

## AN 85-YEAR STUDY OF SAGUARO (*CARNEGIEA GIGANTEA*) DEMOGRAPHY

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**Abstract.** The saguaro population in a 700-ha area at the Desert Laboratory on Tumamoc Hill, Tucson, Arizona, was censused in 1908, one year after livestock were excluded. In 1964, four 10-ha plots were established within the original area to determine the effect of slope aspect on plant growth and demography. The plots were recensused in 1970 and 1993. We developed a model for determining saguaro age, using the growth rates of over 3000 plants from 1964 to 1970. The model was verified with 1993 data. Changes in population size and the estimated age structures were then used to infer regeneration trends.

Saguaro populations on all slope aspects nearly doubled since 1908. Yet, during the same period, relative abundances of saguaros remained higher on the south and east aspects than on the north and west aspects. Higher recruitment and survival of young plants rather than mortality of older ones are largely responsible for the differences between aspects.

The estimated age structures show large, multi-decadal fluctuations in saguaro regeneration. Prior to 1908, populations on all slopes experienced an extended period of decline beginning around the late 1860s. The recent surge in recruitment began in the 1920s and peaked in the 1970s. Populations currently are again in decline. Better regeneration generally corresponds with relatively wet conditions, and poorer regeneration with drier conditions. However, extended periods of decline often included episodes of relatively wet conditions (e.g., from the 1860s to the 1920s), indicating that other climatic and biotic factors also determine recruitment success. Establishment may have been suppressed by colder winters, livestock grazing, and rock quarrying.

This long-term study demonstrates that, despite low regeneration and population decline during much of the last two centuries, saguaros have persisted on Tumamoc Hill because of episodic surges in seedling establishment.

**Key words:** *cactus*; *Carnegiea gigantea*; *climatic effects*; *land use effects*; *long-term studies*; *regeneration trends*; *modeling*; *saguaro demography*; *slope aspect*, *effect on plant demography*; *Sonoran Desert*; *stand age structure*; *survivorship and mortality*.

### INTRODUCTION

The saguaro (*Carnegiea gigantea* [Engelm.] Britton & Rose) is a prominent, long-lived, columnar cactus of the Sonoran Desert, occurring throughout much of southern Arizona, USA, and western Sonora, Mexico (Turner et al. 1995). It has an average life-span of 125–175 yr and a potential life-span of almost three centuries. Like many long-lived, woody plants of the Sonoran Desert, it reproduces episodically when a series of climatic and microhabitat conditions are met (Shreve 1917, Steenbergh and Lowe 1977, Goldberg and Turner 1986, McAuliffe 1988, 1990, Turner 1990, Parker 1993, Bowers 1994, Bowers et al. 1995). As a result, substantial fluctuations in population size and age structure may occur on decadal or longer scales (Goldberg and Turner 1986, Turner 1990, 1992, Parker 1993). Distinguishing long-term population trends from erratic, short-term dynamics requires observations span-

ning several decades, yet demographic studies of plant populations spanning more than two or three decades are rare (White 1985).

In the absence of long-term plot data, regeneration trends through time frequently are inferred from stand age structure. Precise age estimates for many woody desert species are impossible because they lack distinct annual xylem rings. Early work on columnar cacti suggested that careful measurements of plant heights over several years could be used to statistically estimate growth rates, and from these, ages (Shreve 1910). Subsequent work confirmed that saguaro and several other species of columnar cacti are ideally suited for modeling regeneration trends based on age structure because the relationship between annual growth and size is predictable (Hastings and Alcorn 1961, Steenbergh and Lowe 1983, Parker 1988, 1993, Turner 1990, Bowers 1997).

The age structures of populations at single time points have previously been used to forecast the health of saguaro populations (Shreve 1910, Alcorn and May 1962, Niering et al. 1963, Parker 1993). However, single censuses from different decades have suggested that

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the same population was nearing extinction (Alcorn and May 1962, Niering et al. 1963) or dramatically increasing (Turner 1992). Only two previous studies have utilized repeated, long-term observations of population age structure to capture long-term population fluctuations (Turner 1990, 1992). Ours is the first study in which a model for determining saguaro age using growth rates from one observation period was verified using observations from a later separate period.

This study builds on two of the earliest studies of saguaro populations, conducted in 1908 and 1910 at the Desert Laboratory on Tumamoc Hill, in Tucson, Arizona, USA. First, two maps were produced recording the location of all saguaros and their clear preference for steep and south-facing aspects (Spalding 1909: Plates 15 and 16). Two years later, Shreve (1910) reported height-specific growth rates derived from naturally occurring and garden-grown plants. From these he derived population age structure, noting that young saguaros (<60 yr old) were not present in sufficient numbers to maintain the population.

Our recent saguaro censuses (1964–1993) at Tumamoc Hill cover only a portion of the area originally mapped, yet include over 4000 saguaros in four permanent plots. The plots, each ~10 ha in size, are located on the north, south, east, and west slopes of the hill. This placement was designed to compare the effect of slope aspect on saguaro growth and demography. A preliminary report of the 1964 and 1970 population sizes demonstrates a continued preference of saguaros for south and east aspects (Turner and Bowers 1988). We hypothesized that differences in recruitment, growth rates, and mortality across slope aspects would provide insight into factors affecting general patterns of saguaro abundance.

In this paper, we present methods to estimate saguaro ages from their mean height-specific growth rates. We use population age structure to infer regeneration trends when compared to a theoretical age structure defined by a constant, age-specific survivorship rate. We report changes in population size and age structure based on plant surveys from 1908 to 1993 and discuss changes with respect to the influence of climate, weather, and disturbance.

#### *Study area*

Tumamoc Hill is an outlier of the nearby Tucson Mountains, near the northeastern border of the modern saguaro distributional range (Turner et al. 1995). Tumamoc Hill is composed of Tertiary volcanics, primarily basalt, andesite, and rhyolitic tuff (Tolman 1909) and reaches an elevation of 948 m, 245 m above the surrounding alluvial plain. About half of the grounds of the Desert Laboratory (total of 352 ha) are on steep terrain with shallow, clayey soils containing petrocalcic horizons and many colluvial basalt boulders and cobbles; the remainder is level to rolling, composed of sandy soils that are relatively free of rocks (Phillips

1976). The permanent plots extend from the top of Tumamoc Hill to the surrounding base; at least two thirds of each plot occurs on steep, rocky substrate. Substrate composition does not differ substantially among plots.

The vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951, Turner and Brown 1982). A complete species list for Tumamoc Hill has been compiled (Bowers and Turner 1985) and changes in woody and succulent species in permanent plots over a 72-yr period have been reported (Goldberg and Turner 1986).

The Desert Laboratory was fenced in 1907 and has been free of livestock grazing since then (Shreve 1929). Light to moderate grazing by horses and cattle started about 1858 and reached a maximum just prior to fencing (Shreve 1929). Fencing also reduced human activities including the removal of rocks for building material, the removal of vegetation for transplanting, and recreation. Tolman (1909) reported that the surface of Tumamoc and the adjacent two hills were significantly altered by the removal of rocks between 15 cm and 1 m in diameter prior to fencing. Since fencing, the Desert Laboratory has been maintained as an ecological preserve, although easements outside the saguaro plot area (for utilities and a local rock quarry/landfill) have been granted. Despite protection, introduced species now comprise one seventh of its flora (Bowers and Turner 1985, Burgess et al. 1991).

#### METHODS

##### *Field censuses: 1908, 1964, 1970, 1993*

In 1908 all saguaros over a 700-ha area including Tumamoc Hill and the adjacent Sentinel Hill were surveyed using a plane table. The resulting two maps show the location of all saguaros and prominent physical features of the site at a scale of 1:6000 (Spalding 1909: Plates 15 and 16). To determine population size in 1908, we counted the number of saguaros on the maps occurring within the areas defined by our modern plots (Fig. 1).

In 1964 we established four permanent plots (Fig. 1) within the original census area. The north, south, east, and west plots are ~11.1, 11.0, 8.8, and 10.8 ha, respectively. Only those areas with the same slope aspect were included within each plot, hence the irregular shape and the interruption of the north plot (Fig. 1). Every saguaro within the plots was assigned a unique number and located on aerial photographs (scale 1:1800) subsequently used as plot maps. Height (from base to top of the main stem), general condition (type and severity of injuries), and number of branches of each saguaro also were determined. At later censuses (1970, 1993), we gathered the same demographic information; additionally, newly established individuals were located and numbered on plot maps, and deaths of previously censused plants were noted. In 1964 and

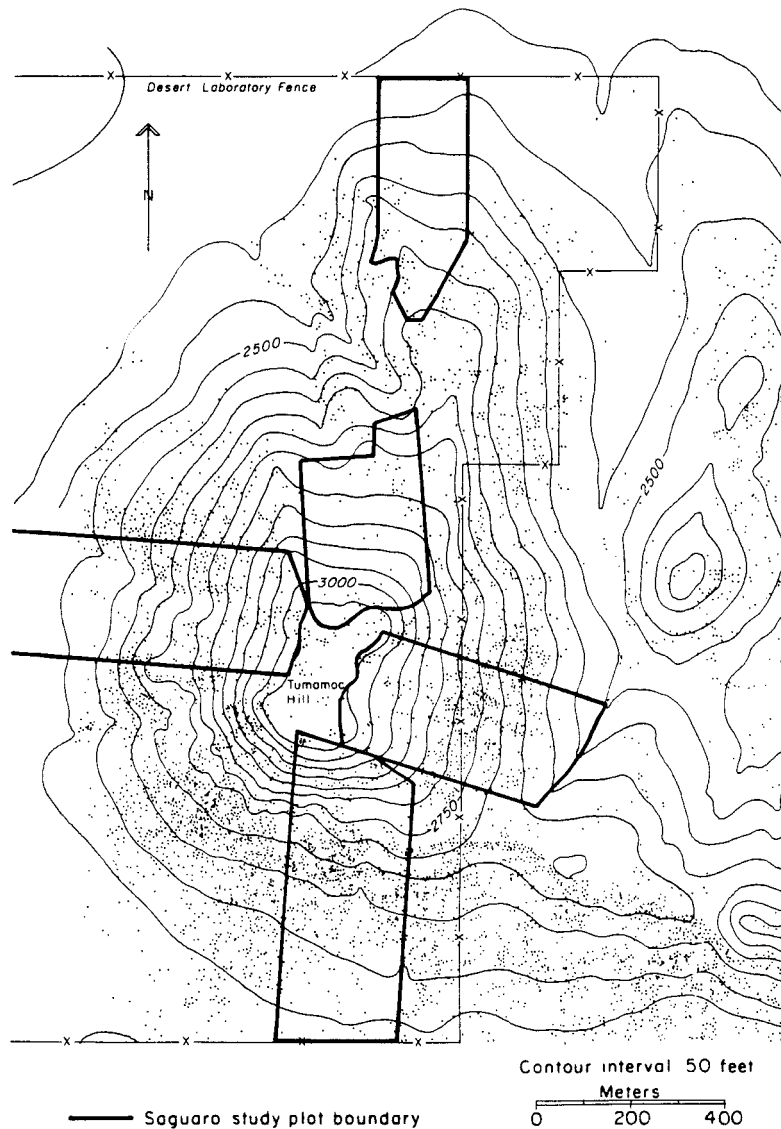


FIG. 1. Reproduction of the 1908 map (Spalding 1909: Plate 15) of Tumamoc Hill, Sentinel Hill, and the surrounding vicinity showing the location of all saguaros (black dots) and slope contour lines. The location of the four permanent study plots established in 1964 are superimposed on the map. Not all of the west plot is shown. (Reprinted from Turner and Bowers [1988: Fig. 1], with permission of the Office of Arid Lands Studies, University of Arizona, Tucson, Arizona, USA.)

1970 heights were measured with a telescoping survey rod. In 1993 the locations of all saguaros were surveyed using an electronic distance meter. Heights of all saguaros  $>2$  m were determined trigonometrically from survey data; heights of smaller plants were measured directly. Data (saguaro presence/absence only) for an additional census conducted on the north slope in 1987 are also given.

#### *Saguaro age determination*

Saguaro age was estimated from the nonlinear relationship between growth rate and height. Growth rates of all saguaros in each plot were determined from the difference in their height measurements in 1964

and 1970. Average height and annual growth during this period were calculated for each plant and then combined into 0.5-m height classes (Fig. 2A). Data from leaning or severely injured plants were not used.

We used a Fortran (IMSL 1991) cubic smoothing spline routine (CSSMH) to fit a curve to the average data using the standard error of the mean growth rate for each height class as a weighting factor. The continuous spline function can be used to generate a matrix of estimated average growth rates for centimeter size classes. Only height classes that contained at least six observations were used to make the spline. For the taller height classes, which have the fewest observations, we sometimes pooled observations into 1-m

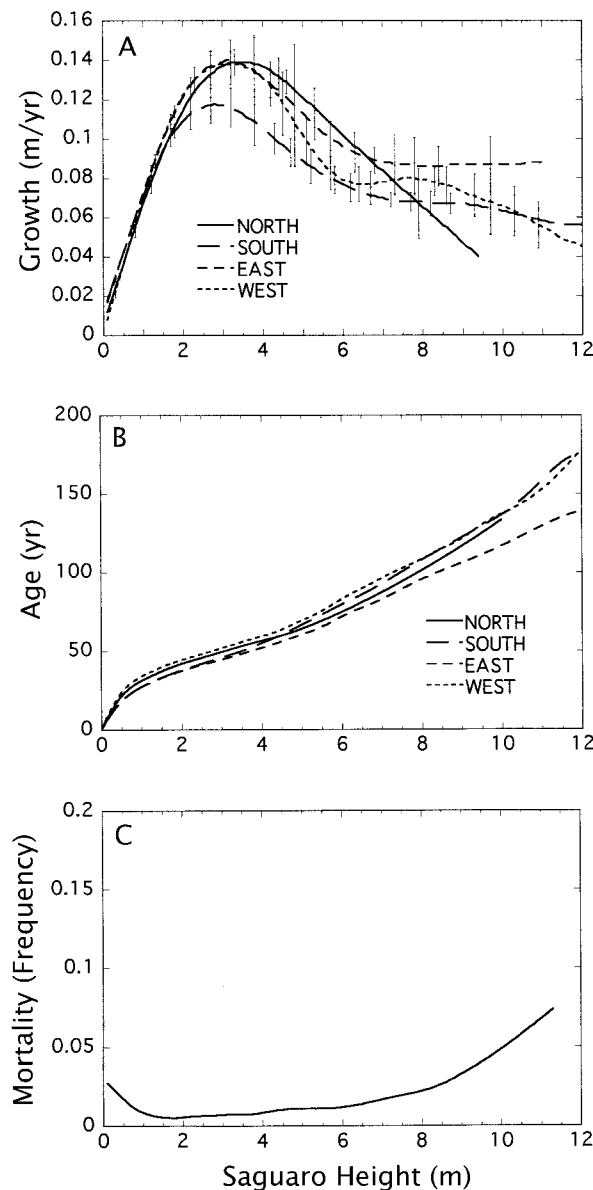


FIG. 2. (A) Saguaro annual growth rate as a function of height for plants located in north-, south-, east-, and west-facing plots. A cubic smoothing spline has been fitted to the average growth rate for individuals in 0.5-m height classes. The standard error of the mean for each height class is indicated by the error bars. (B) Saguaro age as a function of height based on our model of growth rates. (C) The annual mortality rate by height as defined by a cubic smoothing spline. Average annual mortality was estimated from the frequency of deaths observed over the 6-yr interval (1964–1970) summarized by 0.5-m height classes.

classes. We estimated the “goodness of fit” of the spline by plotting the difference between observed and spline-generated average growth rates as a function of height class (Fig. 3A).

The relationship between age and size (Fig. 2B) was determined by integrating the inverse of the spline

function describing the growth rate–height relationship. The age–size relationship for each plot was then used to estimate the age of each saguaro in that plot based on its height. To test the reliability of the age–size model (based on our observations of growth between 1964 and 1970), we compared the estimated ages of saguaros in 1993 based upon their observed height that year with their 1993 age predicted from their estimated age in 1970 plus 23 yr (Fig. 3B). We used regression analysis (SAS Institute 1993: REG procedure) in this comparison (Fig. 3B). The mean difference between age estimates provides a measure of the model’s ability to predict the average age of saguaros as a function of height (Fig. 3C).

#### *Population age structure and analysis of demographic trends*

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 size was corrected to include those plants overlooked, yet undoubtedly present based on their size when discovered. Thus, population sizes reported here differ somewhat from preliminary reports of population sizes in 1964 and 1970, which do not include overlooked individuals (Turner and Bowers 1988). Saguaros for which reliable age estimates could not be made (due to injuries or errors in height measurement) were excluded from the age-structure analysis. Exclusions generally accounted for <15% of the population and were primarily older individuals with broken tops. The annual establishment values are expressed as 5-yr running means to smooth interannual variation (Fig. 4).

A survivorship curve was determined empirically from the pattern of height-specific mortality observed on all four slopes. The deaths were pooled across slopes in order to provide a sufficient number to model. Average annual mortality was estimated from the frequency of deaths observed over the 6-yr interval (1964–1970) summarized by 0.5-m height classes (Fig. 2C). A cubic smoothing spline was used to describe the relationship between mortality and plant height. Similar to the previous application, the continuous spline function can be used to generate a matrix of estimated mortality rates for centimeter size classes. Using this function, age-specific mortality and survivorship were calculated from the age–height function for each plot.

The survivorship curve determined for each plot was then scaled so that the area under the curve was equal to the size of the observed population at each census date (Fig. 4: top panels for each slope; scaling factor = [total population size]/[area under survivorship curve]). The scaled survivorship curve shows the predicted number of individuals in each age class needed to maintain the current population size, given a constant age-specific survivorship rate (i.e., the curve predicts a stable age distribution).

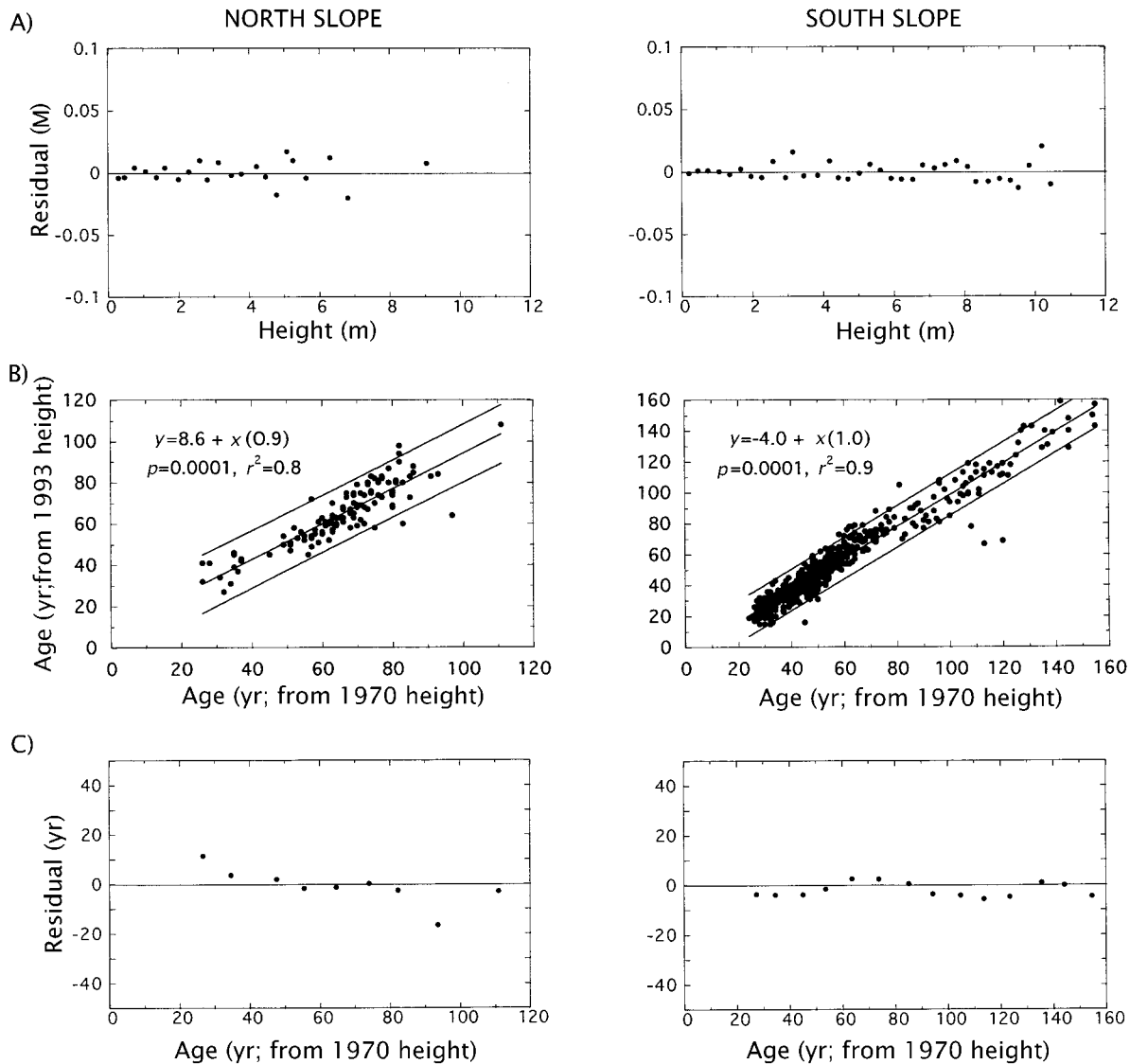


FIG. 3. (A: top four panels) For each slope, residual plots of the difference between the average observed growth rate and the average growth rate predicted by the spline ( $y_{obs} - y_{pred}$ ) for each 0.5-m height class for each slope. (B: middle panels) The age of each saguaro in 1993 predicted from its height in 1993 and from its estimated age at the previous census in 1970. Regression equations,  $P$  and  $r^2$  values, and the lines generated by the regression equation (center line) and upper and lower 95% confidence intervals are given. (C: bottom panels) Residual plots of the difference in average age estimates ( $Age_{[from 1993 ht]} - Age_{[from 1970 ht]}$ ) for each 0.5-m height class.

We used the differences between the survivorship curve and the observed age distribution to highlight periods of time during which regeneration hypothetically was greater than or less than necessary to maintain the current population size. The residual values (differences) were standardized by dividing the difference 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 and then scaled so that the values ranged from  $-1$  to  $1$ , thereby making the range in

positive and negative deviations comparable (Fig. 4: bottom panels for each slope). Because we cannot determine whether deviations from the survivorship curve are a function of recruitment or mortality, we use the term "saguaro regeneration" to encompass both possibilities.

#### *Saguaro reproductive potential*

Saguaro flowers occur mainly at the apices of the primary stem and branches of plants  $\geq 2$  m tall (Fig. 5C). We estimated reproductive potential (number of reproductive stem tips) at each census by adding the total number of plants  $\geq 2$  m tall and the number of



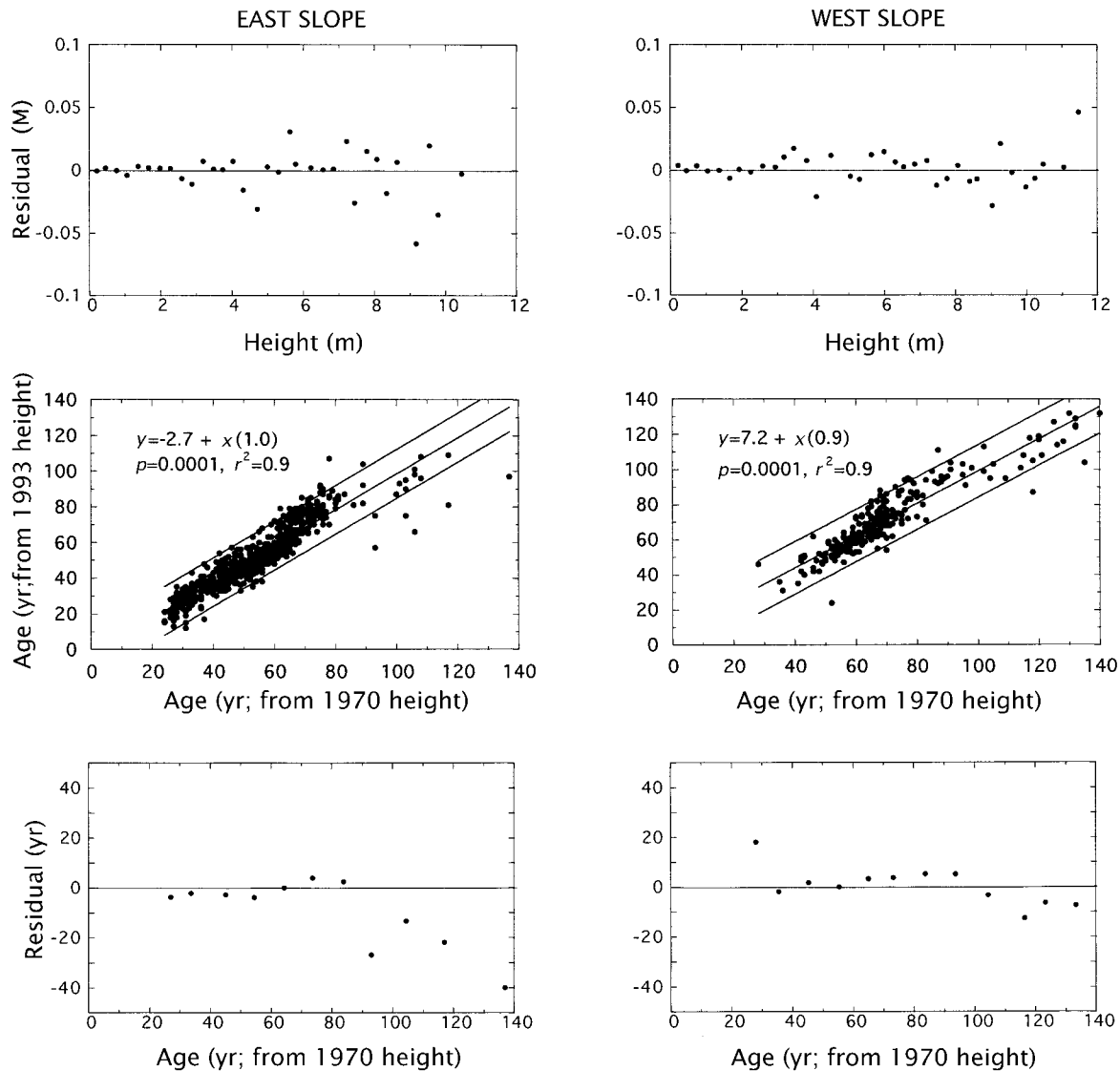


FIG. 3. Extended.

branches on these plants. All branches were considered reproductive, although branches may not reach this status until 2–3 yr after initiation (Steenberg and Lowe 1977).

#### *Summary of climate variables*

Climate was summarized using a series of variables (Fig. 6) including: spring (February–May), summer (June–August), autumn (September–October), and winter (November–January) precipitation; winter (November–March) minimum temperatures; number of days experiencing temperatures below freezing; and number of days above 38°C. These seasons were defined from the synoptic climatologies affecting southern Arizona (Webb and Betancourt 1992). The frequency of severe freezes was expressed as the number of days with temperatures below –8.3°C or the number

of two or more consecutive days with temperatures below –2.2°C (Bowers 1981). Daily climate data were from the University of Arizona weather station in Tucson, Arizona. We also used Palmer Drought-Severity Index (PDSI) values (Alley 1984) derived from these temperature and precipitation records. A measure of the length of favorably wet and unfavorably dry conditions during a year was estimated from the PDSI. For each year, the number of months that were wet ( $\text{PDSI} > 2$ ) and the number of months that were extremely dry ( $\text{PDSI} \leq -3$ ) were calculated. The climate variables were expressed as 5-yr running means to maintain consistency with saguaro regeneration, also expressed as a 5-yr running mean.

We also employed a long-term record of summer PDSI (June, July, August) reconstructed from tree-ring widths based on a generalized tree-ring chronology for

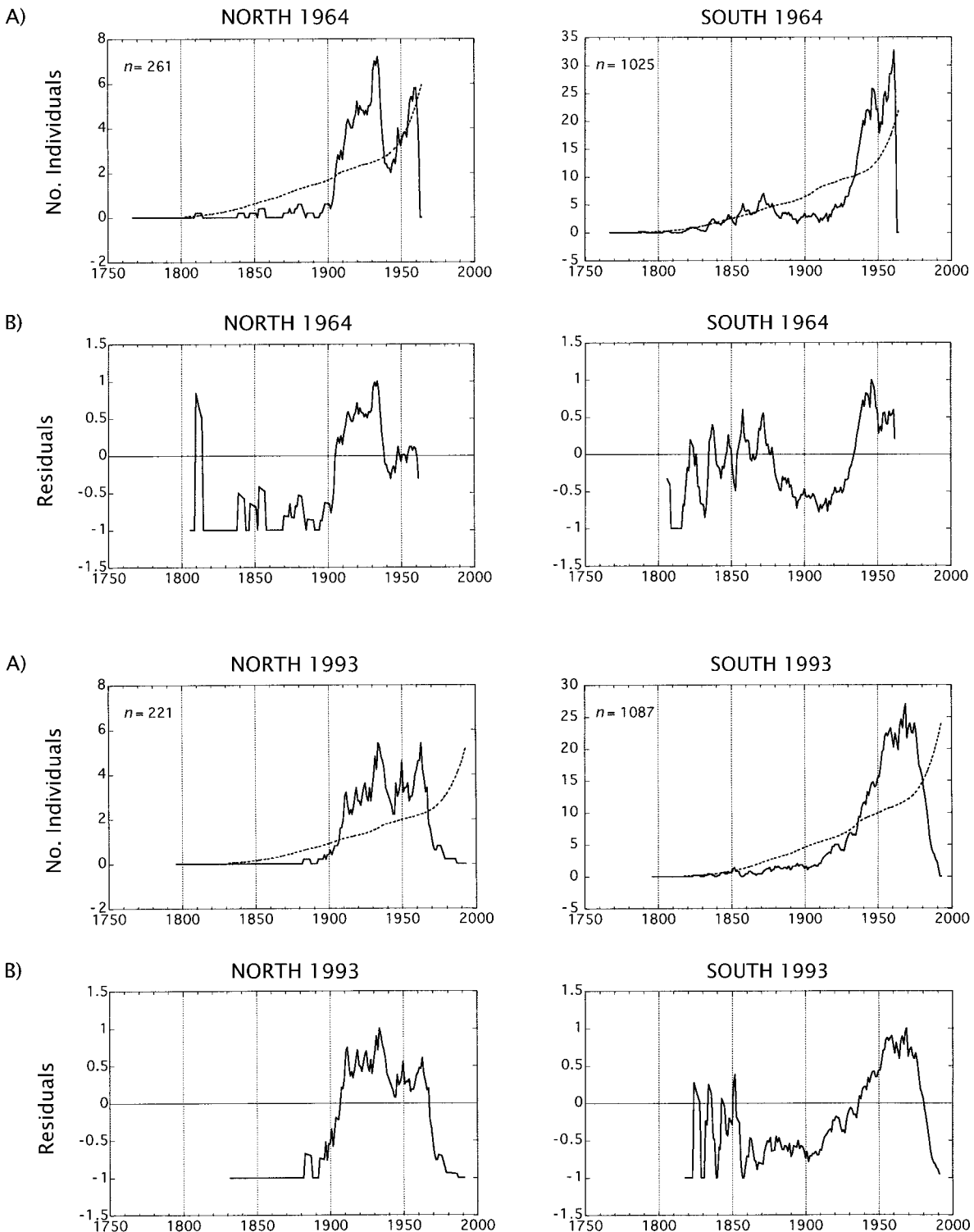
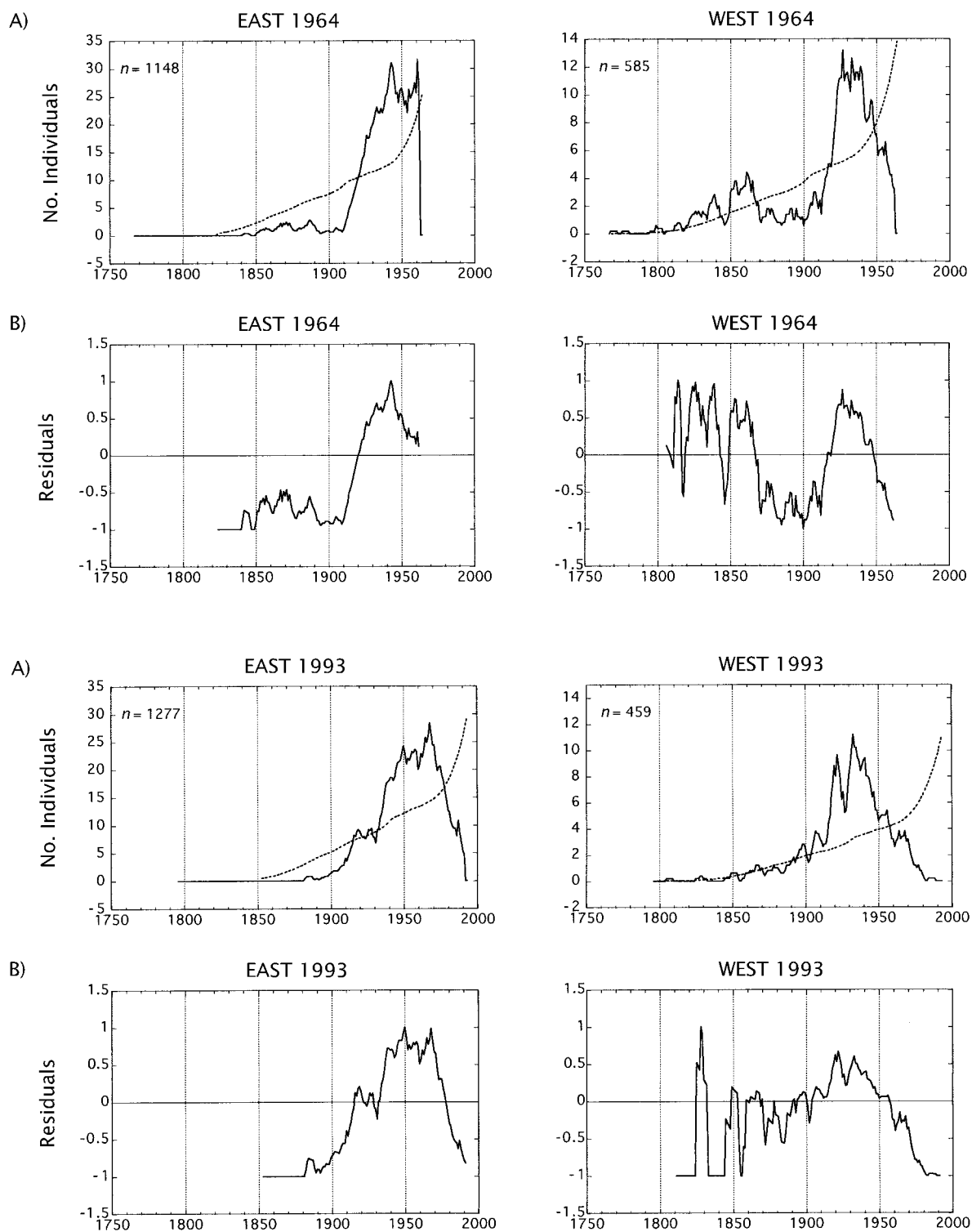


FIG. 4. For each slope, we show (A) observed age distributions expressed as 5-yr running means (solid lines) and predicted age distributions defined by the survivorship curve based on constant age-specific mortality rates (dotted lines) for the first (1964) and last (1993) census dates;  $n$  = no. of saguaros in each age distribution. (B) Residuals based on the difference between the observed and predicted cohort size, standardized to the number of observations at each date, normalized by the mean and standard deviation of the residuals, and scaled to range from  $-1$  to  $1$  for each census.





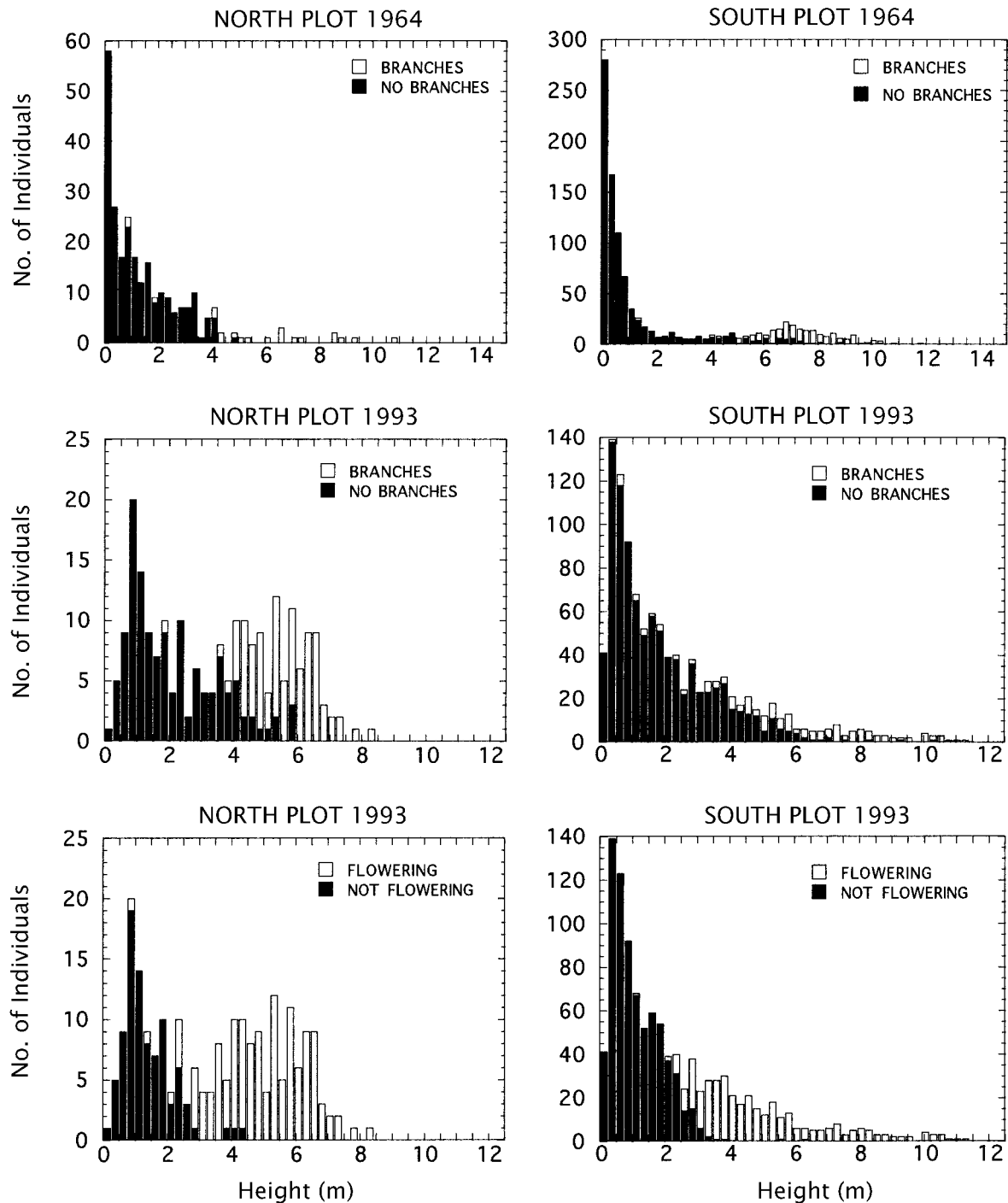


FIG. 5. (Top) For each slope, frequency of saguaros in each plot with and without branches in 1964. (Middle) Frequency of saguaros with and without branches in 1993. (Bottom) Frequency of saguaros with and without flowers in 1993. Data are summarized by 0.25-m height classes. Open and closed bars are stacked to show the total number of saguaros in each height class.

the Tucson Basin (D. M. Meko [Tree Ring Laboratory, University of Arizona], *unpublished data*). The annual PDSI values were summarized using a 10-yr moving average, to show decadal variability in this long-term record.

## RESULTS

### *Saguaro growth rates*

Splines that best fit the growth–height data for each slope are similar, but not identical (Figs. 2A, 3A). In

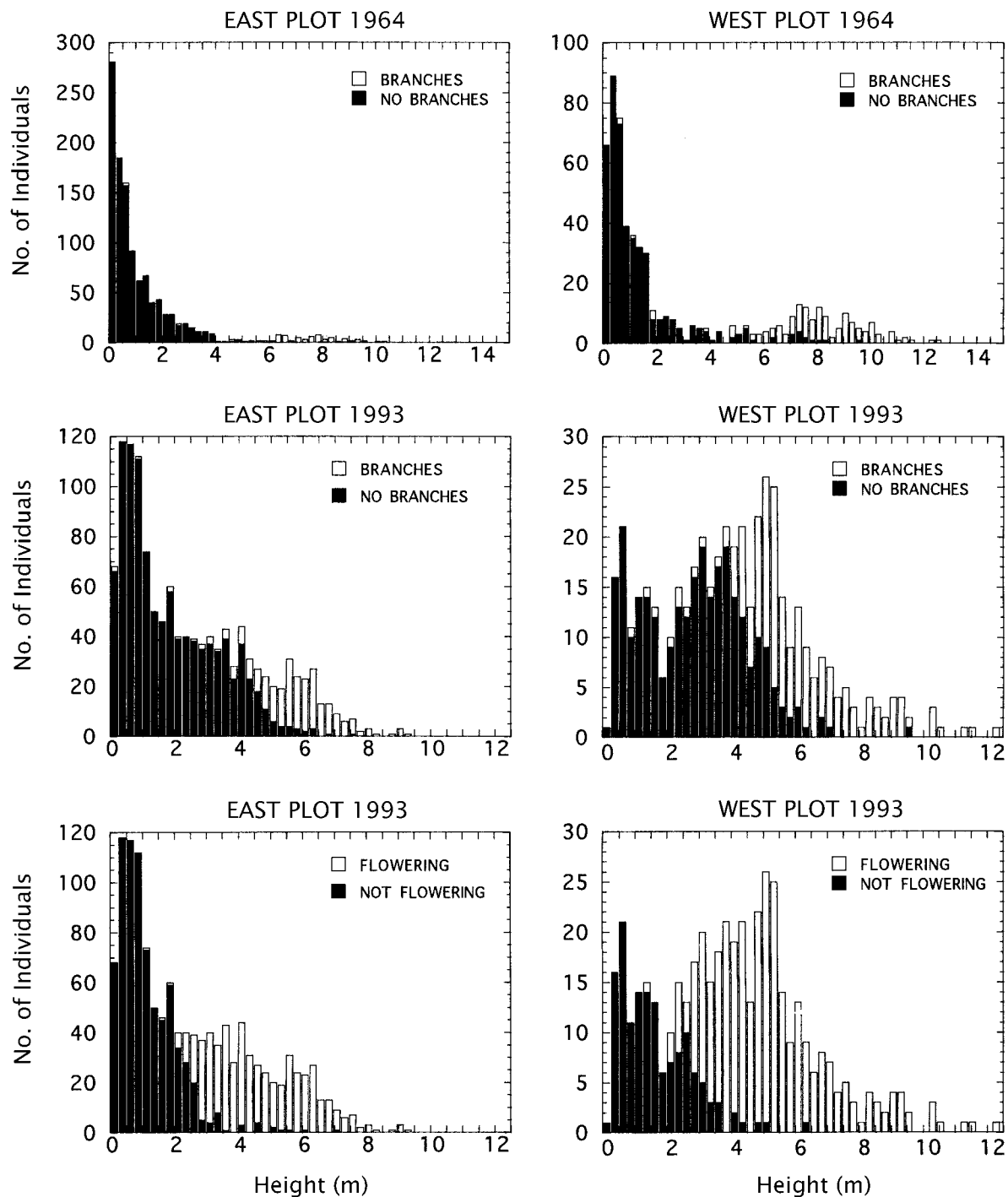


FIG. 5. Extended.

general, annual growth increases rapidly with size to a distinct maximum when saguaros reach a height of 2–4 m, declines steeply to a second inflection at heights between 6 and 7 m, and then decreases at a nearly constant and more gradual rate as saguaros age. Because the small number of saguaros >5 m in height on the north aspect limits our ability to model their growth

rates, the absence of the second inflection for that plot is not significant.

The shape of the growth–height function reflects stages in the phenological and morphological development of the saguaro (Steenbergh and Lowe 1983). The rapid increase in annual growth up to 2 m is a function of the increasing photosynthetic surface area

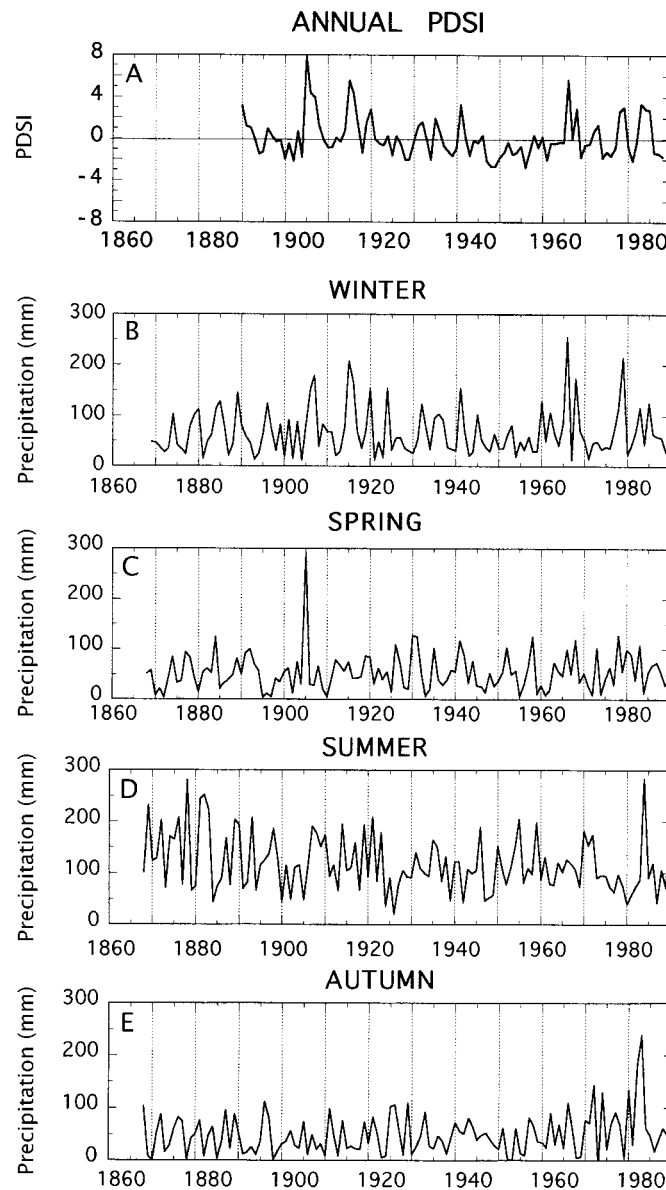


FIG. 6. Climate data for Tucson, Arizona (USA). (A) Average annual Palmer Drought-Severity Index (PDSI). (B)–(E) Precipitation: winter (Nov.–Jan.), spring (Feb.–May), summer (Jun.–Aug.), and autumn (Sep.–Oct.). (F) PDSI indexes showing the number of months with wet conditions ( $\text{PDSI} > 2$ ) and extremely dry conditions ( $\text{PDSI} \leq -3$ ). (G) Winter minimum temperatures and the number of severe freezes. (Note: these cannot be accurately determined for the period from 1960 to 1993 because Tucson temperature data show a pronounced urban heat island effect by 1960 [Cayan and Douglas 1984]). (H) Number of days in which the temperature exceeds  $38^{\circ}\text{C}$ . (I) Long-term data reconstructed from tree-ring chronologies for the Tucson vicinity including annual summer (June, July, August) PDSI and the 10-yr moving averages (lower curves) of annual values. Also shown is the coefficient of variation ( $\text{cv} = \text{standard deviation}/\text{mean}$ ) calculated for each 10-yr interval (upper curve). Low cv (peaks on graph) denotes periods with low variance and high PDSI (i.e., consistently wet summer conditions).

and water storage capacity with increasing plant size. The decline in the mean annual growth of saguaros once they reach 2–4 m coincides with diversion of resources to flowering. We observed that plants on all aspects typically flowered when they reached  $\sim 2$  m (Fig. 5C), as is the case for other Tucson populations (Steenbergh and Lowe 1977). Saguaro are generally

taller at the onset of flowering near their western limits (Brum 1973). When plants reach  $\sim 6$  m, growth rates become essentially constant with increasing plant size. This second inflection is correlated with the proliferation and growth of branches by most members of the population (Fig. 5A and B). Branches increase assimilation of photosynthetically active radiation (Geller

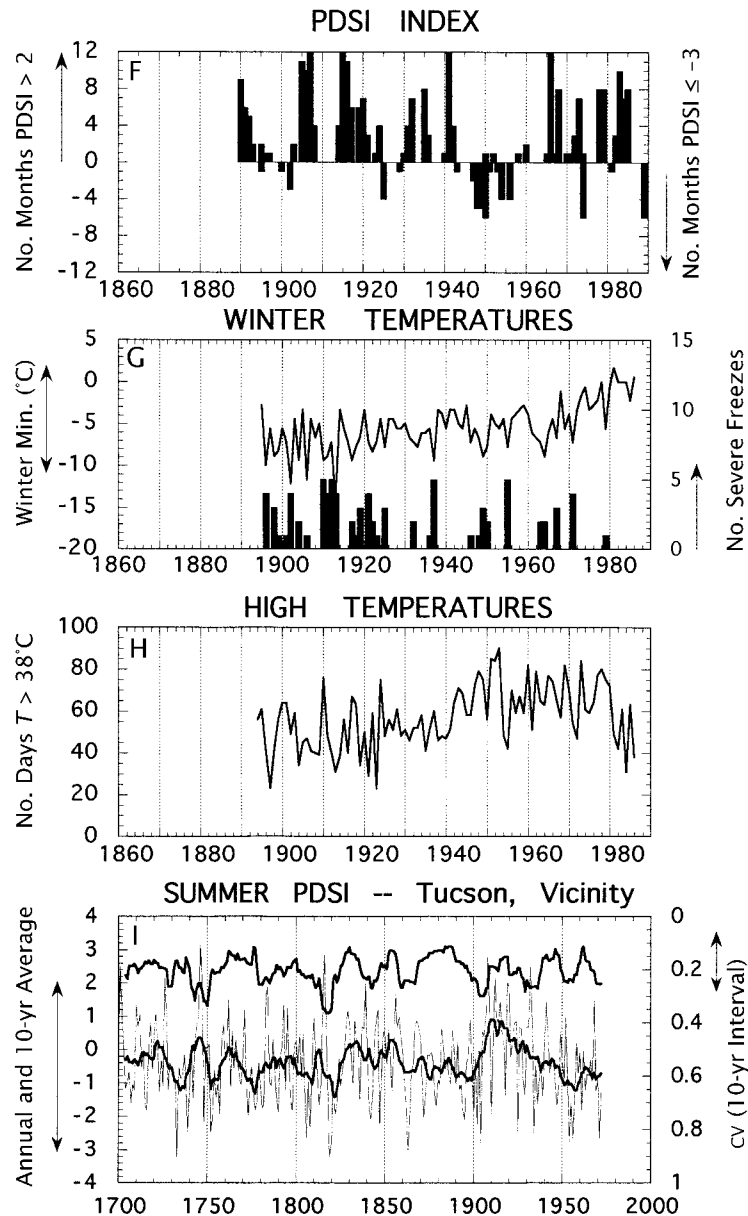


FIG 6. Continued.

and Nobel 1986). However, on Tumamoc Hill, branching does not result in an increased rate of height growth, suggesting that any increase in photosynthetic capacity with branching is largely offset by the energy cost of branch growth and reproduction.

Height-specific growth rates were almost identical on all aspects (Fig. 2A), although growth rates for intermediate size saguaros (2–5 m) were slowest (based on standard errors) on south aspects (Fig. 2A). The height-specific growth rates from 1964 through 1970 were also almost identical to the height-specific rates reported by Shreve (1910) for the north aspect of Tumamoc Hill. Interestingly, height-specific growth rates

were more similar across aspects and through time at Tumamoc Hill than they were to those of other sites within the Tucson vicinity. The general shape of the growth–height functions observed at Tumamoc Hill resembles the one for Saguaro National Park East (SNPE) in Tucson, Arizona, generated by a curve-fitting approach (Hastings and Alcorn 1961), but differs from the one for SNPE generated by a least-squares approach (Steenbergh and Lowe 1983). Discrepancies may reflect differences among sites in average growth rates and phenologies, divergent model-building approaches, or both. Our model probably best describes average growth rates for saguaros on steep, rocky terrain in the

cooler, moister, northeastern portion of the range. It differs from other models that describe growth on more level sites or in xeric populations (Turner 1990).

#### *Saguaro age determination and survivorship*

Several previous studies have used observations of growth rates to develop age–height models (Hastings and Alcorn 1961, Steenbergh and Lowe 1983, Turner 1990); however, none have verified models with repeated censuses. We estimated the accuracy of each age–size relationship (Fig. 2B) by comparing predicted ages of saguaros present in 1993 (based on height measurements in 1970 plus 23 yr) with their estimated ages (based on their measurements in 1993). On all aspects, the slope of the regression equation comparing predicted ages was nearly 1 with an  $r^2$  value  $>0.8$ ; the mean difference between age estimates was  $\sim 2$  yr (1 SD = 7 yr) (Fig. 3B and C). The differences in age estimates consistently were smallest for saguaros between 30 and 90 yr old (residuals, Fig. 3C). Younger saguaros grew faster than predicted on the north and west aspects (hence they are slightly younger than their heights suggest). On all aspects except the south, saguaros  $>90$  yr old grew more slowly than predicted (hence they are slightly older than their heights suggest). This demonstrates that although growth rates have been remarkably constant for most age classes during the last 29 yr, there has been some variability in growth rates for very small and very large individuals. These size classes are typically the most sensitive to climate conditions (Steenbergh and Lowe 1977, 1983).

Mortality was highest among very young ( $<1$  m) and very old ( $>8$  m) individuals (Fig. 2C), consistent with previous observations of saguaro survivorship (Steenbergh and Lowe 1983). Because we located very few saguaros in the smallest size class ( $<10$  cm), our model does not effectively capture the extremely high mortality rates of very young plants observed in seedling studies (Steenbergh and Lowe 1983).

#### *Population age structure*

We found that saguaro populations fluctuated substantially in age structure (Fig. 4) and that our perspective of their health changed over time. In 1910, Shreve reported that saguaro regeneration on Tumamoc Hill had been severely declining since the 1850s and that only 36% of the saguaros  $<5$  m in height had become established over the last 60 yr. He noted: “young plants less than 1 dm in height are so rare, or inconspicuous, that nine botanists who have had excellent opportunities to find them report that they have never done so” (Shreve 1910: 238). Consequently, the age structure was composed primarily of saguaros that had become established prior to 1850.

In contrast to 1910, the age structures in 1964 (Fig. 4) foretold healthy saguaro populations. The poor regeneration during the late 19th century is evident on

all slopes. However, on the south, east, and west aspects, a period of high regeneration occurred in the early 1920s, and on the north aspect regeneration rates increased almost two decades earlier. The age structures of the populations only on south and west aspects, where a large number of older saguaros remained, recorded the relatively high level of saguaro regeneration Shreve observed on the north aspect prior to 1850. The magnitudes of the regeneration residuals (Fig. 4: bottom) suggested that recent regeneration was comparable to rates prior to 1870. The estimated establishment date of the oldest saguaros alive in 1964 was ca. 1770.

By 1993, the forecast for saguaro populations was decline (Fig. 4). Regeneration rates apparently had been too low to maintain the populations since the 1970s on the north and west aspects and since the 1980s on the east and south (Fig. 4: bottom). However, because the newest recruits are the most likely to be overlooked, the extent of the recent decline cannot be accurately determined until the 1980–1990 recruits are older and more visible. By 1993, most individuals with estimated establishment dates of 1850 or earlier had died (Fig. 4), so that evidence of the 19th-century period of high regeneration was almost completely lost.

#### *Saguaro population size and reproductive potential*

We also found striking changes in population size during the 85 yr (Table 1). The surge in regeneration that occurred this century produced populations 2–3 times larger in 1964 than in 1908. Populations have declined since 1964 on the north and west aspects and since 1970 on the south and east aspects. Despite this two- to three-decade decline, populations are still over twice as large as they were in 1908 on all aspects except the west (Table 1).

The greater abundance of saguaros on south and east aspects in 1908 was consistent throughout the 85-yr study (Table 1). Overall recruitment rates from 1964 to 1993 were higher on south and east aspects (38% and 35%, respectively) than on north and west aspects (7% and 8%, respectively). Yet, mortality rates did not differ among slopes over the same period ( $\sim 30\%$ , 35%, 27%, and 38% on north, south, east, and west aspects, respectively).

Changes in age structure during the past 29 yr also affected the reproductive potential of the populations (Table 2). Since 1964, the number of reproductive stems on Tumamoc Hill increased so that they now outnumber individual saguaros on all aspects except the south (Table 2). The increase in reproductive stems is due primarily to the maturation of young unbranched individuals established since the 1920s, rather than to the proliferation of branches on already-mature individuals. Increases in the number of reproductive stems since 1964 has not led to greater establishment rates over the same period; instead establishment has declined. Apparently reproductive potential is not a lim-

TABLE 1. Size of each of the cohorts at each census. Cohort size at each census includes all plants that established on or prior to the census date based on their estimated ages (includes those plants that were overlooked during the census). The 1964 cohort is composed of all the individuals present at the start of the study regardless of establishment date. On the north slope only, data for an additional census conducted in 1987 are also given.

Cohort	Census			
	1964	1970	1987	1993
North plot (1908 population = 90)				
1964	284	264	229	219
1970		1	1	1
1987			2	0
1993				1
Total	284	265	232	221
South plot (1908 population = 584)				
1964	1308	1216		928
1970		100		92
1993				67
Total	1308	1316		1087
East plot (1908 population = 410)				
1964	1367	1279		1029
1970		115		108
1993				140
Total	1367	1394		1277
West plot (1908 population = 339)				
1964	603	564		428
1970		22		22
1993				9
Total	603	586		459

iting factor and does not override other factors that ensure successful establishment.

#### *Analysis of demographic trends relative to climate*

Low-frequency (multiple-decade), high-amplitude peaks and troughs in regeneration demonstrate the same general pattern across aspects and through time: high regeneration in the mid-19th and 20th centuries separated by a longer period of population decline. In contrast, high-frequency (less than a decade), low-amplitude peaks and troughs in regeneration do not align on the same establishment dates across plots or censuses. Regeneration patterns on scales of less than a decade have been used previously in seedling studies, where precise establishment ages are known, to infer the impacts of specific climatic events on saguaro recruitment and survival (Jordan and Nobel 1982, Turner 1992). However, we limit our discussion to the broader trends spanning nearly a decade because our ability to estimate saguaro establishment date is limited to that scale (Fig. 3C).

We observed several generalities regarding long-term regeneration and climate across all four slopes. First, periods of low annual PDSI (Fig. 6A) are generally correlated with low regeneration (Fig. 4). Low regeneration from the 1890s to the early 1900s coincided with severe drought conditions throughout the

southwestern United States from about 1898 to 1904 (Smith and Stockton 1981). Regeneration was also lower relative to the preceding and following decades from the late 1940s to the 1960s (Fig. 4), coinciding with a period of prolonged drought throughout southern Arizona from about 1947 to 1957 (Thomas 1962, Wahl and Larson 1970, Meko et al. 1980).

Second, wet periods often, but not consistently, coincide with high regeneration. For example, the most dramatic increase in saguaro regeneration (Fig. 4) occurred from 1930 through 1942 when moisture was consistently available throughout the year (high PDSI index, Fig. 6F). All aspects also experienced higher regeneration corresponding to high PDSI indices in the 1960s and early 1970s. Additionally, the long-term PDSI record reconstructed from regional tree-ring chronologies (Fig. 6I) demonstrates that regeneration peaks in the 19th century (Fig. 4) coincide with wet conditions during the 1830–1840s and the 1860s.

Notable exceptions to the relationship between wet conditions and high saguaro regeneration are the period from about 1868 to 1898 and the two wet periods from 1905 to 1908 and 1914 to 1920 (Fig. 4). High-intensity summer rainfall occurred in Tucson during several years from 1868 into the 1890s (Fig. 6D), initiating arroyos in southern Arizona alluvial valleys (Cooke and Reeves 1976). Notably intense winter and spring

TABLE 2. Saguaro reproductive potential (mature meristems) at each census, based on the number of individuals that are of reproductive age and the number of reproductive stem tips.

Year	Sample population†	% Mature saguaros‡	% With branches§	Mature meristems
North plot				
1964	273	32	67	186
1970	265	40	43	185
1993	221	66	81	417
South plot				
1964	1148	32	67	856
1970	1133	28	66	771
1993	1087	42	42	702
East plot				
1964	1168	20	82	533
1970	1300	26	55	672
1993	1277	49	58	1298
West plot				
1964	598	36	79	702
1970	586	43	75	673
1993	459	79	60	794

† Sample of total population, which excludes broken saguaros for which reproductive potential cannot be determined (i.e., because plant height or meristem number cannot be accurately determined).

‡ The percentage of the sample population presumed tall enough ( $\geq 2.0$  m) to produce flowers.

§ The percentage of the sample population presumed tall enough to produce branches ( $> 3.75$  m tall) with branches.

|| The number of potentially reproductive meristems in the sample population (the number of mature plants plus the number of branches on these plants).



rainfall events also occurred during some years (floods of 1904–1905, 1908, 1914–1915) at the start of the 20th century. The lack of correlation between regeneration and periods with high-intensity rainfall events suggests that these wet conditions may not favor seedling recruitment and survival.

#### *Sources of mortality*

Between 1964 and 1993 there were 970 saguaro deaths among the tallied plants, although the time between censuses was too long to assign a cause in most cases. Our 1993 observations show that moderate to severe injuries caused by a variety of factors were common among saguaros and varied by type across slopes. For example, the incidence of chewing and tunneling by woodrats (*Neotoma albigula*) was higher on the north (47% of all saguaros) and west aspects (38%) compared to the east (22%) and south aspects (28%). Wounds caused by abrasive contact with other perennial plants, including other saguaros, were equally common across slopes (~40% of all saguaros). Many of these injuries occurred on the apical regions of the primary stem and branches (64% of all wounded saguaros); many plants (12%) also had noticeable constrictions, indicating previous injury to the apical region due to frost, tunneling, or wounding by associated plants. Injuries to the apices are especially significant because they affect stem growth and reproduction. Wounds also were caused infrequently by cavity-nesting woodpeckers (*Colaptes auratus chrysoides* and *Melanerpes uropygialis*), vandals, insects, and lightning. Approximately 1% of all saguaros in 1993 showed evidence of bacterial decomposition caused by *Erwinia cacticida* (Lightle et al. 1942, Alcorn et al. 1991) at the wound site (i.e., the presence of brown or black fluid streaming from a wound).

One of the most dramatic weather events resulting in widespread mortality occurred in August 1982, when strong winds (>100 km/h) toppled more than 140 saguaros within a 15-ha area adjacent to our plots. The winds were preceded by several days of heavy rains, which diminished the resistance of plants to windthrow.

#### DISCUSSION

##### *The effect of slope aspect on saguaro demography and growth*

This long-term study documents changes in saguaro populations located on north, south, east, and west aspects over an 85-yr period. We hypothesized that differences among slope aspects in recruitment, growth rate, reproductive potential, and survival provide insight into the patterns of saguaro abundance across slopes on Tumamoc Hill. The preference of saguaros for south and east aspects in 1908 was consistent throughout the study. Our data indicate that recruitment and survival of small plants are more strongly influenced by aspect than are growth rates, reproductive

potential, or survival of older established plants. Overall recruitment rates from 1964 to 1993 have been 1–2 orders of magnitude higher on south and east aspects than on north and west aspects, whereas there has been little difference among slopes in growth rates and survival of established plants over the same period of time. Apparently, recruitment niche largely defines saguaro abundances across aspects.

The preference of saguaros for south aspects on Tumamoc Hill is in keeping with other observations of saguaros near their northern limit (Niering et al. 1963, Turner et al. 1995). Saguaro, an essentially subtropical species, is limited at higher elevations and near the northern and northeastern margins of its range by the duration and intensity of freezing temperatures (Shreve 1911, Niering et al. 1963, Hastings and Turner 1965, Steenbergh and Lowe 1977, Nobel 1980, 1988). Severe winter freezes can kill large numbers of plants, especially small plants, which are highly susceptible because of their high surface-to-volume ratio (Steenbergh and Lowe 1977). Plants large enough to survive freezes can experience reduced growth and reproduction due to frost injury (Steenbergh and Lowe 1977).

Higher recruitment rates on east and south aspects may be due largely to their earlier exposure to morning sunlight in winter, which reduces the duration of nighttime freezing temperatures. Low recruitment on north aspects particularly may be caused by large seasonal temperature and moisture extremes; north aspects experience the coldest soil conditions in winter and the warmest and driest conditions during the arid foreshummer just prior to saguaro germination (Haase 1970). Previous work has suggested that north and west aspects of mountain ranges also may receive less summer precipitation than south and east aspects because summer storms, critical for seedling establishment, originate from the southeast (Jordan and Nobel 1982); however, on Tumamoc Hill this orographic phenomenon is probably not well developed.

On the north and west aspects of Tumamoc Hill, greater incidence of herbivory by wood rats also may have contributed to lower survival of small plants on these slopes. We also noted more significant colonization of the north and west aspects by winter-annual exotics (especially *Bromus rubens*) since the 1970s and a recent and dramatic expansion of the exotic grass *Cenchrus ciliare* on the east aspect. Because these exotics may utilize regeneration niches of saguaro or saguaro “nurse plants,” they also may have contributed to lower recruitment on the north and west and may become more important as they increase in abundance.

##### *Long-term saguaro regeneration trends in the northern Sonoran Desert*

This study demonstrates that saguaro populations fluctuate substantially in size and age structure. During much of the last two centuries, populations on Tumamoc Hill were in decline due to low regeneration rates.

Although some recruitment probably occurs most years, saguaro persistence apparently is maintained by episodic surges in regeneration resulting in substantial population gains such as those occurring in the middle of the 19th and 20th centuries.

The long time-span and large number of individuals encompassed by this study distinguish it from previous studies using age-structure analysis to study long-term regeneration trends (Hastings and Alcorn 1961, Brum 1973, Jordan and Nobel 1982, Steenbergh and Lowe 1983, Turner 1990, 1992, Parker 1993). Many used the age-size relationships reported by Steenbergh and Lowe (1983), rather than developing site-specific relationships. Our results and those of previous studies (Steenbergh and Lowe 1983, Turner 1990) suggest that growth rates among sites differing in climate and habitat vary enough to warrant age estimates based on local growth rates.

Large fluctuations in saguaro population size and regeneration have been noted by previous studies and many record substantial surges in regeneration beginning around the 1920s, as occurred on Tumamoc Hill. For example, peak regeneration episodes have been observed from 1916 through 1936 in southeastern California (Brum 1973), 1907 through 1959 in the Sierra del Pinacate Reserve in northern Sonora, Mexico (Turner 1990), and 1915 through 1940 at Organ Pipe Cactus National Monument (OPCNM) in southwestern Arizona (Parker 1993). In all of those studies, the regeneration surge was attributed to favorably moist climate.

Studies of seedling establishment patterns demonstrate that saguaro seedling establishment responds to seasonal rainfall patterns (Jordan and Nobel 1982, Turner 1992), and pulses in seedling establishment and survivorship depend on availability of suitable niches and a sequence of favorable years for regeneration. Regional synchronicity in regeneration surges may be driven by decadal-scale variability in cool-season precipitation attributed to low-frequency variations in the upper-air westerlies and sea surface temperatures (SSTs) in the tropical Pacific (Webb and Betancourt 1992, Cayan et al. 1998). Specifically, wet winters and springs occur when the polar jet stream is highly sinuous (meridional) and displaced to the south, steering the storm track over the Southwest. These conditions commonly coincide with warm SST anomalies in the central, equatorial Pacific (El Niño) and an intensified subtropical jet stream that also steers tropical moisture into the Southwest. In contrast, the climatologies affecting summer precipitation over Arizona are more spatially and temporally complex, with little evidence for persistence at the regional or decadal scale (Harrington et al. 1992, Webb and Betancourt 1992). Meridional flow and frequent El Niño events were common in the first and latter third of the century, producing consistently wet winters and springs in Tucson and much of southern Arizona (Fig. 6) and may account

for the synchronicity between the 1920–1940's regeneration surges at Tumamoc Hill and elsewhere.

Our findings—that saguaro recruitment surges do not always coincide with favorably wet climatic conditions—suggest that other climatic factors determine recruitment success. High rainfall intensity (i.e., notable flood years) may be one factor. Subsequent droughts and severe winters may further decouple regeneration and moisture conditions. High mortality rates among seedlings, which are extremely drought and frost sensitive, may mask high recruitment rates for many years both preceding and following such events. For example, small cohorts from the 1880s to the early 1900s and from the 1940s may be the result of the death of these annual cohorts as seedlings during the 1890's and 1950's droughts, rather than low recruitment rates. Similarly, a higher incidence early in the 1900s of severe frosts (Fig. 6G) may have contributed to low regeneration levels during the 1905 through 1920 period when PDSI was high (Fig. 6F). The lack of regeneration during the wet years between 1905 through 1908 and 1914 through 1920 also was observed at OPCNM, where low regeneration was attributed to high frost frequency (Parker 1993). The inconsistency of the relationship between wet conditions and high saguaro regeneration suggests that although moist conditions may be a prerequisite for surges in saguaro regeneration, other climatic factors (including intensity and seasonality of rainfall, subsequent drought, and cold winters) may determine survivorship.

Although most studies agree that climate fluctuations have been the most significant factor affecting saguaro regeneration (Hastings and Alcorn 1961, Brum 1973, Steenbergh and Lowe 1983, Jordan and Nobel 1982, Turner 1990, 1992, Parker 1993), other factors including land use (Niering and Whittaker 1965), herbivores (Niering et al. 1963, Turner et al. 1969), and nurse-plant scarcity (Vandermeer 1980) are also important. Local land-use practices, especially intensive grazing, woodcutting, and rock removal, damage the young seedlings and reduce the number of germination sites due to soil compaction and nurse-plant reduction. Livestock grazing and woodcutting are believed largely responsible for the long decline in saguaro recruitment at Saguaro National Park East in Tucson, Arizona. (Abouhaidar 1992, Niering et al. 1963, Steenbergh and Lowe 1983, Turner 1992). Parker (1993) observed that grazing also has contributed to the recent decline in saguaros at OPCNM and that adverse effects of land use on saguaro regeneration may be more pronounced when climate conditions are stressful. At Tumamoc Hill, limited livestock grazing and removal of rocks may have contributed to lower regeneration rates prior to fencing in 1907 and been intensified by drought during the 1890s and frequent freezes at the turn of the century.

*Need for regional, long-term studies of saguaro and other desert plant species*

Many long-lived desert species, including saguaro, reproduce episodically and so their populations fluctuate on decadal or longer scales (Goldberg and Turner 1986, Turner 1990, Bowers et al. 1995). These changes occur slowly relative to the human life-span so that our perception of the past history as well as our predictions for the future of these populations are often based only on recent trends. As our study demonstrates, observations spanning several decades provide the perspective to discriminate long-term population trends from erratic, short-term dynamics. For example, the current (20 yr) decline does not necessarily signal the demise of the saguaro at Tumamoc Hill. During the last two centuries, Tumamoc Hill populations have frequently declined due to low regeneration rates, but have always rebounded.

Our findings that saguaro regeneration surges do not always coincide with favorably moist conditions, but depend on other climatic and biotic factors, have important implications for regional management of Sonoran Desert species in general. Expansion of suburban areas and land-use practices that destroy native desert vegetation, encourage the spread of exotics, and promote fire are likely to further decouple the relationship between climate and regeneration and may increasingly interfere with regeneration during the infrequent episodes of favorable conditions. Local differences in land use, microclimate, topography, soils, biotic factors, and site history may therefore preclude widespread population responses by long-lived species to regional climate. This in turn, makes predicting responses and managing populations at a regional level extremely difficult. In the future, *long-term studies spanning a broad geographic range* may be needed to distinguish between the influence of regional and local factors in driving population trends of these long-lived episodically reproducing desert species.

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