do not grow or occur in low number due to unfavorable environmental conditions such as high elevation, riparian vegetation, or poorly drained soils. In RMD, saguaro habitat was delineated using the park's vegetation maps, and plots were distributed using an aerially stratified random method (Duriscoe and Graban 1992).



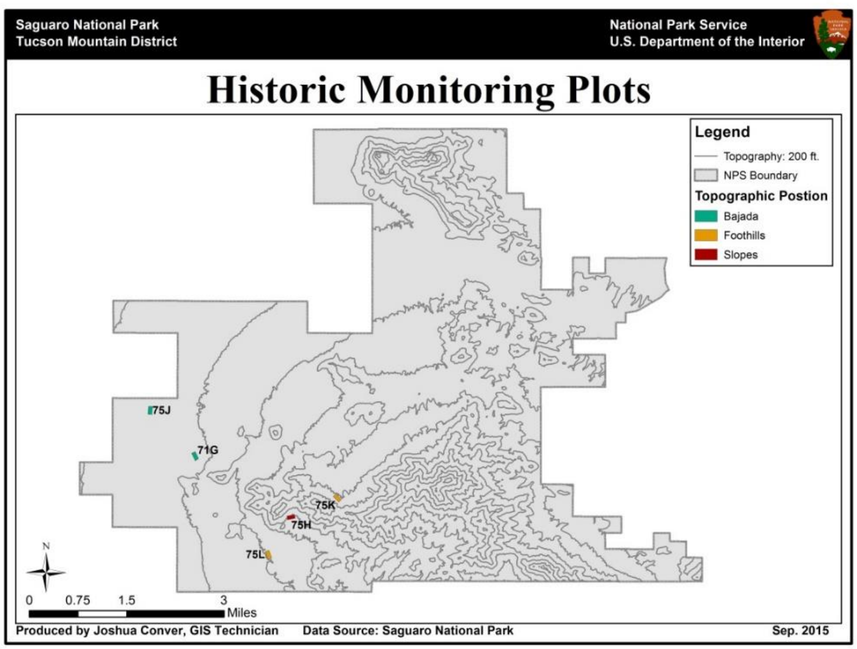
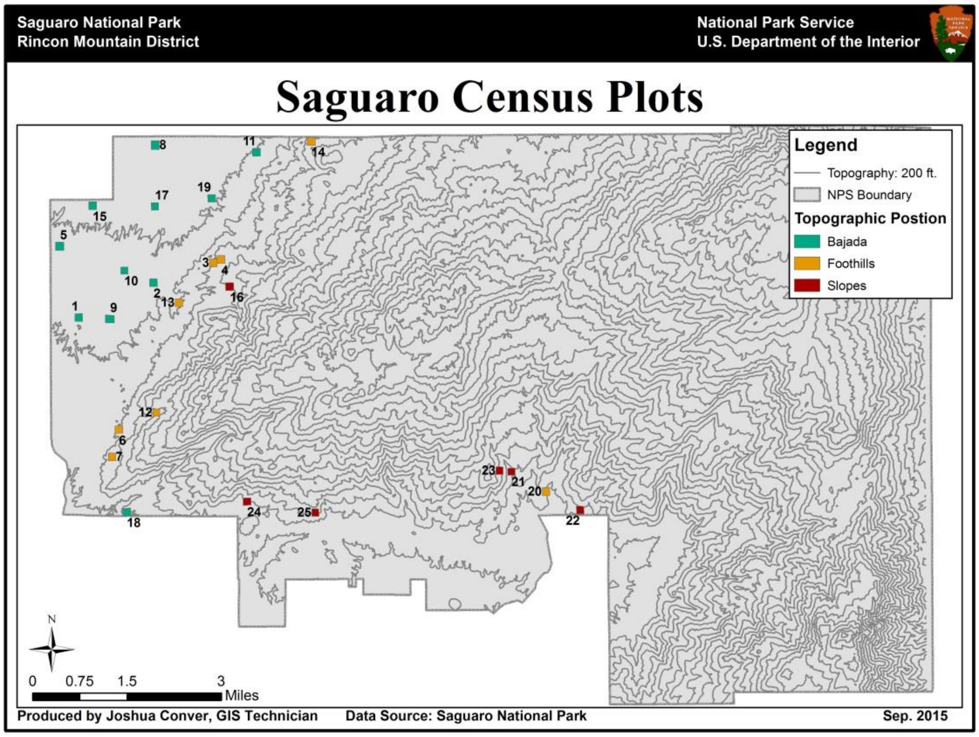


Figure 2 – Historic Monitoring (HM) plot locations in Saguaro National Park. These plots, representative of saguaro habitat in the park, were established in either 1941 or 1975, and surveyed in 2001, 2010, and 2014. All HC plots are 100 x 200 m.



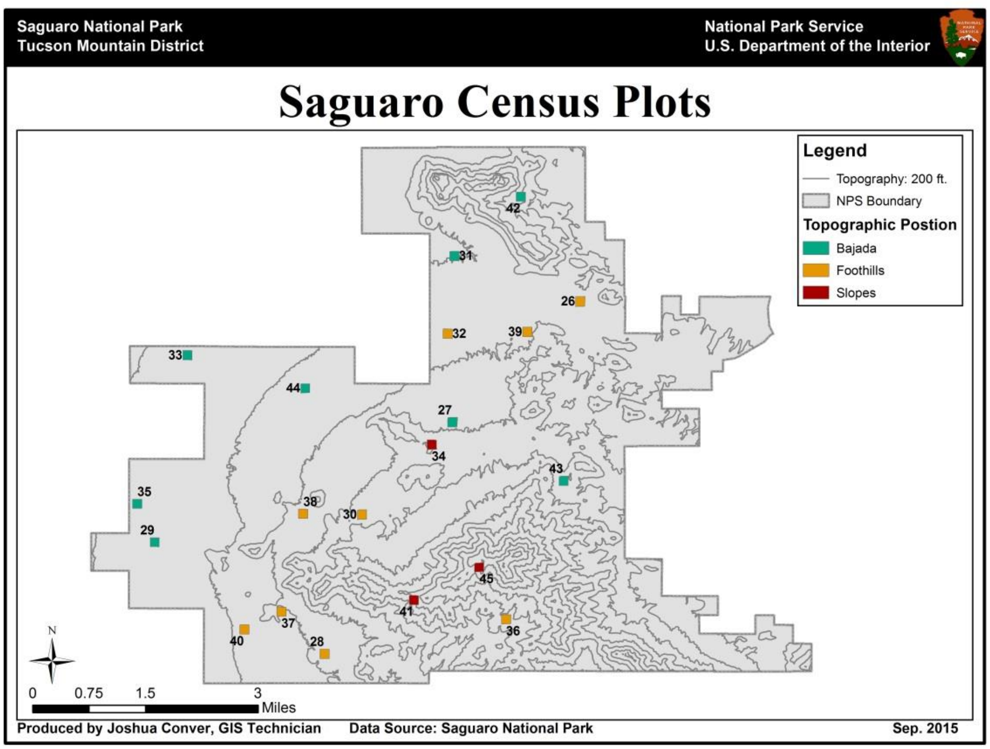


Figure 3 – Saguaro Census (SC) plot locations in Saguaro National Park. These randomly-located plots were established in 1990, and re-surveyed in 2000 and 2010. All SC plots are 200 x 200 m.

Land Types

Saguaros grow in many different habitats across SNP and climate variables may affect cacti differently due to exposure, slope, and substrate. Gill and Lightle (1941) categorized 5 of the 11 HM plots (41A, 41B, 41C, 41D, and 41F) into three categories of topographic habitat: bajada, foothill, or slope, with elevation and slope exposure as the primary criteria used for classification. Steenbergh and Lowe (1983) took the same approach when they added 6 plots in 1975. We used the habitat classifications provided in Steenbergh and Lowe (1983) for the HM plots (Table 1) and used similar criteria to determine the habitat type for SC plots. Plots were classified as bajada if they were under 1220 m at RMD or 685 m at TMD and less than 10% slope. Foothills ranged from 1220 to 1460 m at RMD and 685 to 990 m at TMD and were between 10-25% slope, and plots were in a slope habitat above 1460 m elevation for RMD or 990 m at TMD and had greater than 25% slope. According to this scheme, 17 SC plots were located in bajadas, 13 were in the foothills, and 6 were on slopes for a total of 36 plots. Not all plots were completed in 2010 due to time constraints (O'Brien et al. 2011) and we excluded incomplete plots from our analysis.

	HM Plots		**SC Plots**	
Land Type	*Plot Numbers*	*Total*	*Plot Numbers*	*Total*
RMD Bajadas	41A, 41B, 41D, 41F	4	1, 2, 5, 9, 10, 11, 15, 17, 18, and 19	10
RMD Foothills	41C	1	3, 6, 7, 8, 13, 14, and 20	7
RMD Slopes	75M	1	16, 21, 22, and 24	4
TMD Bajadas	71G, 75J, 75L	3	27, 29, 31, 33, 35, 40, and 44	7
TMD Foothills	N/A	0	26, 28, 30, 32, 38, and 39	6
TMD Slopes	75H, 75K	2	34 and 45	2

Table 1 – Plot distribution among habitat types.

Bajadas

Bajada is a term that refers to constructional alluvial deposits that have coalesced at the base of a mountain range. Bajadas are characterized by broad slopes with a gentle incline (usually less than 10°) that extend from the base of a mountain range into the basin floor. As the sediment eventually grows together, the slope may extend outward from the mountain front to a distance of several miles until the terrain becomes flat. Soils on bajadas at Saguaro National Park range from non-rocky (Figure 4) to coarse and gravelly with large embedded boulders (Steenbergh and Lowe 1983).

Figure 4 – SC plot 9, located in RMD, is a typical non-rocky bajada habitat.

Foothills

Foothills are the transition zone between the bajadas and the upper elevation slopes (Figure 5). They gradually increase in elevation at the base of a mountain range. Foothills form from the rock pediments and erosion surfaces on older basin fill. They typically border mountain ranges or high-plateau escarpments.

Figure 5 – SC plot 16, located in RMD, is an example of a foothills habitat.

Slopes
Slopes are positioned at higher elevations than the foothills and are at a steeper incline (Figure 6). There are several types of slopes: base slope, head slope, side slope, nose slope, and free face. Different slopes are formed based on the tectonic deformations that locally affect the area. Slopes are the starting point of the erosional process that forms the foothills and later the bajadas.

Figure 6 - SC plot 16, located in RMD, is an example of a slope habitat.

METHODS

Field Methods

Saguaro Census (SC) Plots

We utilized data from the 2010 surveys of the SC that have been previously published as a technical report (O'Brien et al. 2010). SC plots were surveyed during the fall, winter, and spring of 2010-2011 using a combination of Resource Management crews, interns, and citizen scientists. Crews moved systematically through the pre-flagged plots. Each area was searched twice with separate crews in an attempt to locate as many small saguaros as possible. Each surveyed saguaro was marked with a pin flag, which was removed after the survey. Height data were recorded on paper datasheets and entered directly into Excel spreadsheets managed by SNP. For further details, see O'Brien et al. (2010).

Historic Monitoring (HM) Plots

We surveyed the 11 HM plots during 2010-2011 and again from May 2014 to February 2015 using a combination of Resource Management crews, interns, and citizen scientists. The plot data, which included plot boundaries, individual saguaro locations, and heights, were downloaded onto Trimble GPS units. Crews moved systematically through the plot, following elevational contours, and used the Trimble for navigation. Each plot was surveyed twice in an attempt to locate as many small saguaros as possible. Crews marked each surveyed saguaro with a pin flag; the flags were removed after the plot was surveyed. We attempted to locate individual saguaros from previous surveys and recorded the current height, number of arms, number of holes, and noted any frost damage or mortality. Signs of frost damage included downturned or broken arms, broken tops, purpling or browning, damage to the original apex of apical branching, and/or growth constrictions (Figure 7). Additionally, we recorded the location of new saguaros not previously in the geodatabase. Data were recorded on paper datasheets and were entered directly into a geodatabase managed by SNP.

Figure 7 – Examples of frost damage on HM plots. From left to right: color darkens from green to purple on the epidermis around the areoles, a shifted apical meristem, and drooping arms and broken tops.

ANALYSIS

We addressed recent establishment by calculating the year of germination for saguaros less than 0.5 meters tall using the Steenbergh and Lowe (1983) age-height curves specific to RMD and TMD. We applied the age-height curve to the 2014 HM Plot survey and the 2010 SC survey datasets in order to determine the year of germination. Because the area surveyed differed greatly between the two datasets, we standardized our results to saguaros per hectare (Table 2). Detectability of saguaros by observers varies with age; in a similar survey conducted annually at the park, detectability was approximately 100% for saguaros >25 years old; 80% for saguaros 20 years old and 20% for saguaros 10 years old (Orum et al. 2010). However, we did not adjust our results for detectability because total numbers were relatively low.

Habitat	*2014 HM Plot Survey Area (ha)*	*2010 SC Plot Survey Area (ha)*
RMD Bajadas	8	40
RMD Foothills	2	28
RMD Slopes	2	16
TMD Bajadas	6	28
TMD Foothills	0	24
TMD Slopes	4	8

Table 2 – Area surveyed, in hectares, for HM and SC plots by habitat location.

We assessed saguaro mortality and frost damage by comparing frost damage and mortality of height classes from the 2010 HM plot survey with our 2014 findings. Every saguaro surveyed during 2010 was mapped using GPS, and some saguaros also had relic tags tied around the base from Steenbergh and Lowe's 1975 survey. We were able to identify older dead individuals that were standing or that had fallen and were decomposing but we did not find remains of all dead saguaros. The number of frost damaged saguaros were summarized for five height classes (0-1.8 m, 1.81-3.66 m, 3.67 – 5.49 m, 5.5 – 7.32 m, and >7.33 m). It was not possible to confirm the cause of mortality as freeze, and because the 2011 freeze affected the entire Tucson area, we do not have control plots for comparison.

RESULTS

ESTABLISHMENT - PARKWIDE

Recent establishment park-wide peaked at 4 saguaros per ha in 1989 but declined throughout the 1990s (Figure 8). Establishment fell to less than 0.25 saguaros per hectare by 2000 and remained at or below this level through 2007, which was the year of germination for the youngest saguaro located during our survey based on the age-height curve. The decline in saguaro establishment corresponds to a shift in climatic conditions. PDSI values for the Tucson Basin indicate that the last 30 years trended towards hot and dry conditions (Figure 8). The park-wide results reflect the decline in the number of saguaro cacti that established in all habitat types for the past three decades but there are distinct differences in the patterns of decline among habitat types.

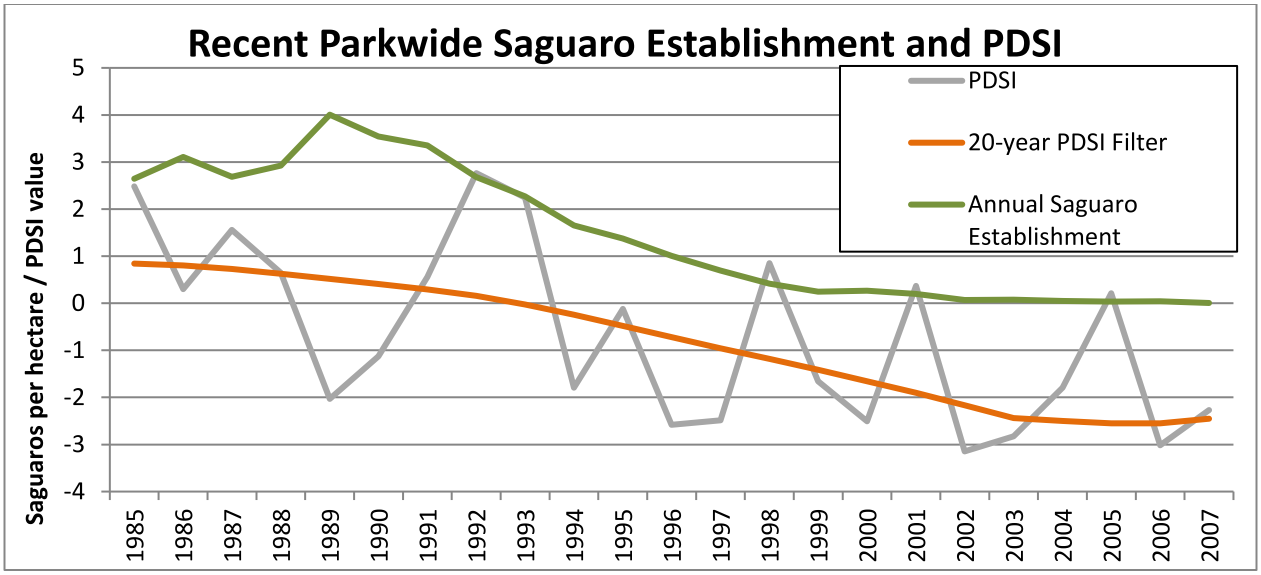


Figure 8 – Estimated year of establishment for saguaros in SNP across all habitats since 1985 on HM and SC Plots. Negative PDSI values indicate drier conditions and positive values indicate wetter conditions.

ESTABLISHMENT BY HABITAT TYPE

Bajada. Recruitment rates in the bajada were the lowest of the three general habitat types, and the decline in establishment is most pronounced in the bajada; we detected little to no establishment of new saguaros in this habitat type at either district for the past 15 years. The results show a recruitment pulse during the mid to late 1980s in both districts of SNP (Figure 9). Recruitment rates reached a peak in 1986 at TMD and 1989 at RMD but declined to near zero by the late 1990s.

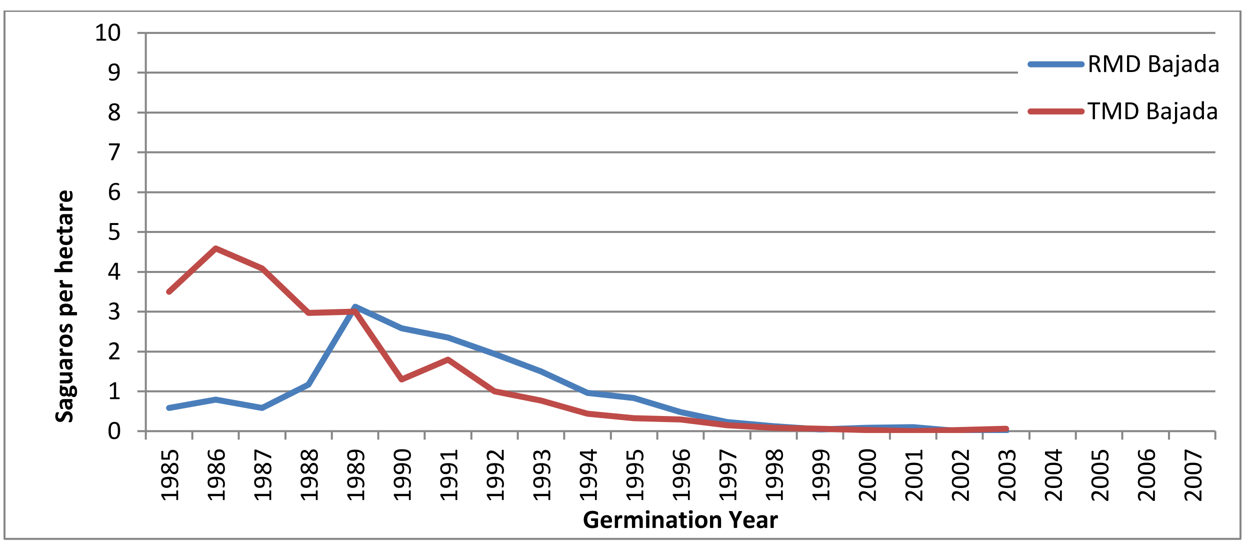


Figure 9 – Estimated year of germination for saguaros under 0.5 meters in the TMD and RMD bajada.

Foothills. The establishment rates in the foothills habitat were higher than in the bajada and reached peak establishment in the same years as the bajada habitat but declined to near zero by 1999 (Figure 10). More juveniles established in the TMD foothills over the last 30 years than any other habitat type in either district, and we located several juveniles ranging from 11 to 13 years old in the RMD foothills. None of the 11 HM plots are located in the TMD foothills, so the TMD results show the 2010 SC plot data only.

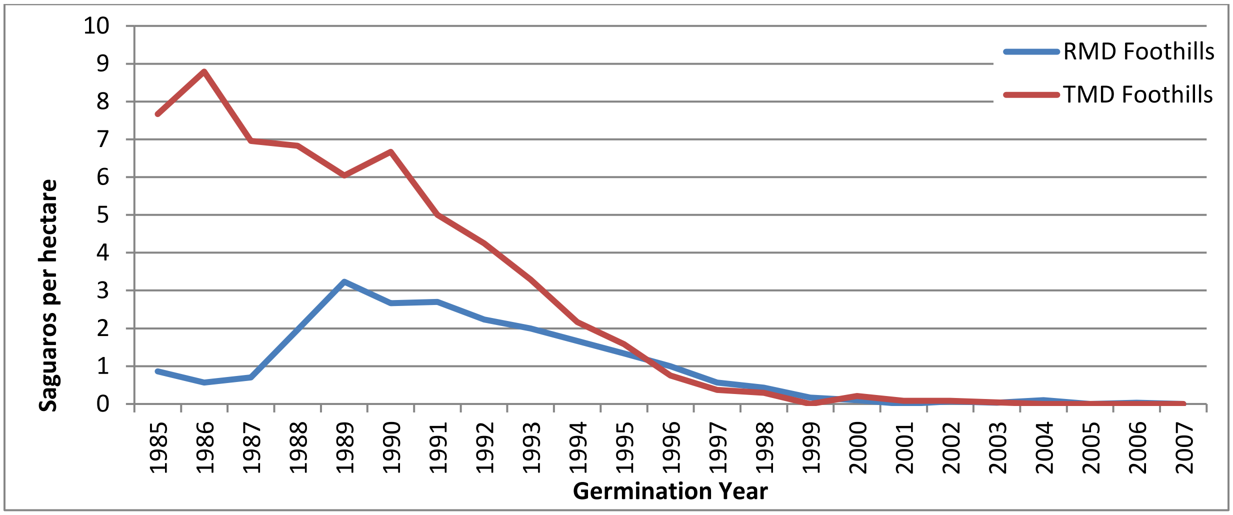


Figure 10 - Estimated year of germination for saguaros under 0.5 meters in the TMD and RMD foothills.

Slopes. Establishment on the slopes varied throughout the late 1980s and early 1990s, but establishment slowed at TMD several years before RMD (Figure 11). The RMD slopes saw a decline in the annual number of established saguaros after 1997, but more juveniles established in this habitat at RMD during 2001-2007 than in any other general habitat type across both districts, and establishment has continued to occur since 2007.

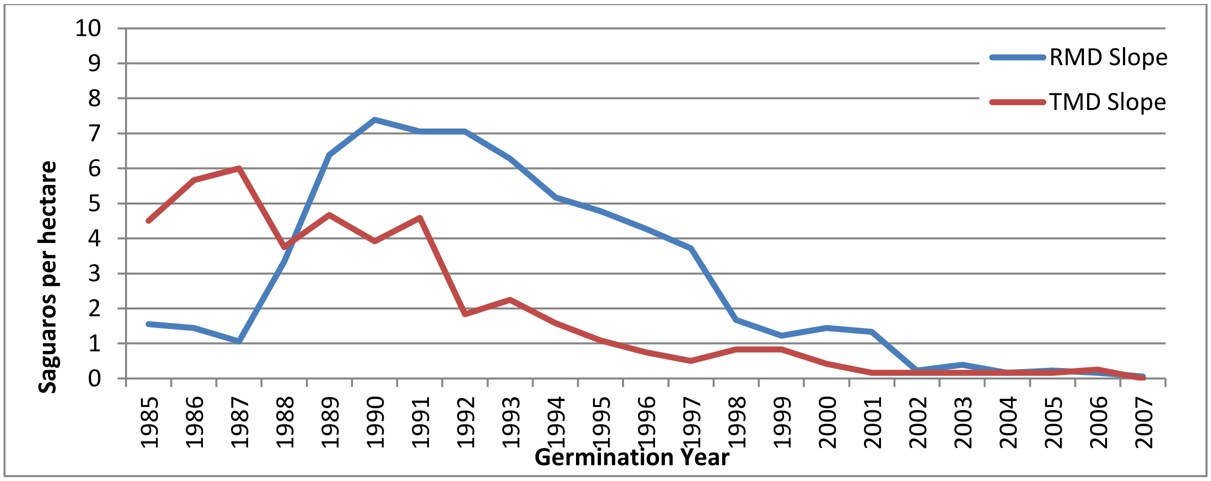


Figure 11 - Estimated year of germination for saguaros under 0.5 meters in the TMD and RMD slopes.

DISTRICT RESULTS

Establishment at TMD surpassed establishment at RMD from 1985 to 1991, but RMD exceeded TMD from 1992 to 2005 (Figure 12). TMD establishment declined steadily from the peak year in 1986, but RMD establishment was low in the early to mid-1980s and surged from 1989 to 1992. RMD establishment fell steadily from 1993 to 2007.

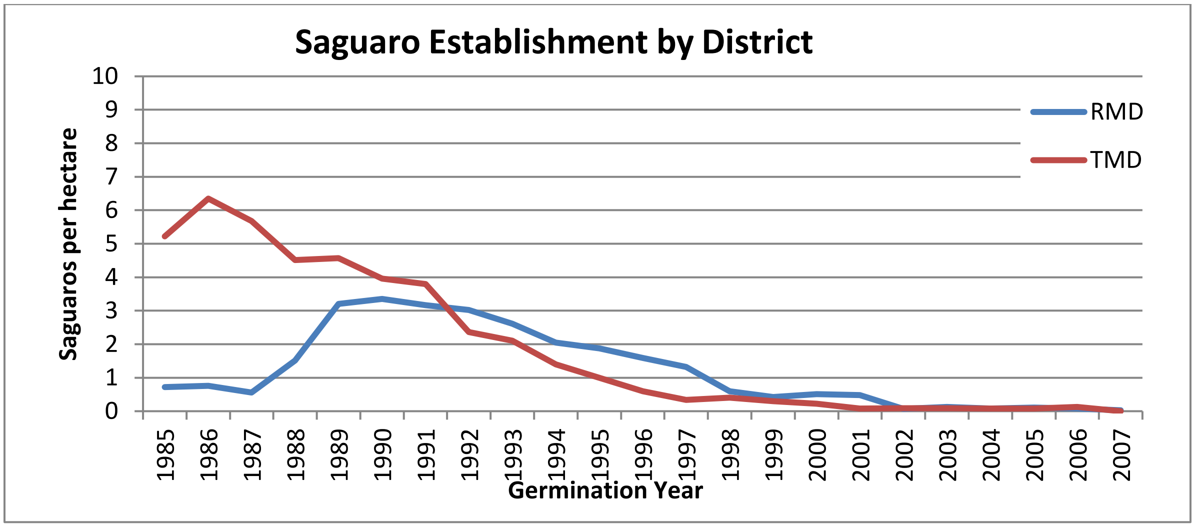


Figure 12 – Recent estimated establishment year by district.

Freeze Effects and Mortality

Our survey results on HM plots indicate that the freeze damaged 6.23% of the saguaro population park-wide (Figure 13). The effects of freezing temperatures affected the habitat types and districts differently. We detected little to no frost damage in the RMD bajada and foothills habitat; plots 41A, 41B, and 41F showed no signs of frost damage, and less that 2% of saguaros were affected on plot 41D. Less than 1% of the saguaros in the RMD foothill habitat showed signs of frost damage. In contrast, the RMD slope plot, 75M, was affected most by the freeze with 26.3% of the saguaros showing freeze damage. 4.5% of all saguaros surveyed at RMD presented frost damage.

At TMD, 8.27% of saguaros showed signs of damage. Nearly 7% of saguaros in the TMD bajada presented indications of freeze damage, in contrast to the RMD bajada (Figure 13). Since no HM plots were located in the TMD foothills, we do not have a result for that habitat type. Similar to RMD, more saguaros were affected by freeze on the TMD slopes (10.3%) than in the TMD bajada.

Frost damage to saguaros was related to height as well as habitat type and district. The chance that a saguaro was damaged due to freezing temperatures increased with height. Older saguaros were affected by freeze at a higher rate than younger saguaros (Figure 14). 28.57% of saguaros taller than 7.33 meters, or older than 85 years, displayed some damage, while 5.49% of saguaros under 1.8 meters, or younger than 36 years, were damaged.

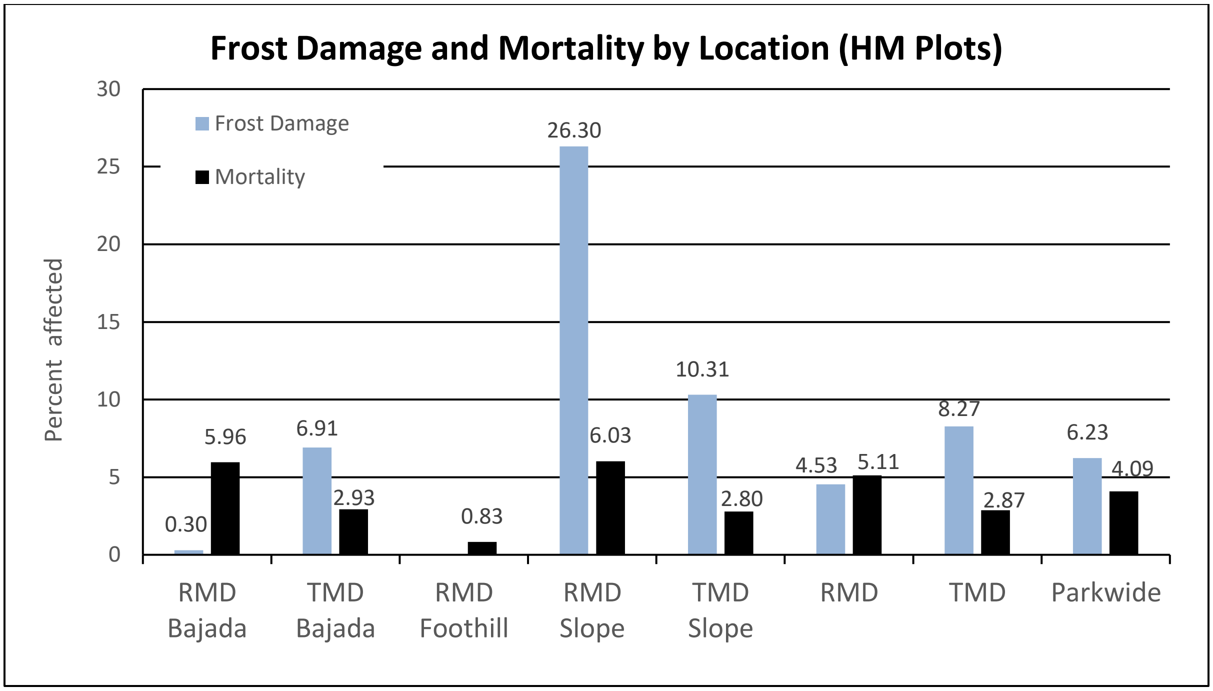


Figure 13 – Frost damage and mortality on HM plots by habitat type, district, and parkwide.

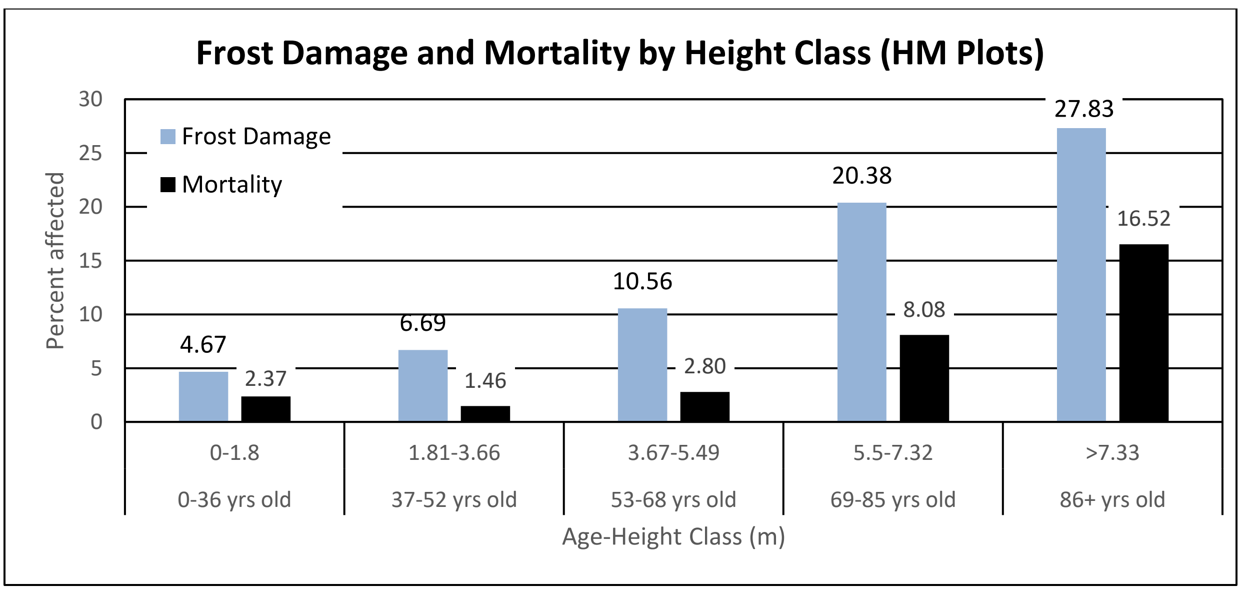


Figure 14 – Percent of saguaros that died or showed frost damage on HM plots between 2010 and 2014 by age-height class, both districts combined.

Four percent of the population on the HM plots died between 2010 and 2014, although the mortality result includes all possible causes of death (Figure 13). Mortality rates were relatively consistent across all habitats within a district; 5.96% of saguaros in the RMD bajada died between 2010 and 2014, while 6.03% died on the RMD slopes. The RMD foothills plot experienced less than 1% mortality. TMD had a lower mortality rate than RMD in the bajada and slopes (2.93% and 2.8% respectively).

Like frost damage, mortality was related to height and age. Mortality rates between 2010 and 2014 were less than 3% for saguaros less than 5.49 meters (Figure 14). The mortality rate was more than twice that (8.3%) for saguaros 5.5 to 7.32 meters tall, and nearly 17% for saguaros greater than 7.33 meters tall. For comparison, independent research conducted in the RMD bajada by a University of Arizona scientist found that frost-driven mortality rates for saguaros 80 years old and younger was less than 2% but approximately 36% for saguaros >80 years old. (Tom Orum, pers. communication).

DISCUSSION

Establishment Park-Wide

After many years of decline, especially in the Cactus Forest area of the Rincon Mountain District where most past studies have occurred, saguaro populations throughout Saguaro National Park surged during the 1960s, 1970s, and 1980s (Turner 1991, Orum 2010, Pierson et al. 2013). This period of high recruitment ended in the Cactus Forest in the early 1990s (Orum et al. 2010; Pierson et al. 2013). Our study confirms that the post-1980s decrease has occurred throughout the park, in both districts and in all habitats, although the habitats vary in the severity of the decrease. Especially since the mid-1990s, recruitment has been less than 15% of what it was in the late 1980s at RMD, and less than 7% of its peak in the mid-1980s in TMD. The >20 year period of declining establishment has coincided with an extended drought in the desert Southwest, with high negative PDSI values that indicate drier conditions (Fig. 8), as well as in Saguaro National Park.

Many studies of saguaros have demonstrated that saguaro recruitment is episodic, which is not unusual in a long-lived species adapted to a highly variable arid environment. Drezner and Balling (2008) have used this variable pattern of establishment, and its dependence on climatic factors such as precipitation and temperature, to suggest that saguaro population structure is related to global drivers of climate such as the El Nino Southern Oscillation (ENSO) and volcanism. The current period of decreased establishment provides perspective on the long period of low recruitment of saguaros in the Rincon Mountain District of the park that occurred during the first six decades of the 20th century. While there is no doubt that anthropogenic factors such as removal of nurse trees and heavy cattle grazing were important factors in this decline, climate certainly also played a role, both in its interaction with these factors and as a driving force, particularly during severe droughts in the 1930s and 1950s.

It is important to point out that a limit to our study is that we used generalized growth rates to estimate year of germination (Figures 8-12). These rates are generalizations only, based on average rainfall for the two districts during the periods when Steenbergh and Lowe conducted their studies. During that period, TMD averaged 10.27 inches/year, and RMD averaged 12.30 inches/year (Steenbergh and Lowe 1983). Growth of individual saguaros is highly dependent on the amount of summer rains, which can vary significantly from year to year and over a small geographic area. Nevertheless, general growth rates combined with saguaro height measurements have been shown to be a powerful tool for understanding general patterns of saguaro recruitment, especially where large sample sizes are available.

Establishment by Habitat Type

While this study focused on recent recruitment, the patterns of establishment across all habitats also change over time. For context, annual saguaro establishment rates by habitat type and district for all 17,039 saguaros measured in 2010 on the SC plots are presented in figure 15. The results indicate that establishment rates vary greatly among habitat types and reinforce the episodic nature of recruitment and establishment. Although establishment of saguaros declined throughout the park since the mid-1990s, we observed striking differences in establishment among districts and habitat types. In general, the decline in establishment is most pronounced in the bajada, is intermediate in the foothills, and is least pronounced on slopes. TMD experienced higher recruitment than RMD in the mid-1980s, while RMD generally experienced higher recruitment later in the decade into the 1990s.

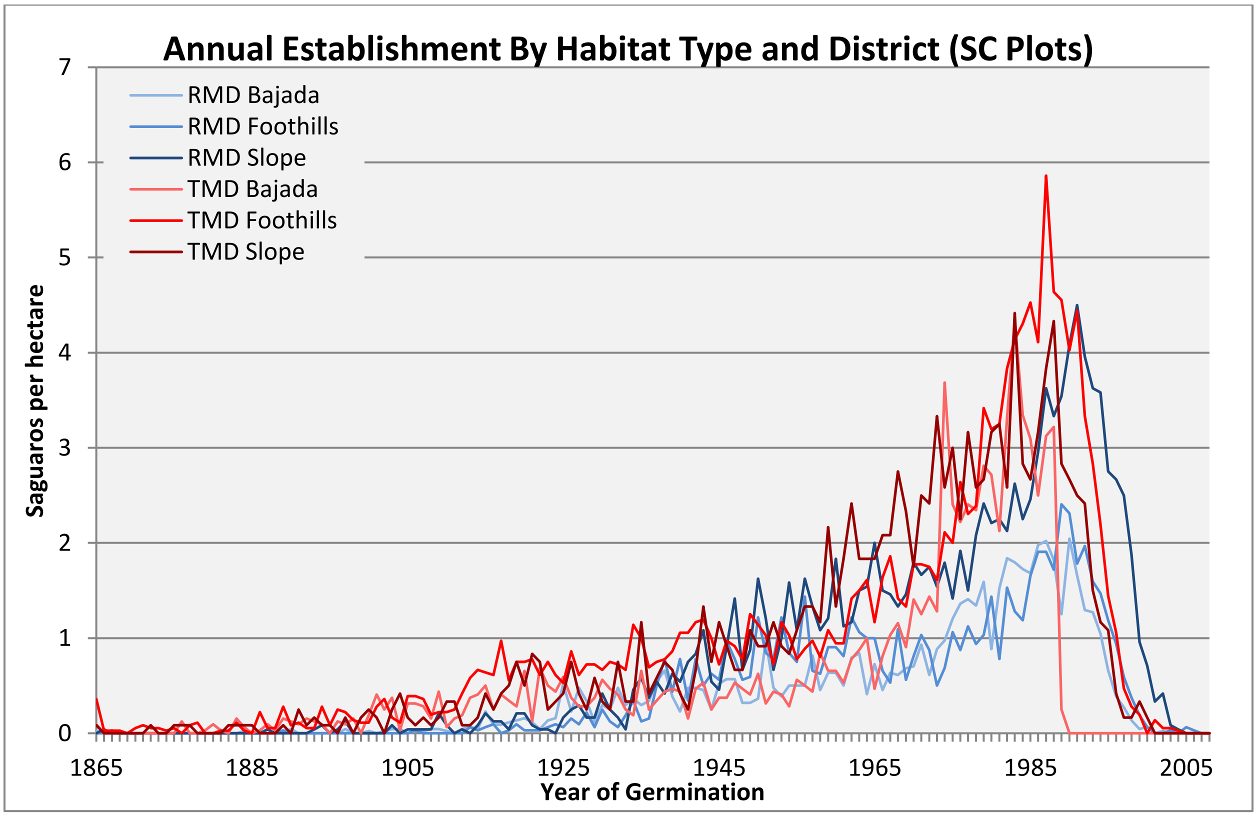


Figure 15 – 140 years of saguaro establishment by district and habitat type. Red colors correspond to TMD and blue colors to RMD. Shades of color increase from light to dark with increasing elevation.

Bajadas. The decline in establishment was significant in the bajada after the early 1990s, and we detected little to no establishment of new saguaros in the bajadas at either district for the past 15 years (Figure 9). The bajada habitat has fewer numbers of saguaros overall, which hinders reproductive potential. It is likely that the low density of mature, seed-producing cacti, unfavorable soil types, and fewer available microhabitats narrows the range of climactic conditions that regulate regeneration. The bajada is the most sensitive habitat to the limiting factors that govern saguaro establishment, and establishment seems to occur only when there is a suite of favorable climatic conditions that occur over several years. Although clearly we have experienced two decades where favorable climatic conditions have not occurred on this habitat, it remains to be seen whether this is a short- or long-term concern. Saguaros are certainly extremely resilient to extended drought, and previous studies have suggested that recruitment of saguaros on the bajada has always been more episodic than in in other areas of the park (Steenbergh and Lowe 1977; O'Brien et al. 2010).

Establishment in the TMD bajada occurs at a higher rate than at RMD. The different in the situation of the bajada plots between the two districts explains some of the variation. The TMD bajada plots are mostly located on the western side of the Tucson Mountains in open Sonoran Desert and tend to be further from the foothills and slopes than the bajada plots at RMD. This allows more cold air to pool on the TMD bajada and accounts for the large number of frost damaged juveniles in the district (Figure 8). Soil type in the bajada also differs between the two districts and may play a role in regulating saguaro presence. Soils with high clay, silt, or sand content prevent seedling establishment and increase seedling mortality by retaining water and rotting young saguaros (Steenbergh and Lowe 1977). The bajada habitat has fewer numbers of saguaros overall, which hinders reproductive potential and the results indicate that it is the most sensitive habitat to the limiting factors that govern saguaro establishment. The current population is not capable of sustaining itself outside of a suite of favorable climactic conditions that occur over several years.

Foothills. At TMD, favorable climatic conditions during the late 1980s and early 1990s (Figure 9) led to increased recruitment compared to bajada populations. More juvenile saguaros established in the TMD foothills during that time period than for any habitat across either district. Establishment on the RMD foothills plots was not as high as the equivalent habitat at TMD or other habitats at RMD. The early 1990s recruitment pulse was not as strong and recruitment peaked much later. This result suggests that the establishment of new saguaros in this habitat depends on a different envelope of climatic conditions than the habitats above or below it in terms of elevation.

Slopes. Our results suggest that climate may not be as influential on the slopes compared to other habitat types park-wide, perhaps because rock features may create more local microhabitats that collect moisture and protect saguaros from temperature extremes. Establishment in the TMD slopes was lower than the foothills habitat but higher than the bajada. Constant establishment is occurring, however, albeit in very low numbers. However, saguaro establishment occurs at a higher rate in RMD. Although establishment is much less in slope areas than in the 1980s, this is the only habitat where meaningful establishment has occurred over the past 15 years. As a result, the slopes may be the most important habitat for saguaro establishment. If new saguaros can establish in this habitat outside of the optimal environmental conditions, then upslope saguaros become a vital source of seed for downslope episodic recruitment in the favorable years.

Freeze Effects and Mortality

Our results show that oldest and the youngest demographics are the most susceptible to the effects of a freeze and that site and situation are strong influences in survival rates after a freeze event. This result conforms to previous research (Steenbergh and Lowe 1976; Orum 2010). 20 to 38% of saguaros in the two oldest age-height classes experienced frost damage, which has serious repercussions for reproductive potential. Damage or mortality to the oldest saguaros may reduce the ability of the species as a whole to propagate as arms fail to produce fruit in the future or fall off completely. Dead cells on the outside of the saguaro reduce its overall health and increase the likelihood of mortality. Despite the high percentage of damage to the oldest age-height classes, we found more saguaros in these two height classes on the HM plots than in 2011. The youngest age-height class had the highest number of affected saguaros (Figure 9), but the saguaro population as a whole is skewed towards this class (Figure 8). Frost damage to juvenile saguaros can slow growth over time and lengthen the time before saguaros are able to produce fruit and seeds.

We could not determine the cause of mortality during our survey, but the mortality results can provide insight into how the freeze affected the population in different habitats and in different districts. RMD plots as a group had higher levels of mortality than TMD, although TMD plots averaged a higher number of damaged saguaros (Table 2). This could indicate that the freeze was more severe at RMD than at TMD.

In terms of habitat type, 5.06% of saguaros in the bajada died in the four years between surveys, but the habitat had the lowest frost damage rate at 3.37% (Table 2). This could be an indication that cold air drainage from the foothills and slopes settles in the bajada and kills saguaros rather than injuring them, but it could also be a response to drought and water stress. Regardless of the cause, saguaros either died or survived with little middle ground. The slope habitat had the highest damage rate and the median mortality rate at 18.01% and 3.58% respectively. Both HM plots on slopes, 75H and 75M, have south-facing aspects, yet plot 75M had the second-highest mortality rate. The foothills HM plots showed the lowest mortality and only 4.1% of saguaros in the habitat showed the signs of freeze damage. These plots have the unique situation of being lower in elevation than slope habitats, so minimum temperatures should be higher than on the slope habitats above and cold air should be funneled downhill by the moderate slope.

Microhabitats are strong influences on saguaro establishment and can mitigate the pressures of climate on establishment (Steenbergh and Lowe 1983). Large rocks on the foothills and slopes retain the daytime heat and radiate warmth through the freezing nights, which can keep established juvenile saguaros alive. The RMD slopes show this effect; despite high damage rates from freeze, the slope habitat was the only RMD habitat to have a net increase in the number of saguaros from 2010 to 2014 (Table 2) and the 2014 HM survey found the most juvenile saguaros that had germinated after the year 2000 in this habitat. Slopes are capable of supporting some recruitment even though current climatic conditions do not support a mass recruitment event across the species' range.

CONCLUSION

This study underscores the need to study establishment among the different saguaro habitats at decadal intervals. The saguaro population as a whole is not in danger of extirpation from SNP, but the decline in establishment since the early 1990s has been unprecedented compared to the previous 7 or more decades. The current period of decline is clearly not related to local anthropogenic factors such as wood-cutting and cattle ranching, which have been eliminated in the park, suggesting that the prolonged drought and higher local temperatures may be responsible. The species may struggle to persist within certain habitats in the future given a changing climate that predicts warmer temperatures and an increased frequency of drought.

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