Seedling Establishment, Mortality and Flower Production of the Acuña Cactus, *Echinomastus erectrocentrus* var. *acunensis* (Cactaceae).

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Abstract: A large number of rare and endangered species of cacti occur in the Southwestern United States. Despite this predominance of rarity, demographic information for this family is limited to the common and conspicuous columnar cacti. Our study provides five years of demographic data for the rare acuña cactus (*Echinomastus erectrocentrus* var. *acunensis*), including establishment, mortality, growth, and flower production. All four of these demographic parameters varied systematically among years; seedling number, growth, and flower number were positively associated with annual rainfall, while mortality was negatively associated with rainfall. Seedlings often occurred at the base of an adult plant, presumably the parent, which provided nurse habitat upon its death. Size of first flowering varied from 25-90 mm in height, with the percentage of plants that flowered increasing to near 100% above 90-100 mm in height. Number of flowers produced increased with plant height but was better correlated with plant volume, probably due to the ability of cacti to expand and store water in wet years. Mortality of small individuals (< 20 mm tall) was negatively correlated with rainfall, while that of larger individuals did not vary among years. This pattern suggests that small individuals are most susceptible to abiotic sources of mortality due to their limited water storage capacity, and larger individuals are mostly affected by biotic factors such as predation.

INTRODUCTION

One of the most prominent and characteristic features of the Sonoran Desert are cactus. Despite this predominance very little is known about population dynamics and growth for species other than the conspicuous columnar cactus including saguaro (*Carnegiea gigantea*), organpipe cactus (*Stenocereus thurberi*), and senita cactus (*Lophocereus schottii*)(Turner *et al.*, 1966, 1990; Steenbergh and Lowe, 1977, 1983; McAuliffe and Janzen, 1986; Parker, 1988). Consequently, population dynamics of cacti and other succulents are poorly understood with only indirect evidence that suggests a correlation between rainfall and patterns of mortality and establishment (Steenbergh and Lowe, 1977; Turner, 1990). For example, estimated establishment by new individuals of hedgehog cactus (*Ferocactus acanthodes*) and desert agave (*Agave deserti*) is highly variable among years and is positively correlated with rainfall (Jordan and Nobel, 1979, 1981, 1982). Additionally, small individuals of both species are highly prone to mortality caused by dessication, while older individuals can store sufficient water to withstand prolonged drought (Nobel, 1988).

This study reports on demography of acuna cactus (*Echinomastus erectrocentrus* var. *acunensis*), which is a rare cactus known to only occur in four locations in Arizona and Sonora, Mexico (Rutman, 1990; Phillips *et al.*, 1982; R. Johnson, unpublished). We examine four demographic parameters in *Echinomastus*, including establishment, mortality, growth, and flower production. These demographic parameters are then examined in relation to rainfall, which is one of the most limiting resource in deserts (Louw and Seely, 1982). Based on high annual variation in establishment and growth in other cactus and succulents (Jordan and Nobel, 1979, 1981; Steenbergh and Lowe, 1977; Turner, 1990), we hypothesize that establishment, growth, and flower production are positively associated with rainfall, and mortality is negatively associated with rainfall. Further, because small individuals cannot withstand drought, we hypothesize that juveniles should experience high mortality during dry years, and vice versa, while adults should be little affected by annual variation in rainfall.

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METHODS

This study was conducted in Organ Pipe Cactus National Monument, Arizona, at elevations of 470-525 m. Vegetation of the area is Arizona Upland (Turner and Brown, 1982), with characteristic species including saguaro (*Carnegiea gigantea*), foothill palo verde (*Cercidium microphyllum*), ocotillo (*Fouquieria splendens*), ironwood (*Olneya tesota*), and organpipe cactus (*Stenocereus thurberi*). Data on seedling establishment, growth, flower production, and mortality were collected in March 1988-1992 from all individuals that occurred in six 20 m x 50 m plots. Two of the plots were searched in late March 1988 so flower production data are incomplete for that year, and some growth data are excluded because they have not yet been analyzed. Plots were scattered across the range of the population within Organ Pipe Cactus National Monument. Precipitation data were obtained from an on-site weather pod or from Organ Pipe Cactus National Monument Headquarters when these data were missing.

The six 0.1 ha plots were searched systematically using 2 m x 20 m subplots in mid-March of 1988-1992. Plots were searched intensively so as to locate all individuals of *Echinomastus erectrocentrus* var. *acunensis*, including seedlings. This required about 100 hours per year, most of which involved searching for new seedlings. We collected demographic data, including plant size, status (alive or dead), and reproductive effort for all individuals. Plants that had not been located in a previous year were also assessed as to whether they were seedlings-of-the-year or plants that had not been located in a previous year; assessments were based on individuals germinated in a greenhouse. Height from the base to the apex, excluding spines, was measured to the nearest mm on the upslope side of each plant. Width was the average of two perpendicular measures at mid-height. Reproductive structures (buds, flowers, and fruits) were counted weekly beginning about one week following the onset of flowering (ca. mid-March to early April). Plants were individually marked using aluminum tags affixed to rocks placed near the plant.

Variation in establishment was analyzed by a Chi-square test using the number of new seedlings located in each of four years. Number of new seedlings was correlated with summer and total annual precipitation to assess which season was more important for establishment; summer rainfall was the total from May through October, during which time water is scarce and drought are most prolonged.

Number of individuals that died over the previous year were divided into two size classes, 0-20 mm tall and > 40 mm tall, for juveniles and adults, respectively; these two groups formed a natural break in size classes of individuals that had died during this study. Percent mortality was used for analysis because the number of individuals in each size class varied among years. Percent annual mortality was the number of dead individuals in a height class divided by the total number of plants in that height class. Annual variation in percent mortality was assessed for each size class by a Chi-square test. Mortality data for juveniles and adults were also correlated with summer and annual precipitation.

Growth was calculated as (height in $year_x$ - height in $year_{x-1}$) and was plotted versus height in $year_{x-1}$. Growth was then compared between years (from 1988-1989 and 1989-1990) using an analysis-of-covariance (ANCOVA) (SAS Institute Inc., 1989), with height as the covariate. Growth data from 1990-1991 are presented but have not yet been analyzed.

Flower production was quantified relative to plant height by calculating the percentage of flower-bearing individuals in successive 10 mm height classes; this percentage was calculated after pooling data across years, which minimized sample error in height classes that had few individuals. Plants were also compared for among-year variation in number of flowers produced using ANCOVA. The ANCOVA was used for plant height and separately for plant volume with height and volume as covariates. Plant volume was approximated using the formula for a cylinder. Only plants that produced flowers in all of three years (1989-1991) were included in analyses. Among-year differences in number of flowers produced were assessed relative to precipitation from 1 April to 31 March, which approximates the annual reproductive cycle of *Echinomastus*.

RESULTS

Number of new seedlings varied significantly among the four years (Chi-square = 44.64, $P < 0.001$). Annual variation in number of new seedlings was positively correlated with summer rainfall ($Y = 0.29X - 7.68$, $R^2 = 0.948$, $P < 0.01$), but not with total annual rainfall ($P > 0.10$; Figure 1).

Percent mortality varied significantly among the four years for individuals <20 mm tall (Chi-square = 18.44, $P < 0.001$), but not for individuals >40 mm tall (Chi-square = 0.22, $P > 0.50$). Additionally, percent mortality of small individuals was negatively correlated with amount of summer rainfall ($Y = -1.3X - 24.79$, $R^2 = 0.94$, $P < 0.01$), but not with total annual rainfall ($P > 0.10$; Figure 2).

Growth in height varied significantly between 1988-1989 and 1989-1990 when using height as a covariate (ANCOVA, least square means, $P < 0.0001$, $N = 422$) (Figure 3). However, there was a signicant interaction between height and year ($P < 0.003$). Mean growth from 1989-1990 did not differ from a slope of 0.00 ($P > 0.26$), while growth was significantly greater than a slope of 0.00 in 1988-1989 ($P < 0.001$). The interaction between year and height indicate that annual growth varied by height such that larger individuals grew more than small individuals in 1988-1989. Data for 1990-1991 are presented but not analyzed; however even without statistics growth from 1990-1991 was obviously greater than for either of the previous two years (Figure 3). Overall, growth during the three years was positively associated with total annual precipitation, being lowest in 1989-1990 (rainfall = 81 mm), intermediate in 1988-1989 (rainfall = 245 mm), and highest in 1990-1991 (rainfall = 329 mm) (Figure 3).

The percentage of *Echinomastus* individuals that produced flowers increased with plant height. The smallest plant to flower was 24 mm tall. The percentage of flower-bearing plants steadily increased in subsequent 10 mm height classes until plants ≥90 mm tall almost always produced flowers (Figure 4). Individuals flowered nearly every year following a previous flowering event; the percentage of plants that produced flowers in the second year after having produced flowers in the previous year was 100% (39 of 39 plants) in 1989, 94.3% (100 of 106 plants) in 1990, and 96.1% (98 of 102 plants) in 1991.

Number of flowers produced varied among years when using either plant height or volume as the covariate. Interaction effects for year by either covariate were non-significant ($P > 0.34$). Individuals produced a similar number of flowers in 1989 and 1991 after factoring out volume as a covariate, but these same individuals produced significantly fewer flowers in 1990 (ANCOVA, $P < 0.005$, $N=91$ plants) (Figure 5). Thus, flower production was greatest during the two wettest years, 1989 and 1991, when precipitation for the annual cycle ending 31 March was 245 mm and 329 mm, respectively, and was significantly lower in 1990 when precipitation was only 81 mm. Number of flowers produced by individuals that bore flowers increased with both height and volume in all three years; in all years, however, R^2 values were more than 0.12 higher when using volume (volume in cm^3, 1989: $Y = 0.0084X + 2.12$, $P < 0.0001$, $R^2 = 0.51$, $N = 107$; 1990: $Y = 0.007X + 1.65$, $P < 0.0001$, $R^2 = 0.47$, $N = 108$; 1991: $Y = 0.0083X + 1.78$, $P < 0.0001$, $R^2 = 0.60$, $N = 129$) (Figure 6).

DISCUSSION

Population dynamics and demographic parameters of *Echinomastus* are closely correlated with rainfall patterns. Such patterns also occur for *C. gigantea* and probably numerous other species (Goldberg and Turner, 1986), and indicate that populations of many desert species including *Echinomastus* fluctuate dramatically in relation to long-term climatic patterns (see also Turner, 1990).

Table 1. Rainfall (mm) at the site used to examine demography of Echinomastus erectrocentrus var. acunensis. Rainfall data are divided into summer (May through September) and winter (October through April), which characterize the bimodal precipitation pattern in the Sonoran Desert.

Year	Summer	Winter	Total
1989	127	118	245
1990	48	33	81
1991	172	157	329
1992	55	144	199

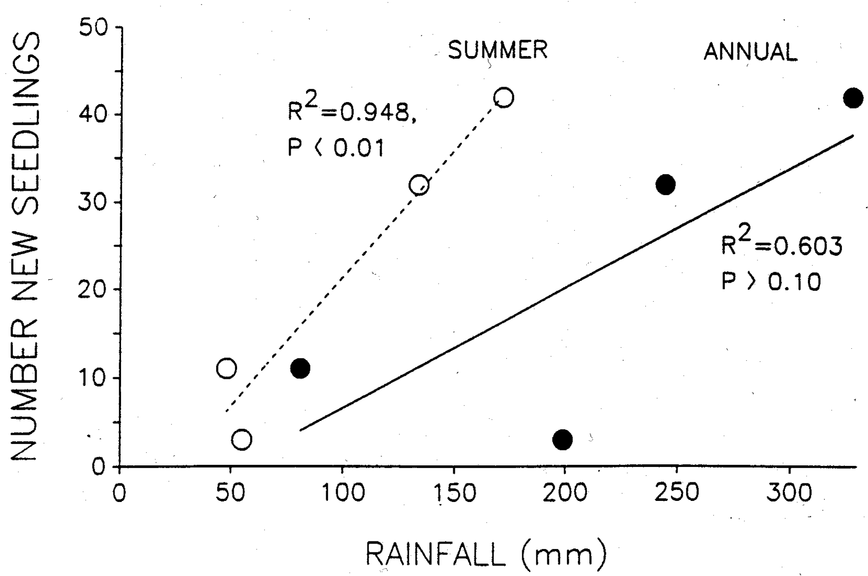

Figure 1. Relationship between rainfall and number of new seedlings of Echinomastus erectrocentrus var. acunensis, Organ Pipe Cactus National Monument, Arizona, March 1989-1992.

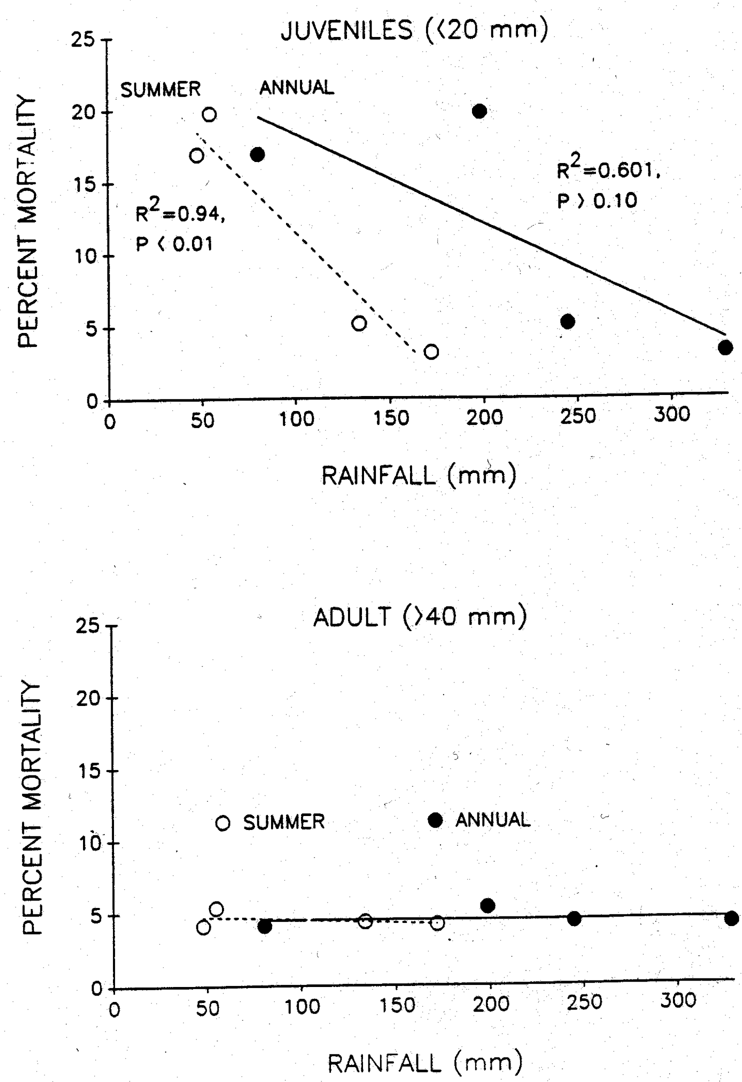

Figure 2. **Relationship between rainfall and mortality for seedlings and adult *Echinomastus erectocentrus* var. *acunensis*, Organ Pipe Cactus National Monument, Arizona, March 1989-1992.**

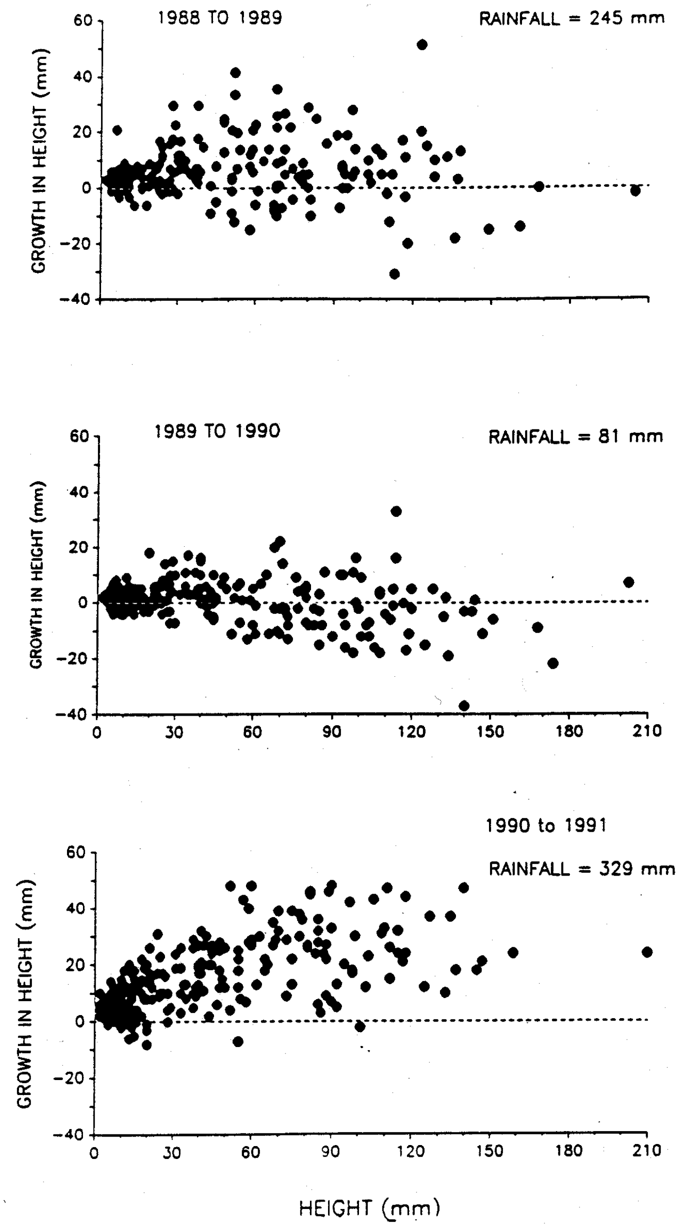

Figure 3. Growth in height by individuals of Echinomastus erectrocentrus var. acunensis, Organ Pipe Cactus National Monument, Arizona, March 1989-1991. Data are presented as growth ove the previous year versus height at the start of the year. The dashed line is the no growth isocline.

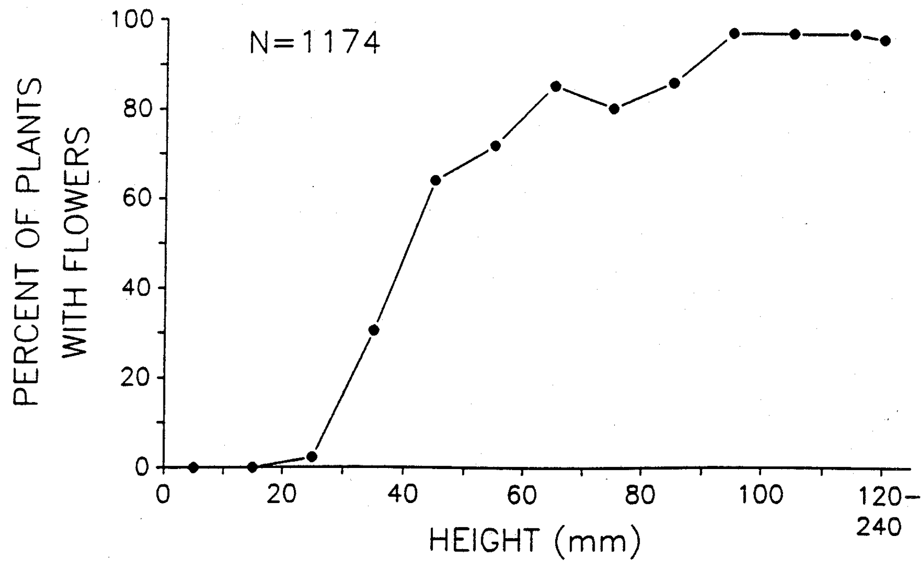

Figure 4. Flower production by Echinomastus erectrocentrus var. acunensis, measured as the percentage of flower-bearing plants in 10 mm height increments, e.g., 0-10 and 10-20. Data were collected in March 1988-1991 from all plants that occurred in six 0.1 ha plots (only four in 1988), Organ Pipe Cactus National Monument, Arizona. Data within each height class are pooled over the four years (reprinted with permission of International Journal of Plant Sciences).

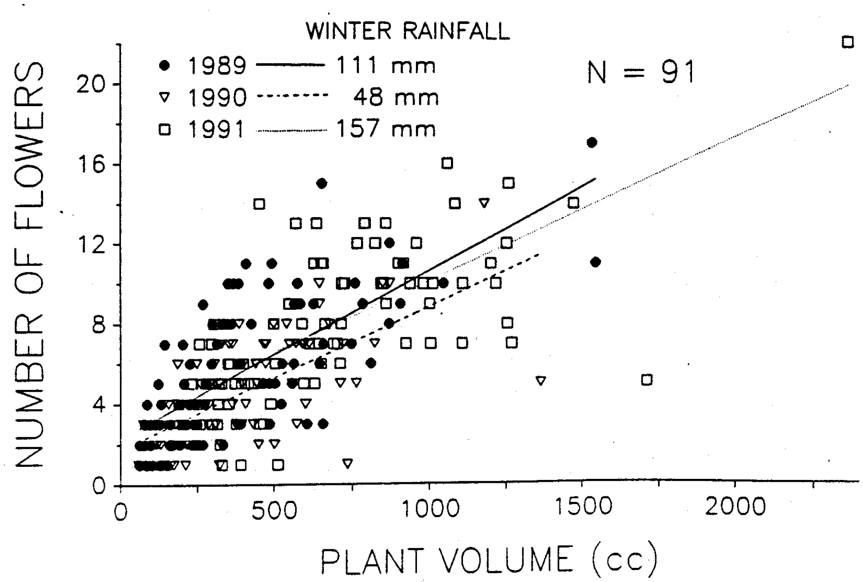

Figure 5. Among-year variation in number of flowers produced by the same individuals, March 1989-1991, Organ Pipe Cactus National Monument, Arizona.

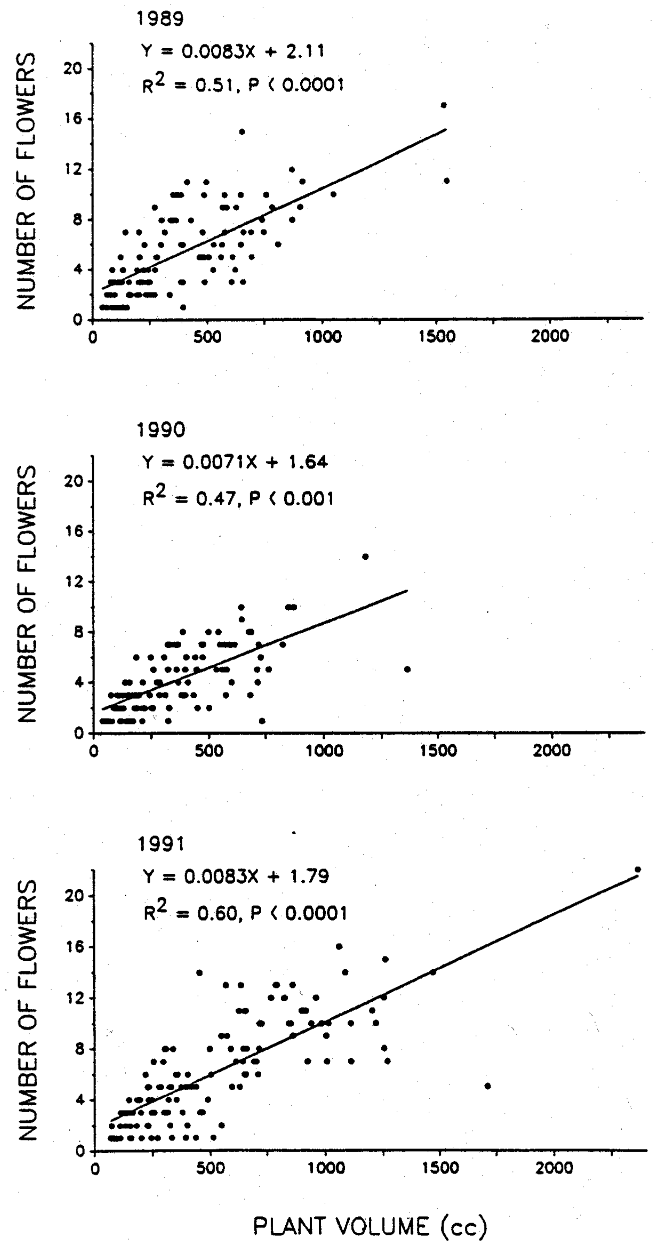

Figure 6. **Relationship between plant volume and number of flowers produced by individuals of *Echinomastus erectrocentrus* var. *acunensis*, Organ Pipe Cactus National Monument, Arizona, March 1989-1991 (reprinted with permission of International Journal of Plant Sciences).**

Significant differences in percent annual mortality between juvenile and adult individuals of *Echinomastus* are likely related to different sources of mortality for the two size classes. Juveniles cannot withstand prolonged drought (Nobel, 1988), and hence manifested high variability in annual mortality that was negatively correlated with summer rainfall. Additionally, juvenile mortality and seedling establishment were more highly correlated with summer than with total annual rainfall, which might be predicted as temperature and water stress are highest and drought is most prolonged during summer. The absence of a correlation between adult mortality and rainfall reflects the ability of larger plants to store sufficient water to withstand prolonged drought. Consequently, adult mortality appears to be caused largely by biotic factors such as disease, predation, and senescence. Larvae of the opuntia borer, *Moneilema gigas* LeConte (Cerambycidae), were observed to kill several adult plants during this study and may be a major source of adult mortality. These larvae typically kill plants by consuming the fleshy interior and severing the root and stem. Larvae of *M. gigas* commonly infest other species of cactus, especially *Opuntia fulgida* and *O. engelmannii* (Crosswhite and Crosswhite, 1985).

Seeds of *Echinomastus* appear to germinate primarily during and following the summer monsoons, though some individuals do establish in winter and spring R. Johnson, pers. obs.). Regardless of the season of establishment, mortality of seedling *Echinomastus* may be high, and is highly correlated with amount of summer precipitation. Establishment is also related to timing of rainfall. Juvenile mortality was higher during 1992 than in 1990 despite a slightly higher summer precipitation during 1992 because summer rains did not begin until late August in 1992, about six weeks later than normal (see also Steenbergh and Lowe, 1977).

Seedlings of *Echinomastus* often occurred at the base of adult plants, presumably the parent, as dispersal is primarily by gravity. Consequently, individuals of *Echinomastus* commonly used conspecifics, possibly relatives, as nurse plants, and grew within the moderated environment provided by the cluster of spines upon death of the adult.

Growth by individuals of *Echinomastus* was also highly positively correlated with annual rainfall, and was also greater for larger plants during wet years, as also occurs for large columnar cacti (Hastings, 1961; Parker, 1988). Seasonality of precipitation is positively correlated with growth patterns in three columnar cacti, though the season of rainfall varies by species; summer precipitation is most important for *C. gigantea* (Hastings, 1961; McAuliffe and Janzen, 1986), and winter precipitation is most important for growth by *S. thurberi* and *L. schottii* (Parker, 1988). Possible seasonal variation in growth has not yet been examined for *Echinomastus*. During a dry year many individuals of *Echinomastus* decreased in size (Figure 3), which reflects growth when water is only sufficient to satisfy the maintenance budget.

The positive association of rainfall and annual variation in number of flowers produced suggests that water availability limits flower production in *Echinomastus* as well as in other cacti (Brum, 1973; Steenbergh and Lowe, 1977; Heins *et al.*, 1981; Johnson, 1992). Such limitation is also indicated by flower number being better correlated with plant volume than with plant height, as also occurs for Simpson's cactus (*Pediocactus simpsonii*) in Colorado (P. G. Kevan, unpublished). Plant volume better reflects total water availability because stems of cacti act like an accordion, expanding from stored water in wet years and contracting in dry years (Nobel, 1988). *Echinomastus* resembles saguaros (*Carnegiea gigantea*) (Steenbergh and Lowe, 1977) in that the percentage of plants with flowers and the number of flowers produced increase with plant height. Mature individuals of *Echinomastus*, like those of other cacti (Nobel, 1988), flowered nearly every year. Occasionally, large plants, i.e., $\geq$90-100 mm tall, did not produce flowers, and these individuals often contained a larvae of *M. gigas* (Johnson, 1992).

Overall, this study demonstrates that rainfall patterns are highly correlated with several demographic parameters, including establishment, mortality, growth, and flower production, which in turn effect the long-term population dynamics of *Echinomastus*. These results provide the first limited data on population dynamics and demographic parameters of a rare cactus species.

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