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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.

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.

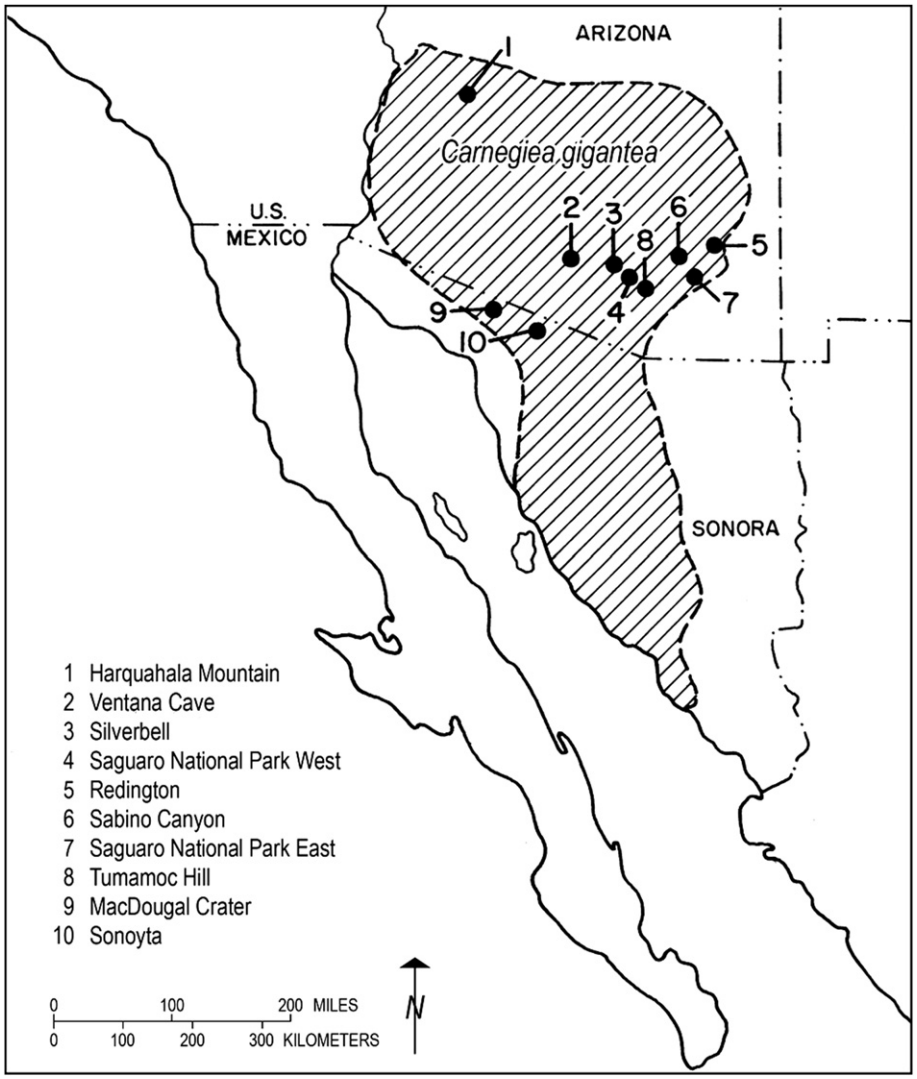

Fig. 1. Map of the saguaro plots used in this study. The locations of ten sites containing permanent plots established between 1959 and 1963 are indicated by circles. The shaded area on the map shows the approximate range of saguaros.