

Episodic recruitment in the saguaro cactus is driven by multidecadal periodicities

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Abstract. Each year, an individual mature large saguaro cactus produces about one million seeds in attractive juicy fruits that lure seed predators and seed dispersers to a 3-month feast. From the million seeds produced, however, only a few will persist into mature saguaros. A century of research on saguaro population dynamics has led to the conclusion that saguaro recruitment is an episodic event that depends on the convergence of suitable conditions for survival during the critical early stages. Because most data have been collected in Arizona, particularly in the surroundings of Tucson, most research has relied on a limited amount of environmental variation. In this study, we upscaled this knowledge on saguaro recruitment to a regional scale with a new method that used the inverse-growth modeling of 1,487 saguaros belonging to 13 populations in a latitudinal gradient ranging from arid desert to tropical thornscrub forest in Sonora, Mexico. Using generalized linear and additive mixed models, we created two 110-yr-long saguaro recruitment curves: one driven only by previous size, and the second driven by size, drought, and soil structure. We found evidence that saguaro recruitment is indeed episodic, with periodicities of 20–30 yr, possibly related to strong El Niño Southern Oscillation events. Our results suggest that saguaros rely on multidecadal periodic pulses of good beneficial years to incorporate new individuals into their populations. Inverse-growth modeling can be used in a wide variety of plant species to study their recruitment dynamics.

Key words: *Carnegiea gigantea; inverse modeling; periodicity; recruitment curves; Sonora.*

INTRODUCTION

Population long-term persistence is determined on average by a balance of births and deaths, but this balance is also regulated by trade-offs in demographic schedules (Franco and Silvertown 1996). For instance, a variety of life-history strategies are thought to evolve in response to the probability of mortality at different stages of the life cycle, creating a fast–slow continuum of population regulation (Stearns 1992). The seedling stage is the most vulnerable in plants (Harper 1977). The probability of mortality of seedlings typically exceeds the mortality of adults. Seedling survival also varies with species life-history strategy. For long-lived iteroparous perennial plants, adult survival is far more important for long-term persistence than seedling survival given that it contributes more to the population growth rate (Franco and Silvertown 2004). As a result, long-lived iteroparous perennials typically have longer periodicities of

recruitment than short-lived semelparous plants (Silvertown and Charlesworth 2009). Environmental influences on plant demography also play an important role in the evolution of a range of life-history strategies (Stearns 1992). Some of the most remarkable examples of long-lived plants come from desert species. Long-term studies on these species have found that periodicities of their vital rates are concordant with environmental periodicities on a global scale (Bowers 2005, Miriti et al. 2007).

The saguaro cactus is an iconic species of the Sonoran Desert that has been subject to extensive long-term observations on their population dynamics. Every year, during the Sonoran Desert dry foreshummer (April to June), saguaros produce large, showy, bat-pollinated flowers. One month later, thousands of seeds contained in large attractive juicy fruits are coveted by primary seed dispersers like bats, woodpeckers, and orioles (Niering et al. 1963, Yetman et al. 2020), secondary dispersers that include most desert vertebrates, and seed predators like white-winged doves and other passerines (Yetman et al. 2020). A large share of the seeds is destroyed by predation before primary dispersal; the first large filter for population recruitment. Furthermore, of the millions of saguaro seedlings emerging

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each summer, most die during the first year due to trampling, seedling predation, desiccation, or unsuitable conditions for establishment (Steenbergh and Lowe 1977).

Grubb's (1977) regeneration niche hypothesis explains well the strong differences between the seedling and adult stages of saguaro. Saguaros can persist well in the present desert environment, where adult saguaros are known to be superbly adapted to grow and survive in extreme desert habitat conditions and have fine-tuned their phenological responses to environmental cues. However, germination and, especially, seedling establishment have a very narrow window of regeneration strongly limited by water availability, high temperatures, and biotic factors during recruitment. Since the seminal work of Shreve (1910), periodic recruitment of saguaro populations has been associated with periods of exceptional rainfall. Most of the observations and data have been gathered in the northern portion of its distribution, mainly from populations near Tucson, Arizona, USA. Periods of low recruitment are coincidental with periods of extreme drought (Pierson et al. 2013, Winkler et al. 2018). Rodríguez-Buriticá et al. (2019), studying the long-term populations that Spalding and Shreve established at Tumamoc Hill, found that recruitment in saguaro was likely to occur in favorable wet periods, but was also influenced by local topographical features. Orum et al. (2016) analyzed a 75-yr saguaro data set that included information on saguaro population's regeneration. They suggested that the success of population regeneration of saguaro depends on a combination of factors, including nurse plants, climate, and local features, but none was strongly correlated with recruitment. Finally, Conner et al. (2017) found that demographic changes in the saguaro population of Saguaro National Park have resulted from climatic factors, especially drought and high temperatures, in combination with local land-use change. All this evidence shows that climate affects saguaro age structure through infrequent events of recruitment.

Population recruitment in iteroparous perennial plants is typically measured through long-term demographic studies by directly counting and following the number of newborns for a number of years. Multidecadal studies are not only labor intensive and costly, but, more importantly, long-term data are very scarce. Even scarcer are those studies that consider recruitment in a variety of habitats within the species' range of distribution. In this paper, we study saguaro recruitment by modeling plant growth of individuals that grow in different population localities. If we know how saguaros grow in different environmental scenarios, we could model their individual-size yearly increments and determine the year of recruitment. This can be achieved by modeling their growth and decreasing their individual heights to a size reached as a yearling. In saguaro, this size is about 1 cm (Steenbergh and Lowe 1977, Ceotto 2009). To our knowledge, this technique has never been applied to the study of recruitment but, recently, general statistical methods have been proposed to fill gaps in demographic

data (González et al. 2016, Brooks et al. 2017, Kindsvater et al. 2018).

We used a 10-yr data set of saguaro heights from 13 populations across the central and southern distributional range of saguaro to reconstruct their recruitment dynamics. We used individual yearly growth rates in response to historical climate variation and variability in soil structure, two environmental variables tightly related to seedling recruitment, to construct inverse growth models: one that was size-driven and another that was size- and environment-driven, in which we iteratively decreased saguaro size to determine individual year of recruitment. We then constructed a recruitment curve that identified the most likely periods of saguaro recruitment. We asked the following questions: (1) is recruitment in the saguaro cactus episodic across populations; that is, are new individuals incorporated in each population over long, sometimes multidecadal, periods instead of continuous recruitment? (2) If so, what is the periodicity and geographic variation of saguaro recruitment on a regional scale?

METHODS

Study species

The saguaro cactus (*Carnegiea gigantea*, Engelmann Britton & Rose) is a keystone species of the Sonoran Desert (Drezner 2014). Its massive trunk can reach more than 12 m in height (Steenbergh and Lowe 1977). Once the adult stage is reached, many individuals can attain a life span of 125–175 yr (Steenbergh and Lowe 1977, Pierson and Turner 1998, Pierson et al. 2013). The saguaro is widely distributed over the Sonoran Desert. It occurs from north of Phoenix, Arizona, USA, to southern Sonora, Mexico (Shreve and Wiggins 1964). In this region, climate varies markedly both spatially and temporally, being the dominant limiting factors controlling saguaro growth water availability and temperature extremes (Steenbergh and Lowe 1977, Pierson and Turner 1998, Félix-Burruel et al. 2019), and recruitment (Pierson and Turner 1998, Drezner and Balling 2002, Drezner 2006a, Donnermeyer and Drezner 2012, Orum et al. 2016, Winkler et al. 2018, Rodríguez-Buriticá et al. 2019). Seedling recruitment is highly correlated with the presence of nurse plants or rocks providing adequate conditions for germination and establishment (Turner et al. 1966, McAuliffe 1984, Drezner 2004, Conner et al. 2020), early life-history processes like seed germination and seedling establishment are known to strongly depend on periods with high humidity and high summer temperatures (Steenbergh and Lowe 1977).

Selection and sampling of populations

In 2006, we established monitoring plots in 13 sites throughout the distribution range of the saguaro in Sonora, Mexico (Fig. 1), starting with an initial sample

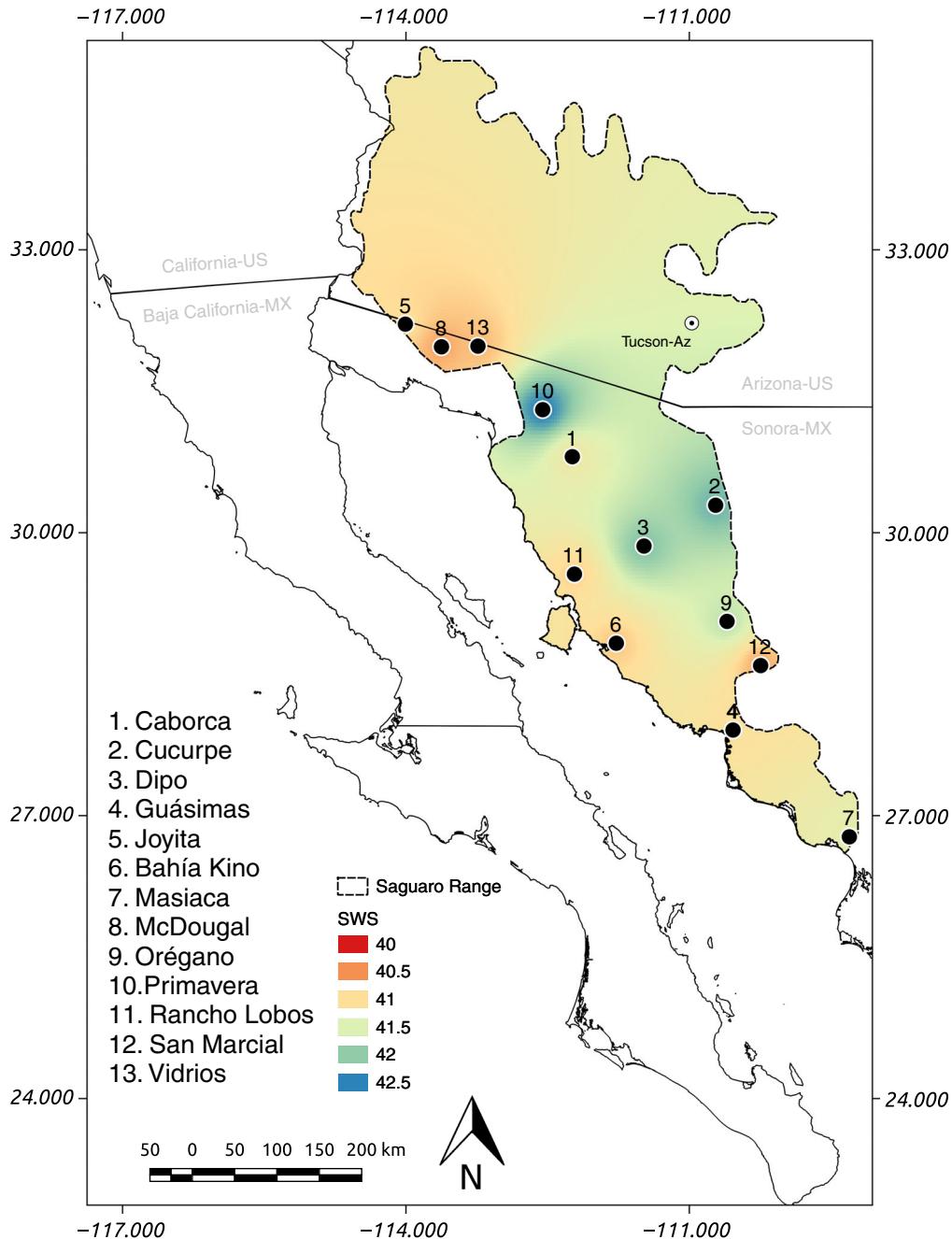


FIG. 1. Geographic location of the 13 saguaro populations studied, represented by numbered black dots, showing mean variation in soil water at saturation (SWS) across the saguaro distribution.

of 1,487 individuals. The selected populations are representative of the four continental subdivisions of the Sonoran Desert: Lower Colorado River Basin, Arizona Upland, Plains of Sonora, and Central Gulf Coast (Dimmitt 2000); we also included the thornscrub transition between the Sonoran Desert and the northernmost portion of the Mexican tropical deciduous forest of the Pacific coast (the foothills of Sonora [Búrquez et al. 1999]).

We sampled contiguous 20 × 20 m quadrats measuring every living saguaro until reaching 100 individuals. We ended up with differently sized plots depending on the density of saguaros in each site. Plots ranged from 0.48 ha to 21.36 ha. Larger plots corresponded to sites with wider spacing between individuals, and smaller plots corresponded to sites with more aggregated individuals. Each saguaro was tagged with a unique ID number attached to its main stem and georeferenced for

subsequent surveys. On each site, we also carefully searched for saguaro seedlings in the whole plot, searching thoroughly under adult saguaros, tree canopies, and rocky outcrops. During the winter seasons of 2014, 2015, and 2016, we recorded the heights (cm) of all individuals and the incorporation of new individuals. Height of saguaros taller than 200 cm were measured from a marked height (about 130 cm) using a telescoping rod with a terminal crossbar (Crain Enterprises, Inc., Mound City, Illinois, USA). Smaller individuals were measured with a tape measure to the nearest centimeter.

Climate data

We used the Palmer drought severity index (PDSI) as a climate variable because it synthesizes precipitation and temperature and their influence on evapotranspiration into a single standardized variable (Palmer 1965). Additionally, we used it because data exist from the beginning of the 20th century to date. The PDSI has been used in previous saguaro studies to explain recruitment or establishment events (Pierson and Turner 1998, Drezner and Balling 2002, 2008, Rodríguez-Buriticá et al. 2019). For each population, we extracted a self-calibrated PDSI from 1901 to 2017 using the KNMI Climate Explorer data (Cook et al. 1999, van der Schrier et al. 2013, Barichivich 2018).

Soil structure

On each site we collected 15 randomly distributed soil samples from 0 to 15 cm depth to determine sand, silt, and clay percentages using the Bouyoucos method (Bouyoucos 1962). Soil samples were processed and analyzed at the Departamento de Ingeniería Química y Metalurgia, Universidad de Sonora, Hermosillo, Sonora, Mexico. To assign soil values to each individual saguaro, we interpolated the soil samples for each site using inverse distance weighting (Shepard 1968). Individual soil particle size fraction allowed the estimation of soil water content at saturation (SWS) through a continuous pedotransfer function based on the van Genuchten function (van Genuchten 1980). This function allows predicting soil water content at a particular point in the water retention curve (Mohamed and Ali 2006):

$$\begin{aligned} \text{SWS} = & 0.6658\text{Si} + 0.1567\text{Sa} - 0.0079\text{Si}^2 - 12.31121/\text{Sa} \\ & - 6.4756\ln(\text{Sa}) - 0.0038\text{ClSi} + 0.0038\text{ClSa} \\ & - 0.0042\text{SiSa} + 52.7526, \end{aligned}$$

where Sa = % sand, Cl = % clay and Si = % silt.

Statistical analysis

To estimate the temporal dynamics of saguaro recruitment, we used a three-step approach: (1) We fitted inverse growth models, using height-monitoring data from 2014–2016 belonging to 13 populations, to predict

individual saguaro heights into the past. The objective of the first step was to decrease the heights of individual saguaros over time to a size that represented the size of recruitment. Inverse growth models were fitted with generalized linear mixed-effects models (GLMMs) and generalized additive mixed-effects models (GAMMs) using saguaro height at time t as the response variable, saguaro height at time $t + 1$, PDSI, and SWS as fixed effects (explanatory variables), and site as a random effect. We fitted a set of models including only saguaro height (S models) and a set of models including height and the environmental variables PDSI and SWS (S+E models) to be able to detect an environmental effect on inverse growth. Inverse-growth models were fitted using 1,142 live individuals in 2016, 1,141 live individuals in 2015, 1,141 live individuals in 2014, and 1,487 live individuals in 2006. We used a leave-one-out cross validation procedure (10,000 iterations) in which we calculated the mean squared error as a measure to select the best predictive S model and the best predictive S+E model (Picard and Cook 1984, Hastie et al. 2009). The best predictive models were used to assign individual saguaros with an estimated age when they reached ≤ 1 cm in height (Steenbergh and Lowe 1977, Ceotto 2009). (2) The second step consisted in the assembly of a time series of recruitment events that described the dynamics of recruitment of saguaro in time. With the year-of-recruitment data, we built frequency distributions of recruitment events as a function of year, going from 1900 to 2016. We built a general recruitment curve where we considered recruitment on a regional scale (pooling all sites) and a series of population-level recruitment curves where we considered each site separately. The year of recruitment was estimated as the number of time units until size-at-recruitment was attained. With these data we constructed two recruitment curves (S and S+E model) with the estimated years-at-recruitment of all individuals. (3) In the third step we used a time-series analysis to explore the periodicity of recruitment events calculated at the regional and site levels using curves from both S and S+E models. We analyzed the periodicity of recruitment events of saguaro with wavelet decomposition analyses. Because we were interested in the periodicity of recruitment, we used the Morlet wavelet, as it has been shown to estimate the location of event frequency better (Mi et al. 2005). This analysis is a more appropriate approach, in comparison with, for example, Fourier analysis, in that it deals with a common feature of ecological time series (Cazelles et al. 2014), namely, their nonstationarity (i.e., time series properties vary with time; Cazelles and Hales 2006). It does so by estimating the spectral characteristics of the time series as a function of time using a mother wavelet. We estimated the periodicity of recruitment on a regional and a population level for both S and S+E recruitment curves, each of which was composed of a regional wavelet power spectra heat map and both regional and population-level periodicity curves. Higher values in the power spectra

heat map indicate higher intensity at which time-frequency recruitment events occur. The power spectra heat map is also analyzed within a “cone of influence,” which delimits the region influenced by edge effects (Cazelles et al. 2008). The spectral characteristic we were interested in was the periodicity curve, and from it, we extracted its local maxima, which corresponded to the most prominent periods in the time series. We analyzed the frequency of local maxima across sites to detect the most frequent periodicities. All analyses were performed in R (R Development Core Team 2020) using packages lme4 (Bates et al. 2015), gamm4 (Wood and Scheipl 2017), and wavScalogram (Bolos and Benitez 2019). See Data S1 for R code details.

RESULTS

Inverse growth models

From a total sample of 1,487 saguaros, we determined the year of recruitment of 1,449 saguaros when using a model without considering environmental variables (2.6% of saguaros were excluded), and 1,403 saguaros when considering environmental variables (5.7% of saguaros were excluded; Appendix S1: Table S1). Because our modeling approach relies on individuals that grow over time, exclusion of some individuals was due to a failure to decrease their height in time based on our models. The best predictive models were GAMM for both the S and S+E models. We chose the smallest mean-square error from both sets of models constructed with the leave-one-out cross validation procedure (Appendix S1: Table S2). The best-predictive S model was a GAMM that included the independent effects of size at $t + 1$ as a fixed effect and site as a random effect. Size at $t + 1$ was positively related with size at t such that every unit increase in size at t corresponded to 0.939 cm in size at $t + 1$. The best-predictive S+E model was also

a GAMM that included the independent effects of size at $t + 1$, SWS, and PDSI as fixed effects and site as a random effect. As expected, there was a positive effect of size at time $t + 1$ on size at t ; and positive effects of SWS and PDSI (Table 1). This result shows that the most important factor for saguaro growth is its prior size. However, environmental variables also played a role in saguaro growth, but this effect was one order of magnitude smaller for the PDSI and two orders of magnitude smaller for the SWS than of prior size (Table 1). Any unit of increase in PDSI contributed 0.09 units of increase in size at time t (Table 1). Similarly, any unit of increase in SWS contributed 0.005 units of increase in size at time t (Table 1).

Reconstruction of recruitment curves

In both regional models (S and S+E), the resulting curves reconstructed the saguaro recruitment dynamics, showing that most of our modeled individuals recruited in the second part of the 20th century (Fig. 2). The two curves show evidence that saguaro populations recruit in an episodic manner, with a large continuous episode of recruitment with varying intensity from 1960 to 2000. Recruitment curves per site suggest the same pattern (Appendix S2: Fig. S1).

Periodicity of recruitment

The wavelet power spectra show that multidecadal periodicities of recruitment have the best predictive power signals for the S model (red color in Fig. 3a) and shorter-term periodicities have the best predictive power signals for the S+E model (red color in Fig. 3c). Additionally, we constructed 26 population-level wavelet power spectra heat maps, which show higher similarity of within-population time-period intensity of recruitment, suggesting differences in the recruitment dynamics

TABLE 1. Summary statistics of inverse growth models: S (GAMM) and S+E (GAMM) models.

Model	Effect	Coefficient	SE	t	P
log(size t) = spline(log(size $t + 1$))	Fixed effects				
	Intercept	-0.003	0.006	-0.516	0.606
	log(size $t + 1$)	0.939	0.01	89.49	<0.0001
	Random effects				
	Plot		0.005		
	Residual		0.002		
log(size t) = spline(log(size $t + 1$) + SWS + PDSI)	Fixed effects				
	Intercept	-0.0507	0.0120	-4.21	<0.0001
	log(size $t + 1$)	0.9340	0.0104	89.005	<0.0001
	SWS	0.0053	0.0039	1.353	0.176
	PDSI	0.0980	0.0049	19.771	<0.0001
	Random effects				
	Plot		0.0115		
	Residual		0.0022		

Note: GAMM refers to: generalized additive mixed-effects models, SE to standard error, SWS to soil water content at saturation, and PDSI to the Palmer drought severity index.

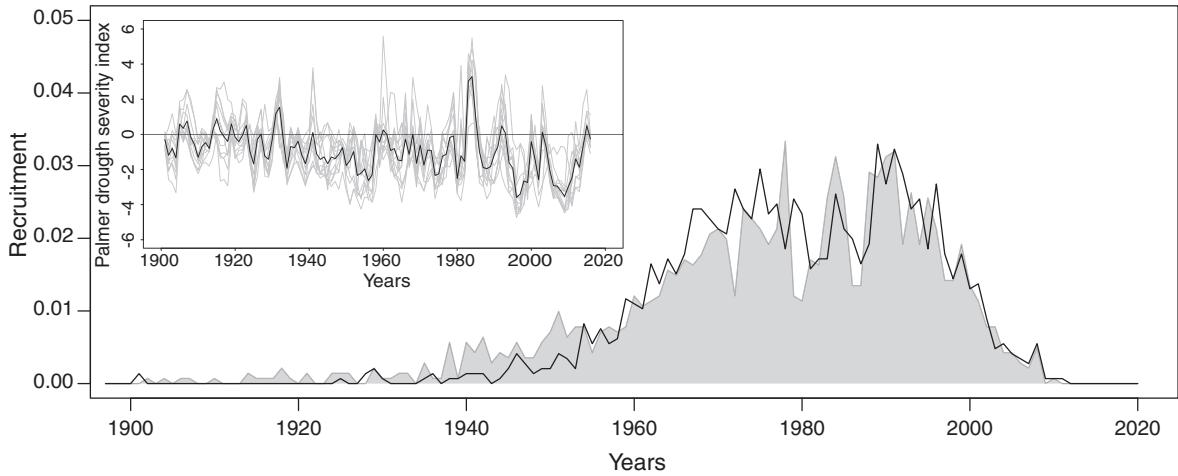


FIG. 2. Saguaro recruitment from 1900 to 2016. The gray line with gray filling on the area under the curve represents the recruitment density curve considering size at $t + 1$ (S model). The black line is the recruitment density curve predicted from the inverse models that considered the size at $t + 1$, Palmer drought severity index (PDSI), and soil water content at saturation (SWS; S+E model). Inset figure represents the time series of self-calibrated PDSI for the same range of years. Black line represents the average PDSI from all populations; gray lines represent PDSI per population.

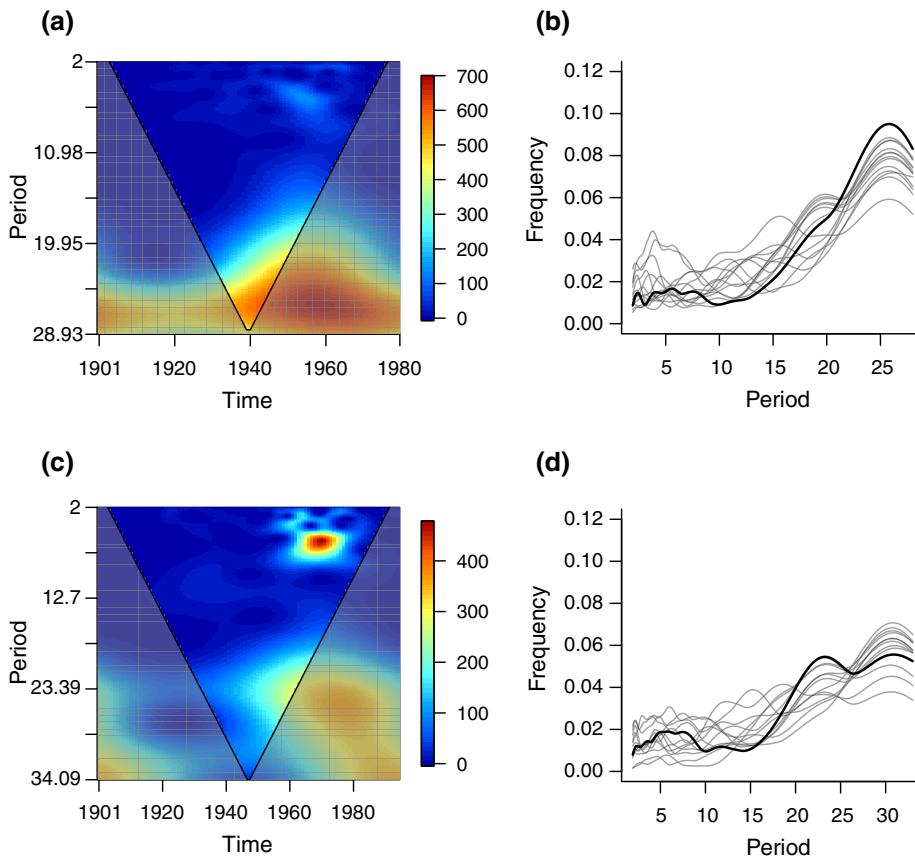


FIG. 3. Periodicity of recruitment of saguaros in Sonora, Mexico, estimated with a wavelet decomposition analysis. (a) and (b) Periodicity of saguaro recruitment from the S model; (c) and (d) periodicity of saguaro recruitment from the S+E model; (a) and (c) display to wavelet power spectra, the range of colors measure the power values of recruitment events, the cone delimited by black diagonal lines represents the zone within which edge effects do not affect periodicity; (b) and (d) refer to periodicity curves extracted from the spectra.

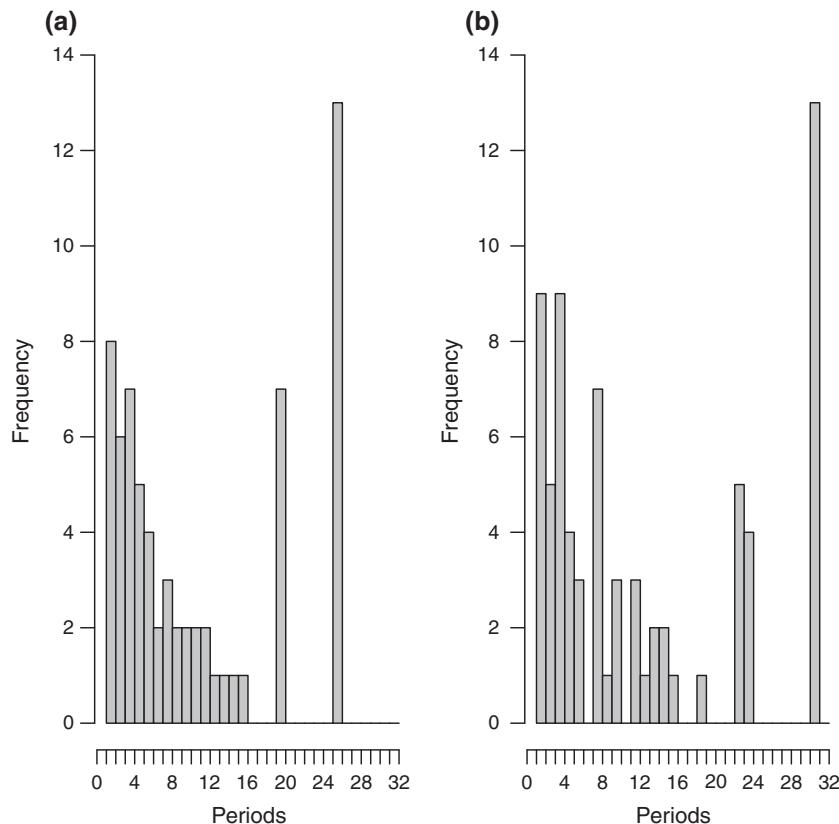


FIG. 4. Frequency of local maxima in years for 13 populations where (a) refers to S model and (b) refers to S+E model. For each site, see Appendix S2: Table S1.

among populations (Appendix S2: Fig. S2). Regionally, there were five modes (local maxima) of episodic recruitment in the S model (2, 4, 6, 8, and 26 yr; black line in Fig. 3b), while in the S+E model there were seven local maxima of recruitment (2, 4, 6, 8, 12, 23, and 31 yr; black line in Fig. 3d). The analysis of frequency of local maxima in recruitment events among sites revealed that long-term periodicities have higher frequency than those of shorter-term periodicities. Long-term periodicities are present in all sites, and short-term periodicities are more variable among sites (Fig. 4; Appendix S2: Table S1).

DISCUSSION

In this paper, we introduced a novel approach to model saguaro recruitment based on the size structure of the population and the year-to-year growth as affected by previous size and two environmental variables related to seedling recruitment: drought and soil characteristics. These models were used to postdict height decrements to a minimum size to assess recruitment time. Inverse growth models allow identifying the likely year of recruitment of individuals by predicting decreases in height and reconstructing the events or peaks of higher recruitment success. With the resulting recruitment curves, we estimated the modes of periodicity to study

the dynamics of episodic recruitment in saguaro. To our knowledge this is the first study that investigates recruitment of a long-lived plant such as the saguaro cactus in combination with environmentally driven inverse-growth models. Our models consider temporal, spatial, and individual variation in recruitment rates of the saguaro cactus in northern Mexico. The drought index represents variation at the temporal (among years) and spatial scales (among sites), and the SWS represents individual and spatial scales.

Long-term studies of plant demography in the North American deserts have repeatedly found complex relationships between demography and climate. For example, in a long-term study in vegetation plots in the Colorado Desert, Miriti et al. (2007) reported the episodic mortality of six common shrubs and one cactus species followed by severe regional drought. Their main finding was the unequal response of the species in the plots in relation to drought. This pattern was also observed by Bowers (2005), using 76 yr of monitoring of plant cover in permanent plots in Tumamoc Hill, Tucson, Arizona, where drought exacerbated the mortality of both long- and short-lived species, but mortality was also species specific. However, the drought effect on mortality was unclear in their study, because high mortality was also observed during periods of average to

better than average precipitation. More recent research by Ehleringer and Sandquist (2018) found that both mortality and recruitment events of three drought-deciduous-leaf shrub species in the Mojave Desert were episodic. They attributed high germination rates during El Niño years and high annual mortality rates during non-El Niño years.

Our results were consistent with the findings by previous saguaro studies linking demographic changes to drought and topographic features. For example, Winkler et al. (2018) found that recent severe drought events coincided with declines in saguaro establishment. Another recent study that used more than seven decades of data from annual demographic censuses found evidence where low recruitment years coincided with the driest decades (Orum et al. 2016). Furthermore, similar results were found by Conner et al. (2017), who concluded that periods of high establishment are followed by many decades of poor establishment. Additionally, land-use changes due to wood cutting and grazing in combination with long periods of drought might cause low rates of recruitment. Moreover, some studies demonstrate that during the past two centuries, patterns of saguaro establishment have varied across different locations, and these variations are highly synchronized to fluctuations in weather factors including large-scale phenomena like the global effects of volcanic eruptions and local topographic effects (Pierson and Turner 1998, Drezner and Balling 2002, 2008, Donnermeyer and Drezner 2012, Pierson et al. 2013).

According to our recruitment curves (Fig. 2), there is evidence of two contrasting recruitment periods during the 20th century. The first part of the period was dominated by lack of recruitment, and higher recruitment during its second part. Although recruitment peaks at the end of the 20th century were reconstructed using living saguaros, the occurrence of recruitment during the first part of the century cannot be determined from our data. It is possible that an absence of recruitment during the first part of the century and gaps in the recruitment curve are not only due to the recruitment dynamics, but also could be ascribed to mortality events during this period. Our data set could not have been able to reconstruct such recruitment periods because none of our sampled individuals were old enough to be traced back to the late 1800s. However, similar centennial patterns have been reported previously for other saguaro populations in the northern part of its distribution (Drezner 2006b, Conner et al. 2017). In fact, Conner et al. (2017) reported the same pattern of recruitment for single localities in the Saguaro National Park.

Our results also suggest that the periodicity of recruitment events fluctuates at short periods of 2–11 yr and longer ones of 20–30 yr. Our analysis also suggests that longer periods have stronger signals than shorter ones in the S model (red areas in Fig. 3a). In the S+E model, the shorter periods have a stronger signal than longer ones (red area in Fig. 3c). Short periodicities are

consistent with modulation by moderate to strong El Niño events, and longer periodicities are related to the upper 10 percentiles in the ranks of El Niño events (Wolter and Timlin 2011). The U.S. National Oceanic and Atmospheric Administration (NOAA) reports that the events of El Niño recur every 2–7 yr and usually last between 9 and 12 months (NOAA 2020).

Our approach is a space-for-time substitution that uses spatial patterns of individual growth to reconstruct long-term temporal recruitment dynamics of saguaro using environmentally driven models. Space-for-time substitution has been used to infer a variety of ecological processes such as biodiversity (Blois et al. 2013), phenological changes due to climate change (Buyantuyev et al. 2012), and ecological succession (Walker et al. 2010). The main critique of space-for-time substitution methods is that time is usually inferred by unknown past environments that are unable to detect transient ecological effects (Pickett 1989). We overcame this caveat by including past site-specific environmental variation (PDSI) with our environment-driven model of saguaro growth. This study, in comparison to other published saguaro recruitment studies (Drezner and Balling 2002, 2008, Orum et al. 2016, Conner et al. 2017, Winkler et al. 2018), aimed to analyze a larger spatial set of populations trying to include multiple sites representing as much environmental variability as possible. Although hot and dry conditions prevail in the Sonoran Desert, the intensity and frequency of wet pulses at a local scale vary substantially in space and time. Some recent studies have included habitat heterogeneity at a local scale to explain differences in recruitment success (Drezner 2006b, Winkler et al. 2018, Rodríguez-Buriticá et al. 2019), or even large numbers of small samples within the same regional locality (Drezner 2006a, Drezner and Balling 2008). These long-term data sets provide highly valuable, very fine temporal resolution, but little spatial variation. We argue that in order to understand the regeneration niche of saguaro seedlings, it is important to include as much variation in environmental variables that better represent the whole geographic distribution of the species.

Drought and uncommon environmental conditions like these related to El Niño events play a major role in the regeneration niche of the saguaro cactus. Seedlings tend to have a smaller range of tolerance for environmental stress than that for adults. This might be related to the volume of larger saguaros that are able to withstand more environmental stress than smaller individuals (Williams et al. 2014, Hultine et al. 2016). As a result, long-lived species such as the saguaro cactus develop highly unsynchronized regeneration niches in relation to ontogeny. Episodic dry periods will result in mortality events for both adults and seedlings. However, adults can tolerate more stress and therefore have a differential lower mortality rate. In terms of population regeneration, it is also important to note that bad years in which high mortality of adults could occur may also

hinder future recruitment by reducing possible nurse sites under large, old saguaros or other large desert perennials that respond to the same environmental cues. Dry periods are eventually followed by wetter periods in which the conditions for seedling recruitment will be permissive. Hence, the length of the periodicity of recruitment will be then influenced by the length of the species life cycle, as Silvertown and Charlesworth (2009) suggested. Results from previous and the present work reaffirm that saguaro population regeneration fluctuates in response to climate and confirms that the intervals of wet periods are sufficient to maintain stable populations. Under the present conditions of global climate change—where extreme events, higher temperatures, and higher evapotranspiration are becoming the rule—slight shifts in the regeneration niche of seedlings and saplings could lead to lack of recruitment for time scales outside the population's tolerance limits, ultimately prompting the local disappearance of otherwise healthy looking adult populations.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3458/supinfo>

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Data (Larios et al. 2021) are available in the Dryad digital repository (<https://doi.org/10.5061/dryad.rn8pk0p99>).