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The influence of climatic variability on local population dynamics of *Cercidium microphyllum* (foothill paloverde)

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Abstract This study investigated correlations among climatic variability, population age structure, and seedling survival of a dominant Sonoran Desert tree, *Cercidium microphyllum* (foothill paloverde), at Tucson, Arizona, USA. A major goal was to determine whether wet years promote seedling establishment and thereby determine population structure. Plant age was estimated from basal circumference for a sample of 980 living and dead trees in twelve 0.5-ha plots. Ages ranged from 1 to 181 years. Age frequency distribution showed that the population is in decline. Most (51.2%) of the 814 living trees were 40–80 years old; only 6.5% were younger than 20 years. The average age of the 166 dead trees was 78 years. Fifty-nine percent of dead trees were aged 60–100 years. Survival of newly emerged seedlings was monitored for 7 years in a 557-m² permanent plot. Mean survival in the 1st year of life was 1.7%. Only 2 of 1,008 seedlings lived longer than 1 year. Length of survival was not correlated with rainfall. Residual regeneration, an index of the difference between predicted and observed cohort size, showed that regeneration was high during the first half of the twentieth century and poor after the mid-1950s. Trends in regeneration did not reflect interannual variation in seasonal temperature or rain before 1950, that is, in the years before urban warming. Taken together, the seedling study and the regeneration analysis suggest that local population dynamics reflect biotic factors to such an extent that population age structure might not always be a reliable clue to past climatic influences.

Keywords Age frequency distribution · Mortality · Regeneration · Sonoran Desert · Survivorship

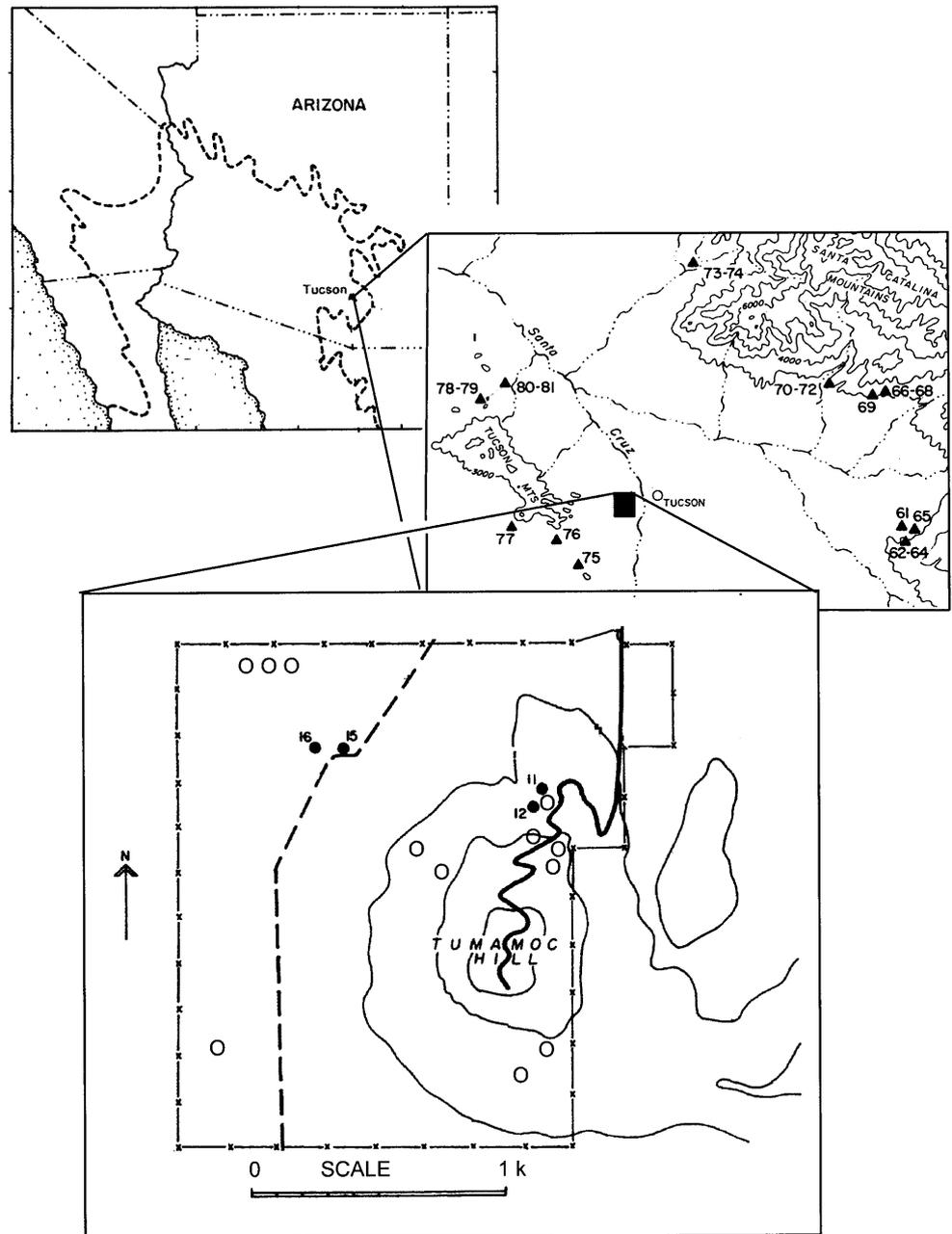
Introduction

Climatic variability has been implicated as a major cause of episodic recruitment among woody plants in arid environments, and, as a result, population age structure has often been assumed to reflect the favorability of particular years or periods for establishment (e.g., Brum 1973; Steenbergh and Lowe 1977; Jordan and Nobel 1979, 1981, 1982; Turner 1990; Parker 1993; Bowers 1997; Pierson and Turner 1998; Swetnam and Betancourt 1998). That certain species can experience high recruitment even in drought years (Brown and Archer 1999) suggests that population age structure at a given site might not always be a reliable clue to past climatic influences. In this study, we investigate correlations between climatic variability, population age structure, and seedling survival for *Cercidium microphyllum* (Torr.) Rose & I. M. Johnston (foothill paloverde), the dominant upland tree in much of the Sonoran Desert (Turner et al. 1995). Our main objective is to discover whether wet years promote seedling establishment and thereby determine population structure. Our study site, an environmental preserve on the northeastern edge of the Sonoran Desert, is particularly well suited for this investigation because (1) it was the location of an early study of *Cercidium* population dynamics (Shreve 1911), (2) long-term permanent plots provide a 78-year record of changes in perennial vegetation (Goldberg and Turner 1986), and (3) domestic livestock have been excluded since 1907 (Shreve 1929).

Recent evidence suggests that at the local scale, climatic variability plays a minor role in the population dynamics of this species. In several sets of matched photographs taken in the Tucson basin during the 50–70 years before 1962 (Fig. 1), *C. microphyllum* increased substantially at several locations (Hastings and Turner 1965: plates 70, 71, 73, 74, 75, 76, 77) while decreasing markedly at others (Hastings and Turner 1965: plates 63, 64, 78, 79) and remaining stable at some (Hastings and Turner 1965: plates 80, 81). Because these sites are <35 km apart and differ in elevation by <215 m, climate should not differ appreciably among them. The inference

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Fig. 1 The Tumamoc Hill study site showing Sonoran Desert boundary after Shreve (1951) (*dashed line*), permanent vegetation plots (*solid circles*), *Cercidium* study plots (*open circles*), and stations used for repeat photography (*triangles*) after Hastings and Turner (1965)



is that other factors drive the dynamics of *C. microphyllum* on a local scale.

In revisiting the *Cercidium* population on Tumamoc Hill, Tucson, Ariz., we determined (1) recent rates of seedling recruitment, (2) the relation between plant size and age, (3) mortality and survivorship, (4) average and maximum longevity, (5) population age structure, and (6) residual regeneration, the difference between the number of plants observed in a cohort and the number needed to maintain a stable age distribution.

C. microphyllum is a small leguminous tree with chlorophyllous bark and drought-deciduous leaves. Flowering is in April and May; after unusually dry winters, trees flower lightly or not at all, and the seed crop is poor (Shreve 1951; Turner 1963). A series of years without

good seed crops eventually brings about a marked reduction in the number of seedlings that emerge (Shreve 1917). The seeds, which ripen in June and July, are consumed by a variety of mammals, including collared peccary, round-tailed ground squirrel, Harris antelope ground squirrel, rock squirrel, several species of pocket mice, and Merriam's kangaroo rat (Hoffmeister 1986; McAuliffe 1986, 1990, personal observation). Heteromyid rodents are important dispersal agents (McAuliffe 1990). Germination occurs during the summer rainy season when minimum air temperatures are $\geq 20^{\circ}\text{C}$ (Bowers 1994). Rain events large enough to trigger germination (≥ 17 mm) occur virtually every summer, typically from July to October (Bowers 1994). Seed coats must be broken for germination to occur (Poole 1958), and it seems

likely that few if any seeds germinate in the year of dispersal (Shreve 1951). Uneaten seeds that do not germinate form a between-year seed bank (McAuliffe 1990; Bowers 1994).

As many as 21.0% of seedlings have been reported to survive their 1st year (Shreve 1917). Establishment is limited by seasonal drought (Shreve 1911, 1917) and by small mammals, particularly cottontail and jackrabbit, that eat seedlings (McAuliffe 1986). Seedlings that emerge in the protection of dense shrubs such as *Ambrosia* spp. have a higher survival rate than those that appear in the open (McAuliffe 1988, 1990). Young plants rarely become established under mature *Cercidium* trees (McAuliffe 1986, 1988). On the basis of tree ring counts, the lifespan has been estimated to be 300–400 years (Shreve 1911). It appears, however, that tree rings are not a reliable means of determining age in this species. Although the greatest increase in stem radius occurs in summer (MacDougal 1936; Turner 1963), a small amount of growth can also occur in spring (MacDougal 1936), making double rings a possibility in some years.

Materials and methods

Study area

Tumamoc Hill (32°13'N, 111°05'W) is an outlier of the Tucson Mountains, Pima County, Ariz., USA (Fig. 1). The study site 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). Vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Between about 1858 and 1907, cattle, horses, goats, and burros grazed the study site (Shreve 1929; Shreve and Hinckley 1937). Stocking rates are unknown; an early observer reported that cattle and goats were present “in considerable numbers” (Bowers 1990). Grazing was apparently heavy enough to bring about a marked reduction in populations of grasses and small perennials (Shreve and Hinckley 1937). Other activities that might have had a substantial effect on vegetation include quarrying of surface rocks in the late 1800s and early 1900s (Spalding 1909) and prehistoric agricultural activities (Ellsworth 1914; Masse 1979). The study site has been protected from grazing and most other impacts since 1907. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter-early spring (November to March), an arid foresummer (April to June), a predictable summer monsoon (July to August), and a highly variable autumn (September to October). Maximum temperatures in summer often exceed 40°C. Winters are generally mild, with occasional freezing temperatures.

Seedling survival

We studied seedling emergence and survival from August 1987 to September 1993 on area A, a 557-m² permanent vegetation plot on the north-facing slope of Tumamoc Hill. This plot was established in 1910 for the purpose of monitoring seedling survival of woody perennials (Shreve 1911, 1917). After summer and autumn rains, we visited the plot and used numbered aluminum tags to mark all recently emerged seedlings. Several times each year, we looked for dead seedlings and removed their tags. In 1993, the final year, we checked for dead seedlings but did not mark any new ones.

For each annual cohort, we calculated seedling survival, S , in the 1st year of life as:

$$S = N_{t+1} \div N_t, \quad (1)$$

where N_t = number of new seedlings emerging during summer and autumn rains and N_{t+1} = number alive at the start of the next summer rainy season. Potential sources of error in our estimates of survival are: (1) we lost track of some seedlings because their tags were removed by animals, and (2) some seedlings doubtless died before we tagged them.

Our censuses in 1987 and 1988 were frequent enough that we could examine seasonal patterns of mortality. Following Shreve (1911), we determined how many new seedlings died during each of four seasons (midsummer, aftersummer, winter, and foresummer). We calculated seasonal mortality for each annual cohort as the number of deaths in a season \div the number of plants alive at the start of the season.

We used linear regression to examine the effect of rain on lifespan of the 1987 and 1988 cohorts. Data from the 2 years were pooled for analysis. We defined seedling lifespan as the number of days between the dates when a seedling was first and last observed. Mean daily rain during the lifespan was calculated by dividing total rain by days of life. Seedlings seen only once were omitted from the analysis. We attempted to assess causes of seedling mortality at the end of the 1987 growing season by categorizing tagged seedlings as: (1) alive, (2) dead and desiccated, (3) dead and chewed, (4) dead and uprooted, and (5) tag found but seedling gone.

Age determination and population age structure

Our examination of seedling survival enabled us to characterize recruitment over the short term. To examine recruitment over a longer period, we first determined the population age structure of a sample of nearly 1,000 established trees. We measured basal circumference to the nearest centimeter of all living and dead trees in 72×72 m plots from December 1998 through May 1999. The 12 plots represented major slope aspects and substrates (Bowers and Turner 2001). We measured basal circumference instead of diameter at breast height because *C. microphyllum* typically branches within a few decimeters of the ground. Dead, highly weathered plants could not be accurately measured and were not used in this study.

We estimated ages for all trees in our sample by determining the relation between plant size and age. In February 1999, we measured the basal circumference of 8 small plants of known age and of 27 additional plants that could be age-dated from historical photographs ($n=2$) and dated disturbances ($n=5$). We assumed that the greatest possible age of the 27 additional plants was close to the actual age; thus, in 1999 the largest plants growing in rubble at the edge of a pipeline dug in 1955 could have been no older than 44 years. Such an assumption can be justified on two accounts. First, rain events large enough to induce germination occur almost every summer, and although survivors of any particular cohort might be few, large cohorts were not needed to build the model. Second, disturbance is not necessarily inimical to *Cercidium* establishment. Construction of buildings, roads, and pipelines typically adds many rocks to the soil surface, and these create safe sites in which seeds and seedlings are protected from herbivores. Altogether, the age-dated sample comprised 35 plants that ranged in size from juveniles with basal circumference <1 cm to mature trees with basal circumference >90 cm. We determined the relation between estimated age and circumference with linear regression, then used the regression equation to assign ages to all plants in the 72×72 m plots.

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; Pier-

son and Turner 1998). We calculated residual regeneration using the sample of trees from the 72×72 m plots. A survivorship curve was determined from the pattern of age-specific deaths in our sample. Because we did not know when the trees died, we could not determine age-specific mortality, that is, proportion of deaths per unit of time for every age class. Instead, we calculated the proportion of dead plants, M , in 5-year age classes as:

$$M = D \div (D+L), \quad (2)$$

where D and L are the number of dead and living plants. We used the Survival Analysis module in SYSTAT (1998) to derive the survivorship curve. The module uses a parametric estimator to determine survival probability of the dependent variable at each time interval. The model can be conditioned upon a covariate, that is, a quantitative predictor variable. Our analysis used age as the survival variable and age-specific deaths (M) as the covariate.

To determine the number of individuals needed in each age class to maintain a stable age distribution, we scaled the survivorship curve [scaling factor=(total population size)÷(area under the curve)] (Pierson and Turner 1998). We then subtracted the number of plants predicted by the survivorship curve from the observed number. To take into account the expected decline in numbers with increasing age, these differences, or 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). Because assigned ages were approximate rather than exact, we expressed residual regeneration as a 5-year running mean.

Environmental correlations

We used 5-year running means of several climatic variables to investigate the relation between climate and residual regeneration from 1914 to 1994. Running rather than annual means were used to maintain consistency with regeneration values. Our expectation was that regeneration would be higher in wetter periods than during dry ones. The climatic variables included total rain in each of four seasons (Table 1), length of drought in each of three seasons (Table 1), and air temperature. For each seasonal drought, we counted the number of days in every rainless period that lasted ≥30 consecutive days, then summed the values. As an indication of interannual variability in temperature, we used the lowest minimum temperature (°C) in every winter and the frequency of extremely high temperatures (≥43°C) in every summer. Missing data were filled in by regression from the record at the University of Arizona, 6 km to the east. Because the maximum temperature record on Tumamoc Hill in the late 1980s is not consistently reliable, we determined frequency of extreme high temperatures from the University of Arizona record.

We used Pearson correlation to examine the strength of association between climatic variables and residual regeneration. Because of urban warming, the annual average temperature in Tucson is now about 3°C higher than in the late 1800s (Comrie 2000). Urban warming has also affected Tumamoc Hill, especially after 1950. To factor out this heat-island effect, we repeated the analysis after separating the data into pre- and post-warming sets, using 1950 as a dividing line.

We also looked for visual correlations between residual regeneration and historic canopy cover on Tumamoc Hill. The canopy and base of all perennial plants on plots 11, 12, and 15 were mapped in 1910, 1928, 1936, 1948, 1957, 1960, 1968, 1978, and 1984 (Shreve 1929; Shreve and Hinckley 1937; Murray 1959; Goldberg and Turner 1986; Raymond M. Turner, unpublished data). We determined for every mapping year the average canopy cover (dm²) of all mapped plants, then plotted cover and residual regeneration as a function of time. Other permanent plots on Tumamoc Hill were excluded from this analysis because they were not mapped as frequently.

Table 1 Definitions of seasonal climatic variables used in correlation analysis

Season	Rain	Drought
Winter	November to March	November to March
Foresummer	April to June	April to July
Midsummer	July to mid-September	—
Aftersummer	Mid-September to October	August to October

Table 2 Survivorship of seedlings of *Cercidium microphyllum* at Tumamoc Hill. Values represent number of seedlings recorded at approximately 12-month intervals. No census of new seedlings was made in 1993

Cohort	Census year						
	1987	1988	1989	1990	1991	1992	1993
1987	155	1	0	0	0	0	0
1988		163	0	0	0	0	0
1989			36	0	0	0	0
1990				170	7	1	0
1991					329	6	1
1992						155	7
Total	155	164	36	170	336	162	8

Results

Seedling survival

Seedlings emerged in every year from 1987 to 1992 and in every month from July to October. In most years, there was more than one emergence event; for simplicity, we treated all seedlings of the same year as a single cohort when we calculated annual survivorship. Average 1st-year survivorship during the 7 years of the study was 1.7% (SE=0.706) (Table 2). Only 2 of 1,008 seedlings survived longer than 1 year (Table 2).

Mean seedling lifespan of the 1987 and 1988 cohorts was 179 days (SD=134.1, $n=303$, range 56–1,029 days). Across the 7 years of the study, the range was 27 to 1,029 days, and the mean was 148 days (SD=122.2, $n=549$); because the analysis omitted seedlings that were seen only once, actual lifespan was probably much shorter. Most seedlings germinated between July and October, then died before the start of the foresummer: survivorship from germination to the following May averaged 5.2% (SD=7.1, $n=6$ years, range=0.0–18.8%).

Attrition of the 1987 and 1988 cohorts followed a distinct seasonal pattern (Fig. 2). On average, almost 50% (SD=6.2) of new seedlings died before the winter rainy season began. The proportion of survivors that died during the winter was considerably lower, an average of about 23% (SD=6.9). It appears that this seasonal pattern was unrelated to rainfall; we found no correlation between mean daily rain and lifespan of seedlings in the 1987 and 1988 cohorts ($r^2=0.02$). Our limited data indicate that the main cause of seedling mortality in 1987 was predation. Of 26 dead seedlings located and evaluat-

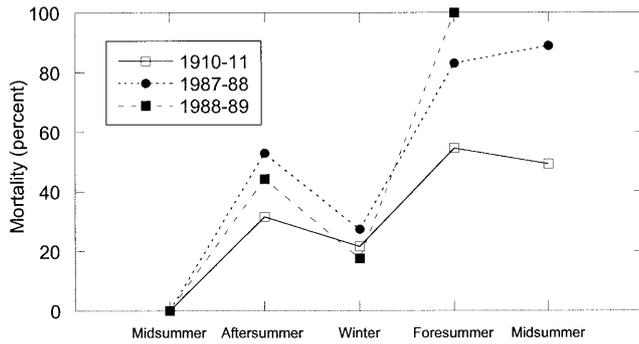


Fig. 2 Seasonal patterns of mortality of *Cercidium microphyllum* seedlings over 3 years

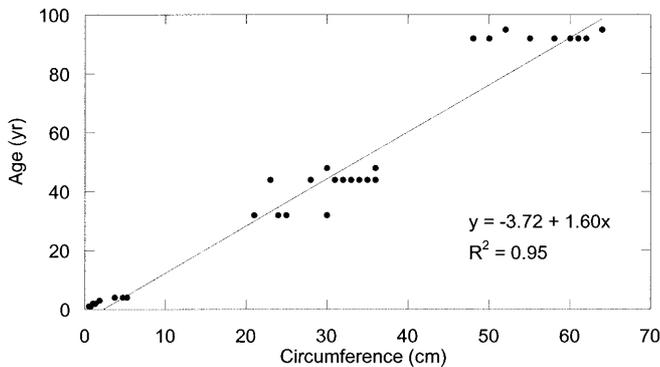


Fig. 3 Relation between basal circumference and age of *C. microphyllum*

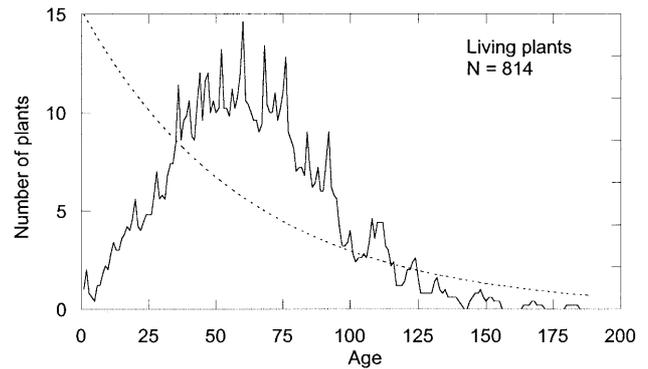
ed in December, two had been uprooted, three had been chewed, and 16 had been removed entirely, presumably by animals. Although the month of November was drier than normal, only 5 seedlings were dead and desiccated. An additional 13 seedlings that died by December somehow escaped categorization.

Age determination and population age structure

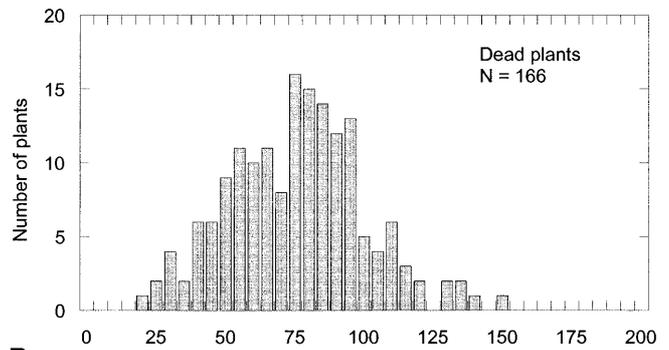
The relation between plant age and basal circumference was linear and could be described as:

$$A = -3.72 + (1.60 \cdot C), \quad (3)$$

where A = age (years) and C = basal circumference (cm) ($r^2=0.95$, $P<0.001$) ($n=35$) (Fig. 3). The average age of the 814 living trees in our sample was 63.0 years ($SE=1.0$; range 1–181). Most (51.2%) were 40–80 years of age; only 6.5% were younger than 20 years (Fig. 4a). For the 166 dead trees, the average age was somewhat higher, 78 years ($SE=1.9$; range 20–152). Fifty-nine percent of dead trees were aged 60–100 years (Fig. 4b). No dead tree was younger than 20 years, a finding that suggests established juveniles have a low death rate.



A



B

Fig. 4 a Age frequency distribution of living *C. microphyllum* in 1999 (solid line) and idealized cohort survivorship (dotted line). Number of plants is expressed as a 5-year moving average. **b** Number of dead *C. microphyllum* in 5-year age classes in 1999

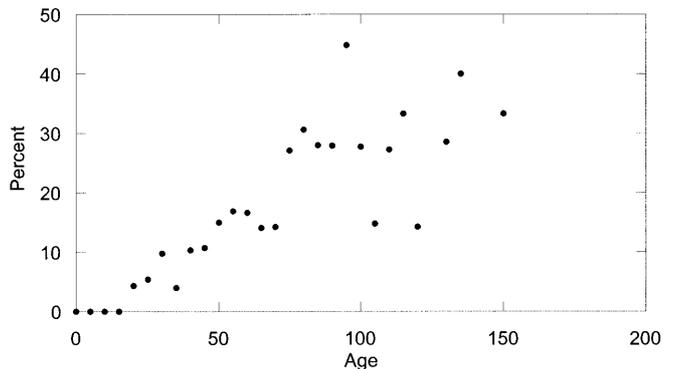


Fig. 5 Proportion of dead *C. microphyllum* in 5-year age classes in 1999

Mortality, survivorship, and residual regeneration

The proportion of dead trees in five-year age classes increased gradually throughout the lifespan (Fig. 5). The shape of the survivorship curve (Fig. 4a) reflects our decision to use an exponential model in the survival analysis (SYSTAT 1998). The exponential model produces a Deevey Type III survivorship curve, in which juvenile mortality is high and adult mortality low, as is typical of many trees (Silvertown 1982).

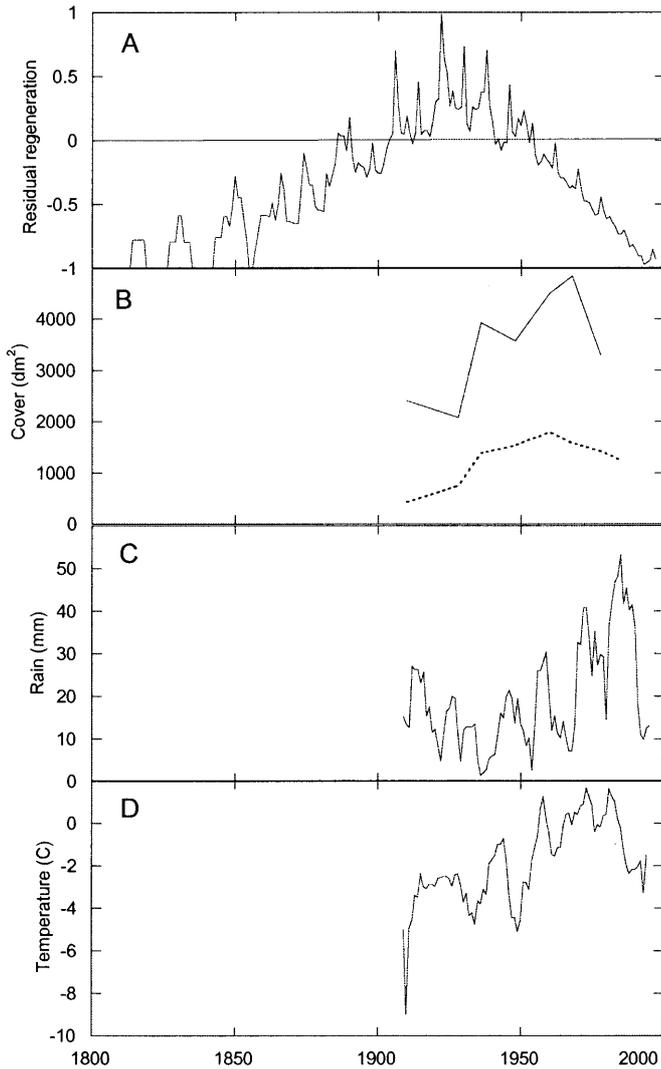


Fig. 6a–g Residual regeneration of *C. microphyllum* as a function of environmental variability. **a** Residual regeneration, expressed here as a 5-year moving average from 1815 to 1995, is an index of the difference between observed and predicted cohort size. Values above the *solid horizontal line* show when cohorts have been large enough to maintain a stable population. **b** Canopy coverage of *C. microphyllum* (*dotted line*) and total canopy cover (*solid line*) on eight observation dates. **c** Aftersummer rain. **d** Lowest winter temperature. **e** Frequency of maximum temperatures $\geq 43^{\circ}\text{C}$. **f** Length of winter drought. **g** Length of aftersummer drought. Except for cover, environmental variables are expressed as 5-year moving averages from 1909 to 1995

Residual regeneration, an index of the difference between observed and predicted population size, is positive when regeneration exceeds the number needed to maintain a stable population and negative when it does not. Regeneration values do not indicate whether an undersized cohort reflects a year of poor recruitment or of high mortality. Both have been involved in the recent decline; dieback in the 1990s removed many older trees from the population (Bowers and Turner 2001), and, at the same time, the number of new plants established was not enough to maintain a stable age distribution. Be-

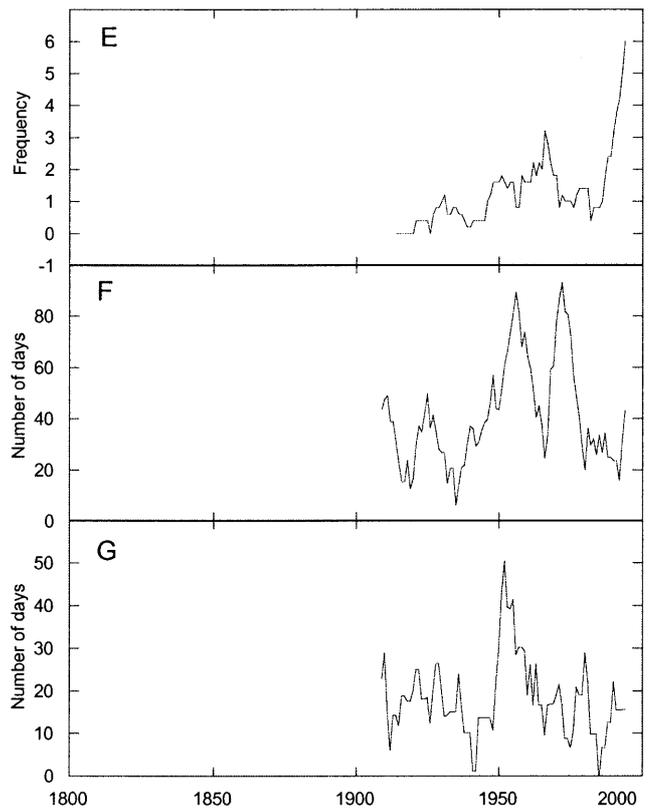


Table 3 Pearson correlations of residual regeneration with nine climatic variables, 1914–1994. Residual regeneration is an index of the difference between observed and predicted cohort size

Climatic variable	Pearson correlation (r)		
	Pre-1950	Post-1950	Entire data set
Foresummer rain	0.25	0.07	0.37
Summer rain	0.17	-0.01	-0.16
Aftersummer rain	-0.30	-0.46	-0.60*
Previous winter rain	0.04	-0.34	-0.35
Aftersummer drought	0.33	0.72*	0.23
Winter drought	-0.01	0.61*	-0.13
Foresummer drought	-0.27	0.35	0.06
Minimum temperature	-0.18	0.01	-0.57*
Maximum temperature	-0.04	-0.37	-0.61*

* $P < 0.01$

tween the early 1900s and the early 1950s, residual regeneration was positive (Fig. 6), that is, cohorts exceeded the number of plants needed to maintain a stable age distribution. Since the mid-1950s, residual regeneration has been negative. Several small pulses of establishment between the 1960s and 1990s are evident as peaks on the downward curve (Fig. 6); evidently none was large enough to generate positive residuals.

Before 1950, residual regeneration was not strongly correlated with any climatic variable (Table 3). After 1950, that is, after urban warming took effect, there were significant ($P < 0.01$) correlations between residual regeneration and drought (Table 3). Surprisingly, the correla-

tions were positive, that is, poor regeneration was associated with brief droughts. In the analysis of the entire data set, residual regeneration was negatively correlated with aftersummer rain, minimum temperature, and maximum temperature (Table 3).

On the three permanent plots, cover of *C. microphyllum* rose steadily during the first part of the twentieth century, reaching a peak between 1948 and 1960, then declined gradually between the 1960s and the 1980s (Fig. 6). Residual regeneration fell below zero about the same time that cover peaked and remained negative thereafter (Fig. 6). Total canopy cover (all mapped species) peaked between 1960 and 1968, then declined (Fig. 6).

Discussion

In revisiting establishment of *C. microphyllum* at Tumamoc Hill, we were able to confirm Shreve's (1911, 1917) results in several respects. The population age distribution was, as in Shreve's day, skewed toward middle-aged plants. Established juveniles had a low risk of mortality. Germination and emergence occurred frequently. In both studies, a high proportion of seedlings died soon after germination.

In other particulars, our results differed. Although Shreve (1911 pp 295–296) reported that of “a great many thousands” of *C. microphyllum* plants in the vicinity of Tucson, he had seen “only two dead trees of full size,” we found substantial mortality among adults, especially in the older age classes. Shreve (1911) estimated that *C. microphyllum* lives 300–400 years, but maximum longevity in our sample was less than 200 years, and most plants did not live longer than 80–100 years. We suspect that Shreve mistook seasonal tree-rings for annual rings, thus doubling the age of individuals in his study. Most notably, our results do not support the hypothesis that seedling survival is limited primarily by drought. Seedling lifespan was not correlated with rainfall, and, in 1987 at least, more seedlings died from predation than drought (see also McAuliffe 1986). In all years, only a small proportion of seedlings survived from germination in summer and autumn until the following May, which means that few had the opportunity to die during the very hot days of early summer. Seedling survival was markedly lower in our study than in Shreve's (1917): 1.7% vs 21.0% in the 1st year of life; 15.5% vs 44.2% in the 2nd year of life; and 0.0% vs 65.6% in the 3rd year of life. These disparities cannot be ascribed to seasonal rains: ANOVA showed little difference between the two studies in rain of the summer, aftersummer, winter, or foresummer (Table 4). It seems unlikely that differences in initial cohort size can account for it either: a *t*-test showed that there was no significant difference between the mean size of annual cohorts in Shreve's sample and ours ($t=0.23$, $P>0.50$).

Residual regeneration showed strong temporal trends, being positive before the early 1960s and negative after-

Table 4 Results of ANOVA: A comparison of seasonal rain during studies of seedling survival from 1910 to 1917 (Shreve 1911) and 1987 to 1992

Source	Sum of squares	df	F-statistic
Season	515.315	3	29.404*
Study	2.344	1	0.401**
Season×study	1.213	1	0.404**

* $P<0.001$; ** $P>0.50$

ward (Fig. 6). At the same time, several climatic variables, most notably temperature and seasonal rains, rose markedly toward the end of the century. Contrary to our expectations, there was no evidence that higher regeneration is associated with wet summers (Table 3). This was true for all three climatic data sets (1914–1950, 1951–1994, 1914–1994) and could reflect the fact that rainfall in most summers exceeds that required for germination and emergence of *C. microphyllum* on Tumamoc Hill (Bowers 1994). We also found no relation in any period between good regeneration and absence of drought (Table 3). Otherwise, analysis of the different climatic periods produced a conflicting picture of the relation between climate and regeneration. In the first half of the century, residual regeneration fluctuated independently of climatic variation, yet after 1950, lower regeneration was associated with brief winter and aftersummer drought, and in the entire data set, residual regeneration decreased as aftersummer rain and minimum temperature increased (Table 3, Fig. 6).

We see no biological basis for any of these correlations. First, in arid regions, gaps between cohorts are typically associated with long dry periods (e.g., Jordan and Nobel 1981, 1982), but on Tumamoc Hill residual regeneration steadily declined between 1976 and 1995, a period that was among the wettest in recent decades (Swetnam and Betancourt 1998). Second, it is not logical that establishment should be hindered by warm-season rains in October but not in July, August, and September. Third, because *C. microphyllum* reproduces during the warmest months of the year, it is difficult to see how an increase in minimum temperature could depress regeneration. Fourth, the highest temperatures of the year occur in June and July before the summer rains begin; arrival of the summer monsoon moderates daily highs. Few seedlings survive long enough to be killed by extreme high temperatures in the foresummer after germination.

If a plant species has particular climatic requirements, it is reasonable to assume that such requirements will remain stable through time. Rather than believe that the relation between regeneration and climate changed after the middle of the century, we conclude that residual regeneration declined after the mid-1950s for reasons that have little or nothing to do with concomitant trends in several climatic variables.

Taken together, our studies of seedling survival and residual regeneration before 1950 do not indicate that climate has controlled the population dynamics of this

species at Tumamoc Hill during the past 100 years. Because germination and emergence do depend on adequate precipitation, we are not suggesting that the population dynamics of this species are independent of climate. Rather, we believe that biotic factors make it difficult to detect the influence of climatic variability in our local area.

One such biotic factor might be herbivory. Shreve's (1911, 1917) studies of seedling survival were conducted before Tumamoc Hill had recovered from grazing by domestic livestock, whereas as ours took place after decades of protection had allowed substantial recovery (Shreve and Hinckley 1937; Blydenstein et al. 1957; Goldberg and Turner 1986). Perhaps regeneration was favored early in the century because competition with livestock for food kept populations of jackrabbits and rodents artificially low, which in turn promoted higher seedling survival of *C. microphyllum*.

A related hypothesis is that rapid suburbanization has indirectly suppressed regeneration in recent decades. In the early 1900s, Tumamoc Hill abutted agricultural fields and open desert. A century later, the hill is nearly surrounded by subdivisions, offices, schools, and thoroughfares. As a result, carnivores such as coyote and bobcat have less opportunity to move between our study site and larger areas of open desert. It is possible, although not certain, that large predators are therefore less frequent on Tumamoc Hill than in the early 1900s. If so, jackrabbit and rodent populations might have grown to such an extent that establishment of *C. microphyllum* has been suppressed in otherwise favorable years.

Another possibility is that exclusion of domestic livestock enabled palatable shrubs such as *Krameria grayi*, *Calliandra eriophylla*, and *Ambrosia deltoidea* to increase markedly in cover and density, and that these species then exerted competitive pressure on *C. microphyllum*, which lost ground. An increase in cover or density of these and other palatable shrubs has been reported several times since the grounds were fenced (Shreve and Hinckley 1937; Blydenstein et al. 1957; Goldberg and Turner 1986). Moreover, Blydenstein et al. (1957) found a decline in numbers of *C. microphyllum* on Tumamoc Hill relative to an adjacent grazed site.

Density-dependent factors might regulate population age structure and obscure the influence of climate. *C. microphyllum* seedlings germinate with equal frequency under the canopies of adults and in the open, but virtually none of the former survive (McAuliffe 1986, 1988). Factors limiting survival under tree canopies might include lack of light and competition with herbaceous plants, as for seedlings of *Prosopis glandulosa* (Bush and Van Auken 1990). Given poor seedling survival under adults, it is of considerable interest that canopy coverage of *C. microphyllum* on Tumamoc Hill increased steadily between the beginning and the middle of the twentieth century (Fig. 5). About the same time that cover reached its peak, residual regeneration began its steady decline. Although the cover data are derived from a small number of trees and therefore must be interpreted with caution, they offer

some support for the idea that high coverage of *C. microphyllum* on Tumamoc Hill has constrained establishment. Recent dieback of *C. microphyllum* has created much bare ground on Tumamoc Hill; if high canopy cover does indeed suppress recruitment, regeneration should again increase as seedlings become established in newly opened spaces between the trees.

Conclusions

Because germination and emergence of *C. microphyllum* depend on adequate precipitation, the population dynamics of this species cannot be entirely independent of climate. Nevertheless, local population dynamics reflect biotic factors to such an extent that age structure might not always be a reliable clue to past climatic influences. Local factors that might swamp climatic effects include ecological processes such as interspecific and intraspecific competition. We suspect that if population data from many sites within the region were integrated, large-scale climatic patterns might well overwhelm such purely local effects.

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