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Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert

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ABSTRACT

Ten saguaro (*Carnegiea gigantea*) populations in the northern Sonoran Desert were monitored from 1959 to 2005 to discriminate how climate influences plant growth, abundance, reproductive potential, survivorship, age structure and regeneration trends. Thousands of saguaros were measured to determine site-specific growth rates and survivorship through time. Observed growth rates were used to predict the ages of saguaros and reconstruct local and regional regeneration patterns back to the late 18th century. Both growth rates and degree of branching generally tracked temperature and moisture gradients. Site-specific age–height models explained 89–97% of variance in observed ages, with a slope of nearly one. Regeneration was more consistent at sites in the western (hotter/drier) than eastern (cooler/wetter) sites, which exhibited clear multidecadal variability in regeneration rates. Averaged across the region, saguaro regeneration rates were highest from 1780 to 1860, coincident with wet conditions and high *Pinus ponderosa* recruitment in the highlands. Milder and wetter winters and protection from livestock grazing likely promoted late 20th century regeneration surges at some sites. Predictions of saguaro population dynamics in the 21st century likely will be confounded by the saguaro's episodic and asynchronous regeneration, continued urbanization, ongoing grass invasions and associated wildfires, and changing climate.

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1. Introduction

The giant saguaro (*Carnegiea gigantea* [Engelm.] Britton & Rose) is a large, multi-branching columnar cactus found in the Sonoran Desert throughout much of southern Arizona, USA and western Sonora, Mexico (Turner et al., 1995). Like many woody plants of the Sonoran Desert, it is long lived (average life-span of 100–175 years) and reproduces episodically. Successful recruitment and survival of many long-lived desert species are associated with favorable climatic and microhabitat conditions including sufficient moisture, mild winters, presence of nurse plants, protection from grazing, and other biotic factors (Bowers, 1994; Bowers and Pierson, 2001; Bowers et al., 1995; Brum, 1973; Butterfield et al., 2010; Drezner and Lazarus, 2008; Goldberg and Turner, 1986; McAuliffe, 1984, 1988, 1990; Parker, 1993; Shreve, 1917; Steenbergh and Lowe, 1977, 1983; Turner, 1990). Episodic recruitment in response to the temporal variability in these conditions yields substantial fluctuations in population size and age structure on decadal or longer time scales (Godinez-Alvarez et al., 2003; Parker, 1993; Pierson and Turner, 1998; Turner, 1990, 1992). These abiotic and biotic factors operate at a range of spatial scales and may influence spatial variability in abundance and age structure (Godinez-Alvarez et al., 2003; Steenbergh and Lowe, 1983). An understanding of the long-term dynamics of populations at the local and regional scale is needed to accurately forecast regeneration trends among long-lived, episodically reproducing species. This is especially challenging where the timing between significant recruitment events approaches the human lifespan (Pierson and Turner, 1998).

Analysis of the age structure of saguaro populations, combined with knowledge of age-specific survivorship, has been used to infer past regeneration trends, extending observations to the establishment date of the oldest individuals (Brum, 1973; Drezner, 2003a; Jordan and Nobel, 1982; Parker, 1993; Pierson and Turner, 1998; Steenbergh and Lowe, 1983; Turner, 1990, 1992). The relationship between annual growth and plant size in columnar cacti is predictable, and measurements of plant heights over several years can be used to estimate growth rates, ages and establishment dates for individual plants (Shreve, 1910).

In this report, we summarize findings from a long-term study of permanent plots established at ten sites across the northern

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portion of the saguaro's distributional range in Arizona, USA and Sonora, Mexico. The ten permanent plots were established between 1959 and 1964, partly in response to growing anxiety over increasing saguaro mortality and lack of recruitment at Saguaro National Park and elsewhere (Alcorn and May, 1962; Niering et al., 1963; Shreve, 1910). The 10 sites are located along regional gradients in temperature and precipitation, which limit saguaro abundances (Niering et al., 1963; Shreve, 1911; Steenbergh and Lowe, 1977; Turner et al., 1995). The goal was to use repeated observations of saguaro age structure at multiple sites over nearly 50 years (1959–2005) to understand saguaro population dynamics across its geographical range.

2. Materials and methods

2.1. Study sites

Permanent plots were established at ten sites across the northern portion of the saguaro's distributional range in Arizona, USA and Sonora, Mexico (Fig. 1). Six of the sites are located in the Tucson area of southern Arizona, where saguaro populations reach high densities across the eastern edge of the saguaro distribution. Four of the sites are near the western and dry limits of saguaro in the western Sonoran Desert (Fig. 1). The six Tucson area populations are Saguaro National Park East (SNPE) near the western base of the Rincon Mountains; Redington (REDI), 55 km northeast of Tucson in the San Pedro River valley; Sabino Canyon (SABI) on the south slope of the Santa Catalina Mountains; Saguaro National Park West (SNPW) near the western base of the Tucson Mountains; Tumamoc Hill (TUMA) an eastern outlier of the Tucson Mountains; and Silverbell (SILV) on the east side of the Silverbell Mountains. The Redington site (REDI) is the coldest site in the Tucson area, and experiences frequent frosts as a result of its proximity to the San Pedro River valley, which funnels cold air drainage. The four western Sonoran Desert populations include Harquahala (HARQ) at the south base of the Harquahala Mountains; Ventana (VENT) at the southern base of the Ventana Mountains on the Tohono O'odham Reservation; Sonoyta (SONO) 10 km southeast of Sonoyta, Sonora, Mexico by Mexico Highway 2; and MacDougal Crater (MACD) on the floor of MacDougal Crater in the Sierra del Pinacate Reserve, Sonora, Mexico. At these four sites, saguaros are limited primarily to habitats that compensate for lower availability of summer precipitation such as mountain slopes, drainages and runnels, or within volcanic crater basins.

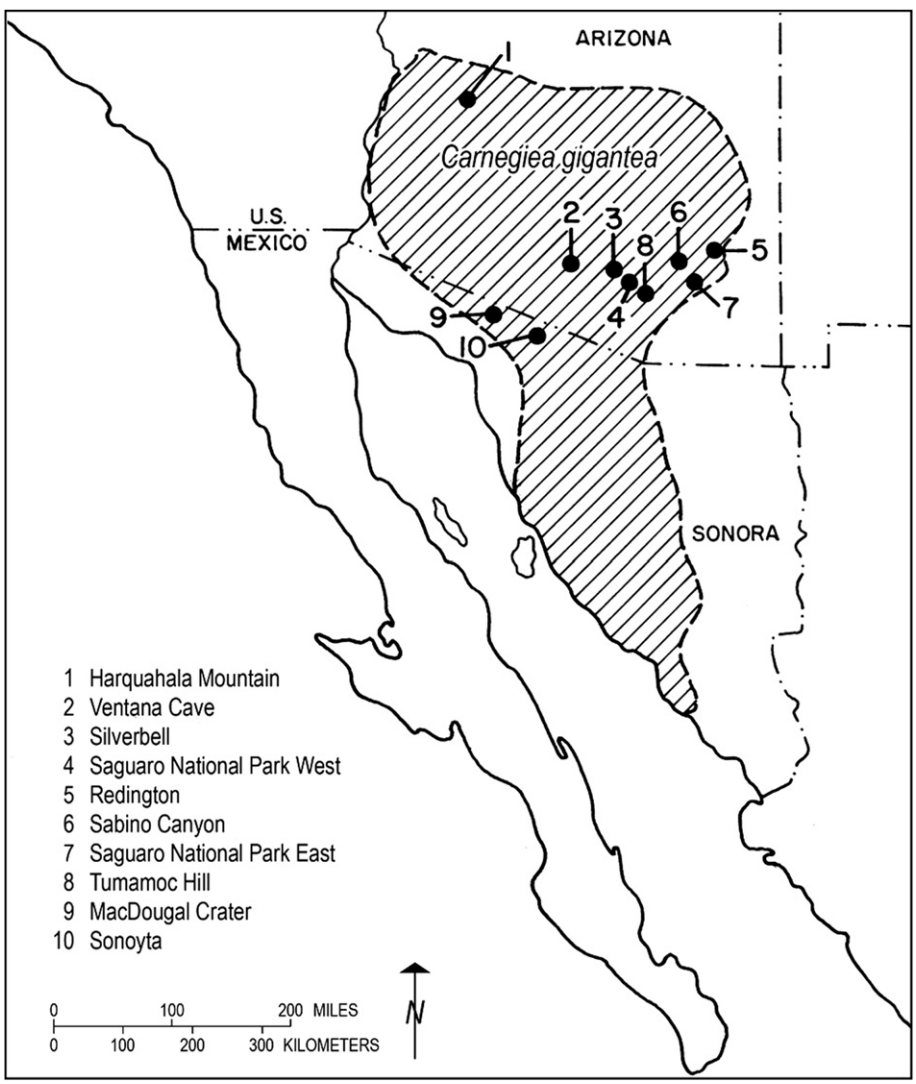

Fig. 1. Map of the saguaro plots used in this study. The locations of ten sites containing permanent plots established between 1959 and 1963 are indicated by circles. The shaded area on the map shows the approximate range of saguaros.

The history of livestock grazing and other human impacts varies across the ten sites. MACD has been continuously protected from livestock and other human impacts. SNPE was grazed by cattle from the late 1870's until 1958 and extensive harvesting of *Parkinsonia* and *Prosopis* for charcoal began just before the start of the 20th Century (Clemensen, 1987). SABI, SNPW and TUMA have been free of livestock since 1961, 1929, and 1907, respectively. Grazing continues today at REDI, SILV, HARQ, VENT, and SONO.

Selecting a plot's location was based on several criteria. Because repeated measurements at each site were the goal, protected areas remote enough to avoid human disturbance were balanced against reasonable access. Locations also were chosen where saguaros occur in high density. More often than not, plots spanned different topoedaphic conditions from rocky slope to piedmont. The study plots at each of the sites (except TUMA) range in size from 0.75 to 4.65 ha, depending on saguaro density at the site. Plot size was adjusted so that the number of saguaros included in the initial census exceeded 125. Additional site information for all of the plots is given in Table 1; vegetation descriptions, including coverage of woody perennials and potential nurse plants, are provided in the Supplementary Online Material (Tables S4 and S5).

Some of the vegetation changes in the plots at MACD (Turner, 1990), SNPE and SNPW (Turner, 1992), TUMA (Pierson and Turner, 1998) have been reported previously. The objectives of the TUMA study were significantly different than for the other nine sites. At TUMA, four plots, each approximately 10 ha in size, were established on north, south, east, and west-facing slopes of the hill within a larger area first mapped in 1908 (Pierson and Turner, 1998; Spalding, 1909). Subsequently, TUMA was censused three times over a 30-year period (1964, 1970, and 1993), whereas the other 9 sites were censused over a 46-year period (Pierson and Turner, 1998). These data are included to augment and inform the regional study.

2.2. Field censuses

Ten permanent plots were established between 1959 and 1964, (Fig. 1, Table 1). Every saguaro was assigned a unique number and mapped using a surveyor's transit. Height (from base to top of the main stem), general condition (type and severity of injuries), and number of branches on each saguaro also were determined during each census. On all visits following the initial one, newly established plants were located and numbered on plot maps, and deaths of previously censused plants were noted (Table S1). Presence of flowers and fruits was noted when visits were made during the appropriate seasons. For a few censuses, only mortality of previously existing plants and establishment of new plants were noted. Height measurements generally were taken at each site on the first and last three census dates (Table 1). Because saguaros complete their annual growth surges in August or September of a given year (Steenbergh and Lowe, 1977), heights measured early in the next calendar year must be correctly assigned to the previous year. Dates presented in Table 1 reflect this adjustment. Heights of all saguaros >2 m were determined either by direct measurement using a telescoping fiberglass rod or trigonometrically from transit data; heights of smaller saguaros were measured directly.

2.3. Saguaro age determination

Saguaro age was estimated from the nonlinear relationship between growth rate and height (Pierson and Turner, 1998). Briefly, growth rates for all saguaros in each plot were determined from the difference in their height measurements between consecutive census dates. For each census interval, the average height and average annual growth rate during that census interval were calculated for each plant, and then all data were combined into 0.5-m height classes. Data from decapitated, leaning, or severely injured plants were not used. At TUMA for this study, data for all saguaros (e.g. within north, south, east, and west plots) were pooled to produce a single growth rate–height relationship for the site. Plot-specific growth rates were published previously (Pierson and Turner, 1998).

A cubic smoothing spline was used to fit a curve to the average height and average annual growth rate data for each plot, as described previously (Pierson and Turner, 1998). Only those height classes that contained at least six observations were used to make the spline. For all plots, it was necessary to pool data from several census intervals to satisfy this contingency. The use of multiple measurements of the same saguaros introduces some pseudo-replication, but could not be avoided. Census dates on which height measurements were used to calculate growth rates are indicated in Table 1. For the less-represented larger height classes, the observations were pooled into 1-m classes. The relationship between age and size was determined by integrating the inverse of

Table 1
Location and climate information for the ten permanent study plots. Table 1 gives site abbreviation, plot size (ha), location (latitude, longitude in degrees and minutes), elevation (m), and estimated annual precipitation (mm) and slope aspect (steeply N, S, E, W, or All aspects; or gently sloping gN, gS, gE, gW; or no slope ns). Precipitation data are from 1:500,000 map, "Arizona Normal Annual Precipitation 1931–1960". At each census for which a date is indicated, demographic data (number of new individuals, number of recently dead individuals) were collected. At some censuses, the heights of all saguaros were measured (designated by an 'h') and used for the calculation of annual growth rates (designated by an 'h^*').

Site	Abbrev.	Size	Location	Elev.	Aspt.	Ppn. (mm)	Census 1^{h*}	Census 2^{h*}	Census 3^{h}	Census 4	Census 5	Census 6^{h*}	Census 7^{h*}	Census 8^{h}
Redington	REDI	0.75	32 27 N, 110 30 W	915	S	335	1960	1965	1973	1979		1988		2003
Saguaro N. P. East	SNPE	3.72	32 12 N, 110 44 W	880	ns	340	1960	1964	1973	1979	1982	1988	1994	2001
Sabino Canyon	SABI	0.82	32 19 N, 110 49 W	880	SE	380	1960	1964	1972	1979		1988		2003
Tumamoc Hill	TUMA	41.7	32 13 N, 111 05 W	824	All	325	1964		1970				1993	
Saguaro N. P. West	SNPW	1.90	32 16 N, 111 13 W	715	gW	300	1961	1964	1972	1979	1982	1988		2001
Silverbell	SILV	1.74	32 23 N, 111 27 W	715	gE	305	1961	1964	1972	1979	1982	1988		2001
Harquahala	HARQ	3.72	33 44 N, 113 29 W	580	ns	205	1960	1964	1973	1979			1991	2005
Ventana	VENT	0.93	32 23 N, 112 14 W	700	S	240	1959	1964	1972	1979			1993	2005
Sonoyta, Sonora	SONO	1.90	31 47 N, 112 53 W	550	gS	190	1961	1964	1972	1979			1992	2004
MacDougal Crater	MACD	4.65	32 00 N, 113 38 W	100	ns	125	1959	1965	1973	1979	1985	1987	1992	2005

the spline function that describes the growth rate–height relationship for each plot. The age–size function for each plot was then used to estimate the age of each plant based on its height, and this age was used to calculate its establishment date at each census.

To test the reliability of the age–size model, height data collected in 1988 (REDI, SNPE, SABI, SNPW, SILV) or in the early 1990's (HARQ, MACD, SONO, TUMA, VENT) were used to estimate the age of all saguaros present in each plot (estimated age). For this analysis, we compared the estimated ages of plants on a particular visit with their age at an earlier census date plus the number of years that had passed between visits (predicted age). For example, at TUMA, the age of every saguaro present in 1993 was estimated based on its 1993 height (Estimated $Age_{93} = Age_{93}$). For verification, 23 years were added to the age of every saguaro present in 1970 (e.g. Predicted $Age_{93} = Age_{70} + 23$). Regression analysis was used to compare the estimated age of each saguaro in 1993 with its predicted age based on its height 23 years earlier. In the present study, we calculated the predicted age at the 1988–1993 census date based on the plant's height at the previous census date (1972–1973). Estimated and predicted ages were compared using regression analysis (SAS Institute, 1993) as described previously (Pierson and Turner, 1998).

2.4. Population age structure and analysis of demographic trends

Analysis of demographic trends using age structure follows Pierson and Turner (1998). The age structure at each census was expressed as the frequency of individuals having the same establishment year. For all censuses prior to the last, the population data were corrected to include those plants overlooked, yet undoubtedly present based on their size when discovered. Saguaros for which precise age estimates could not be made (due to injuries) were excluded from the age-structure analysis. Annual establishment was expressed as five-year running means to smooth internal variation.

A survivorship curve was determined empirically from the pattern of height-specific mortality observed at TUMA (Pierson and Turner, 1998). These data are based on observations over a six-year period (1964–1970) of a population of ca. 3500 individuals. Although the survivorship at each site may differ from this general survivorship curve, use of a single average curve provides a means of comparing regeneration trends at all sites to the same index. The TUMA survivorship curve is our best estimator of survivorship for several reasons: a) it is based on a large population, b) the site is large (40 ha) and encompasses a range of topographic and edaphic conditions, and c) livestock and other land use impacts were minimal since 1907.

A survivorship curve specific for each site was determined using the height-specific mortality from TUMA and the age–height relationship for each site. The survivorship curve was scaled so that the area under the curve was equal to the size of the observed population at each census. The scaled survivorship curve shows the predicted number of individuals in each age class that is needed to maintain the current population size, given a constant, age-specific survivorship rate (i.e. predicts a stable age distribution).

Differences between the survivorship curve and the observed age distribution were used to highlight periods of time during which regeneration was hypothetically greater than or less than necessary to maintain the population size. Data for the first and last census at each site are given (Figs. S1 and S2). The difference values (residuals) were standardized by dividing the difference value at each date by the number of recruits predicted by the survivorship curve for that date. Standardization takes into account the decreasing number of individuals in older age classes. The standardized residuals were normalized with respect to the mean and standard deviation of all residuals. Because deviations from the survivorship curve may be a function of recruitment or survival, the term 'saguaro regeneration' was used to include both possibilities.

Long-term regeneration profiles (Fig. 6) were produced using the standardized residuals from the first and last census dates. Where there was overlap between the data sets, the highest residual value was used (Figs. S1 and S2). This ensured that saguaros that were found in the early census and subsequently died were counted and, similarly, that saguaros found in the later census but missed in the earlier census were counted. These data were then normalized with respect to the mean and standard deviation as described above. Synoptic regeneration trends for the Tucson area, the western Sonoran Desert sites, and all sites were determined by summing the normalized residuals from all sites included in each comparison (Fig. 7).

2.5. Saguaro reproductive potential

A rough index of the ability of a plant population to reproduce is an estimate of the number of seeds produced per unit area. This 'reproductive potential' index is derived easily for saguaros because flowers are produced only at the apical meristems of primary stems and branches (Steenbergh and Lowe, 1977). The reproductive potential (density of reproductive stem tips) at each census was estimated by adding together the density of potentially reproductive plants (heights $\geq$ 2.0 m) and density of branches on those plants. The threshold height of 2 m was selected because saguaros typically become reproductive when they reach that height (Pierson and Turner, 1998; Steenbergh and Lowe, 1977). Newly formed branches begin as small buds and grow in length and diameter with time. Newly formed branches were counted as branches rather than buds when their length exceeded ~15 cm. All branches were considered reproductive, even though branches may not reach this status until 2–3 years later (Steenbergh and Lowe, 1977).

3. Results

3.1. Saguaro density

The density of saguaros varied among sites over the 45-year period, ranging from a maximum of 423 plants/ha at the REDI (1988) to 26 plants/ha at the MACD site (2005), a ~20 fold difference in density across plots (Fig. 2A, Table 2). The mean density (averaged across all censuses) in each plot was not correlated with either plot location (longitude) or annual rainfall along the east–west precipitation gradient (Table 1), ($P > 0.05$, $r^2 = 0.32$, and $r^2 = 0.23$, respectively). This is not unexpected because the locations of plots at each site were selected to maximize saguaro density. Highest densities were observed in plots on steep, rocky, south- or east-facing slopes (TUMA, REDI, SABI, VENT); intermediate densities on gently sloping terrain (SNPW, SILV, SONO); and lowest densities on level to gently rolling terrain (SNPE, HARQ, MACD). In contrast, coverage of woody perennials was correlated with plot location and annual rainfall: mean crown coverage of woody perennials was higher at REDI, SNPE, and SNPW, intermediate at SILV, SABI, and VENT, and lowest at SONO, HARQ, and MACD (Table S4) ($P > 0.05$, $r^2 = 89$ and $r^2 = 80$, respectively).

3.2. Saguaro growth rates

In the present study, a modeling approach, which integrates growth measurements over multiple census dates and considers the standard error of the height-specific growth rates, was used to define the shape of the growth–height function. The growth–size relationship specific to each site (Fig. 2B) was reasonably accurate in predicting the age of saguaros at subsequent censuses. At all sites

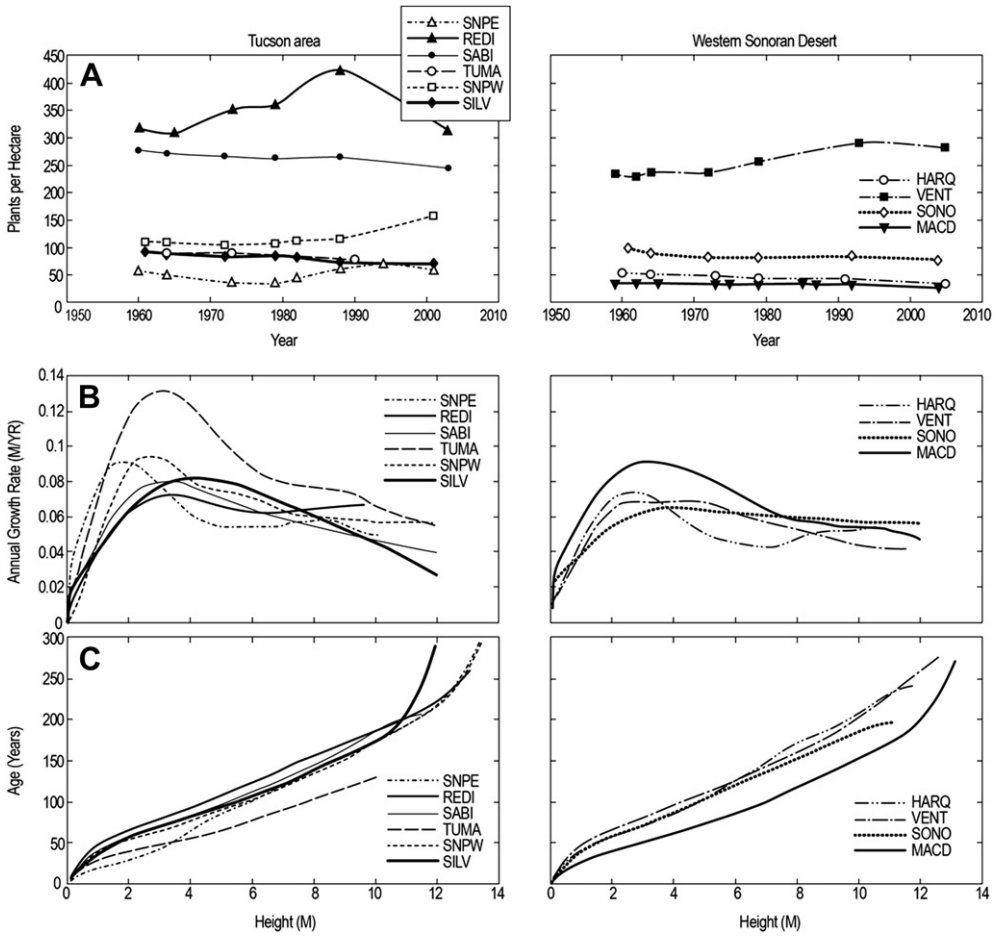

Fig. 2. (A) Saguaro density as a function of time for populations in the Tucson area and western Sonoran Desert. (B) Saguaro annual growth rate as a function of height for both regions. A cubic smoothing spline has been fitted to the average growth rate for individuals in 0.5-m height classes. The standard error of the mean for each height class is typically less than ±1.0 cm for plants less than 2 m and ±2.5 cm for larger plants (data not shown). (C) Saguaro age as a function of height for both regions.

the slope of the regression equation comparing estimated and predicted ages was ~1 with an r^2 value >0.89 (Table S2). Differences among sites in their average size-specific growth rates translate into site-specific differences in the average age–size relationship (Fig. 2C). Saguaros grew the fastest in the wetter Tucson area. For example, 50-year old saguaros range in height (Fig. 2C) from 3.5 m at SNPE and TUMA to less than 1.5 m tall at drier sites (HARQ, VENT, SONO). One hundred-year old saguaros ranged from nearly 8-m (TUMA) to 5.3-m tall in the Tucson area (SNPE, SNPW, SILV, SABI), whereas they were ~4.5 m tall at the cold (REDI) and dry limits (HARQ, VENT, SONO). The notable exception was the MACD site where, despite its location near the western limits, average growth rates were comparable to those measured in the Tucson area (e.g. 50-yr and 100-yr old plants were 3.5 and 7.8 m, respectively).

3.3. Branching and reproductive potential

Saguaros at SNPE and TUMA generally began producing branches reliably at a height of 3.75 m, and in all other plots between 4 and 5 m (data not shown). Although some saguaros produced branches at heights less than 3 m, this commonly was related to injury (especially decapitation). A height of 5 m was set as the low standard for estimating the percentage of plants with branches to prevent the age structure of the population from influencing branching frequency (i.e. even where branching was least frequent, plants 5 m and taller were over 90-years old and would have had sufficient time to branch). The occurrence of branching varied among saguaro populations. The populations with the greatest percentage of 5 m and taller saguaros with branches occurred in the Tucson area (REDI, SNPE, SABI, SNPW), compared to sites located farther west and south (VENT, SONO) (Table S3). The notable exceptions to this relationship were the western HARQ and MACD sites, where high frequencies of branching (78 and 68%, respectively) were observed (Table S3). The average percentage of the population with branches ranged from 87% at SNPE to 26% at SONO.

Due to differences in population density, age structure, and branching frequency, the reproductive potential of the populations varied among sites, ranging from 767 reproductive stems/ha at REDI (1960), a site with a high density of branched plants, to 20 reproductive stems/ha at SNPE (2001), a site dominated by young plants (Table 2).

3.4. Age structure and survivorship

The size and age structures of populations varied among sites and through time (Table 2, Figs. 3 and 4). From the first to the last census, most saguaro populations experienced a decline in size. Notable exceptions were REDI and SNPE, where populations rose and then fell to initial densities, and SNPW and VENT, which increased gradually over time. Changes in population size were brought about by establishment of new plants and the death of established ones (Table S1). Recruitment rates (new plants found

Table 2
The density of plants (plants/ha), the density of potentially reproductive individuals (plants ≥ 2 m in height/ha), the number of branches on potentially reproductive individuals per hectare, and the reproductive potential (the number of potentially reproductive plants plus the number of branches on these plants) per hectare are given. ND indicates site visits when no data were collected on plant height or number of branches.

	Census 1	Census 2	Census 3	Census 4	Census 5	Census 6	Census 7	Census 8
REDI								
Density	315	307	351	360		423		312
Density ≥ 2.0 m	211	201	189	153		149		89
Branches/ha	556	496	460	ND		339		172
Rep. Potential/ha	767	697	649	ND		488		261
SNPE								
Density	58	50	37	35	45	62	71	61
Density ≥ 2.0 m	55	48	32	ND	ND	13	ND	7
Branches/ha	178	151	102	ND	ND	50	ND	13
Rep. Potential/ha	233	199	134	ND	ND	63	ND	20
SABI								
Density	276	272	267	263		265		244
Density ≥ 2.0 m	126	128	127	ND		148		151
Branches/ha	154	152	160	ND		134		99
Rep. Potential/ha	280	280	287	ND		282		250
TUMA								
Density	85		85				73	
Density ≥ 2.0 m	22		24				40	
Branches/ha	32		31				37	
Rep. Potential/ha	54		55				77	
SNPW								
Density	110	109	104	108	113	117		157
Density ≥ 2.0 m	95	95	89	ND	ND	77		63
Density branches	164	176	229	ND	ND	171		105
Rep. Potential/ha	259	271	318	ND	ND	248		168
SILV								
Density	93	87	85	86	83	74		70
Density ≥ 2.0 m	52	52	51	ND	ND	49		48
Branches/ha	19	22	23	ND	ND	58		67
Rep. Potential/ha	71	74	74	ND	ND	107		115
HARQ								
Density	52	49	46	42			39	29
Density ≥ 2.0 m	38	34	31	28			23	15
Branches/ha	82	69	54	ND			34	13
Rep. Potential/ha	120	103	85	ND			57	28
VENT								
Density	232	228	235	235	255		290	281
Density ≥ 2.0 m	85	ND	96	108	118		128	138
Branches/ha	3	ND	35	38	ND		47	55
Rep. Potential/ha	88	ND	131	146	ND		175	193
SONO								
Density	95	87	78	78			82	75
Density ≥ 2.0 m	49	45	41	41			33	28
Branches/ha	25	19	18	ND			9	4
Rep. Potential/ha	74	64	59	ND			42	32
MACD								
Density	33	32	31	32	33	31	31	26
Density ≥ 2.0 m	21	23	22	ND	ND	22	22	21
Branches/ha	26	29	35	ND	ND	ND	47	36
Rep. Potential/ha	47	52	57	ND	ND	ND	69	57

expressed as a percentage of the original population size) were the highest (>50%) in the SNPE, SNPW, REDI, and VENT plots. Over the same period, survivorship of plants present at the start of the study was lowest at SNPE (6%) and REDI (33%), underscoring the importance of recruitment for maintaining these populations.

How did the actual survivorship rates compare to those predicted by our generalized survivorship curve? This curve is based on observations of height-specific mortality in a population of ~3500 individuals at TUMA over a six-year period. Predicted survivorship for individuals in the same 10-yr age class was determined from the plot-specific survivorship curve (Figs. 3 and 4). In general, the actual survival rate over the course of the study was greater than or equal to what was predicted by the generalized survivorship curve. The notable exceptions are the SNPE and REDI sites. In most plots, the greater survivorship observed than predicted was due almost entirely to higher survival by plants between 20 and 120 years old; for older plants, there was good agreement between observed and predicted survivorship. Despite these site and age differences in survivorship, a single survivorship curve provided the best common denominator for comparing regeneration trends across sites and censuses.

3.5. Regeneration trends

We evaluated how site differences might have influenced regeneration trends across the ten sites. We considered how changes in age structure affected reproduction potential and whether ensuing regeneration correlated with this potential.

3.5.1. Tucson area

The greatest time depth for any site in the northern Sonoran Desert was obtained at SNPE, allowing characterization of age structure and regeneration trends back to ~1750. The 1960 census shows that a large number of plants were established ~1780–1860

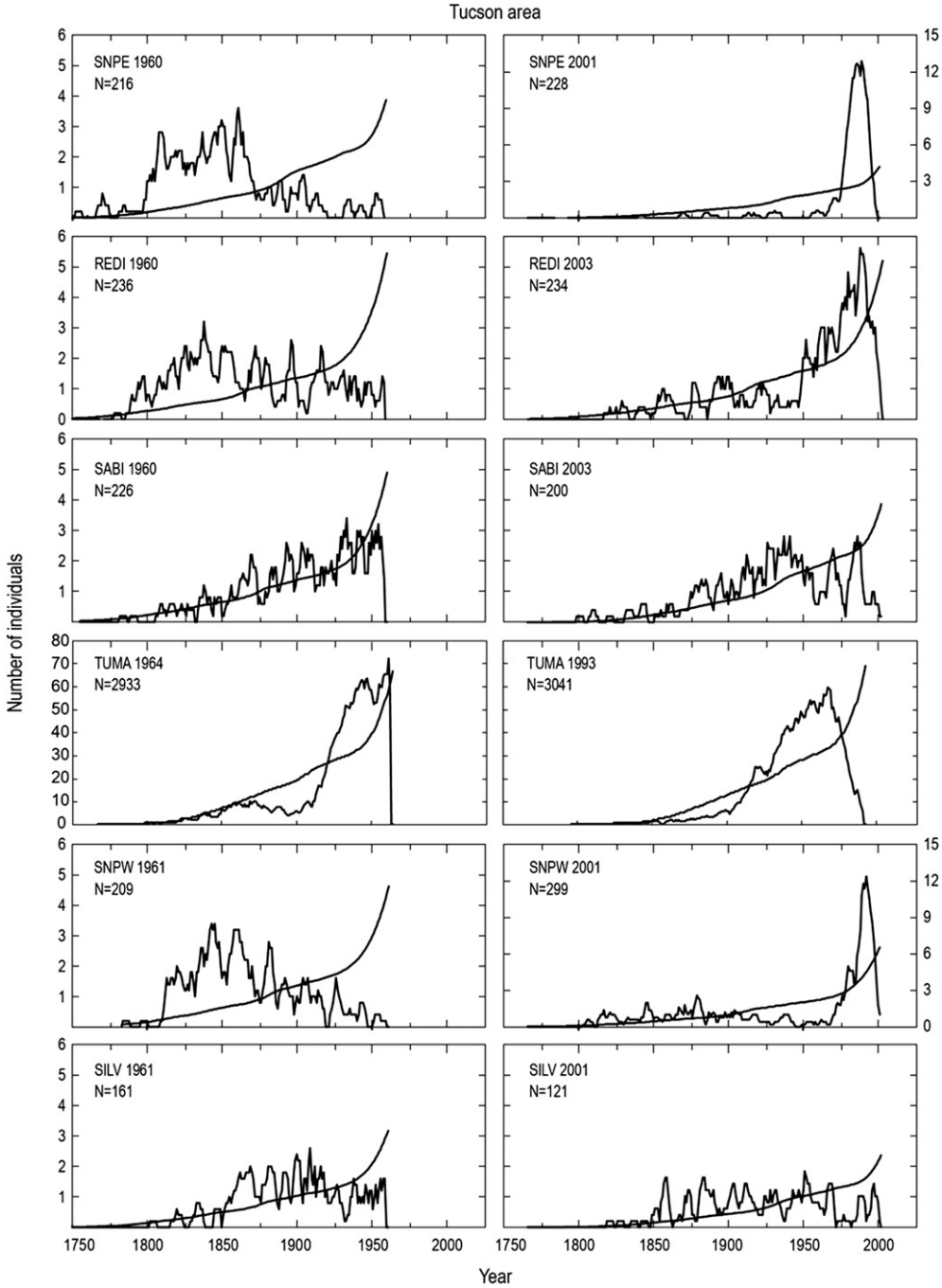

Fig. 3. Age distributions with survivorship curves for each of the Tucson area plots at the first and last census dates. For each site, we show observed age distributions expressed as 5-year running means (solid lines) and predicted age distributions defined by the survivorship curve based on constant age-specific mortality rates (smooth curve) for the first and last census dates. Tucson area plots include Saguaro National Park East (SNPE), Redington (REDI), Sabino Canyon (SABI), Tumamoc Hill (TUMA), Saguaro National Park West (SNPW), and Silverbell (SILV).

(Fig. 3), when regeneration rates also were very high at REDI and SNPW. The SNPE population in 1960 was composed primarily of mature individuals (95% of individuals were >2 m in height), many of which became established prior to 1860. This large cohort of older plants, clearly visible in photographs from the 1930s (Fig. 5), accounted for the dense "cactus forest" that motivated establishment of the Monument at SNPE in 1933. From 1960 to 2001, the older cohort steadily declined until only 6% of the 1960 population remained (Figs. 3 and 5). The age structure of the population in 1960 indicated that post-1860 establishment/survival of recruits was well below that required to maintain the population at its current size for nearly 100 years (Fig. 3). By 1979, the loss of the oldest saguaros coupled with the lack of recruits resulted in a 40% decrease in population density. In contrast, the strikingly skewed 2001 age structure shows that saguaros became established in large numbers starting in the mid 1970's, and this surge led to a steady increase in population size. The poor regeneration during the 100-year period from 1870 to 1970 was still evident in the 2001 age structure (Fig. 3, Fig. S1). These changes markedly altered the appearance of the population over time (Fig. 5). A period of high regeneration from the

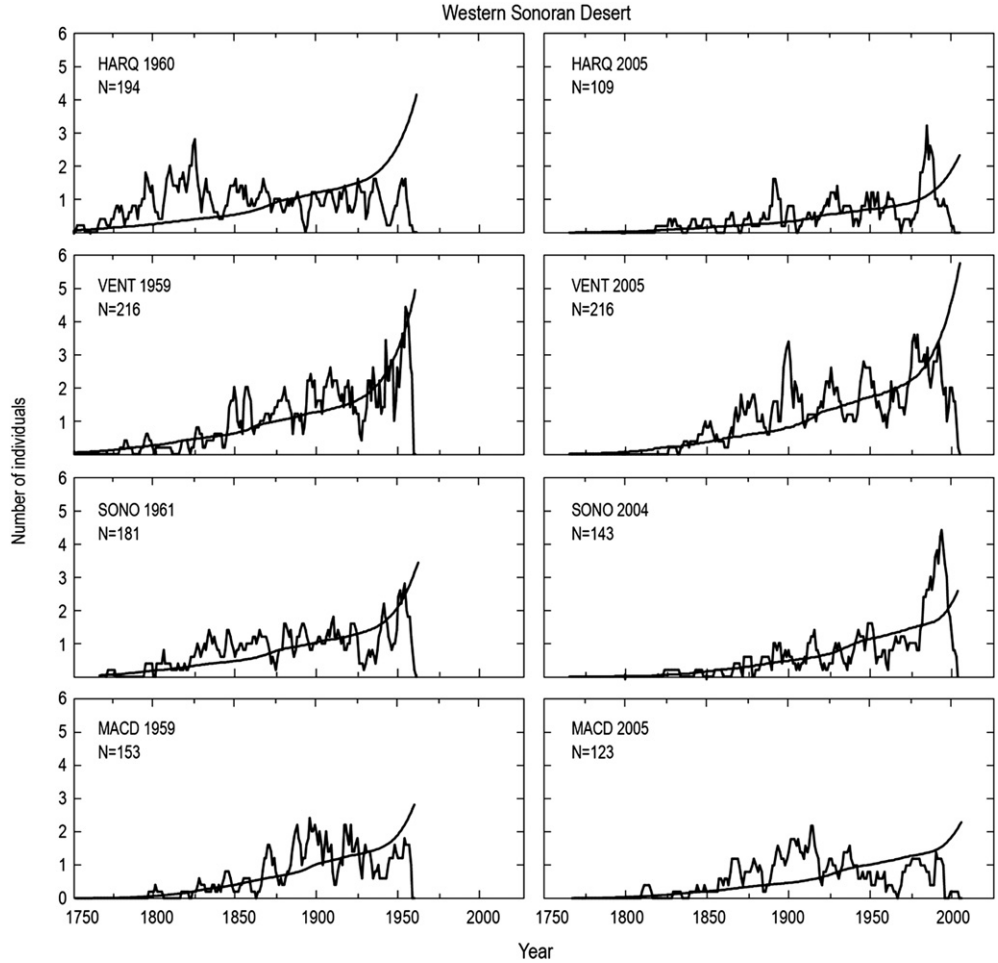

Fig. 4. Same as Fig. 3, but for western Sonoran Desert plots, including Harquahala (HARQ); Ventana (VENT), Sonoyta (SONO) and MacDougal Crater (MACD).

mid 1970's through 2001, however, restored the population density to the 1960 level. This surge in establishment may be related in part to the large number of mature plants with branches present in the 1960 population; in 1960 the number of reproductive meristems exceeded population density (Table 2). Despite the resurgence in saguaro density from 1979 to 2001, only 11% of the saguaros in 2001 were of reproductive size (e.g. over 2 m in height) and only 4% had branches, indicating a reproductive potential of only 20 meristems/ha (10 fold less than in 1959) (Table 2).

A similar cyclic regeneration pattern was observed at SNPW and TUMA where high regeneration rates throughout much of the 19th century were followed by 60 years of low regeneration (ca. 1900–1960 at SNPW and ca. 1860–1920 at TUMA), and by a steady increase in saguaro regeneration since then (Fig. 3, Fig. S1). At SNPW, the 2001 population was composed primarily of immature plants below 2 m in height and was experiencing a significant decline in reproductive potential. At TUMA, by 1993 the maturation of the saguaros established during the mid-1900s led to a subsequent increase in reproductive potential (Fig. 3, Fig. S1).

In contrast, recruitment at SABI was remarkably constant during the period from 1800 to the late 1940's conforming to a nearly stable age distribution (i.e., the shape of the age structure conforms to the survivorship curve, indicating the occurrence of sufficient recruitment/survival to replace older individuals as they die) (Fig. 3, Fig. S1). No surge in recruitment of the magnitude seen at SNPE and SNPW was observed at SABI. In fact, the number of young plants establishing and surviving to 2003 has been slightly below the number needed to maintain the population. Reproductive potential at SABI remained constant from the first census to the 1988 census and, like regeneration, has declined slightly recently. The regeneration pattern at SILV is somewhat similar to that observed at SABI (Fig. 3, Fig. S1).

The regeneration pattern for REDI, the coldest site in the Tucson area, is less variable than that observed at SNPE or SNPW. At REDI, a decline in regeneration occurred between 1900 and 1950, but this was smaller in magnitude than that experienced at SNPE or SNPW (Fig. 3, Fig. S1). As at SNPE, the reproductive potential at REDI in 1960 far exceeded the density of plants (767 meristems compared to 315 plants) (Table 2). A surge in recruitment correlated with this peak in reproductive potential has largely offset the loss of two-thirds of the 1960 population. The 2003 population was composed primarily of plants less than 2 m (Table 2).

3.5.2. Western Sonoran Desert

Long-term regeneration trends for populations near the western, dry limits of the saguaro's distributional range vary from a nearly stable age distribution at VENT and SONO to cycles in recruitment at MACD and HARQ. Similar to populations in the Tucson area, at HARQ the 1960 age structure records that the period from 1760 to 1860 was favorable for saguaro establishment and survival (Fig. 4, Fig. S2). This period was followed by almost a century of decline, although the magnitude of the decline is not as great as observed at SNPE and SNPW. Beginning about 1970, there was a surge in regeneration at both HARQ and SONO (Fig. 4,

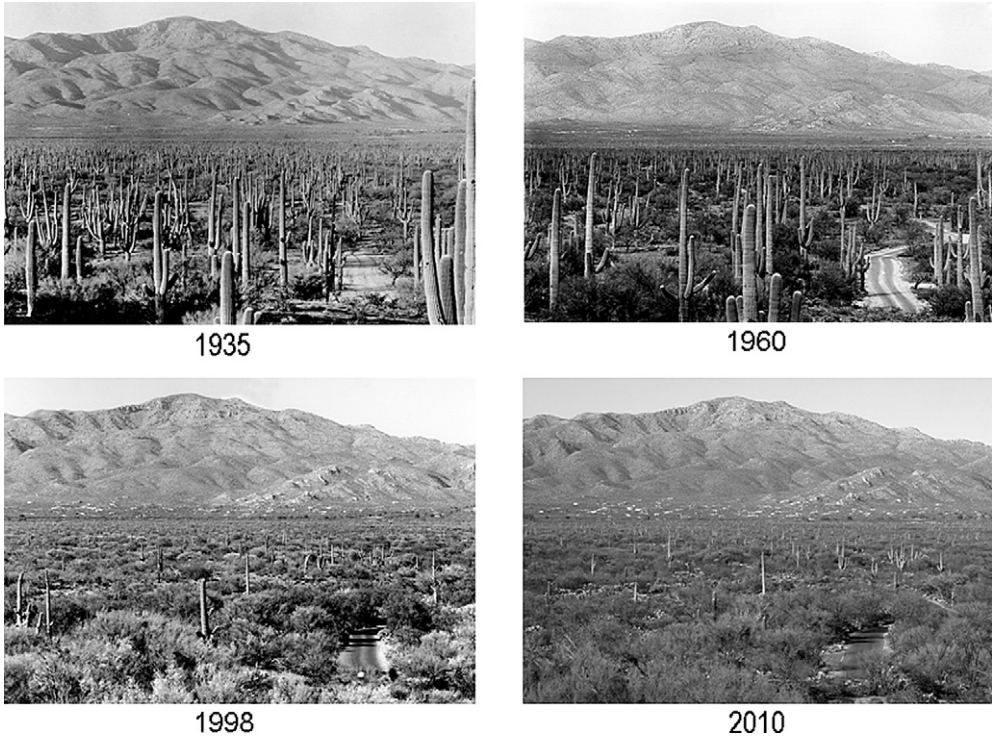

Fig. 5. Photographs of general area encompassing permanent plot at Saguaro National Park East (SNPE) in 1935 (unknown photographer), 1960 (J.R. Hastings), 1998 (R.M. Turner); and 2010 (R.M. Turner).

Fig. S2). At both sites, this surge follows a period of maximum reproductive potential in the 1960s. In contrast to the SNPE, SNPW, TUMA, and HARQ regeneration trends, at MACD the period from 1870 to 1930 was notable for saguaro regeneration, whereas at the other sites during the latter half of the 19th century and recently, regeneration rates have been low (Fig. 4, Fig. S2). The age structure of the population at VENT has been stable over time and does not record the cyclic patterns observed elsewhere (Fig. 4). Reproductive potential and density at VENT have increased steadily (Table 2).

4. Discussion

4.1. Regional patterns in saguaro density, growth rate, and branching

4.1.1. Saguaro density

This study documents changes in saguaro populations located across the northern portion of the saguaro's distributional range. The goals of the study were to look at regional variation in saguaro density, growth rate, reproductive potential, and age structure and to determine the degree of regional synchrony in saguaro regeneration patterns. It was expected that differences between populations at different sites would be determined largely by regional and temporal patterns in precipitation and temperature. Instead, we found a lack of correlation between saguaro growth rate, branching frequency and abundance, and a complex relationship between these variables and precipitation. The density of saguaros differed dramatically among populations, and there was no correlation between saguaro density and average annual precipitation or longitude. In the driest sites, saguaros were constrained primarily to microhabitats that likely compensated for the low precipitation regimes, e.g. to slopes and bajadas of mountain ranges such as at VENT, and ultimately to runnels where moisture is augmented by flow from higher terrain such as at MACD and HARQ. Overall, the highest densities occurred in plots located on steep, rocky, south- or east-facing slopes (REDI, SABI, TUMA, VENT), intermediate densities on gently sloping terrain (SNPW, SILV, SONO), and the lowest densities on level to gently rolling terrain (SNPE, HARQ, MACD). These findings suggest that the influence of local conditions (e.g., slope aspect, substrate, microclimate and/or biotic factors) on saguaro densities obscures that of regional climatic gradients.

As reported previously, slope aspect has a significant effect on saguaro density with densities being higher on south- and east-facing slopes (Niering et al., 1963; Pierson and Turner, 1998; Spalding, 1909; Turner et al., 1995). For example, at TUMA where observations of saguaro density on north-, south-, east- and west-facing slopes span the period from 1908 to 1993, saguaro densities and recruitment rates were consistently higher on south- and east-facing slopes than north- and west-facing slopes. In contrast, over the same period of time there was little difference among slopes in the growth rates or survival of established plants suggesting that recruitment niche is an important determinant of saguaro abundance across aspects. The preference of saguaros for south and east aspects may result from differences among slope aspects in the intensity and duration of freezing temperatures (Parker, 1993; Pierson and Turner, 1998), the intensity and duration of sun exposure during summer (Pierson and Turner, 1998), the availability of summer precipitation (Jordan and Nobel, 1982), and the susceptibility/dependence of small plants to freezing temperatures and summer precipitation, respectively (Bowers and Pierson, 2001; Brum, 1973; Steenbergh and Lowe, 1977, 1983). At the time our studies were initiated in the 1950's, the relationship between slope aspect and saguaro density was not yet appreciated. Plot selection was based on choosing a location at a site with the highest plant density, which produced a bias in plot location on south and east-facing slopes.

4.1.2. Saguaro growth rates

High population density also did not necessarily correlate with high growth rates, suggesting that the climatic and biotic factors affecting recruitment niche are not the same as those affecting plant growth. Saguaros grew fastest at sites located in the Tucson area as compared to sites located in drier parts of the range. Previous studies have suggested that summer rains contribute significantly to saguaro growth (Hastings and Alcorn, 1961; Steenbergh and Lowe, 1983). Because monsoonal rains decrease in frequency and increase in patchiness from east to west, we expected slower saguaro growth rates in the western Sonoran Desert. The notable exception was the MACD site where, despite its location near the western limits, average growth rates were comparable to those measured in the Tucson vicinity. This site, located on the floor of a volcanic crater, may experience wetter soils than predicted from rainfall records due to extensive runoff into the crater. Standing water has been observed inside the crater, outside the saguaro plot (Turner, 1990, 2007).

Similar to this study, slower main stem growth rates have been reported for saguaro populations located in the western portion of the saguaro's range as compared to populations at SNPE and SNPW (Drezner, 2005; Steenbergh and Lowe, 1983). In the Drezner study, growth rates of saguaros at 10 sites in Arizona located across an east–west gradient were correlated positively with summer rainfall. Saguaros at our coldest site (REDI), however, had one of the slowest growth rates observed. Apparently, the gradient in highest to lowest growth rates as you move from east to west breaks down at the colder limits of the range. Steenbergh and Lowe (1983) observed that plants large enough to survive freezes may experience reduced growth and reproduction due to frost injury. Repeated exposure to freezing temperatures may contribute to the slower growth rates. Density-dependent factors (McAuliffe and Janzen, 1986) also may affect growth, particularly at the two sites (REDI and VENT) where saguaro density exceeds 300 plants/ha. We have no experimental evidence for why REDI experiences the highest population densities, but the slowest main stem growth rates. Finally, we acknowledge that atmospheric CO_2 enrichment probably increased saguaro photosynthesis and growth (Drennan and Nobel, 2000) over the demographic history of saguaros in our study. If such is the case, our stationary age–height models may

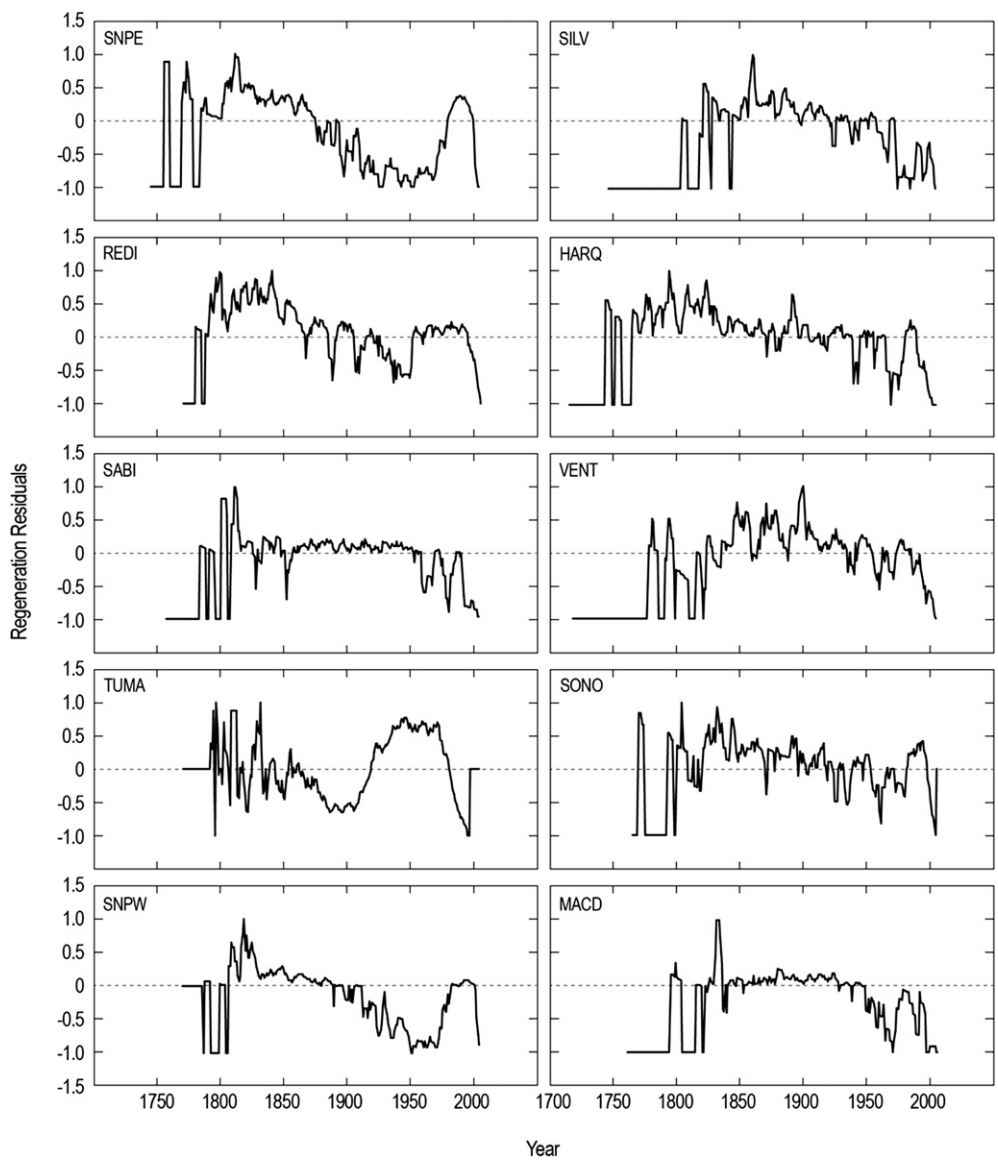

Fig. 6. Residuals for each plot merged across all census dates. Residuals range from 1 to −1 and identify periods of time when regeneration was theoretically greater than (positive) or less than (negative) needed to maintain the most recent population size.

underpredict the age of the oldest saguaros, particularly in the earliest censuses.

4.1.3. Saguaro branching

We also observed differences among plots in the allocation of plant growth to height versus branch production. Branching in saguaros 5 m and taller was greatest in the Tucson area (REDI, SNPE, SABI, SNPW), compared to sites located farther west and south (SILV, VENT, SONO). This trend has been observed previously and attributed to the fact that more mesic habitats can support faster growing and more vigorous plants (McAuliffe and Janzen, 1986; Steenbergh and Lowe, 1983; Yeaton et al., 1980). There does not seem to be a clear relationship, however, between mesic habitat, main stem growth rate, and/or branch production. For example, the frequency of branching at the MACD and HARQ sites, located near the arid limits, is comparable to the frequency observed in eastern populations. Notably higher growth rates observed at the MACD site compared to others near the arid limits (Fig. 2B) suggests that branching may be related to plant vigor. At HARQ where plants are restricted to habitats of compensation in runnels, plants experience more mesic conditions than indicated from nearby rainfall records. Although branch proliferation is among the highest at this site, main stem growth rates and plant densities are among the lowest. At the cold extreme (REDI), population density and arm proliferation are high, but saguaro height growth is slow.

4.2. Long-term and regional patterns in saguaro regeneration

One goal of this study was to understand what was "typical" for saguaro regeneration patterns temporally and regionally. Given that saguaros reproduce episodically, could we expect to find stable age distributions or variable ones dominated by broad synchronous or asynchronous trends in regeneration? To what extent might the degree of synchroneity be related to climate? How might human influence (livestock grazing or protection from it) or other local factors contribute to asynchroneities?

Observations of saguaro age structure over the 46-yr period encompassed by this study provide information on saguaro regeneration patterns spanning ~250 years. Fig. 6 integrates the regeneration residuals across the first and last census (Figs. S1 and S2) and demonstrates that, during the past two centuries populations have remained relatively stable at some sites but fluctuated dramatically at others. In the Tucson area, perhaps the most striking comparison is the difference in regeneration history observed at SABI compared to that observed at SNPE (Fig. 6). During the census period, populations at SABI remained remarkably constant and regeneration rates since the early 1800's appear to have been sufficient most years to maintain the population. At SNPE, saguaro populations fluctuated substantially in density and age structure. The regeneration history suggests that regeneration peaks at this site were separated by almost a century (Fig. 6). Despite nearly a 40% decline in density during the study period, the SNPE population densities at the first and last censuses were equivalent, confirming that regeneration surges occurring at ~century intervals are sufficient to maintain population sizes. However, an order of magnitude decline in reproductive potential over the census period from 200^{+} to 20 meristems/h suggests that a time lag can be expected before the current population is again capable of producing a regeneration surge. Apparently once populations become cyclic in their regeneration, to the extent observed at SNPE, the cyclic pattern of regeneration may be perpetuated by the age structure of the population. Episodic regeneration also is indicated from the regeneration histories at nearby REDI, SNPW, and TUMA (Fig. 6).

The first census, based on observations made from 1959 to 64, predates all previous observations of saguaro age structure (except Shreve, 1910) and at many sites records a significant regeneration peak not captured by later studies (Figs. S1 and S2, Fig. 6). For example, at six of the ten sites (REDI, SNPE, SNPW, TUMA, SONO, and HARQ) predicted regeneration rates were higher prior to 1870 than during the period from 1870 to ~1960. At the other four sites, predicted regeneration rates were either relatively constant (SABI, SILV, MACD) from 1800 to 1960 or difficult to interpret (VENT). Data from the last census indicate that a regeneration peak occurred during first third of the 20th century at SABI, SILV, and MACD and the last third of the 20th century at REDI, SNPE, SNPW, HARQ and SONO (Figs. S1 and S2, Fig. 6). In contrast, regeneration was high during the middle of the 20th century at TUMA, and decreased gradually at VENT throughout the century.

Synoptic regeneration trends for the Tucson area, the western Sonoran Desert, and for all sites were determined by summing the normalized residuals of the sites included in each comparison (Fig. 7) and show the following regional trends. Regeneration was highest across the northern Sonoran Desert from 1780 to 1870, broadly peaking between 1780 and 1860, particularly in the Tucson area (Fig. 7A). A secondary peak happens in the western sites ~1880–1900, but regeneration there generally declined or held steady from 1870 to the present (Fig. 7B). Large fluctuations in saguaro population size and regeneration have been noted in previous studies with substantial peaks occurring during the first and last third of the 20th century (reviewed Danzer and Drezner, 2010; Pierson and Turner, 1998). As observed here, there is little correspondence regionally in the exact dates of peaks and troughs in regeneration or in the magnitude of changes in populations in

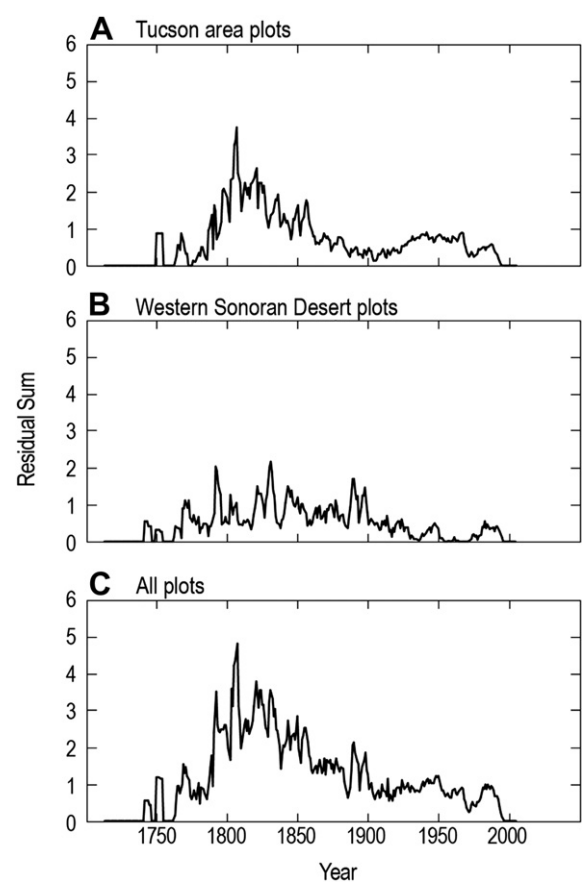

Fig. 7. Sums of normalized residuals for A) Tucson area plots, B) western Sonoran Desert plots, and C) all plots in the northern Sonoran Desert.

these studies. Pierson and Turner (1998) previously hypothesized that regional synchroneity in regeneration peaks may be driven by decadal- to century-scale variability in cool season precipitation and mild winter conditions.

To evaluate this hypothesis, regional regeneration patterns were compared to climatic reconstructions using tree-ring data. Given that temperature variability is broadly similar across the region, we relied on tree-ring reconstructions of summer temperature from bristlecone pine (*Pinus aristata*) growing at upper treeline north of Flagstaff, AZ (Fig. S3, upper) (Salzer and Kipfmueller, 2005). For moisture, we relied on gridded tree-ring reconstructions of the Palmer Drought Severity Index (PDSI) for gridpoints in southern and central Arizona (Fig. S3, lower) (Cook et al., 1999). The broad peak in saguaro regeneration from 1780 to 1860 corresponds to a generally wet 80-yr period that shifted from warm to cool around 1810. Furthermore, the peak in saguaro regeneration in the late 18th–early 19th century at all ten sites, shown in Fig. 7C, matches one of the two major peaks (1810–1860, 1890–1930) in ponderosa pine (*Pinus ponderosa* var. *scopulorum*) recruitment throughout the southwestern U.S. attributed to exceptionally wet periods at a time of reduced El Niño Southern Oscillation (ENSO) variance (Swetnam and Brown, 2010). Swetnam and Brown (2010) suggest that ecological responses to favorable conditions in the late 18th–early 19th century represent one of the most important and ecologically effective climatic changes in southwestern forests over the past three centuries. Our regional demographic history for saguaro, the only desert species for which we have long-term demographic data, would suggest that these impacts extended to the southwestern deserts.

For analysis of more recent regeneration trends, we used mean precipitation patterns for the 16-month interval from June to September of the following year across Pima County, Arizona (which encompass our Tucson Basin sites and also REDI and VENT sites). The 16-month average was typically above the 100-year average in the early and late 1900's with peak conditions in the 1980's (Fig. S4). Of significance, mean monthly minimum winter temperatures (based on a 3-month period ending in February), demonstrate a 1 °C step increase in winter minimum temperatures beginning about 1976 (Fig. S4; see also Weiss and Overpeck, 2005). Milder winters, combined with moist conditions, could have promoted late 20th century regeneration surges at several of the sites in this region. On the other hand, higher regeneration at some sites in the early (TUMA) and latter part (SNPE, SABI, and SNPW) of the 20th century corresponds with removal of livestock grazing from these parks and reserves. Of interest, REDI which also experienced a late 20th century regeneration surge has received no such protection.

The lack of regeneration at some sites during certain favorably wet periods has been attributed to other climatic and biotic factors, land use history, and the interaction among these factors. High rainfall intensity, droughts, or severe winters may decouple regeneration and moisture conditions because these factors may cause high mortality rates among seedlings. Successful establishment of young plants also is based on climatically-driven effects on the fitness and commitment to reproduction of existing mature saguaros. For example, branching, flower production and ultimately viable seed production may be influenced by climatic factors several months to years prior to successful recruitment (Bowers, 1996; Drezner, 2003b; Parker, 1993). As is evident from this study, population age structure is a major determinant of reproductive potential, which may limit regeneration during favorable climatic periods. Biotic factors including the presence of sufficient 'nurse plant' coverage, pollinators and seed dispersers and the impact of seed predators and herbivores also may influence regeneration patterns and may themselves be influenced by local and climatic factors. In this study, the crown coverage of woody perennials and the frequency with which perennials were associated with young saguaros varied by site and through time (Tables S4 and S5). Intensive grazing, woodcutting, and rock removal may reduce recruitment locally due to seedling damage and the reduction in germination sites from the soil compaction and nurse-plant destruction (Pierson and Turner, 1998). At SNPE, livestock grazing and woodcutting until 1959 are believed largely responsible for the long decline in saguaro recruitment. Parker (1993) observed that grazing also contributed to saguaro decline at Organ Pipe Cactus National Monument and that this impact may have been amplified by prolonged drought. At TUMA, the effects of livestock grazing and rock removal may have been intensified by drought and frequent freezes (Pierson and Turner, 1998). These biotic and land use factors influence regeneration patterns at local scales and are probably largely responsible for the lack of regional correspondence in the dates of peaks and troughs in regeneration and the magnitude of changes in regeneration among sites.

5. Conclusions

In scaling up from stand to the region, one of the most difficult extrapolations involves the degree of regional synchroneity in long-term demographic trends. Regionalization of plot data is especially problematic for long-lived plants that exhibit episodic establishment and mortality. Our observations demonstrate that, whereas climate may have a strong impact on the demographics of saguaro, patterns of recruitment, growth, mortality, and abundance can be determined by local abiotic and biotic factors. This long-term study across a broad environmental range indicates that saguaro populations are highly variable in their patterns of regeneration. Populations may experience nearly stable age distributions at century scales punctuated by multidecadal-scale variability in regeneration. Alternatively, populations may experience dramatic changes in population size and age structure. Although it is likely that some recruitment occurs most years at these sites, saguaro population size and perhaps persistence may depend upon large, infrequent peaks in regeneration with intervals between peaks being on the order of 50–100 years. Changes in population size and age structure also drive changes in reproductive potential and population-wide probabilities of mortality. If the timing between regeneration peaks is too great (>100 years), it is possible that there may be insufficient reproductive potential to produce a regeneration surge large enough to maintain the population, regardless of favorable climatic or biotic conditions. These findings have important implications for regional management of Sonoran Desert species in general. Given the complexity of the regeneration niche, land use practices that fragment natural landscapes, reduce native desert habitat, encourage the spread of exotics, and promote fire may interfere increasingly with regeneration during the infrequent episodes of favorable conditions.

Also of significant concern is trying to predict how rising temperatures (Weiss and Overpeck, 2005) and increasing aridity (Seager et al., 2007) associated with buildup in greenhouse gases will affect all aspects of the structure and function of Sonoran Desert communities, including those factors that contribute to long-term saguaro persistence. By the end of the 21st century, bioclimatic modeling suggests that a 5 °C increase in mean annual temperatures hypothetically could shift saguaro's cold limit ~500 km northward and ~600 m upward in the Southwest (Rehfeldt et al., 2006). Though the suitable habitat may shift significantly, saguaro spread and population dynamics will be sluggish at the leading edge of migration. Prediction of these dynamics, decades and even centuries ahead, will be difficult, given the episodic nature of saguaro regeneration, the lack of regional synchrony, the impacts of urbanization and other human land use, and novel wildfire regimes

driven by non-native grass invasions (Olsson et al., 2012) and climate change (Abatzoglou and Kolden, 2011).

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Appendix A. Supplementary material

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2012.08.008.

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