Influence of climatic variability on local population dynamics of a Sonoran Desert platyopuntia

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Abstract

Age-based population dynamics of *Opuntia engelmannii*, a shrubby cactus with flattened cladodes, were investigated at a Sonoran Desert site protected from grazing since 1907. Demographic statistics were determined from births and deaths on six permanent vegetation plots mapped four times between 1968 and 2001. Moderate longevity (13–56 years) and modest per capita annual survival (0.9298) were associated with fairly rapid turnover; cycles of population growth and decline were thus evident over relatively short periods. Age–frequency distribution, determined for subpopulations in two neighboring habitats in 1996 and 2003, was used to calculate residual regeneration, an index of the difference between observed cohort size and idealized survivorship. Establishment peaks occurred in the late 1970s, the mid-1980s, and the early to mid-1990s and coincided with increased winter moisture in the years before germination, ample summer rain in the year of germination, and decreased drought in the years after germination, reflecting favorable conditions for fruit production, seed germination, and seedling survival. Regionally, pulses and gaps in establishment coincide with the frequency and amplitude of large-scale climatic phenomena that affect cycles of moisture and drought on decadal and interdecadal scales. Because of local factors, however, subpopulations within a few km of one another can experience virtually identical climates yet differ strikingly in age structure and density.
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Keywords: Demography; El Niño-Southern Oscillation; Longevity; Pacific Decadal Oscillation; Survivorship; Turnover

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1. Introduction

Proliferation of *Opuntia* (Cactaceae), especially the platyopuntias or prickly-pears, has been noted at many times and locations, as on the Great Plains in the 1930s (Turner and Costello, 1942; Cook, 1942), in southern Arizona in the latter half of the 20th century (Humphrey, 1960; Turner et al., 2003), in southern Africa in the 1980s (Hoffman et al., 1998), in Spain since the 1960s (Gimeno and Vilà, 2002), and in Australia in the 1910s and 1920s (Dodd, 1940). Populations of certain species, such as *Opuntia rastrera* Weber in the Chihuahuan Desert, can reach densities of >4000 plants/ha (Mandujano et al., 2001). Proliferation or invasion of platyopuntias has been variously attributed to grazing, drought, efficient dispersal of seeds, disturbance, absence of predators, released competitive pressure, or a combination of these and other factors (Cook, 1942; Turner and Costello, 1942; Humphrey, 1960; Houston, 1963; Burger and Louda, 1995; Hoffman et al., 1998; Gimeno and Vilà, 2002). Some ranchers and land managers consider platyopuntias to be pest species that require biological or chemical control (Humphrey, 1960; Hoffman et al., 1998), but in their native range, platyopuntias are an integral component of food webs, providing a reliable source of food and moisture for insects, birds, and mammals at a time of year when little else is available. In addition, platyopuntias can be an important element of community structure in arid and semi-arid North America.

Whether platyopuntias are native or introduced, pulses of establishment are necessarily demographic phenomena. With a few exceptions, however, little attention has been paid to their population age structure. Size-class distributions have been used as a substitute for population age structure (e.g. Gimeno and Vilà, 2002) but cannot be conveniently correlated with dated events in the past such as disturbance or seasonal rainfall. Age-based analysis makes it possible to correlate peaks and troughs in establishment with climatic trends over the lifetime of a population. Although platyopuntia wood does not form annual growth rings, age can be estimated from the relation between annual growth and plant size, that is, number of cladodes (Bowers, 1996a). Height-growth models have long been used to estimate ages of columnar cacti (Shreve, 1910; Steenbergh and Lowe, 1977, 1983; Jordan and Nobel, 1982; Turner, 1990; Parker, 1993; Bowers, 1997a; Pierson and Turner, 1998; Drezner, 2003). Such age estimations, along with repeated censuses, have been powerful tools for understanding cycles of population growth and decline (Pierson and Turner, 1998).

I investigated age-based population dynamics of *Opuntia engelmannii* Salm-Dyck. (Engelmann prickly-pear) in the northern Sonoran Desert, USA, at a site protected from domestic livestock since 1907. *Opuntia engelmannii*, a shrubby cactus that reaches about 1 m in height, is widely distributed in the southwestern United States at elevations of 300–2000 m above sea level (Turner et al., 1995). Fecundity is highly variable from year to year, depending on winter rain (Bowers, 1997b), predispersal seed predation (Mann, 1969), and meristem allocation (Bowers, 1996b). Germination occurs during the summer rainy season (July–September) and requires $\geqslant 43$ mm rain during $\leqslant 14$ days (Bowers, pers. obs.). Seeds can persist in the soil for at least 19 months and probably much longer (Bowers, pers. obs.). The paucity of

O. engelmannii seedlings in 7- and 6-year studies of woody plant recruitment (Shreve, 1917; Bowers et al., 2004) suggests that establishment is infrequent. Adult mortality increases during severe drought (pers. obsv.). Plants reach reproductive maturity at 9–11 years of age (Bowers, 1996a). Few individuals live longer than 25–30 years (Shreve, 1935; Goldberg and Turner, 1986; Bowers, 1996a). Plants can reproduce vegetatively when detached cladodes become rooted in the ground.

In the last half of the 20th century, populations of *O. engelmannii* in the northern Sonoran Desert increased markedly at many locations (Turner et al., 2003). At one site near Tucson, Arizona, 85% of the 1995 population was established after 1978 (Bowers, 1996a). Similarly, in the nearby desert grassland, density increased three-fold between 1975 and 1997 (McClaran et al., 2002a, b). Given the capacity of platyopuntias for rapid advance across landscapes, recent growth of these populations might not seem remarkable; on the other hand, judging from repeat photography, *O. engelmannii* was a minor constituent of Sonoran Desert vegetation during the first 50–70 years of the 20th century, and its populations were generally stable (Turner et al., 2003). The pattern bears some resemblance to the boom-and-bust dynamic described for *O. fulgida* Engelm., a cylindropuntia that experiences multi-decadal cycles of population growth and decline (Tschirley and Wagle, 1964; Martin and Turner, 1977).

To gain a better understanding of the population dynamics of *O. engelmannii*, I integrated data from several sources. From censuses made in 1996 and 2003, I determined population age structure in two neighboring habitats, then identified years of peak establishment when cohorts were larger than necessary for a stable age distribution. From historical maps of permanent vegetation plots, I assessed changes in population size over several decades and also calculated average annual survival, longevity, and turnover. My ultimate objective was to determine how a species with moderate life-span, variable fecundity, and episodic establishment can persist, much less increase, in a climatically variable environment where severe drought can last a decade or longer.

2. Methods and materials

2.1. Study site

Tumamoc Hill (32°13′N, 111°05′W) is an outlier of the Tucson Mountains, Pima County, AZ, USA (Fig. 1). The study site, established as the Desert Laboratory of the Carnegie Institution of Washington in 1903, encompasses about 352 ha and includes Tumamoc Hill proper, a rocky, basaltic-andesitic knoll (760–948 m above sea level), and the level or gently rolling plain to the west (725–760 m above sea level). Historically significant permanent vegetation plots currently monitored at Tumamoc Hill include nine 100-m^2 plots established in 1906 (the Spalding–Shreve plots), a 557-m^2 plot established in 1910 (Area A), and a set of eight contiguous 100-m^2 plots established in 1928 (Area B) (Shreve, 1917; Shreve, 1929; Shreve and Hinckley, 1937; Goldberg and Turner, 1986). Their monitoring history is complex
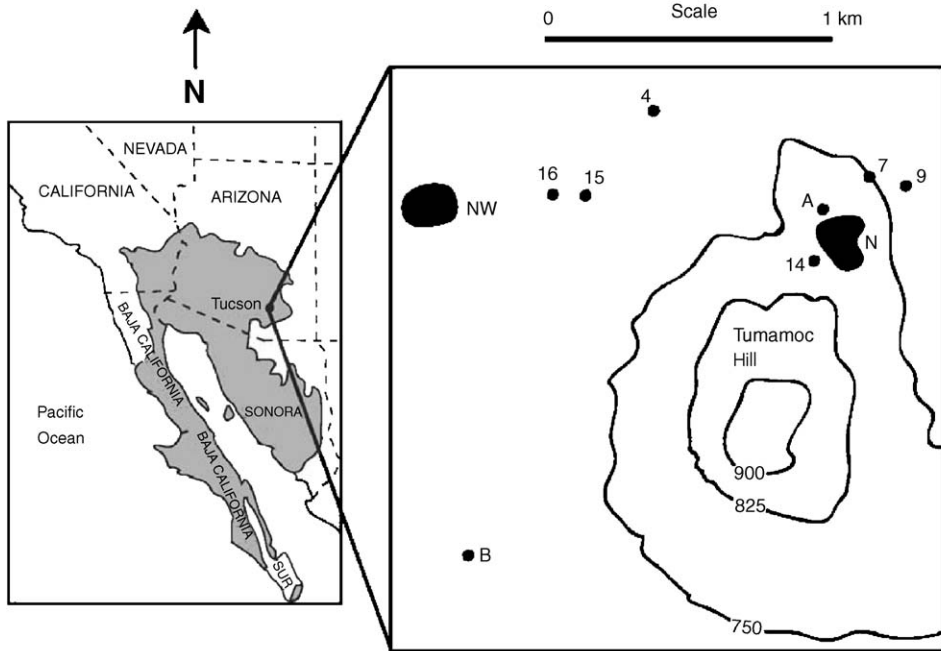
Fig. 1. Location of the Tumamoc Hill study site in the Sonoran Desert, showing Sonoran Desert boundary after Shreve (1951); and Tumamoc Hill, showing locations of selected permanent vegetation plots (numbered circles) and *Opuntia engelmannii* study plots (N = North Slope plot, NW = Northwest Corner plot).

(Goldberg and Turner, 1986) and will not be described here except to note that of the plots established in 1906, only four were consistently monitored after 1906 and before 1968. Starting in 1968, perennial plants on the Spalding–Shreve plots have been mapped about once per decade. Area B has been mapped about as often since 1928. Area A has never been mapped, but woody plants on the plot have been counted occasionally; in addition, seedlings of perennial plants were monitored from 1910 to 1917 and again from 1987 to 1993 (Shreve, 1917; Bowers et al., 2004). Plot maps show locations of canopies and stem bases, making it possible to track persistent plants from one census to the next, to recognize new individuals, and to detect deaths (Shreve, 1929; Shreve and Hinckley, 1937; Goldberg and Turner, 1986). Decadal monitoring is consistent with the characteristic cycling of wet and dry periods in the region (Goldberg and Turner, 1986) and is appropriate for assessing longevity and survival of woody desert plants (Goldberg and Turner, 1986; Cody, 2000).

Study-site vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve, 1951; Goldberg and Turner, 1986). In addition to *O. engelmannii*, dominants include *Cercidium microphyllum* (Torr.) Rose and Johnston, *Carnegiea*

gigantea (Engelm.) Britton and Rose, *Larrea tridentata* (Sessé and Moç. ex DC.) Cov., *Fouquieria splendens* Engelm., *Ambrosia deltoidea* (A. Gray) Payne, *Encelia farinosa* A. Gray, and *Ferocactus wislizeni* (Engelm.) Britton and Rose. Domestic livestock have been excluded from the study site since 1907. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter–early spring (November–March, 110 mm), an arid late spring (April–June, 20 mm), a predictable summer monsoon (July–August, 120 mm), and a highly variable autumn (September–October, 50 mm). Average maximum and minimum daily temperatures are 18.6 and 2.4 °C during January, the coldest month, and 37.9 and 22.8 °C in June, the hottest month (Sellers et al., 1985).

2.2. Historical populations on the permanent plots

I examined maps of the permanent vegetation plots to track changes in population during the 20th century. For Areas A and B (Fig. 1), I simply determined the number of *O. engelmannii* plants mapped or recorded at every census date. Census dates were 1910, 1928, 1936, 1968, 1978, and 1999 for Area A, and 1928, 1936, 1948, 1957, 1968, 1978, 1984, and 2001 for Area B. For six of the Spalding–Shreve plots (plots 4, 7, 9, 14, 15, 16; Fig. 1), I determined number of *O. engelmannii* plants mapped in 1968, 1978, 1984, and 2001. Three Spalding–Shreve plots were excluded from this study: one was not mapped in 1984, and *O. engelmannii* was absent from the other two in the years of interest.

I calculated survival, longevity, and turnover on the same six Spalding–Shreve plots. First, I determined from plot maps the number of individuals that persisted, died, and became established between successive census years (1968–1978, 1978–1984, and 1984–2001), then I summed values for the six plots within intercensus periods. I calculated periodic survival, S_p, for each period after Cody (2000) as

$$S_p = P/(P + D),$$

where P is the number of plants that persisted and D the number that died. I further calculated per capita yearly survival probability, S, for each period after Cody (2000) as

$$S = 10^{\frac{\log(S_p)}{t}},$$

where t is the length of period in years. Note that S is not age-specific survivorship but, rather, an average for the population.

S was extrapolated after Cody (2000) to give $E_{0.5}$, the age achieved by 50% of the sample, $E_{0.25}$, the age reached by 25% of the sample, and $E_{0.05}$, the age reached by 5% of the sample. The equations used were

$$E_{0.5} = -0.301/\log(S),$$
$$E_{0.25} = -0.602/\log(S)$$

and

$$E_{0.05} = -1.301/\log(S).$$

Average values for survival and life-spans were calculated from the intercensus values.

2.3. Population age distribution in 1996 and 2003

In April 1996 and again in March 2003, a census of the *O. engelmannii* population was made in two large, unmarked plots on and near Tumamoc Hill. The North Slope Plot (Fig. 1) encompassed about 1.2 ha on the rocky, north-facing slope of the hill. The Northwest Corner Plot (Fig. 1), located on gently rolling alluvial terrain about 1.5 km to the northwest, encompassed about 1.4 ha. At each census, plant size was determined for living plants by counting number of cladodes. Only plants that originated from seed were sampled; they could be readily recognized by the lowermost cladode, which is more or less cylindrical, forming a short trunk. Ages of sample plants in 1996 and 2003 were estimated from the relation between plant size (number of cladodes) and probable age (Bowers, 1996a). Plants were grouped into annual cohorts, and population age distribution was plotted as a function of estimated age.

The model used to age-date *O. engelmannii* (Bowers, 1996a) was based on plants that originated from seed. The size-age relation for *O. engelmannii* plants of vegetative origin was unknown, and clones were therefore omitted from the census. They were not common on either plot in 1996 or 2003.

2.4. Residual regeneration

Residual regeneration is an index of the difference between observed and predicted cohort size, that is, between the number of plants observed in a cohort and the number needed to maintain a stable age distribution (idealized survivorship) (Parker, 1993; Pierson and Turner, 1998). Residual regeneration was calculated separately for the North Slope and Northwest Corner plots in each census year to highlight periods of good and poor regeneration.

First, the Survival Analysis module in SYSTAT (2002) was used to derive a survivorship curve from dates of first and last appearance of 40 *O. engelmannii* individuals on the six Spalding–Shreve plots from 1968 to 2001 and of eight individuals on Area A from 1987 to 1993. Because plots were monitored at long intervals, the exact life-span of any particular plant was not known. The lower bound for life-span in years was determined by subtracting the date when a plant was first observed from the date when it was last observed. The upper bound was calculated as the difference between the date when a plant was first observed and the date when it was first recorded as absent. Given the upper and lower bounds of life-span, the Survival Analysis module estimated where, in that interval, the probability of death occurred, then, from the proportion of plants failing at that point, calculated the survival probability (Weibull distribution) (SYSTAT, 2002).

Next, to estimate the number of individuals needed in each age class to maintain a stable age distribution, the survivorship curve was scaled (scaling factor = [total population size] ÷ [area under the curve]) (Pierson and Turner, 1998). For each

annual cohort, the number of plants predicted by the survivorship curve was then subtracted from the observed number; these differences were the residuals (Parker, 1993). Because assigned ages were approximate rather than exact, the observed number was expressed as a 3-year running mean.

Finally, to take into account the expected decline in cohort size with increasing age, the residuals were divided by the number of recruits predicted by the survivorship curve (Pierson and Turner, 1998). The resulting values (residual regeneration) were standardized with respect to the mean and standard deviation, then scaled to range from −1 to 1, thus making the range in positive and negative deviations comparable (Pierson and Turner, 1998). Positive deviations indicated periods when regeneration was greater than that required for a stable age distribution. Large positive deviations represented peaks in establishment.

2.5. Establishment peaks and climatic variability

The influence of climatic variability on establishment was examined using principal components regression, a procedure that combines principal components analysis (PCA) with stepwise multiple regression. PCA was used to extract major climatic components from 17 original climatic variables (see below). PCA was used to alleviate problems associated with multi-collinearity among independent variables. The PCA solution was rotated to facilitate interpretation of the components. Factor scores were saved for use as dependent variables in stepwise multiple regression. The principal components with eigenvalues <1 were eliminated from further consideration. The remaining components were interpreted on the basis of component loadings.

The original climatic variables, calculated as 3-year running means from 1970 to 2000, represented various measures of seasonal precipitation and drought. For the purpose of this analysis, the climatic year began in October and ended in September. Precipitation variables, selected to reflect conditions that might favor abundant seed germination in $year_0$, above average fruit production in the previous years, and good seedling survival in the following years were: (1) total summer rain (July–September) in $year_0$, $year_{+1}$, and $year_{+2}$, (2) single largest summer storm in $year_0$, (3) number of summer storms large enough to trigger germination in $year_0$, and (4) total cool-season rain (October–March) in $year_0$, $year_{-1}$, and $year_{-2}$ (Fig. 2). Drought variables, selected to reflect conditions for seedling survival immediately after germination and in the following years, were calculated as number of consecutive days $\geqslant 30$ without measurable rain during the following seasons: (1) autumn (September–October) of $year_0$, $year_{+1}$, and $year_{+2}$, (2) winter (November–March) of $year_{+1}$, $year_{+2}$, and $year_{+3}$, and late spring (April to June) of $year_{+1}$, $year_{+2}$, and $year_{+3}$ (Fig. 2).

The relation between principal climatic components and residual regeneration was examined with stepwise multiple regression. Residual regeneration in 1996 or 2003 was used as the dependent variable. Factor scores of those principal components with eigenvalues >1 were used as independent variables. The North Slope and
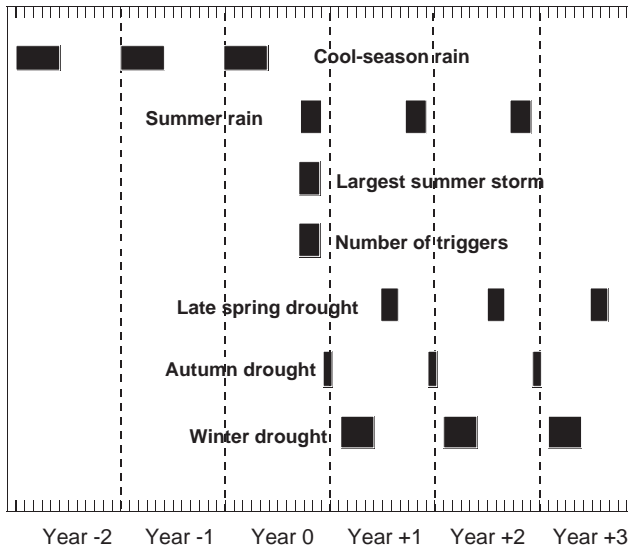
Fig. 2. Diagrammatic representation of original climatic variables used in PCA, showing how variables were lagged with respect to year of germination (year$_0$).

Northwest Corner plots experience virtually identical climates and were pooled for this analysis.

3. Results

3.1. Historical populations on the permanent plots

On Area A (557 m^2; Fig. 3a), *O. engelmannii* numbers rose from three in 1910 to 15 in 1968, then dropped to nine in 1978 and finally to zero in 1999. On Area B (800 m^2; Fig. 3b), three to four plants were mapped in 1928, 1936, and 1957. By 1968, none were left. No new individuals appeared at the 1978 or 1984 censuses; then, at the 2001 census, 12 new plants were recorded. From periodic sampling of Area B, it appears that gaps in establishment can extend for more than a decade. The six Spalding–Shreve plots (total area = 600 m^2) supported 25 individuals of *O. engelmannii* in 1968, 26 in 1978, 26 in 1984, and 16 in 2001. Births and deaths during the three periods were as follows: 1968–1978, 15 births, 14 deaths; 1978–1984, four births, four deaths; 1984–2001, 12 births, 22 deaths. Thus, between 1968–1984, the total number of plants on the plots remained stable despite relatively high turnover. After 1984, high turnover was accompanied by a large drop in total population. Per capita annual survival probability on the Spalding–Shreve plots was 0.9298. About 50% of the population was expected to live to 13 years of age, about 25% to 27 years of age. Life expectancy of the oldest five percent was 56 years.
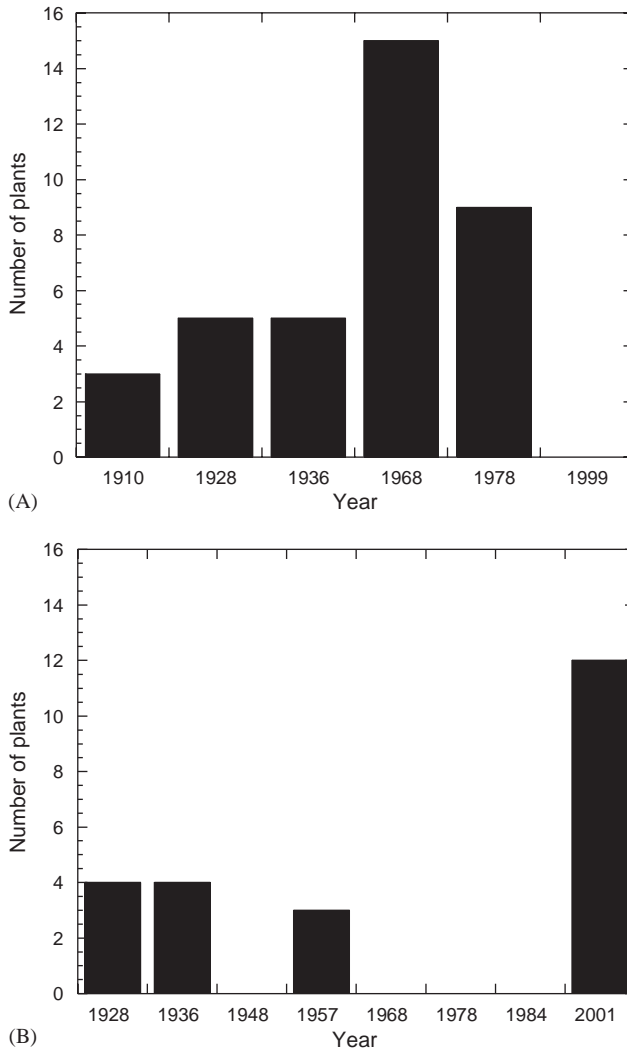
Fig. 3. Density of *Opuntia engelmannii* on two permanent plots, Tumamoc Hill, Tucson, AZ. (A) Area A, 557 m^2. (B) Area B, 800 m^2. *X*-axis shows only those years when plants were counted or mapped; plots were not always monitored in the same year.

3.2. Population age distribution in 1996 and 2003

The North Slope plot (1.2 ha) and Northwest Corner plot (1.4 ha) presented strikingly different age structures (Fig. 4). In 1996, the Northwest Corner sample ($n = 152$) was young, with an average age of 12.8 ± 4.3 years. The North Slope sample ($n = 88$) was older on average, 18.1 ± 4.7 years. During the eight years between censuses, the North Slope subpopulation declined from 73 plants/ha to 56 plants/ha,
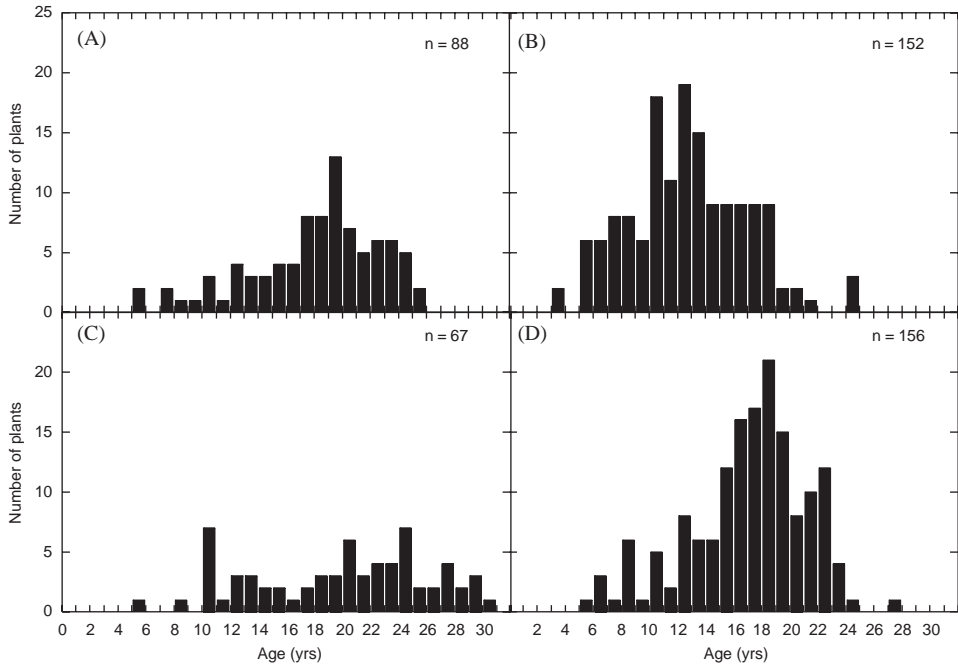
Fig. 4. Population age structure of *Opuntia engelmannii*, Tumamoc Hill, Tucson, AZ. Bars represent number of plants in 1-year age classes. (A) North Slope plot, 1996. (B) Northwest Corner plot, 1996. (C) North Slope plot, 2003. (D) Northwest Corner plot, 2003.

while the Northwest Corner subpopulation remained stable, with 106 plants/ha and 108 plants/ha in 1996 and 2003, respectively. Despite the loss of many individuals, average age of the North Slope sample in 2003 remained steady at 17.7 ± 6.2 years. The Northwest Corner subpopulation reached an average age of 17.0 ± 4.2 years in 2003, about the same as for plants on the North Slope.

3.3. Residual regeneration

Plotting residual regeneration as a function of time revealed three major establishment peaks from about 1975 to about 1995, equivalent to a rate of one peak every 7 years. Peaks evident in the 1996 census could be assigned to the late 1970s and possibly to the mid-1980s on the North Slope plot, and to the mid-1980s and possibly to the early 1990s on the Northwest Corner plot (Figs. 5a and b). At the 2003 census, the late 1970s and mid-1980s peaks were still evident on the North Slope plot, and a strong peak in the early to mid-1990s had become apparent (Figs. 5c and d). The mid-1980s peaks was still a prominent feature of the subpopulation on the Northwest Corner plot in 2003, but that of the 1990s was not (Fig. 5d). The large cohorts of the mid-1980s and early to mid-1990s on Tumamoc
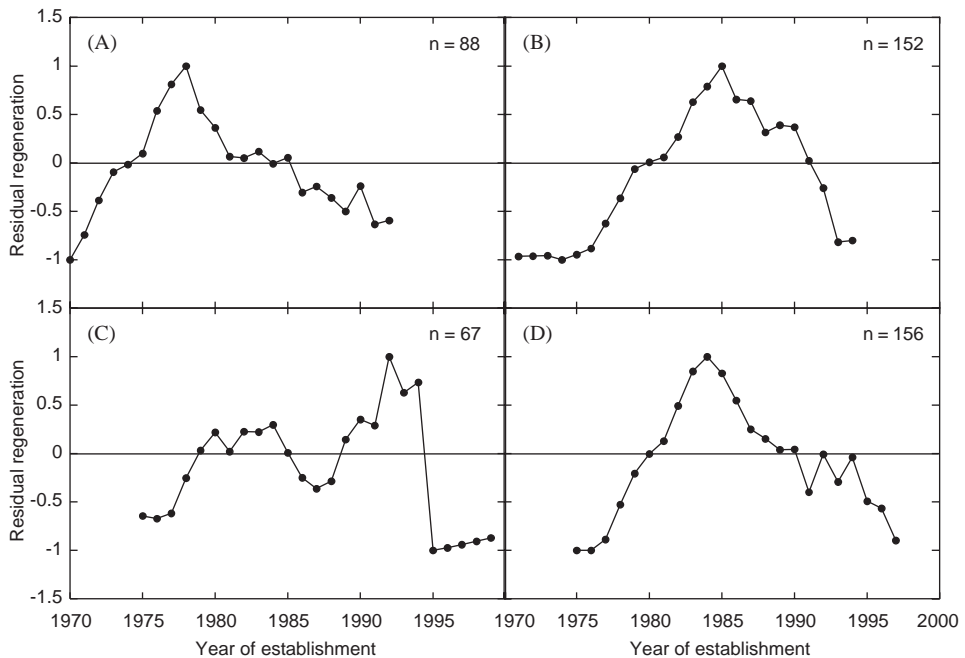
Fig. 5. Patterns of establishment of *Opuntia engelmannii*, Tumamoc Hill, Tucson, AZ. (A) North Slope plot, 1996. (B) Northwest Corner plot, 1996. (C) North Slope plot, 2003. (D) Northwest Corner plot, 2003. Values represent residual regeneration, an index of the difference between observed cohort size and idealized survivorship.

Hill have not been matched in the past decade, and a large drop in population is likely as these cohorts become senescent and die.

3.4. Establishment peaks and climatic variability

In the PCA, five components had eigenvalues >1. From loadings (Table 1), it appeared that these components represented (1) summer rain in the year of germination and the following year (Warmwet); (2) late spring drought and cool-season moisture in the years before and after germination (Springdry); (3) autumn drought in the year of germination and following years (Autumndry); (4) winter drought in the years after germination (Winterdry); and (5) cool-season rain in the years before germination (Coolwet). Together the five components accounted for 78.7% of the total variation associated with the original 17 climatic variables.

In stepwise multiple regression, residual regeneration in 1996 was negatively related to Springdry, Autumndry, and Winterdry, showing that small cohorts were associated with lengthy droughts. The combination explained 62% of the variation in residual regeneration ($p < 0.001$). Coolwet in combination with Springdry, Autumndry, and Winterdry explained 64% of the variation in residual regeneration

Table 1
Eigenvalues and rotated factor loading for the principal components generated in PCA

	Principal component				
	Warmwet	Springdry	Falldry	Winterdry	Coolwet
Eigenvalue	4.137	3.525	2.723	1.669	1.322
Proportion of variance explained	0.218	0.200	0.153	0.101	0.115
Original rainfall variables					
Cool season, $year_0$	0.139	−0.819[a]	0.053	0.025	−0.009
Cool season, $year_{-1}$	−0.159	−0.666[a]	−0.019	−0.079	0.571[a]
Cool season, $year_{-2}$	−0.140	−0.175	−0.144	−0.099	0.884[a]
Summer, $year_0$	0.919[a]	−0.179	0.001	0.179	−0.113
Summer, $year_{+1}$	0.844[a]	0.025	0.051	−0.340	0.051
Summer, $year_{+2}$	0.515	0.188	0.214	−0.509	0.376
Largest summer storm	0.875[a]	0.141	0.135	0.205	−0.217
Number of germinating rains	0.915[a]	−0.054	−0.036	0.277	0.005
Original drought variables					
Autumn, $year_0$	0.303	0.082	0.823[a]	0.021	0.049
Autumn, $year_{+1}$	0.054	−0.019	0.965[a]	−0.030	−0.071
Autumn, $year_{+2}$	−0.204	−0.139	0.841[a]	0.025	−0.270
Winter, $year_{+1}$	0.184	0.176	0.206	0.760[a]	−0.202
Winter, $year_{+2}$	0.182	0.298	−0.175	0.692[a]	0.272
Winter, $year_{+3}$	0.025	0.431	−0.332	0.191	0.511
Late spring, $year_{+1}$	0.100	0.783[a]	0.008	0.104	−0.298
Late spring, $year_{+2}$	−0.017	0.853[a]	0.026	0.081	−0.011
Late spring, $year_{+3}$	−0.016	0.701[a]	−0.041	0.252	0.325

Seasons for original rainfall and drought variables are as follows: cool season, October to March; summer, July to September; autumn, September and October; winter, November to March; late spring, April to June. $Year_0$ = year (October to September) of hypothetical germination event.

[a] Variables represented by each component on the basis of loadings.

in 2003 ($p < 0.001$). The relation was positive for Coolwet, negative for the other three variables. Larger cohorts were thus associated with increased cool-season moisture before germination and decreased seasonal drought after germination Warmwet did not contribute significantly to either regression.

4. Discussion

Opuntia engelmannii, like other Sonoran Desert cacti (Tschirley and Wagle, 1964; Pierson and Turner, 1998), experiences natural cycles of population growth and decline. On Tumamoc Hill, cycles occurred in the absence of grazing by domestic livestock and resulted from the interaction of life-history traits and climatic variability, especially conditions that favored establishment. Moderate longevity (13–56 years) and modest annual survival (0.9298) were associated with fairly rapid turnover, thus cyclical fluctuations were evident over relatively short times. Censuses

made in 1996 and 2003 suggested that rapid population growth occurs during periods of favorable climate for regeneration and that declines are precipitated as large cohorts reach the end of their natural life-span (Fig. 5). Drought-related mortality might play a role in declines as well.

Permanent plots maintained at Tumamoc Hill illustrate the pattern of rising and falling populations. Between 1968 and 1984, numbers of *O. engelmannii* on the Spalding–Shreve plots remained essentially stable because births and deaths were approximately equal; between 1984 and 2001, deaths outnumbered births, resulting in a marked decline. The pattern of gain and loss was even more marked on larger plots. On Area A, *O. engelmannii* increased five-fold between 1910 and 1969, then gradually dropped to zero in 1999 (Fig. 3a). On Area B, the pattern was essentially the same, but the timing differed. A small population present from 1928 to 1957 disappeared by 1968 and was not replaced until 2001, when there were 12 new plants (Fig. 3b).

On the North Slope and Northwest Corner plots, there were three major establishment peaks from about 1975 to about 1995 (Fig. 5), equivalent to a rate of one peak every 7 years. This rate seems barely adequate for a species with a median life-span of 13 years, especially given the potential for decade-long gaps in major pulses of establishment (Fig. 3). A 10-year gap is longer than the reproductive life-span of most individuals. An estimated five percent of plants might live as long as 56 years; such extended longevity is probably crucial for population persistence during long periods of little or no recruitment. It seems likely that subpopulations can rebound from declines as long as a few old, highly fecund plants remain in the vicinity. In addition, persistent seed banks and vegetative reproduction doubtless help maintain populations until favorable climatic conditions again promote regeneration from seed.

Although some platyopuntias increase under drought conditions, that is not the case for *O. engelmannii*. Major establishment peaks on the North Slope and Northwest Corner plots occurred in the late 1970s, the mid-1980s, and the early to mid-1990s in conjunction with briefer autumn, winter, and spring droughts after germination and higher cool-season rain before germination (Fig. 6). Each factor plays a unique role in regeneration. Average or better-than-average cool-season moisture is associated with good fruit set (Bowers, 1996b), hence large seed crops, but because seeds remain dormant for a year or longer after dispersal (Bowers, pers. obsv.), there is a lag between wet winters and germination events. A series of wet cool seasons might promote development of a large seed bank and, eventually, large seedling cohorts. Length of seasonal drought likely affects seedling survival directly via desiccation and indirectly via predation by rodents, with seedlings at greater risk for predation during drier seasons. Autumn and late spring are normally dry in the study area; amelioration of the usual seasonal drought seems to be a prerequisite for establishment of large cohorts. Summer rains induce germination, apparently producing larger cohorts in wetter summers, but did not explain a significant proportion of the variation in residual regeneration in 1996 or 2003. Establishment peaks in the mid-1980s and early to mid-1990s clearly coincided with peaks in total summer rain (Figs. 6a and c). That the late 1970s peak apparently did not was an
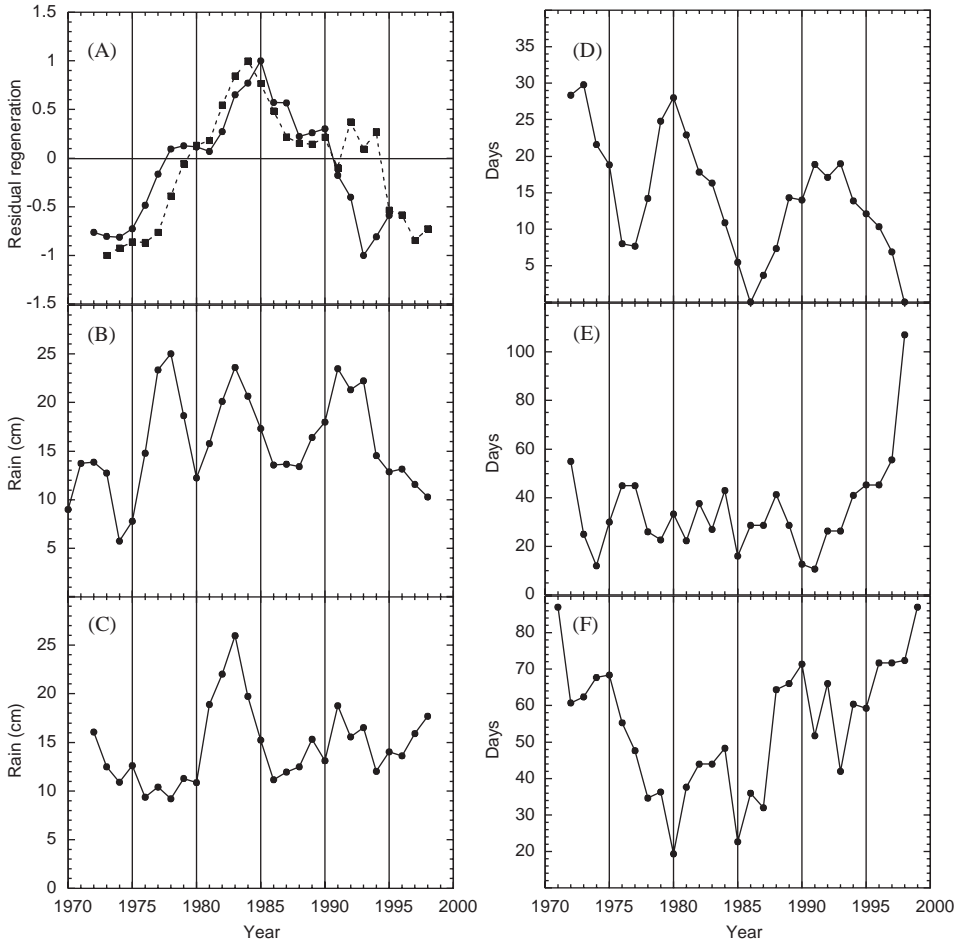
Fig. 6. Climatic variability and establishment of *Opuntia engelmannii*, Tumamoc Hill, Tucson, AZ. (A) Residual regeneration in 1996 (circles) and 2003 (squares), North Slope and Northwest Corner plots pooled. (B) Cool-season rain (October–March). (C) Summer rain (July–September). (D) Autumn drought (September and October). (E) Winter drought (November–March). (F) Spring drought (April–June). Length of drought calculated as number of consecutive days ⩾30 without measurable rain. Climatic variables are 3-year running means.

artifact of data summarization. Although summers in the late 1970s were drier than normal, producing the dip seen in Fig. 6c, single large storms in 1978 and 1979 probably stimulated abundant germination, thus accounting for the establishment peak of the late 1970s (Fig. 6a).

As with other patterns showing regional synchronization (Swetnam and Betancourt, 1998), the recent resurgence in *O. engelmannii* at locations across southern Arizona (e.g. McClaran et al., 2002a; Turner et al., 2003) can probably be ascribed to large-scale climatic phenomena. One major source of inter-annual

variability in winter rain in the region is the El Niño-Southern Oscillation phenomenon (ENSO). When the Southern Oscillation index is negative, autumn and spring tend to be wetter than normal (El Niño conditions); when it is positive, winters can be very dry (La Niña conditions) (Andrade and Sellers, 1988; Webb and Betancourt, 1992; Cayan et al., 1999). In the southwestern United States, insect outbreaks, wildfires, and tree demography are driven by decadal-scale climatic variability associated with ENSO (Swetnam and Betancourt, 1998). Similarly, peaks of *O. engelmannii* establishment at Tumamoc Hill since 1975 have all coincided with periods of frequent El Niño conditions: the late 1970s peak with the El Niños of 1976–1978 and 1979–1980; the mid-1980s peak with the El Niños of 1982–1983 and 1986–1987; and the early to mid-1990s peak with prolonged El Niño conditions from 1991 to 1995. *Opuntia engelmannii* populations elsewhere in southern Arizona grew rapidly during the same period of frequent El Niño years (e.g. McClaran et al., 2002a, b).

A concurrent source of climatic variability in the region is the Pacific Decadal Oscillation (PDO). Like ENSO, PDO exerts a strong influence on cycles of drought and wetness, but over periods lasting two to three decades (McCabe and Dettinger, 1999; Mantua, 2002). Negative values of PDO are associated with severe drought in the southwestern United States, as from 1942 to 1957 (Schmidt and Webb, 2001). Because PDO can influence both winter and summer rain (Cayan et al., 1998; Barlow et al., 2001), prolonged negative PDO should have a deleterious effect on all aspects of regeneration, including fecundity, germination, and seedling survival, resulting in long periods with little regeneration. As noted earlier, *O. engelmannii* populations in southern Arizona tended to be stable and rather small between 1890 and 1985 (Turner et al., 2003), overlapping with mostly negative PDO from 1890 to 1924 and again from 1947 to 1976 (Mantua, 2002). In the late 1990s, PDO shifted to negative values (Mantua, 2002), and on Tumamoc Hill there has been little regeneration since then. If PDO stays negative, as some observers think likely, *O. engelmannii* establishment will remain low for two to three decades.

Although regional population cycles of *O. engelmannii* reflect the influence of global atmospheric circulation, climatic variability interacts with other factors in controlling population cycles of *O. engelmannii* on a local scale. For example, repeated seed germination without successful establishment could deplete *O. engelmannii* seed banks, especially during dieback of old plants, which, because of their high fecundity, are the likeliest source of additional seeds. Other local factors might include pathogens and insects. Tschirley and Wagle (1964) believed that cyclical declines in *O. fulgida* populations could be attributed to build-up of pathogens in the soil; the same might true of *O. engelmannii* and is worth investigating. In addition, at least 13 species of insects attack *O. engelmannii* cladodes, flowers, or fruits (Moran, 1980), and these doubtless check population growth to some extent. Once *O. engelmannii* disappears entirely from a site, recolonization can be a slow process, as seen on Area B after 1957 (Fig. 3b). Presumably because of local effects, *O. engelmannii* subpopulations within a short distance of one another can experience virtually identical climates yet differ strikingly in age structure and density. The North Slope sample in 1996 had

experienced little recruitment in recent years and was much older on average than the Northwest Corner sample, where recent recruitment had been strong (Figs. 5a and b). Similarly, density of *O. engelmannii* in 1969 was about 2.7 plants/$100 \, m^2$ on Area A, 0 plants/$100 \, m^2$ on Area B. The situation was reversed in 2001, when *O. engelmannii* was absent from Area A, and density on Area B was about 1.5 plants/ $100 \, m^2$.

The patchiness of increase and decline at the study site suggests that population dynamics on a larger scale should form a mosaic in which some populations are increasing in response to favorable climatic signals while others remain out of step, perhaps because deaths from disease or old age have diminished recruitment to the point where favorable climate cannot reverse a decline. Metapopulation dynamics of this and other platyopuntias is a subject worthy of further research.

Acknowledgements

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