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DEMOGRAPHIC PATTERNS OF *FEROCACTUS CYLINDRACEUS* IN RELATION TO SUBSTRATE AGE AND GRAZING HISTORY

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Bob - If you see anything to change or drop or add, please point it out. I meant to give you a copy of This before now - I guess I thought I had, Then forgot about it

Jan

Three subpopulations of *Ferocactus cylindraceus*, a short-columnar cactus of the Sonoran and Mojave deserts, were sampled in Grand Canyon, Arizona, U.S.A., at sites representing a range of substrate ages and grazing histories. Age-height relationships were determined from annual growth, then used to estimate probable year of establishment for each cohort.

On the oldest terrace, which was never grazed by domestic livestock, most plants were between 6-15 years in age. Older plants (>29 years) were relatively few; however, the oldest plants in the study--aged about 49 years--grew on the ancient terraces. Most plants on the young terrace (which was also ungrazed) were fewer than 17 years in age, and no plants were older than about 30 years. At the grazed site, 28- to 29-year-old plants were the most abundant age class, and the oldest plants were aged about 43 years. Young plants were under-represented, and several age classes younger than 39 years were not represented at all. Decades of heavy grazing may have reduced the shrub canopy to such an extent that *Ferocactus* seedlings, which grow best under nurse plants, have not become established even in climatically favorable years.

On the ungrazed sites, peaks in *Ferocactus* establishment occurred in the late 1940s, the early 1950s, the mid-1960s, the early to mid-1970s, and the early to mid-1980s. Notable troughs in establishment were registered in the mid-1950s and the mid-1970s. A combination of abundant warm-season rains and a subsequent year of normal or greater-than-normal rain coincided with periods of peak establishment. Favorable establishment years seemed to be correlated with El Niño-Southern Oscillation conditions, which suggests that large pulses of rainfall are an important aspect of *Ferocactus* regeneration and that somewhat unusual climatic conditions are necessary if populations are to replace themselves.

Introduction

Intermittent establishment is typical of many woody plants in the arid southwestern United States with far-reaching effects on demographic patterns (Shreve 1917; Barbour 1968; Sheps 1973; Ackerman 1979; Sherbrooke 1989; Parker 1993; Bowers 1994). The resulting populations, composed of cohorts spaced several to many years apart, are vulnerable to declines or even local extirpation if seedlings are not numerous enough to replace old plants as they die (e. g., Shreve 1910; Niering et al. 1963; Steenbergh and Lowe 1977, 1983; Helbsing and Fischer 1992). Populations with intermittent establishment can also be particularly vulnerable to human-induced perturbations such as grazing by domestic livestock (Niering et al. 1963; Martin and Turner 1977; Webb and Bowers 1993; Parker 1993).

Ferocactus cylindraceus (Engelm.) Orcutt [=*F. acanthodes* (Lem.) Britt. & Rose], a columnar cactus common on rocky slopes and cliffs in the Sonoran and Mojave deserts, exemplifies these demographic patterns. Seedling establishment of *Ferocactus* spp. in the southwestern United States is intermittent, apparently in response to length of drought (Jordan and Nobel 1981, 1982), to frost (Ehleringer and House 1984), and to grazing disturbance (Reid et al. 1983). *Ferocactus* populations in which very small plants are the most numerous size class are known (Jordan and 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 and House 1984; Jordan and Nobel 1982). *Ferocactus cylindraceus* is limited in its distribution by opportunities for establishment and does not occur where fewer than 1 in 10 years offer suitable conditions (Jordan and Nobel 1982).

Grand Canyon, Arizona, is an ideal setting for further investigation of *Ferocactus* demography. Most of the river corridor has never been grazed by domestic livestock, which provides a control for the few reaches where feral burros once grazed in large numbers.

Variation in substrate age, from one to thousands of years, makes it possible to compare young populations with long-established populations. The goal of this study was to sample Grand Canyon *Ferocactus cylindraceus* subpopulations at climatically similar sites that represent a range of disturbance histories and substrate ages. All sites were located in desertscrub vegetation along the Colorado River. Questions asked were: 1) Are periods of establishment associated with unusual climatic events; 2) What is the growth rate of Grand Canyon populations; 3) Does the population structure differ on grazed versus undisturbed sites or on old versus young surfaces; and 4) How quickly does *Ferocactus* colonize recently deposited debris flow terraces?

Methods

STUDY SITE

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 (fig. 1). The climate is hot and arid. From 1967 to 1982, annual rainfall at Phantom Ranch (783 m above sea level) averaged 231 cm 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 may be slightly warmer and drier. Lees Ferry, which has a longer weather record (1944 to the present), is located 141.5 km by river upstream of Phantom Ranch and is somewhat drier and colder.

The Prospect Canyon site (fig. 1) is characterized by debris flow terraces ranging in age from several decades to 4000 years (Melis et al. 1994). It is inaccessible to domestic livestock and has been grazed only by small populations of bighorn sheep (Webb and Bowers 1993). The Indian Canyon site (fig. 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. Gray) Payne, a palatable drought-deciduous subshrub, and in accelerated turnover of several other species (Webb and Bowers 1993).

FEROCACTUS SAMPLING

At Indian Canyon, all *Ferocactus* 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), was a triangle with sides approximately 40 m long and a base about 30.5 m long. Each *Ferocactus* plant in the plot was numbered and tagged, and its height and diameter were 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, *Ferocactus* subpopulations were sampled on three debris flow terraces of known age (55, 490 and 4000 years) (Melis et al. 1994) and an undated prehistoric terrace (Robert H. Webb, personal communication). The two younger terraces and the undated terrace were walked from one end to the other in March 1993, and the heights of the first 75 plants encountered on each terrace were measured. On the 4000-year-old surface, another permanent plot was established based on an historic photograph (Robert B. Stanton #620, 1890). It too was a triangle with 40-m sides and a 30.5-m base. In February 1991 all *Ferocactus* plants on the plot were numbered, tagged and measured as for the Indian Canyon plot, and in March 1993 heights above the nail and diameters were measured again so that average annual growth could be calculated.

DATA ANALYSIS

Growth Curves.--The height-diameter allometry of plants on the permanent plot in Prospect Canyon was determined by regression, using the 1993 heights and diameters.

The ages of columnar cacti can be readily determined from their heights (Shreve 1910; Jordan and Nobel 1982; Steenbergh and Lowe 1983; Turner 1990; Parker 1993). Using the average annual growth for each 5-cm height class as the dependent variable, a Kolmogorov-Smirnov two-sample test was performed to determine whether growth rates at the two permanent plots differed significantly. Average annual growth for every plant was plotted as a function of its 1991 height or its 1991 diameter, and curves were fitted to the data. Mean annual growth for each 5-cm height class was plotted as a function of mean class height or diameter. Plants that were diseased, injured, strongly leaning, or dead were omitted from these calculations, as were the few plants that failed to grow. A regression equation was used to estimate the amount of annual growth expected at different heights. The resulting growth increments were summed for successive years, producing an estimate of plant height at any age. Probable years of establishment were determined from the age-height relationship.

Population Structure.--For each of the five samples, the 1993 heights were grouped according to 5-cm height classes and the number of individuals in each class determined. Preliminary analysis with a Kolmogorov-Smirnov two-sample test showed that height distributions on the three oldest terraces at Prospect Canyon were not significantly different from one another, and they were therefore pooled for subsequent analyses. Height distributions on the Indian Canyon plot and the 1940 Prospect Canyon terrace were significantly different from one another and from the pooled Prospect Canyon sample, and they were treated separately. Numbers of individuals in each height class were plotted for the Indian Canyon plot, the 1940 Prospect Canyon terrace and the pooled Prospect Canyon sites.

Climatic Data.--Because there were no weather stations at the study sites, climatic data from Phantom Ranch were used as a reasonable approximation. Monthly rainfall totals were available for Phantom Ranch from 1967 to the present. Monthly values prior to 1967 were estimated by regression, using total monthly precipitation from Lees Ferry as the independent variable. The regression equation was $y = -11.53 + 1.49x$ ($R^2 = 0.72$, $P < 0.001$), where y = study site precipitation (mm) and x = Phantom Ranch precipitation.

Results

GROWTH RATES AND AGE-HEIGHT RELATIONSHIPS

Plant heights overall ranged from 1 to 135 cm, plant diameters from 2 to 42 cm. Plant height and diameter were closely correlated ($R^2 = 0.913$, $n = 75$), especially at heights below 35 cm (fig. 2).

Of the 40 plants originally measured on the Indian Canyon plot, growth could be determined for 23. On the Prospect Canyon plot, growth was determined for 68 of the original 75 plants. All but one of the regressions of growth versus height or diameter were statistically significant and explained 36.7 to 83.0% of the variance in annual growth (table 1). The regression of 5-cm diameter classes against annual growth accounted for the highest proportion of the variance, but, because radial growth essentially stopped at 35-40 cm while vertical growth continued, this equation was not useful in predicting annual growth for tall plants. Among the height regressions, the equation that accounted for the highest proportion of the variance, 69.7%, was derived from the Indian Canyon subpopulation of 39 individuals. Although the regression equation based on the Prospect Canyon subpopulation did not explain as much variance, the greater number of plants (225) seemed likely to provide a more reliable estimate of growth at various heights. Furthermore, growth rates at Indian Canyon did not differ significantly from those at Prospect Canyon ($p < 0.09$). The most suitable equation, therefore, based on 5-cm height classes at Prospect Canyon, was $y = -0.38 + [2.41 \cdot \log(x)]$, in which y = mean annual growth and x = mean height (fig. 3).

The regression equation used to assign ages on the basis of height was $y = -17.59 + 3.06x$, where y = height and x = age. Except for plants 0-5 cm high (0-5 years old), each height class represented an age span of 2-3 years.

POPULATION AGE STRUCTURE

At Prospect Canyon, slightly more than half of the 1993 subpopulation on the old terraces was between 6 and 25 cm in height (fig. 4a), or about 6 to 15 years in age (fig. 5a). Older plants (>66 cm or 29 years), were relatively few; however, the oldest plants in the study--aged about 49 years--grew on the ancient terraces. There was a marked difference between the age structures of subpopulations on the old and young terraces at Prospect Canyon. The subpopulation of the 1940 terrace was mostly less than 17 years in age. There were no plants older than about 30 years (figs. 4b, 5b). The tallest plant (115 cm) on this 53-year-old terrace was dead when first observed in 1993. The carcasses can remain on the ground for several years, so this plant was probably about 45 years old at the time of its death. Assuming that it belonged to the first cohort to become established on the terrace, it would appear that *Ferocactus* colonization lags behind terrace formation by about 8 years.

The age structures on the ungrazed terraces at Prospect Canyon and the grazed plot at Indian Canyon differ noticeably (figs. 4, 5). At Indian Canyon, the most abundant height class was 61-65 m (fig. 4c), or about 28-29 years (fig. 5c). The oldest plants were aged about 43 years. Young plants were underrepresented relative to Prospect Canyon. Several height classes below 100 cm (<39 years) were not represented at all.

The Kolmogorov-Smirnov two-sample tests showed significant differences in the height distributions, and therefore the age structures, of two sets of subpopulations: the old terraces versus the young terrace at Prospect Canyon ($p < 0.008$); and the ungrazed old surfaces at

Prospect Canyon versus the grazed old surfaces at Indian Canyon ($p < 0.004$). The height distribution of the subpopulation on the 1940 terrace was not significantly different from that at Indian Canyon ($p < 0.30$), which perhaps reflected the paucity of old plants in each subpopulation.

Distinct peaks and troughs are evident when the number of individuals in each cohort is plotted according to probable year of establishment (figs. 5a, 5b, 5c). Because of mortality, the number of individuals in a cohort necessarily decreases with time, and recent cohorts are generally composed of more survivors than older cohorts. The larger cohorts of recent years do not necessarily indicate that these years were more favorable for establishment than past years. In the absence of mortality data, it is assumed that the peaks and troughs are reliable indicators of relatively good or poor establishment years but that their magnitude does not necessarily convey useful information.

Discussion

The accurate dating of establishment peaks depends in part on the reliability of the annual growth measurements. For this study, determination of growth rates on the basis of two sampling dates only two years apart seemed adequate. Because most growth occurs in response to warm-season rains (Nobel 1986), and average March-October rainfall during the two years of this study was within 11% of the 20-year average, it seems likely that growth was neither unusually high nor unusually low. For small plants (< 8 cm high), the age-height relationships determined in this study agree well with those reported by Nobel (1988); according to both, a seedling about 8 cm high (or 8 cm in diameter) is about 7-8 years old. According to Nobel (1977), plants 29 cm high grew 3.2 cm/year, a value that agrees closely with plants of the same height in Grand Canyon. The results of the two studies diverge for taller plants, however. Nobel (1988), using a model based on an index of environmental productivity, predicted that a

90-cm-tall plant at the Deep Canyon Desert Research Center, California, would be 90 years old, whereas the Prospect Canyon growth curve would put its age at 36-37 years. Reasons for the discrepancy might be: 1) the Deep Canyon site is more arid (annual rainfall is 109 mm [Zabriskie 1979]), resulting in a slower growth rate, or, 2) the low growth rate (about 9 mm/year) measured for young plants overestimates plant age when projected linearly throughout the life of the plant.

At Prospect Canyon, peaks in *Ferocactus cylindraceus* establishment occurred in 1946-47, 1947-48, 1950-51, 1953-54, 1957-58, 1960-61, 1961-62, 1965-66, 1966-67, 1972-73, 1978-79, 1979-80, 1981-82, 1983-84, and 1986-87 (figs. 5a, 5b). Notable troughs in establishment were registered in the mid-1950s and the mid-1970s (figs. 5a, 5b).

The seed ecology of this species plays a large part in creating these peaks and troughs. *Ferocactus cylindraceus* seeds are dispersed in late spring and summer. Like those of *F. wislizenii* (Engelm.) Britt. & Rose (Jordan and 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 and Lowe (1977) have shown for the columnar cactus *Carnegiea gigantea* (Engelm.) Britt. & Rose. Germination probably requires heavy rains, as is the case for *Carnegiea gigantea*, which germinates only in response to rains ≥ 38 mm (Steenbergh and Lowe 1977). *Ferocactus cylindraceus* germination occurs at a temperature range of 21-34°C, with an optimum of 29°C. These high temperatures suggest that most germination occurs in summer and early fall (Jordan and Nobel 1981). Given unseasonable May or June rains, germination presumably can occur in late spring as well.

In sum, it is likely that heavy rains some time between May and October are required for germination and emergence of *Ferocactus cylindraceus* seeds. The survival of a newly emerged seedling depends largely on whether it has enough water-storage capacity to last it through the next rainless period (Jordan and Nobel 1981). The smaller the seedling, the more susceptible it is to drought (Jordan and Nobel 1981), therefore it seems likely that seedling water requirements are relatively high for the first 12-18 months after germination. If seedlings are to survive autumn and late spring droughts, rain in the first year probably must equal or exceed the annual average. Weather records from Grand Canyon show that in 14 of 15 establishment years, May-October rain equalled or exceeded 90% of the long-term average. Rain of the following 12 months (November-October) equalled or exceeded 90% of the long-term average in 10 of 15 establishment years, and in 14 of 15, it was at least 80% of the long-term average. A connection between unusually wet years and major periods of *F. cylindraceus* establishment has already been noted (Jordan and Nobel 1981; Ehleringer and House 1984). At Grand Canyon, the combination of abundant warm-season rains and a subsequent average or better-than-average year (fig. 6) corresponds well to the periods of peak establishment (figs. 5a, 5b, 5c).

As in other arid regions, the climate in Grand Canyon is characterized by alternating wet and dry periods. During the past 100 years, the wettest periods coincided with El Niño-Southern Oscillation (ENSO) conditions. ENSO involves the appearance every 3-5 years of unusually warm currents in the equatorial eastern and central Pacific Ocean (Rasmusson 1985; Enfield 1989). In the southwestern United States, ENSO conditions bring increased variability of precipitation and more intense and frequent winter frontal storms (Webb and Betancourt 1992). They also increase the frequency and intensity of warm-season rainfall on the Colorado Plateau (Hereford and Webb 1992).

The relation between the Southern Oscillation and seasonal rainfall in Grand Canyon has not been specifically investigated. In the Great Basin region to the north, ENSO conditions typically enhance April-October rain (Ropelewski and Halpert 1986). In the Sonoran Desert to the south, they enhance October-April rain (Webb and Betancourt 1992). The Grand Canyon, location in a transition zone between these two regions, may reap the benefits of both, with

ENSO conditions providing wet summers for *Ferocactus* germination and a subsequent wet year for seedling establishment. If this is the case, it is not surprising that many peaks in *Ferocactus cylindraceus* establishment seem to be correlated with ENSO conditions. For example, the rebound in establishment of the early 1970s apparently coincided with the onset of ENSO conditions in mid-1972. Another surge in establishment occurred in the late 1970s, perhaps in response to the ENSO period that lasted from mid-1976 to early 1978. Thereafter, establishment remained high through 1986 except in 1980-81 (fig. 5b). During this time, ENSO conditions prevailed from mid-1982 to mid-1983 and from mid-1986 to early 1987 (Webb and Betancourt 1992; Julio Betancourt, pers. comm.). The smaller establishment peaks of the late 1940s, early 1950s and mid-1960s also coincided with ENSO conditions (fig. 5a, table 2). In all, 9 of 11 recent ENSO periods (table 2) were apparently times of *Ferocactus* establishment in Grand Canyon (fig. 6).

Other populations show a similar pattern of establishment. In southwestern Utah, a major period of establishment from 1937-1947 (Ehleringer and 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 and Nobel 1982) coincided with ENSO conditions. Although Jordan and Nobel (1982) suggested that failure to establish can be correlated with length of drought, the apparent match between ENSO years and establishment peaks at Grand Canyon and elsewhere suggests that large pulses of rainfall are equally important in determining *Ferocactus* regeneration. It also suggests that as for *Fouquieria splendens* Engelm., *Agave deserti* Engelm. and some other woody desert plants, somewhat unusual climatic conditions are necessary if populations are to replace themselves (Jordan and Nobel 1979; Bowers 1994).

As the subpopulation on the 1940 terrace indicates, *Ferocactus cylindraceus* is clearly capable of occupying recently deposited surfaces along with early successional species such as

Encelia frutescens A. Gray, *Bebbia juncea* (Benth.) Greene, *Brickellia longifolia* Wats. and *Hymenoclea salsola* Torr. & Gray (Bowers, unpublished data). Developing populations have somewhat different dynamics than established populations (figures 5a, 5b). On the 1940 terrace, only 4% of the subpopulation fell between the ages of 26 and 30, whereas this age group made up about 11% of the subpopulation on the old terraces nearby. This suggests that the rate of population increase on the recent terrace falls short of the rate on the old terraces, presumably because the number of initial colonizers was small and because it takes about 13 years for the plants to reach reproductive age (assuming that reproductive age occurs at a height of about 20 cm as for *Ferocactus wislizenii*). The oldest living plant encountered on the 1940 terrace was about 30 years old. If any of the initial colonizers had survived to 1993, they would have been about 45 years in age. Assuming a small initial population, it is not surprising that none of these very old plants remain.

Establishment trends in the Indian Canyon subpopulation contrast sharply with those at Prospect Canyon. In general, peaks and troughs of establishment seem much more pronounced at Indian Canyon, probably a result of the small number of plants involved. Plants younger than 10 years are underrepresented compared to the Prospect Canyon subpopulations. Plants of this age would have become established in the early to mid-1980s, a favorable period at Prospect Canyon. The establishment peak of the mid-1960s coincided with ENSO conditions of mid-1963 to mid-1966 (fig. 5a, table 2).

The histogram of the Prospect Canyon subpopulation (fig. 4a) roughly fits a Deevey Type III survivorship curve, which suggests that the population is in equilibrium; that is, young plants are numerous enough to replace old ones. In contrast, the Indian Canyon subpopulation is clearly not in equilibrium (fig. 4c). The Prospect and Indian canyon sites differ in topography and substrate, but these differences seem unlikely to affect population age structure, nor should climate, which differs little between the two sites. The main difference between them is that

Prospect Canyon has never been grazed by domestic livestock, whereas Indian Canyon was heavily grazed by feral burros before 1981 (Webb and Bowers 1993).

As noted above, feral burros in Grand Canyon have demonstrably accelerated turnover of several dominant shrubs and have been implicated in the near extirpation of *Ambrosia dumosa* at Indian Canyon (Webb and Bowers 1993). Evidently the effects of burro grazing also extend to *F. cylindraceus*, as seen in the populational disequilibrium at Indian Canyon. A similar situation might have occurred in the Organ Mountains, New Mexico, where examination of height class of *F. wislizenii* revealed that the subpopulation was not in equilibrium (Reid et al. 1983) (fig. 7). The site had been heavily grazed, which perhaps had long-term effects on the establishment rate (Reid et al. 1983).

Grazing at Indian Canyon ended in 1981, but there has been little rebound in establishment in the 0-15 cm height classes since then (fig. 4c), even though much of the 1980s were apparently quite favorable for establishment at Prospect Canyon. *Ferocactus cylindraceus* establishes best under the canopies of nurse plants (Nobel 1984, 1989) such as *Ambrosia dumosa*. If the shrub population has not recovered from decades of burro grazing, the continued decline in *F. cylindraceus* establishment is not surprising.

Future research will focus on obtaining mortality rates for the various subpopulations so that a survivorship curve based on the current age structure can be produced. At that point, deviations between expected and actual establishment can be computed and the results used in regression analysis to more precisely define the climatic variables involved in germination and establishment.

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Table 1. Results of 12 regressions showing the relationship between annual height growth of *Ferocactus cylindraceus* and plant height or diameter in Grand Canyon, Arizona. Annual height growth was the dependent variable in every case.

Independent Variable	Regression Equation	Regression R^2
PROSPECT CANYON		
Diameter (individuals)	0.445 + 0.123x	0.518[a]
Diameter (individuals)	-1.282 + 3.317 · log(x)	0.367[a]
Diameter (5-cm classes)	1.139 + 0.096x	0.830[b]
Diameter (5-cm classes)	0.437 + 2.102 · log(x)	0.518
Height (individuals)	1.470 + 0.039x	0.428[a]
Height (individuals)	-0.136 + 2.130 · log(x)	0.386[a]
Height (5-cm classes)	1.782 + 0.035x	0.626[a]
Height (5-cm classes)	-0.307 + 2.405 · log(x)	0.676[a]
INDIAN CANYON		
Height (individuals)	0.717 + 0.052x	0.612[a]
Height (individuals)	-1.688 + 2.987 · log(x)	0.444[b]
Height (5-cm classes)	0.966 + 0.051x	0.697[a]
Height (5-cm classes)	-0.384 + 2.251 · log(x)	0.423[c]

[a] $p < 0.001$

[b] $p < 0.005$

[c] $p < 0.05$

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

From	To
Mid-1939	Early 1942
Early 1946	Late 1946
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

FIGURE CAPTIONS

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

Figure 2. Relationship between height and diameter of *Ferocactus cylindraceus*, Prospect Canyon, 1993 (n = 75).

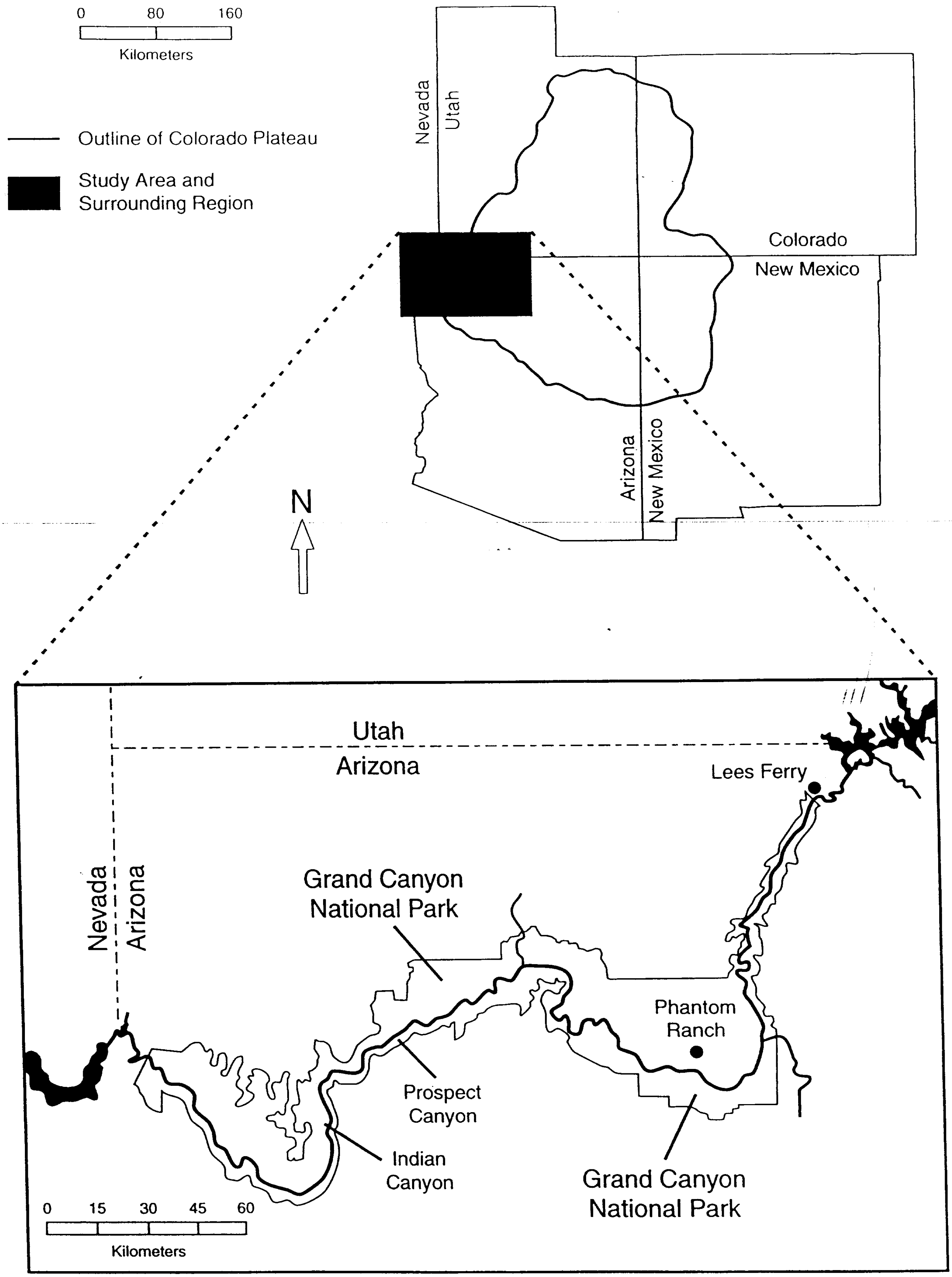
Figure 3. Annual growth in *Ferocactus cylindraceus* as a function of plant height, based on 5-cm height classes.

Figure 4. Height-class distributions of *Ferocactus cylindraceus* at Grand Canyon, Arizona, 1993. A, Prospect Canyon, old terraces, n = 225; B, Prospect Canyon, 1940 terrace, n = 75; C, Indian Canyon, n = 39. The X-axis depicts 5-cm height classes. Note that the vertical scales are not the same.

Figure 5. Population trends of *Ferocactus cylindraceus* at Grand Canyon, Arizona. A, Prospect Canyon, old terraces, n = 225; B, Prospect Canyon, 1940 terrace, n = 75; C, Indian Canyon, n = 39. Note that the vertical scales are not the same.

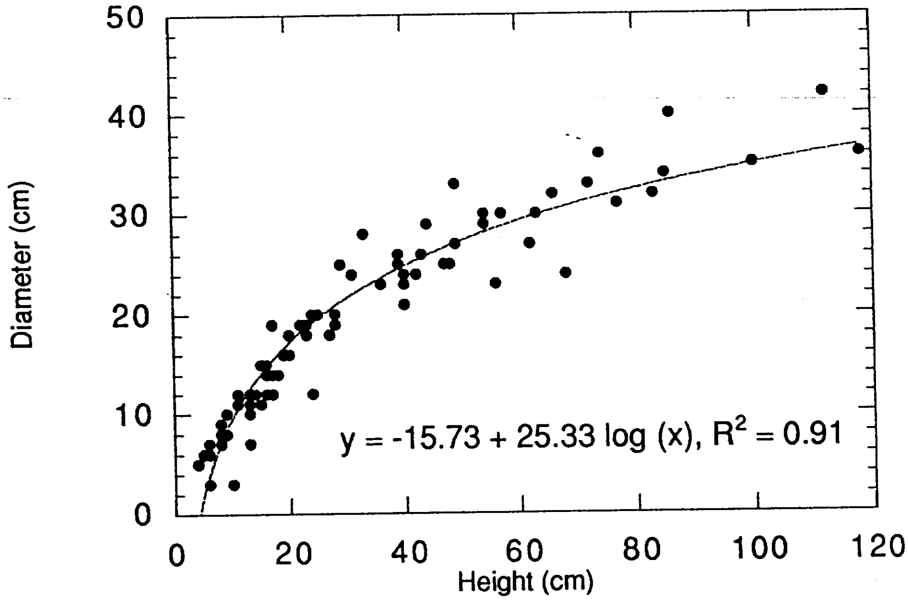
Figure 6. Precipitation at Phantom Ranch, Grand Canyon, 1944-1993. Bars represent summer rainfall (May-October) and rainfall of the following 12 months (November-October). Asterisks show peak *Ferocactus cylindraceus* establishment years at Prospect Canyon: A, 1946-47; B, 1947-48; C, 1950-51; D, 1953-54; E, 1957-58; F, 1960-61; G, 1961-62; H, 1965-66; I, 1966-67; J, 1972-73; K, 1978-79; L, 1979-80; M, 1981-82; N, 1983-84; O, 1986-87.

Figure 7. Height-class distributions of *Ferocactus wislizenii*, Organ Mountains, New Mexico, n = 280 (data from Reid et al. 1986).



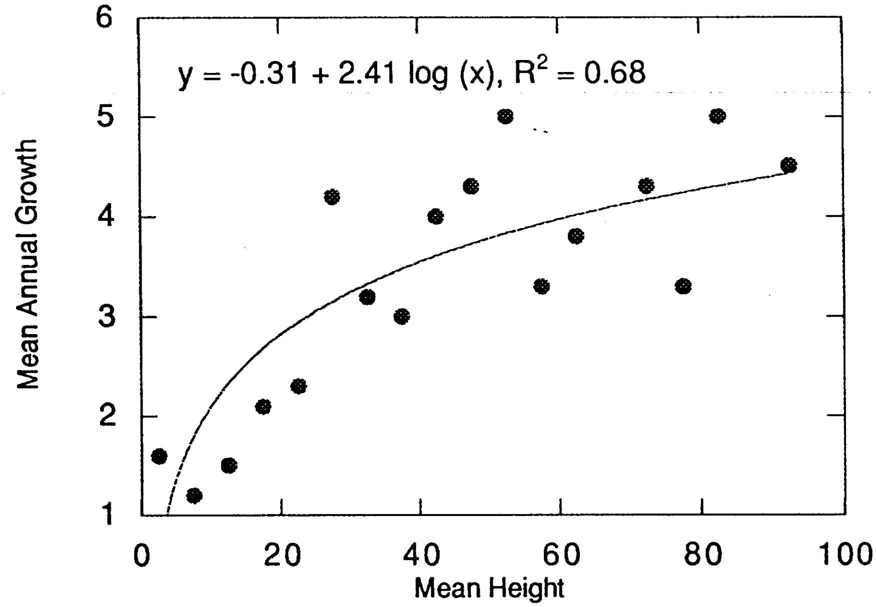
0 80 160
Kilometers
Outline of Colorado Plateau
Study Area and Surrounding Region
Nevada
Utah
Colorado
New Mexico
Arizona
New Mexico
N
Utah
Arizona
Lees Ferry
Nevada
Arizona
Grand Canyon National Park
Phantom Ranch
Prospect Canyon
Indian Canyon
Grand Canyon National Park
0 15 30 45 60
Kilometers

Fig. 2



50
40
30
20
10
0
Diameter (cm)
y = -15.73 + 25.33 log (x), R2 = 0.91
0
20
40
60
80
100
120
Height (cm)

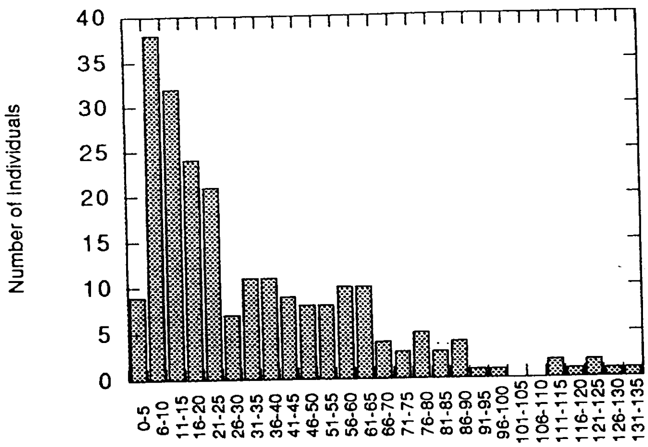
Fig. 3



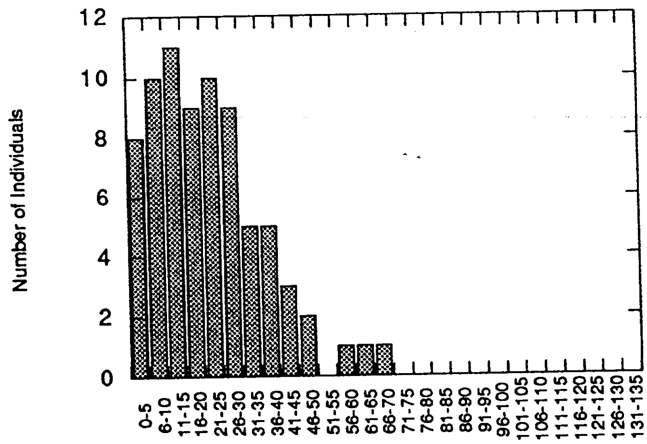
$y = -0.31 + 2.41 \log(x), R^2 = 0.68$
Mean Annual Growth
Mean Height
6
5
4
3
2
1
0
20
40
60
80
100

Fig. 4

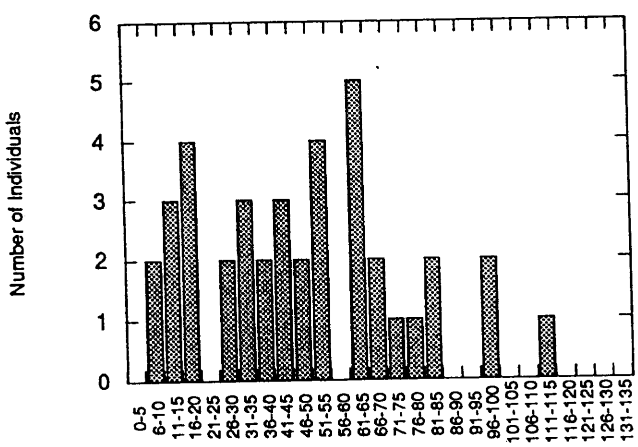
Prospect Canyon (old terraces)

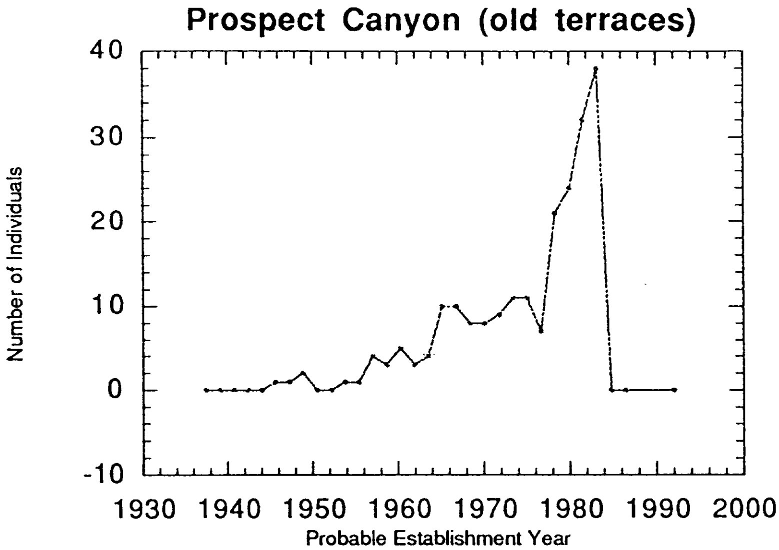


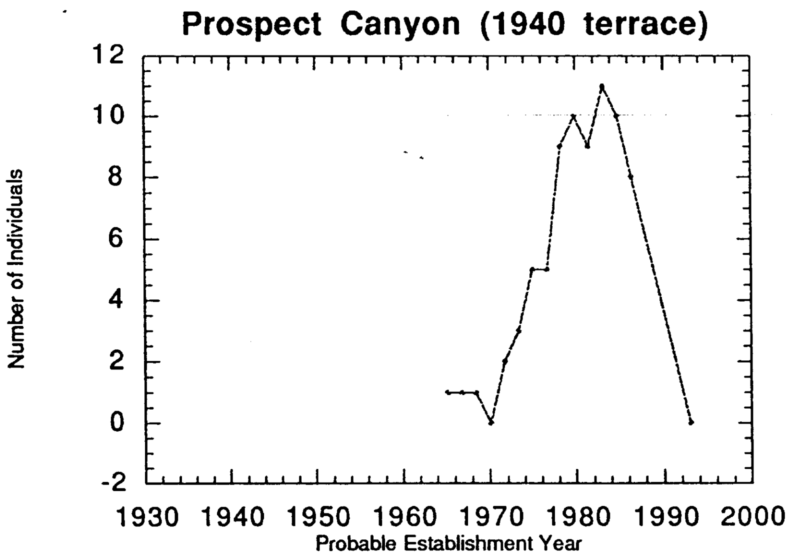
Prospect Canyon (1940 terrace)



Indian Canyon




Prospect Canyon (old terraces)
Number of Individuals
40
30
20
10
0
-10
1930 1940 1950 1960 1970 1980 1990 2000
Probable Establishment Year


Prospect Canyon (1940 terrace)
Number of Individuals
12
10
8
6
4
2
0
-2
1930 1940 1950 1960 1970 1980 1990 2000
Probable Establishment Year

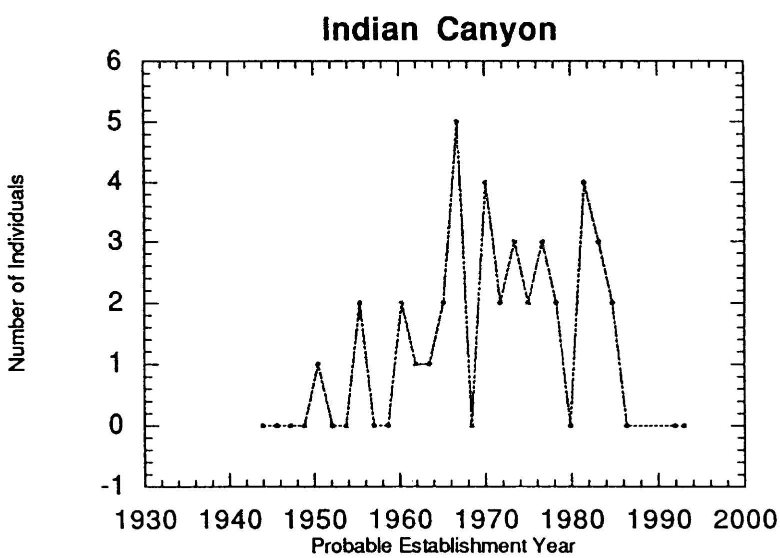
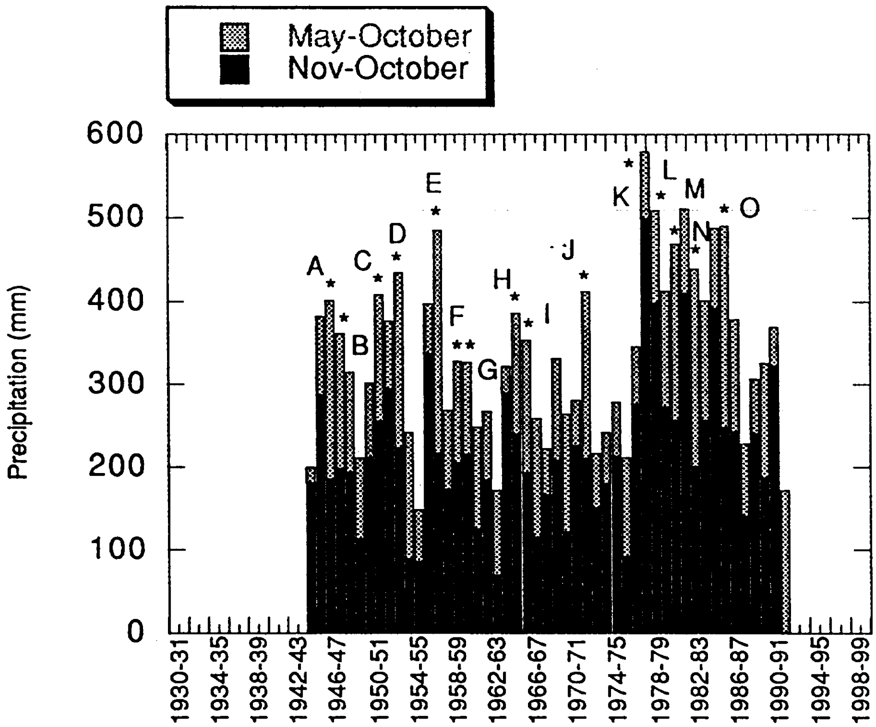
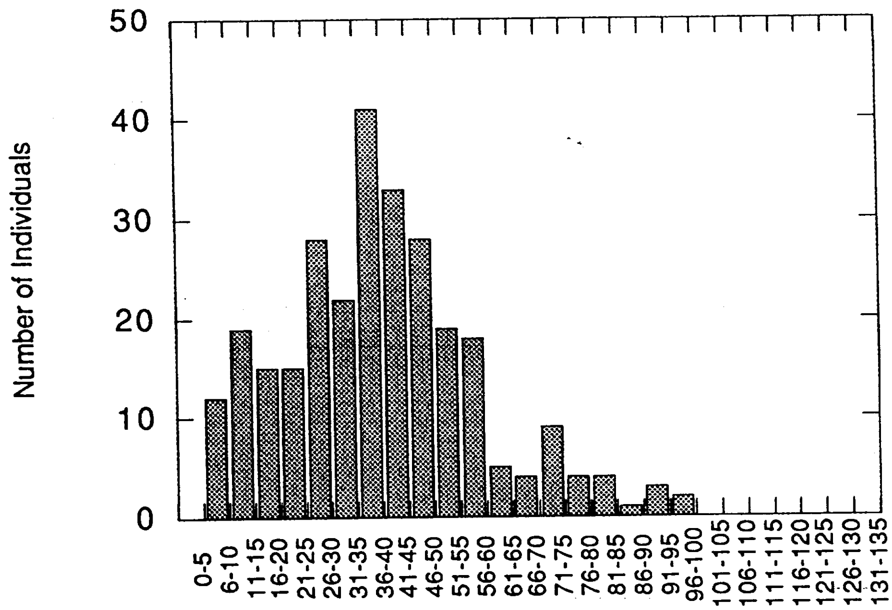

Indian Canyon
Number of Individuals
6
5
4
3
2
1
0
-1
1930 1940 1950 1960 1970 1980 1990 2000
Probable Establishment Year

Fig. 6



May-October
Nov-October
Precipitation (mm)
600
500
400
300
200
100
0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
1930-31
1934-35
1938-39
1942-43
1946-47
1950-51
1954-55
1958-59
1962-63
1966-67
1970-71
1974-75
1978-79
1982-83
1986-87
1990-91
1994-95
1998-99

Fig. 8



Number of Individuals
50
40
30
20
10
0
0-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85
86-90
91-95
96-100
101-105
106-110
111-115
116-120
121-125
126-130
131-135