

Demographic patterns of *Ferocactus cylindraceus* in relation to substrate age and grazing history

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Abstract

Three subpopulations of *Ferocactus cylindraceus*, a short-columnar cactus of the Sonoran and Mojave deserts, were sampled in Grand Canyon, Arizona, USA, at sites representing a range of substrate ages and different grazing histories. Age-height relations were determined from annual growth, then used to estimate probable year of establishment for each cohort. Eight years between 1944 and 1992 were especially favorable for establishment. Six of these 8 years coincided with El Niño-Southern Oscillation conditions, indicating that as for many woody plants in arid regions, somewhat unusual climatic conditions are necessary if populations are to replace themselves.

Comparison of age structures showed that established and developing populations have somewhat different dynamics in that the rate of population increase was slowest on the youngest terrace. On the ancient terraces, about half the plants were less than 25 years old. Plants older than 40 years were few; however the oldest plants in the study (about 49 years) grew on the ancient terraces. On the recent terrace, 76% of the subpopulation was 25 years or younger, and the oldest living plant was about 36 years of age. The age structures of subpopulations on grazed and ungrazed sites also differed markedly. On ungrazed sites, subpopulations were more or less at equilibrium, with enough young plants to replace old ones as they died. In contrast, the subpopulation on the grazed site was in a state of marked disequilibrium. Grazing before 1981 largely extirpated a palatable subshrub that was probably an important nurse plant. Until the shrub population at Indian Canyon recovers from decades of burro grazing, a rebound in *F. cylindraceus* establishment is not to be expected.

Nomenclature:

Hickman, J. C. (ed.) 1993. The Jepson manual: Higher plants of California. University of California Press, Berkeley.

Introduction

Intermittent establishment, typical of many woody plants in the arid southwestern United States, can have far-reaching effects on demographic patterns (Shreve 1917; Barbour 1968; Sheps 1973; Ackerman 1979; Sherbrooke 1989; Parker 1993; Bowers 1994). Composed of cohorts spaced several to many years apart, the resulting populations may undergo prolonged decline when seedlings are too few to replace old plants as they die, as has been the case for the columnar cactus *Carnegiea gigantea* (Shreve 1910; Niering et al. 1963; Steenbergh & Lowe 1977, 1983; Helbsing & Fischer

1992). Such populations are particularly vulnerable to the disturbance created by grazing livestock (Niering et al. 1963; Martin & Turner 1977; Webb & Bowers 1993; Parker 1993).

Ferocactus cylindraceus, a short-columnar cactus common on rocky slopes and cliffs in the Sonoran and Mojave deserts, exemplifies these demographic patterns. Germination of *F. cylindraceus* likely occurs under warm, wet conditions (Jordan & Nobel 1981). Seedling survival in the following months probably requires normal or greater-than-normal rains and winters that are not unusually cold (Jordan & Nobel 1981, 1982; Ehleringer & House 1984). Grazing disturbance

might hinder establishment, as is the case for *F. wislizeni* (Reid et al. 1983). *Ferocactus cylindraceus* populations in which very small plants are the most numerous size class are known (Jordan & Nobel 1982), but these may be less common than populations in which the height distribution is positively skewed with a peak in the 31- to 40-cm class (Reid et al. 1983; Ehleringer & House 1984; Jordan & Nobel 1982). The species does not grow where fewer than 1 in 10 years offer suitable climatic conditions for establishment (Jordan & Nobel 1982).

Grand Canyon, Arizona, is an ideal setting for further investigation of *F. cylindraceus* demography. Most of the river corridor has never been grazed by livestock. Ungrazed reaches provide a control for the few sites where feral burros once grazed in large numbers. In addition, variation in substrate age, from one to thousands of years, makes it possible to compare young and long-established populations. The goal of this study was to sample *F. cylindraceus* subpopulations at climatically similar sites that represented a range of substrate ages and different grazing histories. All sites were located in desert scrub vegetation along the Colorado River in Grand Canyon National Park. Questions asked were: (1) What is the relation between annual growth and height, and between height and age; (2) To what extent is establishment associated with unusual climatic events; and (3) Does population age structure differ on grazed versus ungrazed sites and on old versus young surfaces?

Methods

Study area

Grand Canyon, Arizona, a gorge incised as much as 2000 m into the Colorado Plateau, lies between 35°30' and 37° N longitude, and between 111°35' and 113°30' W latitude (Figure 1). The climate is hot and arid. From 1967 to 1982, annual rainfall at Phantom Ranch (783 m above sea level) averaged 231 mm with peaks in January–March and July–August (Sellers et al. 1985). The average daily temperature in July was 32.8 °C, in January, 7.3 °C (Sellers et al. 1985). The two study sites, Prospect Canyon (511 m above sea level) and Indian Canyon (448 m above sea level), are, respectively, 147.3 and 191.0 km by river downstream of Phantom Ranch and might be slightly warmer and drier. Lees Ferry, which has a longer weather record

(1944 to the present), is 141.5 km by river upstream of Phantom Ranch and is somewhat drier and colder.

The Prospect Canyon site (Figure 1) is characterized by debris-flow terraces ranging in age from 1 year to at least 2900 years (Webb et al. 1996). It is inaccessible to livestock and has been grazed only by small populations of bighorn sheep (Webb & Bowers 1993). The Indian Canyon site (Figure 1), a level sandstone bench partly covered by colluvium, has not been dated but was no doubt exposed by fluvial erosion and mass wasting many millennia before the present. This site was grazed by feral burros for an unknown number of years before 1981, resulting in a marked decline in numbers of *Ambrosia dumosa*, a palatable subshrub, and in accelerated turnover of several other species (Webb & Bowers 1993). Grazing was terminated in 1981.

Plant sampling

At Indian Canyon, all *F. cylindraceus* plants in a permanent plot were mapped as part of a vegetation study in February 1991. The plot, established to coincide with the field of view in an historic photograph (Robert B. Stanton #643, 1890, Still Picture Branch, National Archives), was a triangle with 40-m sides and a 30.5-m base. Each *F. cylindraceus* plant in the plot was numbered and tagged, and its height was measured. The heights were taken from an average ground level to the plant apex, that is, the highest green part of the plant. In addition, a long nail was hammered into the ground near the base of each plant, and a second height was taken from the top of the nail to the plant apex. In March 1993, the height from nail to apex was again measured for each plant, and average annual growth was calculated.

At Prospect Canyon, annual growth of *F. cylindraceus* was determined in a permanent plot established to coincide with the field of view in another historic photograph (Robert B. Stanton #620, 1890, Still Picture Branch, National Archives). This plot, which was also a triangle with 40-m sides and a 30.5-m base, was located on a debris flow terrace that had been deposited about 2900 years ago (Webb et al. 1996). In February 1991 all *F. cylindraceus* plants on the plot were numbered, tagged, and measured as for the Indian Canyon plot, and in March 1993 heights above the nail were measured again so that average annual growth could be calculated.

To get a better understanding of population age structure on surfaces of different ages, additional

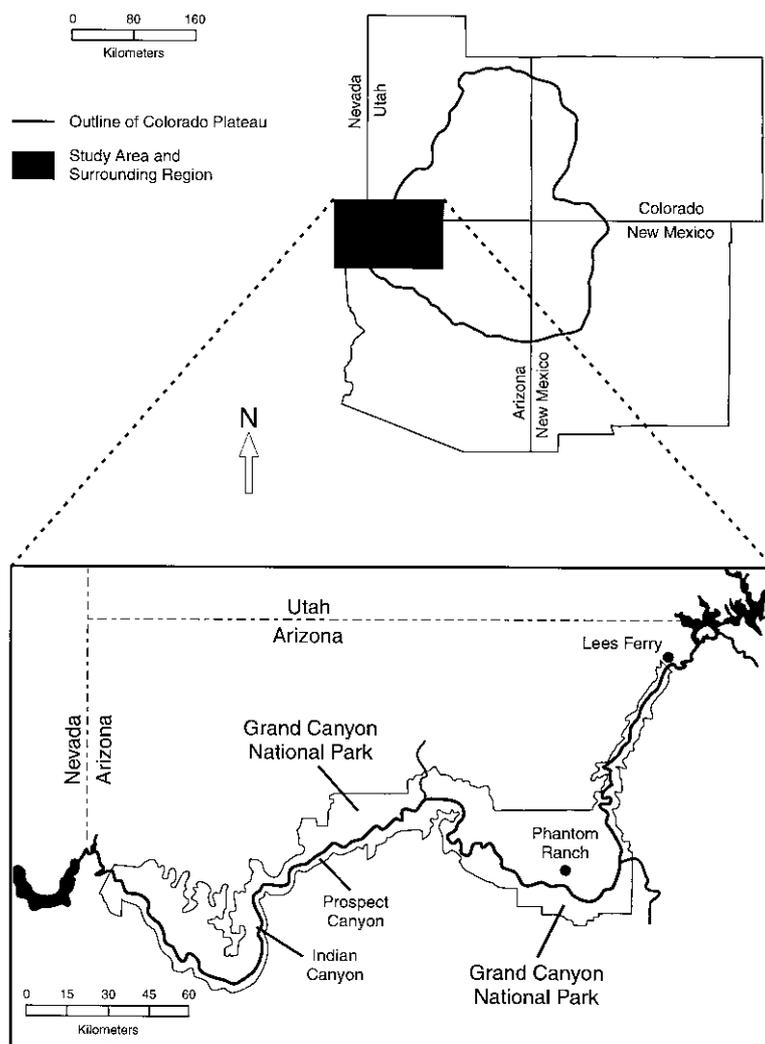


Figure 1. Location map of the Grand Canyon region showing study sites and other features of interest.

height data were collected in March 1993 on three more terraces in Prospect Canyon. One, deposited in 1939, was 55 years old; another was about 490 years old (Webb et al. 1996). The third, although undated, was more than several centuries in age (Robert H. Webb, personal communication). On each terrace, two observers simultaneously walked from one end toward the other end, carefully searching for plants of all sizes. Heights of the first 75 plants encountered were measured and recorded. (Sample size was chosen to match the number of plants found in the permanent plot at Prospect Canyon.) *Ferocactus cylindraceus* density on the ancient terraces ranged from 1000–1300 plants ha^{-1} (Bowers et al., in press). On the 1939 terrace, there

were about 400 plants ha^{-1} (Bowers et al., in press). Plants appeared to be randomly distributed with respect to height on all terraces. Except on the 1939 terrace, where lower *F. cylindraceus* density made it necessary to sample a larger area, these unmarked plots each covered about the same amount of ground as the permanent plots.

Growth curves

The ages of columnar cacti can be readily determined from their heights (Shreve 1910; Jordan & Nobel 1982; Steenbergh & Lowe 1983; Turner 1990; Parker 1993). The process involves measuring apical growth over

several years or longer, then calculating average annual growth for each plant in the sample. The sample plants are used to define the relation between annual growth and height; the resulting regression equation makes it possible to calculate annual growth at a range of heights. Annual growth increments are then summed, producing an estimate of expected height after a given number of years. Because radial growth in *F. cylindraceus* essentially stops at 35–40 cm while vertical growth continues (Benson 1982; Ehleringer & House 1984), the relation between diameter and annual growth is not useful in estimating the ages of tall plants.

Average annual growth was determined for all plants on the two permanent plots except for plants that were diseased, injured, strongly leaning, or dead. Next, individuals were grouped by height in 5-cm height classes, and mean annual growth for each height class was plotted as a function of mean class height. Using the average annual growth for each 5-cm height class as the dependent variable, a Kolmogorov–Smirnov two-sample test was used to evaluate the difference in growth rates among the various sites.

Regression analysis was used to estimate the amount of annual growth expected at different heights. Annual growth values from the two permanent plots were combined by averaging them within 5-cm height classes; the averaged values were then used in regressions of mean class height versus average annual growth. In addition, all growth values from the two permanent plots were plotted individually as a function of plant height, and curves were fitted to the data points with regression. Linear, semi-logarithmic, and log-log models were examined for both data sets. The regression equation that best fit the data was used to estimate annual growth at a range of heights. These annual growth increments and their corresponding heights were summed such that expected annual growth in the first 12 months after germination = height at age 1; height at age 1 + expected annual growth at that height = height at age 2; etc. The heights were plotted as a function of age so that age at any height could be read from the graph. Unfortunately, the permanent plots did not contain enough very small plants for a meaningful estimate of annual growth in the smallest size class. According to Jordan & Nobel (1981), newly germinated *F. cylindraceus* seedlings attain a height of about 1.5 cm in 12 months; 1.5 cm was therefore used as the starting point for summation of heights and annual growth increments at the end of the first year.

A disadvantage to estimating heights by summation is that variation in error from prediction of any one height is incorporated into the next height. To evaluate how propagation of errors affected the height-age model, the process of estimating annual growth at different heights was repeated twice, substituting a different x coefficient in the height-growth regression equation each time. These substituted values were obtained by increasing and decreasing the x coefficient by its standard error. In other words, a regression equation having the form $\hat{Y} = a + bX$ was altered to $\hat{Y} = a + [(b + SE) \cdot X]$ and $\hat{Y} = a + [(b - SE) \cdot X]$. The unmodified equation estimated median annual growth at a range of heights; the maximum and minimum annual growth expected at each height was provided by the altered equations. Growth increments were then summed with heights as described above to estimate a maximum and a minimum height for every age of interest.

Peaks of establishment

To correlate years of peak *F. cylindraceus* establishment with calendar years, plants were assigned to annual cohorts. Preliminary analysis indicated that 3-, 5-, and 10-cm height classes generally spanned > 2 years, whereas 1-cm height classes spanned 1 year or less, except for the smallest classes. All individuals within each of the five 1993 samples were therefore grouped by 1-cm height classes, then the age of each class was estimated from the graph of height versus age. Like-aged height classes were grouped into annual cohorts, and the probable establishment year for each cohort was determined from its presumed age in 1993. The number of individuals in each annual cohort was plotted as a function of establishment year. Separate histograms were made for the five study sites individually and for all sites combined. Keeping in mind that recent cohorts are generally larger than older cohorts as a result of plant deaths, peak establishment years, defined as those years when an unusually large number of plants became established, were identified by inspecting the histograms.

Population age structure

Identifying establishment years for annual cohorts made it possible to compare population age structures among sites. Preliminary analysis with a Kolmogorov–Smirnov two-sample test showed that age distributions on the three oldest terraces at Prospect Canyon were

not significantly different from one another, and they were therefore pooled for this and subsequent analyses. Age distributions on the 1939 Prospect Canyon terrace were significantly different from the pooled Prospect Canyon sample, and they were treated separately. Age histograms were therefore plotted for the Indian Canyon plot, the 1939 Prospect Canyon terrace, and the pooled Prospect Canyon sites.

Climatic analysis

To correlate climatic events with years of peak establishment, it was necessary to construct a proxy climatic record, there being no weather stations at the study sites. Monthly precipitation data, available for Phantom Ranch from 1967 to the present, were used directly in the climatic analysis. Monthly rain prior to 1967 was estimated by regression using total monthly precipitation from Lees Ferry as the independent variable. The regression equation was $\hat{Y} = -11.53 + 1.49x$ ($R^2 = 0.72$, $P < 0.001$), where \hat{Y} = study site precipitation (mm) and x = Lees Ferry precipitation.

Kruskal-Wallis tests were used to evaluate the strength of the correspondence between peak or non-peak establishment years and several climatic variables. These variables were defined to reflect the supposed germination and establishment requirements of seeds and seedlings. Monthly rains were grouped into several seasonal categories and summed for each year of interest: (1) May–October (the summer germination season), (2) November–April (the first cool season after the germination season), (3) November–October (the first 12 months after the germination season), and (4) the largest monthly total during the May–October germination season. The lowest winter minimum temperature at Lees Ferry was used directly as an index of winter severity. Although winters at the study sites were doubtless warmer than those at Lees Ferry, the relative severity of winter cold from year to year was probably similar at all locations.

Results

Growth rates and age-height relationships Growth could be determined for 23 of the 40 plants originally measured on the Indian Canyon plot. Of the remaining 17, 6 could not be relocated (tags or nails were missing), 4 were strongly leaning, 6 were injured or diseased, and 1 was dead. On the Prospect Canyon

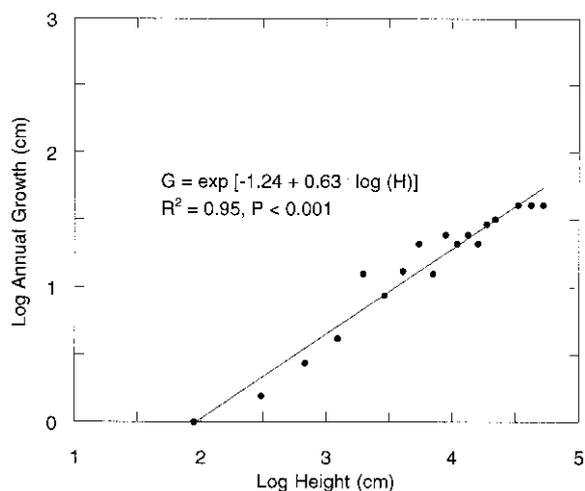


Figure 2. Annual growth (G) in *Ferocactus cylindraceus* as a function of plant height (H), based on 5-cm height classes.

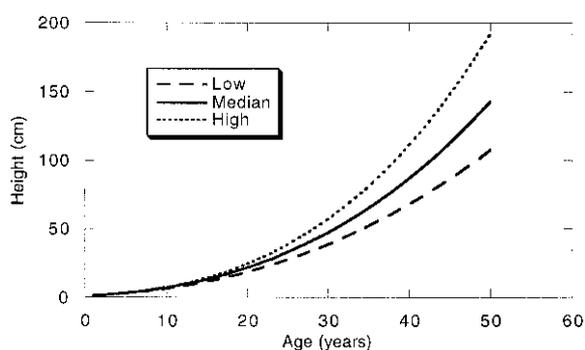


Figure 3. The effect of propagation of error on estimation of height. The three curves represent heights calculated using the height-growth regression equation and three different values for the x coefficient: the unmodified coefficient (median height estimate), the coefficient minus the SE (low height estimate), and the coefficient plus the SE (high height estimate). The median estimate was used to model the age-height relation for *Ferocactus cylindraceus* at Grand Canyon, Arizona.

plot, 1 plant was dead; growth was determined for the remaining 74 plants. Growth rates at Indian Canyon did not differ significantly from those at Prospect Canyon ($p > 0.80$), and the samples were combined for regression analysis. Regressions based on 5-cm height classes accounted for a higher proportion of the variation in annual growth than regressions based on individual heights; the log-log model of data from the combined sites provided the best fit (Table 1). The log-log model was further refined by eliminating two outliers that had large leverages. The regression equation used to estimate annual growth at various heights was $G = \exp[-1.24 + 0.63 \cdot \log(H)]$, in which $G =$

Table 1. Results of regressions showing the relation between annual growth (G) of *Ferocactus cylindraceus* and plant height (H) in Grand Canyon, Arizona. The independent variable was mean height of each 5-cm height class represented at the site.

Site	Regression Equation	Regression r^2	n
Prospect Canyon	$G = -0.49 + 2.45 \cdot \log(H)$	0.67 ^a	19
Indian Canyon	$G = -3.43 + 4.58 \cdot \log(H)$	0.50 ^b	13
Combined Sites	$G = \exp [0.43 - 0.46 \cdot \log(H)]$	0.77 ^a	19

^a $p < 0.001$. ^b $p < 0.05$

mean annual growth (cm) and H = mean height (cm) ($R^2 = 0.95$, $p < 0.001$) (Figure 2).

The model relation between age and height is depicted as the 'median' curve in Figure 3. Propagation of error had negligible effect on the predicted heights of plants younger than 20 years, as shown by the close correspondence between the low, median, and high estimates of height (Figure 3). For older plants, the effect was more pronounced; a 25-year-old plant, for example, could range in height from 27.5 to 38.6 cm. This result was not unexpected; because of natural variation in growth rates, plants of the same age will not all be the same height.

Population age structure

The Kolmogorov-Smirnov two-sample tests showed significant differences among subpopulations in age structure: the old terraces versus the young terrace at Prospect Canyon ($p < 0.001$); the old and ungrazed surfaces at Prospect Canyon versus the old and grazed surfaces at Indian Canyon ($p < 0.001$); and the young Prospect Canyon terrace versus the old Indian Canyon Terrace ($p < 0.004$). On the old terraces at Prospect Canyon, about 59% of the 1993 subpopulation was less than 25 years (Figure 4a). Although plants older than 40 years were few, the oldest plants in the study (about 49 years) grew on the ancient terraces. In contrast, 76% of the subpopulation of the 1939 terrace was younger than 25 years, and no plants were older than about 36 years (Figure 4b). The tallest plant (115 cm) on the 1939 terrace was dead when first observed in 1993. It was about 45 years old at the time of its death and likely belonged to the first cohort established on the terrace. At Indian Canyon, the 26-year-old cohort was the best represented age class by far (Figure 4c). The oldest plants were about 41 years, and young plants were underrepresented relative to Prospect Canyon.

Years of peak establishment and climatic variation

Distinct differences in the number of survivors in each annual cohort are evident in individual subpopulations (Figure 4) and to an even greater extent in the pooled samples (Figure 5). Unusually large cohorts are associated with the years 1953, 1958, 1959, 1965, 1967, 1973, 1977, and 1982 (Figure 5). These 8 peak establishment years were strongly correlated with wetter conditions than non-peak years, in particular with the biggest monthly rain total from May–October (Mann-Whitney $U = 66.00$, $p < 0.015$). The largest monthly rain during the May–October germination season was on average 1.50 cm (SD = 0.677) in the 38 non-peak years but 2.81 cm (SD = 0.644) in the 8 peak years. None of the other climatic variables were significantly associated with peak or non-peak years.

Discussion

The accurate dating of establishment peaks depends in part on the reliability of annual growth measurements. Total annual growth in cacti depends in part on plant size and in part on environmental factors such as rain, solar radiation, and temperature (Nobel 1986). Most *F. cylindraceus* growth occurs during the warm season (Nobel 1986). During this study, average warm-season (March–October) rain was within 11% of the 20-year average. It therefore seems likely that annual growth from 1991–1993, insofar as it was influenced by rain, was neither unusually high nor unusually low. Nobel (1977) reported a growth rate of 3.2 cm year⁻¹ for plants 29 cm high; plants of the same height in Grand Canyon grew 3.1 cm year⁻¹. This also supports the assumption that growth rates during this study were not atypical. For this study, determination of growth rates on the basis of two sampling dates only two years apart seemed adequate.

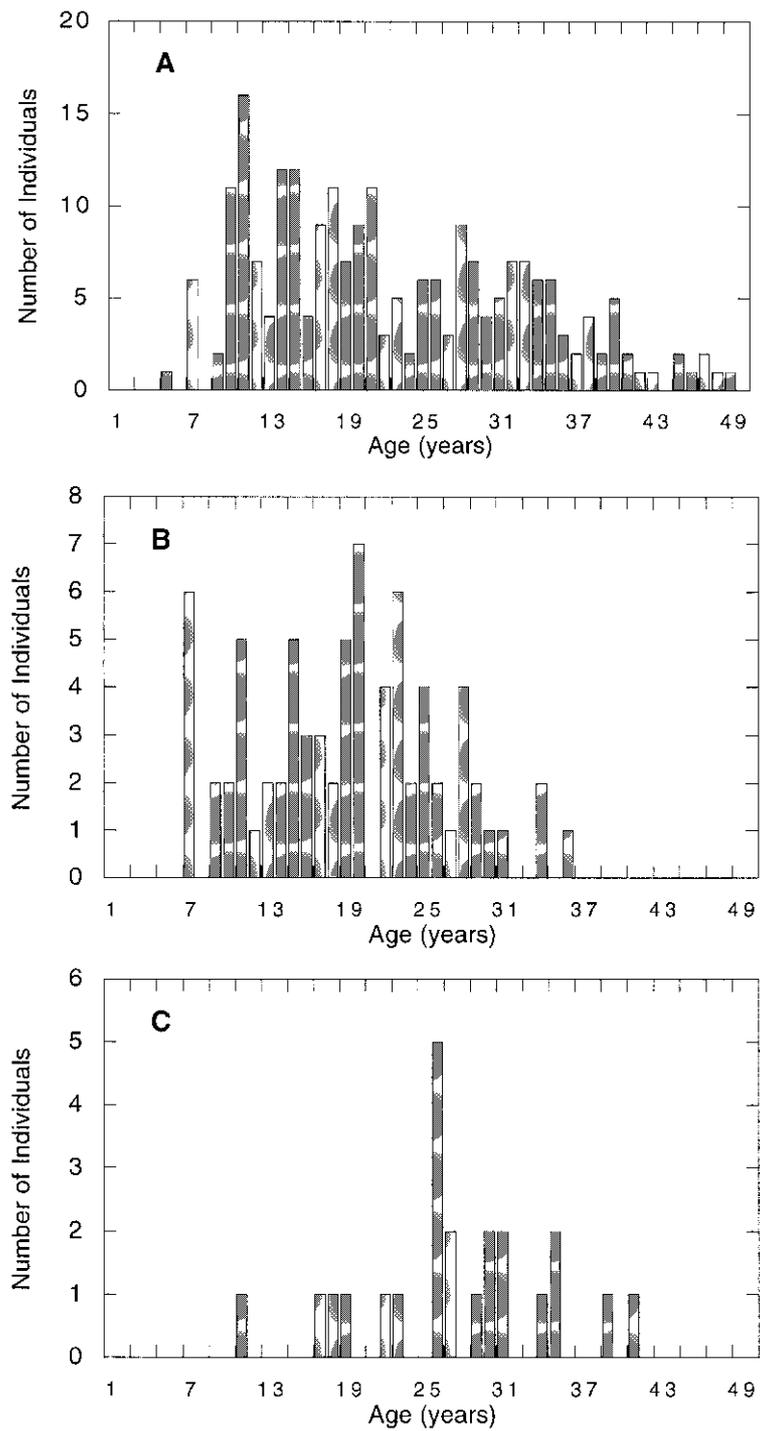


Figure 4. Age structure of *Ferocactus cylindraceus* at Grand Canyon, Arizona, 1993. A, Prospect Canyon, old terraces, $n = 225$; B, Prospect Canyon, 1939 terrace, $n = 75$; C, Indian Canyon, $n = 39$. Note that the vertical scales are not the same.

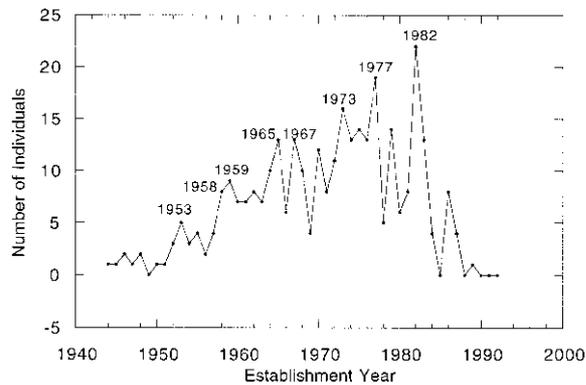


Figure 5. Establishment of *Ferocactus cylindraceus* at Grand Canyon, Arizona, from 1944–1992. Years of peak establishment are labeled.

Even when growth estimates are reliable, no age-height model can be applied to all plants with perfect accuracy, a consequence of natural height variation within cohorts. In the example discussed above, a 25-year-old plant that was 27.5 cm in height would be assigned a model age of 23 years; a 38.6-cm-tall plant from the same cohort would be treated as if it were 28 years of age. One way around this problem is to assume that annual growth within a given cohort follows a Gaussian distribution. In this case, the mean height of a cohort by definition corresponds to the actual age of that cohort, and a histogram of height-derived ages would show a distinct peak at the actual age. Similarly, if the x axis represented establishment years rather than age, the peaks would indicate actual establishment years. Adjacent years would seem to show some establishment, but this would be an artifact of natural variation in growth rates and heights, with slower growing plants to one side of the peak and faster growing plants to the other.

Nobel (1977, 1988) presented two different growth models for *F. cylindraceus*. Using the earlier model, Nobel (1977) estimated that plants 8, 34, and 90 cm in height would be, respectively, 4, 26, and 54 years in age. These estimates were extrapolated from growth over a 12-month period and measurements of net CO_2 uptake. The age-height model from Grand Canyon agrees well, putting the same plants at 4, 26, and 41 years. Later, Nobel (1988) refined his original model by including a water index, thus taking into account the amount of growth expected given the moisture conditions in a particular year. According to this model, a 90-cm-tall plant would be 90 years. The conflict among models can be resolved, at least for Grand

Canyon plants, by examining pairs of matched photographs from Grand Canyon. Of 264 *F. cylindraceus* plants visible in photographs taken in 1890, none survived until the early 1990s, nor did any of the 70 plants apparent in photographs taken in 1923 (Bowers *et al.* 1995). If *F. cylindraceus* typically survived 90 years in Grand Canyon, at least a few 70-year-old plants should have persisted from 1923 until the early 1990s.

Plotting the subpopulations as a group (Figure 5) makes it appear that some establishment occurred in most years; as noted above, however, the values distributed around peak establishment years might well represent plants that grew faster or slower than the majority of their cohort. Assuming that this is indeed the case, 8 years between 1944 and 1992 were especially favorable for *F. cylindraceus* establishment in Grand Canyon: 1953, 1958, 1959, 1965, 1967, 1973, 1977, and 1982 (Figure 5). (These are ‘biological years’ that begin with the May–October germination season.) Notable troughs in establishment were registered in the mid-1950s, the early and late 1960s, the late 1980s, and the early 1990s (Figure 5). The absence of cohorts in the 1990s may be real, or it may reflect the difficulty of finding plants only 1–2 cm high.

The absolute number of survivors in any cohort is a function of recruitment and mortality. High recruitment followed by high mortality in one cohort could produce the same number of survivors as low recruitment and low mortality in another cohort. Direct mortality or recruitment figures could not be determined from the data gathered for this study; nevertheless, there are several reasons why adult mortality is likely to be relatively constant. First, although *F. cylindraceus* seedlings are susceptible to prolonged drought (Jordan & Nobel 1981, 1982) and temperature extremes (Ehleringer & House 1984; Nobel 1984), mature individuals are extremely drought resistant and, within their native range, frost tolerant (Nobel 1977, 1980). Second, herbivores large enough to inflict significant damage are uncommon in the study area, and, in fact, little such damage was evident on mature plants. Herbivores are probably responsible for few adult deaths. Third, tall plants typically lean as they grow; many eventually lean so far that they fall to the ground, which is probably a major cause of death in old plants. If adult mortality is indeed relatively constant, the highest peaks in plant numbers (Figure 5) should reflect actual establishment events, and, by the same logic, the troughs should indicate periods of little or no establishment.

The seed and seedling ecology of this species plays a large part in creating establishment peaks and troughs. *Ferocactus cylindraceus* seeds are dispersed in late spring and summer. Like those of *F. wislizeni* (Jordan & Nobel 1981), they probably can remain viable for several years, but it seems likely that in most years predation quickly reduces the seed crop to a tiny fraction of its original size, as Steenbergh & Lowe (1977) have shown for the columnar cactus *Carnegiea gigantea*. Germination probably requires heavy rains, as is the case for *C. gigantea*, which germinates in response to rains ≥ 38 mm (Steenbergh & Lowe 1977). The optimum germination for *F. cylindraceus* is 29 °C, and most germination doubtless occurs in summer and early fall (Jordan & Nobel 1981). Survival thereafter depends largely on whether seedling water content is high enough for the plant to endure the inevitable water losses of the ensuing rainless periods (Jordan & Nobel 1981). Because the smallest seedlings are the most susceptible to drought (Jordan & Nobel 1981), it might seem that seedling water requirements should be relatively high for the first 12 to 18 months after germination. This is apparently not the case, however; peak establishment years in Grand Canyon were not correlated with total rain during the germination season or with total rain in the following 6- or 12-month periods. In other words, given a rain large enough to trigger germination, seedlings seem likely to survive most climatic fluctuations except for long droughts.

A connection between wet years and major periods of *F. cylindraceus* establishment has already been noted (Jordan & Nobel 1981; Ehleringer & House 1984). Identification of peak establishment years in Grand Canyon makes it possible to define these wet climatic events more precisely. During the past century, the wettest periods in the southwestern United States have coincided with El Niño-Southern Oscillation (ENSO) conditions (Webb & Betancourt 1992). In the Great Basin region to the north of Grand Canyon, ENSO typically enhances April–October rain (Ropelewski & Halpert 1986). In the Sonoran Desert to the south, it enhances October–April rain (Webb & Betancourt 1992). On the Colorado Plateau, ENSO increases the frequency and intensity of warm-season rains (Hereford and Webb 1992). The Grand Canyon, by virtue of being located on the Colorado Plateau between the Great Basin and Sonoran deserts, might experience enhanced precipitation all year when ENSO conditions prevail. For *F. cylindraceus*, this could mean wet summers for germination and a subsequent year in which rains were frequent enough for seedlings to maintain

Table 2. Years during the past four decades in which El Niño-Southern Oscillation (ENSO) conditions prevailed in the southwestern United States (data from Webb & Betancourt 1992).

From	To
Early 1951	Late 1951
Early 1953	Late 1953
Early 1957	Mid-1958
Mid-1963	Early 1964
Early 1965	Mid-1966
Early 1969	Late 1969
Mid-1972	Early 1973
Mid-1976	Early 1978
Mid-1982	Mid-1983
Mid-1986	Early 1987

adequate water contents. If this is the case, it is not surprising that 6 of the 8 *F. cylindraceus* establishment peaks at Grand Canyon occurred during ENSO conditions (Table 2, Figure 5). For example, the peak establishment year of 1972 apparently coincided with the onset of ENSO in the middle of that year. Another surge in establishment occurred in 1977, perhaps in response to the ENSO that lasted from mid-1976 to early 1978. The very high establishment peak of 1982 might have corresponded to prevailing ENSO conditions from mid-1982 to mid-1983. Smaller establishment peaks in 1958 and 1965 also coincided with ENSO. At Indian Canyon, the establishment peak consisting of 26-year-old plants coincided with ENSO conditions from early 1957 to mid-1958 (Figure 4c, Table 2). Not every ENSO event brought about *F. cylindraceus* establishment; of the 10 ENSO periods from 1951–1987, only 6 corresponded to establishment peaks in Grand Canyon (Table 2, Figure 5). Clearly, establishment depends upon other factors in addition to adequate rain for germination and survival.

Ferocactus cylindraceus populations elsewhere show a similar pattern of establishment. In southwestern Utah, a major period of recruitment from 1937–1947 (Ehleringer & House 1984) occurred in conjunction with ENSO conditions from mid-1939 to early 1942 and from early 1946 to late 1946. In southeastern California, the peak establishment years of 1958 and 1966 (Jordan & Nobel 1982) coincided with ENSO. Although failure to establish can be correlated with length of drought (Jordan & Nobel 1982), the apparent match between ENSO conditions and establishment peaks at Grand Canyon and elsewhere suggests that large pulses of rainfall are equally important for

F. cylindraceus regeneration. It also suggests that as for *Fouquieria splendens*, *Agave deserti*, and certain other woody desert plants (Jordan & Nobel 1979; Turner 1990; Bowers 1994), somewhat unusual climatic conditions are necessary if populations are to replace themselves.

The population age structures of columnar cacti studied to date generally show Deevey Type III survivorship in having high juvenile mortality and low adult mortality (Steenbergh and Lowe 1977, 1983; Parker 1993). On the ancient terraces at Prospect Canyon, slightly more than half the plants were 25 years or younger (Figure 4a). Overall, plants comprised a wide range of ages, from 5–49 years. Except for the paucity of plants in the youngest age classes, the subpopulation roughly fits a Deevey Type III curve (Figure 4a) indicating that for the time being, young plants are numerous enough to replace old ones. Historical photographs show that *F. cylindraceus* has occupied the ancient terraces at Prospect Canyon for at least a century (Bowers et al., 1995). During that time as many as 6 generations could have become established (assuming that plants become reproductive around 10 years of age, as is the case for *F. wislizeni* [Bowers, unpublished data]). Clearly, the ancient terraces support a well-established subpopulation.

In contrast with the ancient terraces, the 1939 terrace at Prospect Canyon was only 55 years of age at the time of this study. Comparison of age structures on the ancient and 1939 terraces shows that established and developing populations have somewhat different dynamics. On the 1939 terrace, 76% of the subpopulation was 25 years or younger (Figure 4b), and the oldest living plant was about 36 years of age. The lack of old plants and the small number of middle-aged individuals indicate that the rate of population increase has been slower on the 1939 terrace than on the ancient surfaces. The slower increase is presumably a function of a small number of initial colonizers and the length of time required for plants to reach reproductive size. The dead plant estimated to be 45 years old must have established in the first decade after the terrace was deposited. If any of the initial colonizers had survived to 1993, they would have been more than 45 years old. Assuming a small initial population, it is not surprising that none of these very old plants remains.

Another sharp contrast can be seen between establishment trends on the ancient Prospect Canyon terraces and the Indian Canyon site. In general, peaks and troughs of establishment seem much more pronounced at Indian Canyon (Figure 4c), which probably reflects

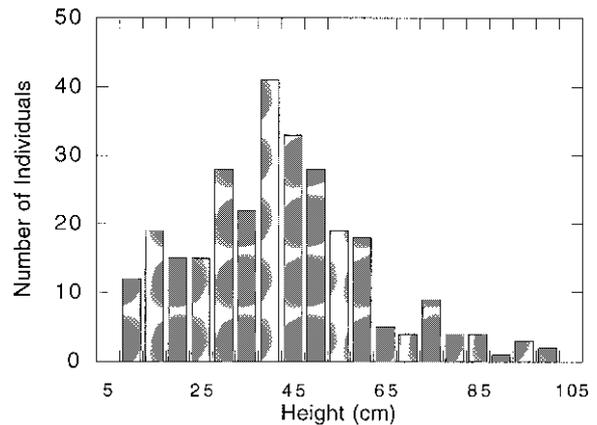


Figure 6. Height-class distributions of *Ferocactus wislizeni*, Organ Mountains, New Mexico, U.S.A., $n = 280$ (data from Reid et al. 1986).

the small number of plants involved. Moreover, the Indian Canyon subpopulation is clearly not in equilibrium. Young plants are greatly underrepresented, even though rainfall favored establishment in 1977 and 1982, and many cohorts appear to be missing. The differences between the Prospect and Indian canyon subpopulations cannot be accounted for by substrate age, since ancient surfaces are involved in both cases, nor is it likely that the climate of the two sites differs in any substantive way. The two sites do differ in topography and parent material, however, and they also differ in grazing history. Prospect Canyon has never been grazed by livestock, whereas Indian Canyon was heavily grazed by feral burros before 1981 (Webb & Bowers 1993).

Although the data are pseudoreplicated, confounding site with topography and grazing history, it is possible to draw some cautious conclusions about the effect of grazing on *F. cylindraceus* establishment. As noted above, feral burros in Grand Canyon demonstrably accelerated turnover of several dominant shrubs and were implicated in the near extirpation of *Ambrosia dumosa* at Indian Canyon (Webb & Bowers 1993). Nurse plants such as *A. dumosa* facilitate seedling survival by moderating soil and air temperatures, by hiding plants from herbivores, and by preventing excess transpiration (Turner et al. 1966; Nobel 1984, 1989; McAuliffe 1988). The disappearance of *A. dumosa* from Indian Canyon was no doubt a serious loss for *F. cylindraceus*, which establishes best under the canopies of nurse plants (Nobel 1984, 1989). By eliminating many potential nurse plants, grazing at Indian Canyon also eliminated many potential establishment

sites, making it difficult for seeds to respond to germinating rains and for seedlings to survive between rains. A similar situation might have occurred in the Organ Mountains, New Mexico (Reid et al. 1983), where a heavily grazed site supported a population of *F. wislizeni* that was clearly not in equilibrium (Figure 6). Reid et al. (1983) speculated that grazing had suppressed or prevented establishment for many years.

There has been little regeneration at Indian Canyon since grazing ended in 1981 (Figure 4c). One reason is doubtless that, except in 1982, climatic conditions have not favored establishment. Another is most likely that the virtual absence of an important nurse plant has hindered establishment for some years. Until the shrub population at Indian Canyon recovers from decades of burro grazing, a rebound in *F. cylindraceus* establishment is not to be expected.

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