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Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette[1]

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Agave macroacantha can sexually reproduce by seeds and propagate vegetatively by aerial bulbils and ground-level basal shoots and rhizomes. It forms compact patches apparently generated by the multiplication of ground-level offshoots. We experimentally evaluated the establishment and survival of bulbils and seedlings of *A. macroacantha* in the Tehuacán Valley, Mexico, between 1991 and 1994 and studied comparatively the effectiveness of sexual reproduction against vegetative propagation.

Seedlings showed low survival rates. Cohorts placed outside nurse plants died in less than 1 yr, while 1–10% of cohorts under nurse plants survived for more than 2 yr. Herbivores negatively affected seedling survival in non-nursed plots. In rainy years, survival rates increased. Bulbils showed higher survival rates than seedlings.

The excavation of rosettes showed that most are derived from vegetative shoots, as indicated by remains of rhizomes in their base. Most rosettes had ground-level vegetative offspring totaling almost three shoots per rosette.

In *A. macroacantha*, the establishment of seedlings and bulbils is a rare event that possibly only occurs under nurse plants in rainy years, while ground-level cloning is highly effective as a propagation mechanism. These results are consistent with the aggregated spatial pattern of the species.

Key words: Agavaceae; *Agave macroacantha*; bulbil; seedling establishment; sexual reproduction; shoot; survivorship curves; vegetative propagation.

Plant populations are demographically maintained and regenerated through two mechanisms: (1) reproduction, which involves the production of either sexually derived seeds or apomictic seeds, and (2) vegetative growth, which involves the production of vegetative offshoots or clones (Harper, 1977, 1985). Both processes may give rise to new individuals, but in reproduction the new plant is originated from a zygote, while in vegetative propagation the new plant is originated from a meristem (Harper, 1977). Plants showing both processes, normally known as clonal plants, are very common in nature (Abrahamson, 1980; Cook, 1985).

From a morphological point of view, the development of a plant may be interpreted as a process of modular construction in which growth is determined by the addition of new morphological units or modules. In clonal plants, each independent unit of modular growth is called a ramet and corresponds to clonally originated individuals. Similarly, a genetic individual, or genet, is defined as the array of ramets derived from a common zygote, i.e., the set of clonal individuals that originated from a common parental stock and thus have the same genotype (Harper, 1977, 1985). In clonal plants, a single genet may occupy large areas extending hundreds of meters (Cook, 1985).

The propagules and diaspores (both seeds and vegetative offspring) produced by clonal plants seem to play different roles in the life cycle of the plant. In highly unpredictable or extreme environments, clonal multiplication operates as a safe strategy to perpetuate the genotype in a given habitat, while sexual reproduction seems to constitute a strategy that involves greater risks and mostly serves as a mechanism to explore new environments (Abrahamson, 1980; Silander, 1985; Eriksson, 1989, 1992). Although normally the successful establishment of sexually derived seedlings involves a very low proportion of all the seeds produced, it nonetheless plays an important role in genetic recombination and in maintaining the genetic variation of the population (Silander, 1985; Ellstrand and Roose, 1987). Furthermore, the clonal propagation of a genet may also increase the chance of successful sexual reproduction of a single genet, which may reproduce repeatedly, at different times and in different places, through its constituent ramets (Cook, 1985).

The amount of sexual diaspores produced by a clonal plant is regulated by environmental factors such as the availability of resources and the trade-off between sexual reproduction and vegetative growth (Cook, 1985; Silander, 1985; Eriksson, 1992). The theory of resource allocation predicts that the amount of resources available for a plant is limited and that the onset of reproduction necessarily implies a competitive reduction in resources available for vegetative growth (Watson, 1984). In some plants, this trade-off between clonal growth and reproduction is related to direct competition for the same reserves in such a way that resource allocation for either one of these two processes develops at the expense of the other (Harper, 1977; Willson, 1983; Arizaga and Ezcurra, 1995).

Although the dispersal ability of sexual diaspores is an extremely important element in the demography of plants (Harper, 1977; Grime, 1979), the probability of successful establishment of seedlings is often extremely low and frequently constrained to narrow windows of opportunity in space or time (Thomas and Dale, 1975; Cook, 1985). In contrast, clonal propagules have the advantage of being linked to the parental
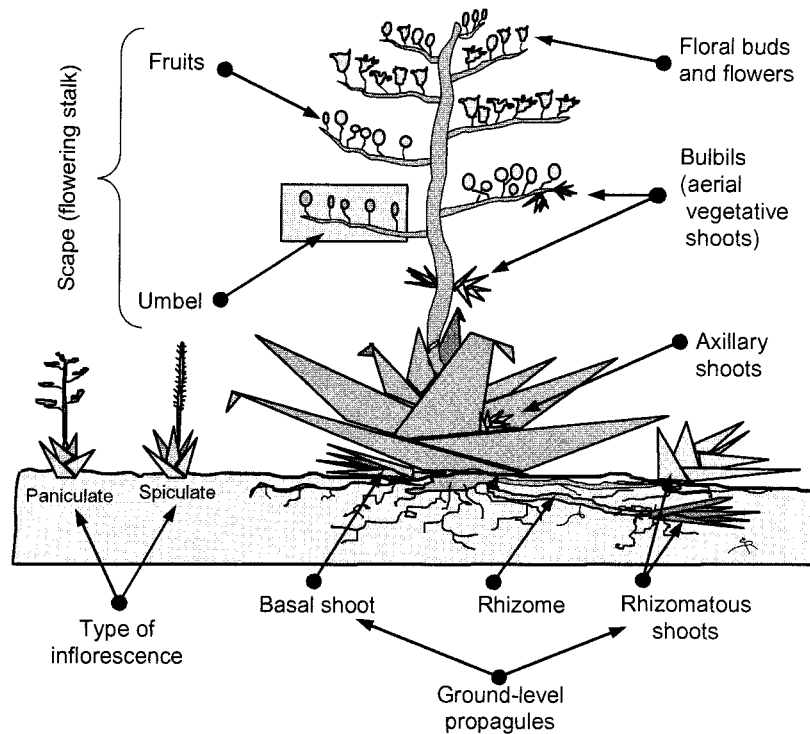
Fig. 1.   Simplified morphology of a rosette of a paniculate *Agave*.

plant during their early stages through their vascular systems, a fact that allows them a much higher probability of survival in extreme environments (Harper, 1985; Pitelka and Ashmun, 1985).

Within the group of succulent rosette plants that form the genus *Agave*, numerous species present both propagation mechanisms, i.e., sexual reproduction and cloning. The latter can be achieved in different species through the development of clonal shoots in different parts of the rosette, including: (1) aerial bulbils produced in the flowering scape, (2) lateral shoots produced in leaf axils, (3) short basal shoots produced below the rosette, or (4) long rhizomatous shoots that emerge from the ground at a distance from the parental plant (Gentry, 1972, 1982; Fig. 1). As is the case with other xerophilous succulents such as cacti (Nobel, 1984; Elheringer, 1985; Valiente-Banuet and Ezcurra, 1991), the establishment and seedling stages represent the most vulnerable phases of the *Agave* life cycle. Seedlings have a limited amount of reserves, a low capacity to absorb water, and are exposed to the high variations in surface ground temperatures that characterize arid environments. Thus, their successful establishment is usually confined to rainy seasons (Turner et al., 1966; Nobel, 1977, 1984; Jordan and Nobel, 1979; Raphael and Nobel, 1986). In terms of survival probabilities, cloning seems to be a more efficient mechanism of propagation (Gentry, 1972, 1982).

The genus *Agave* is formed by a group of rosette plants with succulent leaves that are endemic to the American continent (Gentry, 1982; Álvarez, 1989; García-Mendoza, 1995). They are native to North America, Central America, the Caribbean, and South America and range in latitude from 40° N to 6° N. The highest species diversity of the genus is found in Mexico (Gómez-Pompa, 1963; Álvarez, 1989; Rzedowski, 1991; García-Mendoza, 1995). Agaves have been used by humans since pre-Columbian times and are still widely used as sources of food, beverages, fibers, construction materials, and natural medicines (Gonçalves y Lima, 1956; Callen, 1965; Felger and Moser, 1970; Gentry, 1982). Although most of the economic uses of agaves depend on plants from wild populations, some species are commercially cultivated.

Although many *Agave* species are characteristic elements of arid lands, little information exists on the production of different types of propagules and diaspores in natural conditions. This is a study on the reproductive and propagation strategies of *A. macroacantha*, a clonal species with monocarpic rosettes (i.e., semelparous ramets).

METHODS

Study area—This study was conduced in the "Helia-Bravo" Botanical Garden, located in Zapotitlán Salinas (18°20′ N, 97°28′ W), 30 km south of Tehuacán, in Puebla, Mexico (Fig. 2). In spite of its name, the garden contains some 30 ha of native dry scrub, surrounded by a larger area of hundreds of hectares of natural vegetation, and we shall refer to it in the rest of this paper as the "reserve." Elevation is 1407 m, and the climate is arid to semiarid with summer rainfall (Zavala-Hurtado, 1982). Mean annual rainfall is 380 mm, mean annual temperature is 21.4°C, and annual evaporative demand is on the order of 2000 mm (García, 1987; Peters, 1993).

The main vegetation is a xerophilous scrub (Rzedowski, 1978), and the dominant species is the giant columnar cactus *Neobuxbaumia tetetzo*, growing in association with other cacti, succulent rosettes, xerophytic shrubs, and annuals (Zavala-Hurtado, 1982). Zapotitlán Salinas is one of the many small valleys that converge into the large Tehuacán Valley, which in turn forms part of the Tehuacán-Cuicatlán Biosphere Reserve in the border region between Oaxaca and Puebla. The ranges of the Eastern Sierra Madre, known as Sierra de Zongolica and Sierra de Juárez, create a rain shadow that constitutes the main cause of the aridity of the Tehuacán Valley (Smith, 1965; Villaseñor, Dávila, and Chiang, 1990). In contrast with other arid zones, the short rainy season in the Tehuacán Valley is relatively predictable. The rainy period normally starts in late May and continues until late September. Hurricanes may
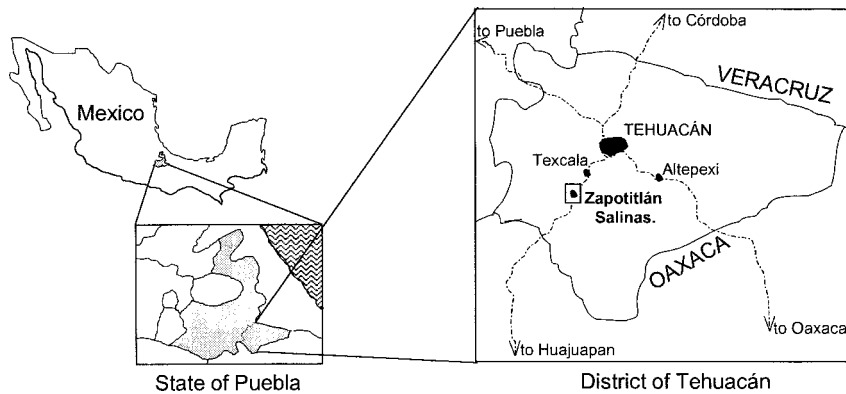
Fig. 2.   The study area, Zapotitlán Salinas, located within the District of Tehuacán, Puebla, Mexico.

extend the rains into October and, rarely, into November. In August, a mid-summer drought frequently occurs (Valiente, 1991).

The soils of the Tehuacán Valley are shallow and rocky, derived from calcareous sedimentary rocks, and are frequently halomorphic, with varying degrees of salinity and alkalinity. In some hills, the soils form typical limestone rendzinas. In general, soils have loamy textures, light colors, alkaline pH, low organic matter, and high carbonate contents (Aguilera, 1970).

The economy of Zapotitlán Salinas is based on extracting and processing onyx, extracting salt from briny aquifers, and grazing the natural scrub with goats. Agriculture is limited to the valley bottoms. The collection of wild fruits and wild plants is common, but mostly oriented towards self-supply and not aimed at external markets.

Study species—*Agave macroacantha* is a midsize paniculate agave, endemic to the Tehuacán Valley (Gentry, 1982; García-Mendoza, 1995). It is locally known as "maguey espadita" (little sword), and its rosettes are occasionally planted to delimit land plots with hedge-like rows of different plants. It grows mostly on low-grade slopes forming small colonial aggregations, possibly as a result of its cloning ability. It flowers in early summer, between April and June, coinciding with the end of the dry season. As in all other paniculate agaves, the flowers in the scape of *A. macroacantha* are developed in lateral "branches," which are lateral umbellate clusters. For the sake of brevity, we shall refer to these structures as "umbels." The flowers are protandrous and the crossing system is mainly allogamous. Its reproductive success is extremely dependent on the presence of nocturnal pollinators, chiefly nectar-feeding bats and, to a lesser extent, moths (Arizaga and Ezcurra, 1995; Arizaga et al., 2000a, b). The fertile capsules are formed in late summer, between June and October (Arizaga et al., 2000a). Most of the seedlings and many solitary rosettes are observed growing in association with higher shrubs, a fact that suggests that these agaves may profit in the early stages of their life cycle from the shade of nurse plants. Another interesting aspect of the ecology of *A. macroacantha* is its capacity to produce a large amount of bulbils in the scape if pollinators fail to arrive or if grazing damages the flowering stem (Arizaga and Ezcurra, 1995).

Evaluation of rosette morphology and spatial distribution—During the reproductive period (April to November) of 1992, we selected 188 clumps or colonies of *A. macroacantha* localized within the study area, all located in a gentle (14° or 23%) southwestern slope. A clump is normally formed by a group of rosettes growing less than 1 m apart. Previous excavations of plants showed that rhizomatous shoots are normally generated less than 1 m away from the parental rosette. Hence, we assumed that rosette clumps, which are clearly distinguishable in the field, are formed by a population of ramets belonging to a single genet. In each clump, we counted the number of rosettes (ramets) and measured the height and diameter of each one. In reproductive rosettes, we also measured the size of the scape.

Quantification of propagules—*Seeds (reproductive diaspores)*—*1. Seed production*—Between April and November 1992, we counted the number of

floral buds and the number of fruits that developed from them (i.e., the fruit set) in all the flowering rosettes located within the study area, totaling 53 scapes. During fruiting season (July to November) we took a random sample of 219 capsules that had not yet reached dehiscence from 38 randomly chosen individuals (we collected 5–6 unopened capsules per scape). In each capsule we counted the number of fertile seeds, which are black in color, and the number of aborted seeds, which are light brown. The estimate of total ovules is determined by summing the numbers of the fertile and aborted seeds. With both the fruit- and seed-set data, we estimated the mean fecundity of the ramets as the product of the mean number of capsules formed in a scape and the mean number of viable seeds formed within each capsule.

2. Seed germination—Once the fruits mature, the flat seeds are dispersed by wind. Some fall directly on the ground, where they either germinate rapidly or are subject to predation, while others fall in rock cracks, which act as safe sites where radiation conditions are less intense and where escape from predation is more likely. Additionally, a significant proportion of the seeds remain in the dry capsules up in the scape. This aerial seed bank is released gradually during the next 1–2 yr by the slow, progressive opening of the capsules. Taking into account the variation in seed age, we quantified the germination capacity of seeds by applying the following treatments: (1) Fifteen lots of 100 seeds each ($N = 1500$) were germinated in 1% agar plates in the laboratory at 23°C and under 12 h light, 12 h darkness conditions. These seeds were produced in 1992 and were approximately 1 mo old when germinated. (2) Five lots of 100, 1-mo-old seeds ($N = 500$) were germinated as in (1), but under total darkness by covering the tray with aluminum foil (24 h darkness at 23°C). (3) Eight lots of 100 seeds ($N = 800$) collected in 1991, i.e., older than 20 mo and stored under laboratory conditions, were germinated under the same conditions of treatment (1).

Vegetative aerial propagules—*1. Bulbil production*—To evaluate the effect of goat grazing on bulbil production, we quantified bulbil production in two areas with varying degrees of protection: (1) In the botanical reserve (i.e., the "protected" treatment), we evaluated herbivore damage during four reproductive seasons (1992–1994 and 1996) and counted bulbil production in all flowering rosettes found within the reserve, totaling 254 rosettes. The reserve is intended to be protected from grazing, but goats often break in and so only partial exclusion from herbivores was accomplished in this treatment. (2) For the "unprotected" treatment, we evaluated herbivore damage in a grazing commons, 1.3 km south of the reserve, that belongs to the community of Zapotitlán. During two reproductive seasons (1995–1996), we counted bulbil production in all flowering rosettes found in the grazing area, totaling 129 rosettes.

2. Fate of bulbils—For the two areas described above (protected and unprotected for the period between 1992 and 1996), we marked at the end of each reproductive period all the bulbils produced in 86 bulbiferous rosettes (48 rosettes in the protected area and 38 in the unprotected one), totaling 518 bulbils. At monthly intervals during the 5-yr period we returned to both sites and followed the fate of the recorded bulbils, registering the mortality of

bulbils in the scape, the abscission of bulbils from the scape, and their final fate on the ground.

3. Axillary shoot production—We conducted periodic observations in the same rosettes ($N = 383$) in the protected and unprotected areas to determine the number of lateral shoots produced above ground, in the axils of the leaves.

4. Basal and rhizomatous shoots (vegetative ground-level propagules)—We excavated ten randomly selected clumps (genets) by carefully removing the top layers of the soil (see Böhm, 1979) until the underground stems, rhizomes, and lateral root system were exposed. In each rosette (ramet) we registered: (a) the diameter and height of the rosette, (b) the vertical buried depth of the main stem, (c) the number of basal shoots and their respective size, and (d) the number and size of rhizomatous shoots.

Propagule establishment dynamics—Seedling establishment—To evaluate the establishment dynamics of *A. macroacantha* seedlings, we performed a factorial experiment with two levels of radiation (open space and under a nurse plant), two levels of predation exposure (exposed to predators and excluded), two planting seasons (dry and rainy season), and three replicates within each treatment. Three cohorts of nursed seedlings from seeds collected in 1991 and germinated in 1% agar gel at 25°C were planted under one of three randomly selected *Mimosa luisana* shrubs with canopy cover of about 2 m². Flores-Martínez (1994) estimated a minimum shrub cover of 0.235 m for the nurse plant to effectively have some protective effect on cactus establishment. The open space cohorts were planted 30 cm north of three randomly selected *A. macroacantha* rosettes, with no other canopy shading them. Each cohort was planted in a 30 × 30 cm plot. Vertebrates and larger insects were excluded by covering the plots with 12-mm wire mesh; smaller insects were excluded by applying a contact insecticide (Clordane) in the perimeter of the plot each week for the first 70 d. The seedlings were planted 1 wk after germinating. Planting was done in the following two contrasting periods: (1) Dry season establishment was simulated by planting the seedlings in December 1991. Seedlings were hardened off after planting by watering them daily for the first 2 wk and every 4 d thereafter for three more occasions. The survivorship analysis was done on the seedlings that survived the acclimatization period. (2) Rainy season establishment dynamics were evaluated by planting the seedlings in early June 1992, at the beginning of the rainy season. Because the soil was wetter at this time, the acclimatization of the seedlings was done by watering only for the first week.

We planted 100 seedlings in each plot. Because of the high seedling mortality during acclimatization, the plots in the dry period treatment were uniformly thinned to an initial number of 75 seedlings at the beginning of the survival counts, while the wet season treatment retained the original density of 100 seedlings per plot when counts started. Surviving seedlings in both treatments were then periodically counted after 1 wk, thereafter at increasing intervals of 2, 5, and 10 wk. Both experiments were ended in April 1994. To characterize the environmental conditions of the site, we placed two rain gauges (Peters, 1993) and a maximum-minimum thermometer on the southwest-facing slope where the experiments were done.

Bulbil establishment—To evaluate the establishment dynamics of *A. macroacantha* bulbils, we used 102 bulbils collected in 1991 from flowering scapes. Due to the low number of bulbils, this experiment was reduced to analyzing the effect of bulbil size as a factor leading to successful establishment. We divided the bulbils into three categories: small (<4.0 cm height, $N = 48$), intermediate (4.0–5.9 cm, $N = 30$), and large bulbils (≥6 cm, $N = 24$). The bulbils were planted under three nurse shrubs (*Acacia coulteri*) of similar size, excluding in all cases larger predators with 12-mm wire mesh. At the time of planting (November 1991), the bulbils had not yet developed roots. The bulbils were planted in a 40 × 40 cm plot, 30 cm north of their nurse shrub. Rows of bulbils of different sizes were mixed within the plot in order to avoid the systematic placement of a given bulbil size in a fixed position under the canopies. Survival counts started in mid-November 1991 and were performed at increasing intervals of 1, 2, 5, and 10 wk for 30 mo.

Analysis of survivorship curves—To evaluate the characteristics of the survivorship process we used a nonlinear model developed for this study. We
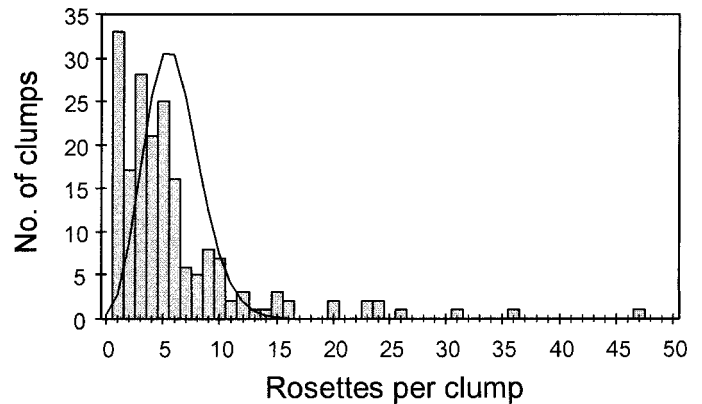

Fig. 3. Frequency distribution of clump size in 188 *A. macroacantha* colonies. The line shows the prediction of the Poisson distribution under the assumption of random clumping.

started with the assumption that the mortality of a cohort, which defines the survivorship curve, may belong to one of three basic types: (1) type I mortality, in which the initial mortality rate (k_0) increases with time (i.e., the risk of mortality increases with the age of the cohort); (2) type II, in which the mortality rate is constant (the mortality risk is the same for any age); and (3) type III, in which the risk of mortality decreases with time (i.e., the initial mortality rate k_0 decreases with time). Mathematically, this can be written as a system of two simultaneous differential equations: $\partial n/\partial t = -kn$, and $\partial k/\partial t = bk$, where t = time; n is the number of survivors, k is the instantaneous mortality rate, and b is a shape parameter that describes the type of survivorship process. If $b > 0$, then k will increase with time, and the resulting curve will be of type I. If, on the other hand, $b < 0$, then k will decrease with time, and the resulting curve will be of type III. Finally, if $b = 0$, then k will remain constant with time, and the survival dynamics will be of type II.

Integrating the two previous equations, we get the nonlinear survivorship function: $n_t = n_0 \exp[-k_0/b \, (\exp(bt) - 1)]$, where n_t is the number of survivors at time t; n_0 is the initial size of the cohort (at time $t = 0$); k_0 is the initial mortality rate (at $t = 0$); and b is a parameter, defined above, that describes how k_0 changes with time.

This model was fitted to both the seedling and the bulbil survival counts by means of nonlinear regression. Once the parameters of the function (k_0 and b) were estimated, we compared them by means of t tests. These results were corroborated with the test of Peto and Peto for survivorship curves (Pyke and Thompson, 1986).

RESULTS

Rosette morphology—The nonreproductive adult rosettes of *A. macroacantha* had an average diameter (±1 SE) of 25.3 (±0.3) cm and an average height of 29.4 (±0.3) cm ($N = 1092$). In contrast, reproductive rosettes were significantly larger, with an average diameter of 41.5 (±1.9) cm and an average height of 33.6 (±1.8) cm ($N = 53$). The scapes had a mean height of 2.14 (±0.13) m and an average of 12.5 (±0.5) umbels, which occupied the top 70.0 (±7.0) cm of the scape. The density of rosettes in each colony varied between 1 and 47 ramets. The distribution, however, was highly skewed, with a mode of 1 rosette per clump and a mean of 5.9 rosettes (Fig. 3). This distribution of ramet clump densities differs significantly ($\chi^2 = 435.0$; df = 12; $P \ll 0.0001$) from the predictions of the Poisson distribution (Fig. 3). Clumps with only one rosette, and also clumps with more than 12 rosettes, are significantly more abundant than could be expected by chance alone, a fact that highlights the highly aggregated nature of ramet development.

Quantification of propagules—Seeds (reproductive diaspores)—*1. Seed production*—The scapes of *A. macroacantha* ($N = 53$) formed on average 170 (± 16) floral primordia. Some of these floral buds were grazed by domestic cattle, to a lesser degree by caterpillars of microlepidoptera, and other buds were aborted. Only a mean of 24 (± 4) fertile capsules formed in each scape, i.e., 14.0% fruit set. Each capsule carried a mean of 117 (± 4) fertile seeds, representing 59.8% of the total number of seeds per capsule. The total mean fecundity in *A. macroacantha* was of 2808 seeds per scape (24 capsules $\times$ 117 seeds).

2. Seed germination—Four days after initiation of the experiment, recently collected seeds germinating under alternating light/darkness conditions had the highest germination rate (76%; $\pm 2\%$); seeds germinated in total darkness had 70% ($\pm 2\%$) germination, and the seeds that had been stored for 20 mo had 59% ($\pm 2\%$) germination. These differences are statistically significant ($\chi^2 = 18.4$, df = 2, $P = 0.0001$) and suggest that older seeds lose some of their germination ability. Biologically, however, the differences seem to be relatively minor: 8 d after initiation of the experiment, the stored seeds had increased their germination rate to about 85%, a value not significantly different from that of the recently collected seeds.

Bulbils—*1. Bulbil production*—Highly significant differences ($\chi^2 = 57.4$, df = 5, $P < 0.0001$) were found between the unprotected and the protected areas in terms of the number of grazed scapes. Only 38% of all scapes ($N = 254$) were grazed in the reserve, whereas 85% were grazed in the unprotected area ($N = 129$). Although these differences were obtained by comparing different years for both sites, and hence represent an invalid replication, a similar trend was observed when bulbil production was measured at both sites simultaneously in 1996. Additionally, significant variation in the proportion of grazed scapes ($\chi^2 = 32.4$, df = 3, $P < 0.0001$) was found within the reserve, ranging from 5% damage in 1996 (a year in which protection was successfully enforced) to 64% damage in 1994 (a year in which enforcement was very low).

In both sites, the grazing commons and the botanical reserve, a similar proportion (37% for the pooled data set) of the grazed scapes formed bulbils, and 26% of the bulbiferous scapes shed some of their propagules to the ground. In contrast, only 5% ($\pm 1\%$) of scapes that were not grazed ($N = 156$ in the reserve and $N = 19$ in the unprotected area) formed bulbils, possibly as a result of deficient pollination (Arizaga and Ezcurra, 1995). The proportion of ungrazed scapes forming bulbils was similar in the reserve and the grazing unprotected area. In both sites, 26% of all scapes that formed bulbils shed some of these to the ground (± 1 SE) (3.9 ± 1.0 bulbils per plant were shed). No significant differences were found between years or between sites.

2. Fate of bulbils—Under field conditions we observed that bulbils may have the following final fates: (1) Some bulbils are predated in the scape by insects (mostly by caterpillars and secondarily by grasshoppers) and to a lesser degree by goats and cattle. (2) A certain proportion, which varies significantly according to the site and the year ($\chi^2 = 63.8$, df = 4, $P < 0.0001$), are shed and fall to the ground. In 1992, 1994, and 1996, 32%, 34%, and 0%, respectively, of all bulbils were shed in the reserve and only 4% were shed in the grazed commons in 1995 and 1996. Shedding may be related to the density of neighboring canopies that brush against the drying scape. The plants that do shed bulbils dropped a mean of 3.9

bulbils. The shedding scapes in the reserve dropped a mean of 5.6 (± 0.8) bulbils, while the plants in the grazing commons shed 2.2 (± 0.8) bulbils. (3) Of those bulbils that fall to the ground, a small proportion may eventually become established. However, this seems to be a rare event in the arid environments of Zapotitlán. In our 5 yr of observations, we only counted four successfully established bulbils from a total of 78 bulbils that were followed after shedding. These four bulbils were shed in 1992, a relatively wet year (Fig. 4), and fell under the nurse plants *M. luisana* and *Jatropha neopauciflora*. In all other years, bulbils that were shed failed to take root on the ground. (4) Sixty-six to 96% of the annual crop of bulbils that are produced remain in the scapes and slowly dry up with them, remaining viable for a year or more until they die (Fig. 1).

Axillary shoot production—Of the 383 plants observed over a 5-yr period, only one plant showed the development of two lateral shoots that originated in the axils of the rosette leaves (Fig. 1). These results, coupled with the fact that axillary shoots are rarely observed in the field, suggest that this propagation mechanism in *A. macroacantha* is highly infrequent.

Basal and rhizomatous shoots—Agave colonies ($N = 10$) contained 1–7 well-defined ramets each, totaling 44 adult rosettes with a mean diameter of 28.0 (± 1.5) cm, a mean height of 22.9 (± 2.7) cm, and a vertical underground depth of the main stem of 6.6 (± 0.5) cm. We found 80 live rhizomes of variable length, the longest one being 78 cm, mostly unbranched, with a mean diameter of 2.9 cm (± 0.6; $N = 64$). Eighteen of the 80 rhizomes (23%) were starting to develop small terminal rosettes (i.e., they were transitioning from undetermined to determined growth; Bell, 1991), while the rest were still in the exploratory, undetermined growth phase. We also counted 47 basal shoots, with a mean diameter of 8.9 (± 2.4) cm and a mean height of 5.8 (± 1.0) cm. In short, we found a mean of 2.9 offspring ground-level shoots for each adult rosette, including 1.1 basal shoots, 0.4 determined (i.e., established) rhizomes, and 1.4 undetermined (i.e., exploratory) rhizomes (Fig. 1).

Propagule establishment dynamics—Seedling establishment—*1. Dry season establishment dynamics (1991 cohorts)*—Seedlings placed in open, non-nursed plots showed rapid mortality, and none survived after 245 d (Fig. 5a, b). Initial mortality was higher in the plots that were exposed to predators, and in both treatments (exposed to predators and excluding predators) the shape of the curve was type I (i.e., the initial mortality tended to accelerate with time; see parameters in Table 1). In contrast, the initial mortalities in seedlings planted under the shade of the nurse plant *M. luisana* tended to decrease with time resulting in a type III curve (Fig. 5c, d and Table 1). No significant differences were found between shaded plots exposed to predators and those excluding them. At the end of the 30-mo experiment, 2.4% (± 1.1) of the initial seedlings had successfully established and survived in these plots.

2. Rainy season establishment dynamics (1992 cohorts)—The curves in this experiment showed similar trends to those observed in the previous cohort: non-nursed plants showed a convex, type I survivorship curve with rapidly increasing mortalities. All non-nursed plants had died at the end of the first 3 mo (Fig. 6a, b and Table 1). Nursed plants showed concave,
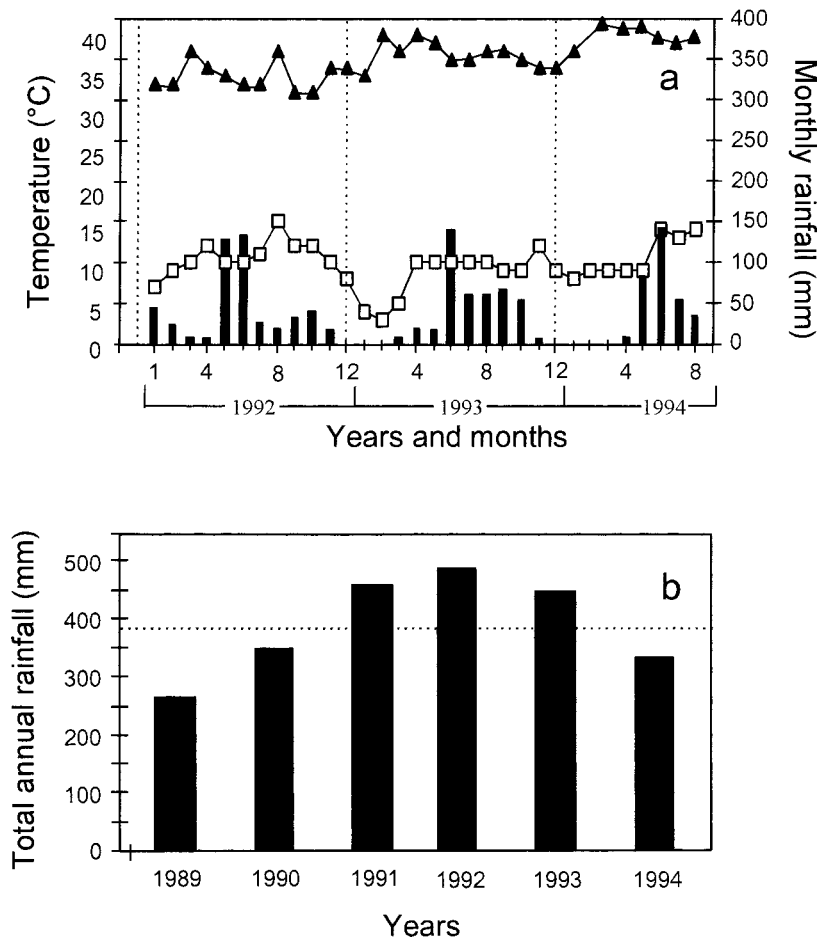
Fig. 4. Climatic conditions at Zapotitlán Salinas: (a) Climatic diagram for the study site. Precipitation is shown in black bars, monthly minimum temperature in open squares, and monthly maximum temperature in closed triangles. (b) Total annual precipitation in the study site from 1990 to 1994. The long-term mean annual rainfall is 380 mm (García, 1987; broken line). The values for 1990 and 1991 were taken from Flores-Martínez (1994); all other values were taken from the present study.

type III curves, with initial mortalities leveling off with time (Fig. 6c, d). Similarly to the dry-season cohort, at the end of the 22-mo experiment, 2.4% (± 1.1) of the initial seedlings had successfully survived in the nursed plots. No significant differences attributable to grazing could be found in the experiments involving nursed seedlings.

3. Cohort comparison—When both cohorts were compared, we found that the survivorship curves of the nursed seedlings did not differ in their parameters (Table 1). However, it was found that both the initial mortality (k_0) and the shape parameter (b) had higher values in the rainy season cohort, i.e., the non-nursed plants died faster when planted during the rainy season. Identical conclusions were obtained from the test of Peto and Peto for survivorship data. It is interesting to note that 1992 was an anomalous year; it had an abnormally high amount of rain in January and February (a normally dry season), high rainfall in the early summer (May and June), and an extremely dry late summer and fall (July–October; see Fig. 4a, b, for 1992). This contrasts with the normal precipitation pattern, which is markedly seasonal with high rainfall in June–October (see Fig. 4a, b for 1993 and 1994).

Bulbil establishment—No significant differences were found in bulbil survivorship between the three size classes, either

with the survivorship curve analysis or with Peto and Peto's test. Hence, we pooled the different size-specific bulbil counts under each nurse tree into a single data series and fitted one survivorship curve for all bulbil sizes. Once established, bulbils had lower initial mortality than seedlings, and these initial mortalities tended to decrease rapidly with time, in a markedly concave type III curve (Fig. 7 and Table 1). Thirty months after being placed under a nurse tree, 56% (± 4.04) of the initial bulbils had successfully rooted and survived in the plots.

DISCUSSION

The importance of seed production, germination, and establishment—*Seed production*—In most plants, only a fraction of the flowers develop into fertile fruits because flowers are predated, may fail to pollinate successfully, or may abort after pollination (Stephenson, 1981; Herrera, 1987). On average, a rosette of *A. macroacantha* produces some 2800 seeds (24 fertile capsules per scape $\times$ 117 fertile seeds per capsule). This is only 14% of the approximately 20 000 seeds that could be potentially produced if the average 170 flowers present in a scape developed. This fecundity seems low when compared to other agaves (Table 2), although many of these other esti-
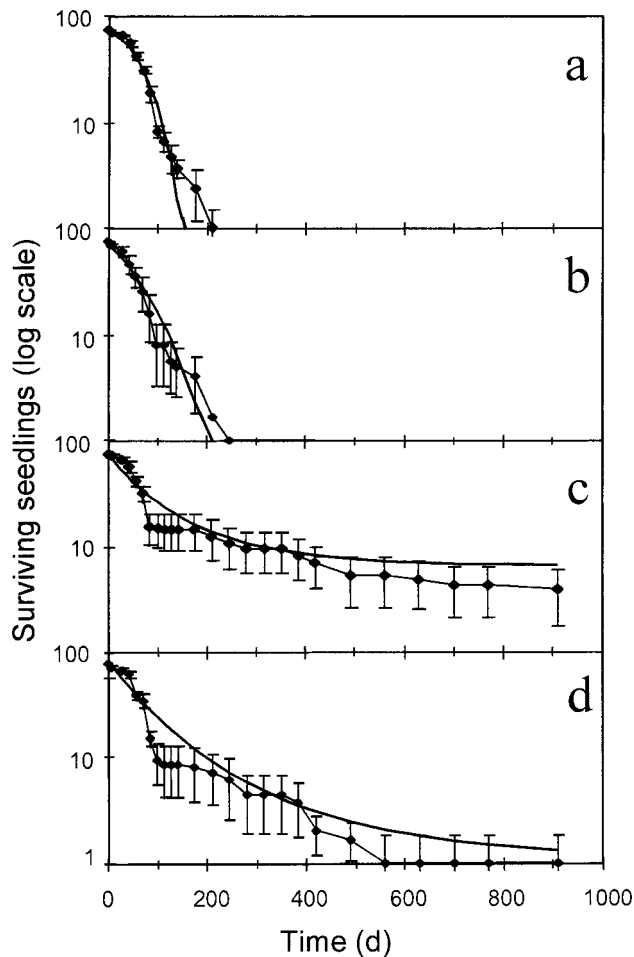
Fig. 5. Survivorship curves and data for *A. macroacantha* seedlings planted during the dry season (December 1991 cohort): (a) non-nursed, nonexcluded; (b) non-nursed, predator-excluded; (c) nursed, nonexcluded; and (d) nursed, predator-excluded. Vertical interval lines show 1 SE (see Table 1).
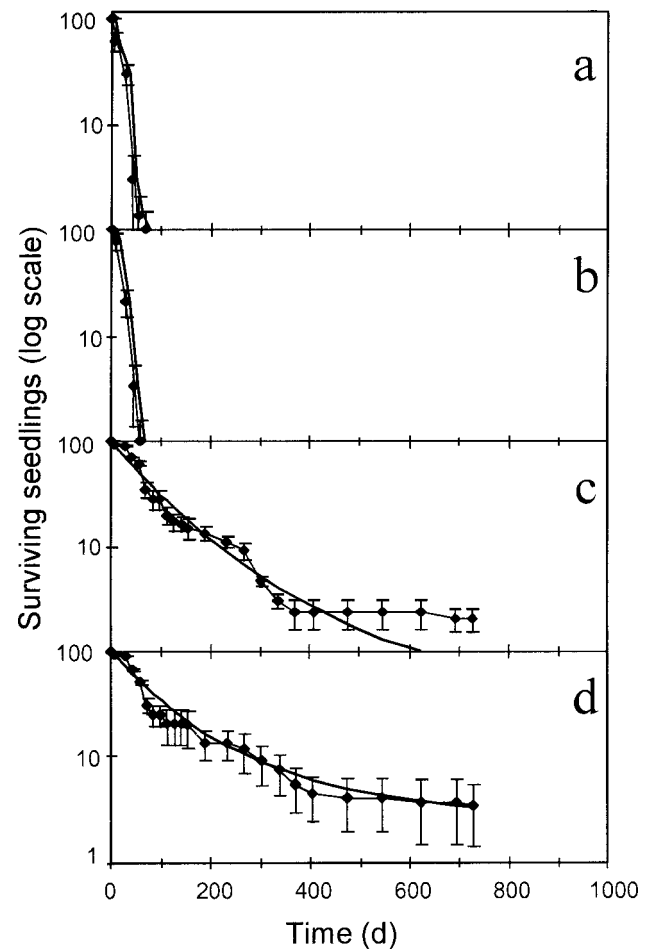

Fig. 6. Survivorship curves and data for *A. macroacantha* seedlings planted during the rainy season (June 1992 cohort): (a) non-nursed, nonexcluded; (b) non-nursed, predator-excluded; (c) nursed, nonexcluded; and (d) nursed, predator-excluded. Vertical interval lines show 1 SE (see Table 1).

mates of seed set lack an explicit explanation of the methodology used and may possibly be only the result of extrapolations. Three main factors seem to playing an important role in decreasing the fecundity of *A. macroacantha*: (1) Predation of reproductive structures by insects and principally by goats was an important factor throughout our study. Goats consumed 85% of all scapes in the grazed unprotected area and predated

38% of all scapes in the protected reserve. Other authors (e.g., Smith, 1965; Meyrán, 1980; Gentry, 1982) have long reported the damaging effect of goats on these natural systems. We have also identified evident goat damage in many other agave species in Tehuacán, such as *A. kerchovei, A. marmorata, A. peacockii, A. potatorum, A. salmiana* var. *ferox, A. stricta,* and *A. triangularis*. (2) The local winds may also have a strong effect

TABLE 1. Parameters of the nonlinear survival curve for the different seedling treatments and for bulbils. The 1991 cohort was planted during the dry season, and the 1992 cohort was planted during the wet season: k_0 = initial mortality rate, b = shape parameter, r^2 = fit (variance fitted by the model/total variance), and SE = standard error. Similar superscript characters indicate values of the two parameters that do not differ significantly at $P = 0.05$.

| Cohort	Nursing	Predation	k_0	SE(k_0)	b	SE(b)	r^2
1991	Open	Excluded	0.0462[A]	0.0043	0.1173[A]	0.0133	0.98
1991	Open	Non-excl.	0.0780[B]	0.0125	0.0422[B]	0.0230	0.92
1991	Nursed	Excluded	0.0973[B]	0.0103	−0.0400[C]	0.0088	0.82
1991	Nursed	Non-excl.	0.1013[B]	0.0102	−0.0234[C]	0.0098	0.88
1992	Open	Excluded	0.2810[C]	0.0437	0.2500[D]	0.0885	0.99
1992	Open	Non-excl.	0.2590[C]	0.0471	0.3180[D]	0.1064	0.99
1992	Nursed	Excluded	0.1040[B]	0.0062	−0.0220[C]	0.0060	0.96
1992	Nursed	Non-excl.	0.1078[B]	0.0084	−0.0350[C]	0.0069	0.88
Bulbils	—	—	0.0387[A]	0.0046	−0.0757[C]	0.0109	0.66
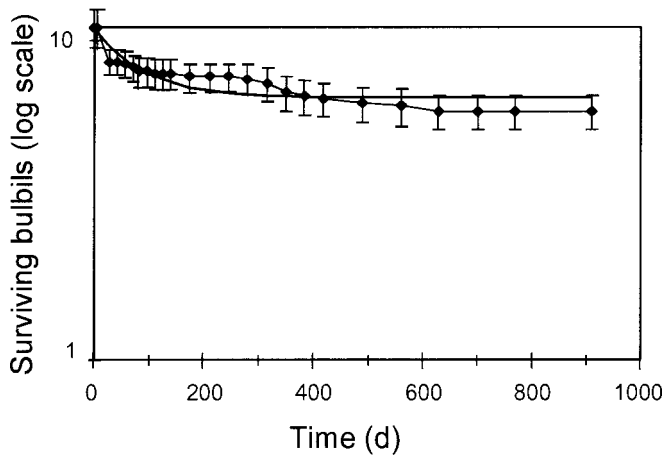
Fig. 7. Survivorship curves and data for *A. macroacantha* bulbils planted in November 1991 under nursing shade. Vertical interval lines show 1 SE (see Table 1).

on flower and bulbil retention. This seems to be especially important in dense scrubs, where under windy conditions the spiny canopy of neighboring plants often detaches the reproductive structures from the scape. (3) Lastly, *A. macroacantha* is pollinized chiefly by bats and secondarily by moths, and its fertilization is strongly pollinator limited (Arizaga et al., 2000b). The failure of bat pollinators to arrive in sufficient numbers in some years may decrease significantly the number of fertile capsules produced in a given scape (Arizaga and Ezcurra, 1995).

Germination—The seeds of *A. macroacantha* showed a high germination capacity (>80% after 8 d), high longevity (85% germination rate in 8 d after 20 mo in storage under laboratory conditions), and did not seem to be very sensitive to photoperiod stimuli. This hardy behavior contrasts with reports for the related *Manfreda* (*Agave*) *virginica*, a plant of temperate zones that requires alternating temperatures to break its dormancy and greatly decreases its germination with long-term storage (Baskin and Baskin, 1971). Freeman (1973, 1975), however, has reported germination values for *A. lechuguilla* and *A. parryi* that are similar to ours, while Jordan and Nobel

(1979) found 92% germination rate in recently collected *A. deserti* seeds.

Seedling establishment—All seedlings planted in open, non-nursed space died within 3–8 mo. Seedlings planted under nurse shrubs survived for 2.5 yr, but the demographic toll was considerable; only some 2.4% of the initial cohorts survived. Similar high mortalities have been reported for the Sonoran Desert where planted seedlings died within the next 63 d (Nobel, 1977; Jordan and Nobel, 1979).

Seed predation, principally by ants, showed detectable but quantitatively low effects in the 1991 cohort and in open spaces. Survival behavior was very similar in the 1991 and the 1992 cohorts. In all cases, the main factor controlling seedling establishment was the protective shade of a nurse plant. These results suggest that *A. macroacantha* depends critically on nurse plants for the survival of seedlings during the establishment phase in the hot tropical desert of Zapotitlán, in the same manner as cacti and other succulents depend on nurse plants in most deserts (Turner et al., 1966; Steenbergh and Lowe, 1969; Jordan and Nobel, 1979; Valiente-Banuet and Ezcurra, 1991).

There was a surprising lack of differences between the 1991 "dry" cohort and the 1992 "rainy" cohort. In reality, the 1991 cohort started during an abnormally wet winter and spring, while the 1992 cohort had to start its survival process during an exceptionally dry summer and fall (Fig. 4). It is likely that in a more normal year the cohorts planted in midsummer would survive better, but this remains to be tested. In any case, our results highlight the potentially critical importance of atmospheric anomalies in the establishment of this desert species and possibly of many others.

In follow-up sampling done in 1998, we found that the established seedlings of the 1991 cohort had decreased from eight to four, while the 1992 cohort still maintained the four survivors it had in 1994. This new value brings the 7-yr survival probability of nursed seedlings to 1.5%. This value is possibly overestimated as the experiment started with germinated seedlings that were watered for a few days to allow them an initial advantage. It is difficult to estimate at this point what the probability is that the seeds in a scape will produce successful offspring. Our establishment experiment showed that

TABLE 2. Production of different propagation structures in the genus *Agave*, according to published literature. *Agave chrysoglossa* and *A. vilmoriniana* are the only species belonging to the subgenus *Littaea*; all the rest belong to the subgenus *Agave*. Asterisks denote cultivated species, zero values indicate that the trait is reported as not found on that species, and dashes indicate lack of published information on that particular trait.

Species	Seeds	Bulbils	Vegetative shoots	Source
*A. americana**	—	0	5	Gentry, 1982; Granados, 1993
*A. angustifolia**	—	100	8–15	Gentry, 1982; Granados, 1993
A. chrysoglossa	500 000	0	—	Gentry, 1972
A. deserti	65 000	0	—	Nobel, 1977
*A. fourcroydes**	0	many	5–8	Gentry, 1982; Benítez, 1965
A. macroacantha	2800	5–7	2.3–10	This work
A. macroacantha	2064	0	—	Arizaga et al., 2000b (with pollinators)
A. macroacantha	153	17 (0–50)	—	Arizaga et al., 2000b (without pollinators)
A. palmeri	38 000	0	—	Howell and Roth, 1981 (with pollinators)
A. palmeri	1600	0	—	Howell and Roth, 1981 (without pollinators)
A. salmiana	—	0	4–7	Martínez-Morales and Meyer, 1985
*A. sisalana**	0	2000–3000	—	Álvarez, 1987
*A. tequilana**	—	—	15–20	Valenzuela, 1994
*A. vilmoriniana**	10 000	>2000	0	Gentry, 1982; Szarek and Holmesley, 1996

none of the seeds that fell in the open survived and that only a fraction of less than 1.5% of seeds that fell under a nurse plant survived. However, no data is available regarding the number of seeds predated, the proportion of seeds that fall under nurse plants, the chances of successful germination in the field, or the probability of establishment if no acclimatization is given to the seedlings.

In any case, these very low survival numbers suggest that seedling establishment is an extremely rare event, a fact that seems to be confirmed by the very small number of seedlings that have been observed in the field. Between 1991 and 1998, we failed to detect any new seedlings that established naturally in the study site. Sampling done in 1997 in the reserve revealed the presence of 16 isolated juvenile plants with some evidence of having established from seed: they had a rounded underground stem quite different from the funnel-like base that results from rhizomes and basal shoots. Furthermore, these plants were grown in isolation, without any other colony nearby from which they could have been derived as bulbils. These juveniles showed a mean diameter (± 1 SE) of 7.9 (± 0.8) cm, a mean height of 5.3 (± 0.6) cm, and 8.4 (± 1.9) photosynthetic leaves. Based on a size-age model we developed (see Arizaga, 1999), we estimated the age of these plants to be about 14 yr. This would set the age of establishment around 1983, a year that brought an unusually high rainfall to central Mexico.

Various authors (Gentry, 1972; Nobel, 1977; Raphael and Nobel, 1986) have also pointed out that recruitment from seed in agaves is an extremely rare event. Additionally, it has been reported that atmospheric anomalies may play a role in releasing harsh environmental restrictions: Jordan and Nobel (1979) found a strong correlation between unusually rainy years and the establishment of *A. deserti* seedlings under nurse plants.

The importance of vegetative shoots—*Bulbils*—A direct consequence of the abatement of fecundity or reproductive failure in *A. macroacantha* is the formation of bulbils from bracteal meristems in the main scape, lateral umbels, or even in the floral pedicels (Arizaga and Ezcurra, 1995). As was the case with seeds, most authors report a much higher productivity of bulbils for other agave species (Table 2), but the exact methodology of these calculations is unclear. Bulbils are commonly used to clonally propagate commercial species such as *A. fourcroydes*, *A. sisalana*, *A. angustifolia*, and many others (Benítez, 1965; Gentry, 1982; Álvarez, 1987). Although it is clear that reproductive failure in *A. macroacantha* induces bulbil formation, the effectiveness of these propagules as a means of cloning is less certain. Only 37% of damaged plants produced bulbils, and of these, only 26% shed one or more bulbils to the ground. Plants that shed bulbils dropped a mean of 3.9 bulbils and only 5% of these eventually rooted and survived (in the field we counted four successfully rooted bulbils out of 78 shed ones; our establishment experiment showed that if bulbils fall under a nurse plant their survival is much higher, but this does not always occur under natural field conditions). In short, the expectation that a damaged plant will produce bulbils, shed them in time, and that bulbils will root is around 2% (0.37 × 0.26 × 3.88 × 0.05). That is, 98% of all bulbiferous scapes will not produce offspring. Even so, any chance, however small, of clonally recovering from reproductive failure may be adaptive.

Basal shoots and rhizomes—In contrast with the questionable importance of bulbils as reliable mechanisms for clonal propagation, basal and rhizome shoot production was undeniably very effective as a cloning mechanism. Most (98%) of the rosettes excavated had one or more ground-level vegetative offspring, either consisting of basal shoots, developed rhizome propagules, or developing rhizomes, totaling almost three offspring shoots per rosette. Most of the independent rosettes were formed from similar vegetative shoots, as indicated by the remains of dead rhizomes in the base of the stem and by their funnel-like form. Of the 44 randomly selected plants, only one small individual, 8 cm in diameter, had a rounded stem base and no traces of decomposed rhizomes, a fact that suggests that it was originated from seed. The idea that ground-level cloning is the main propagation mechanism in *A. macroacantha* is also consistent with the highly aggregated spatial pattern of the clumps.

The formation of basal and underground shoots may vary significantly in different *Agave* species from less than 5 to 15 or more clonal offspring per rosette (Table 2). Other authors have also reported basal shoots and rhizomes as a main mechanism of colonization that has a demographic quantitative importance that surpasses that of sexual reproduction (Gentry, 1972, 1982; Freeman and Reid, 1985; Raphael and Nobel, 1986). A consequence of this natural trait is the widespread use of cloning to propagate cultivated agaves, with the consequence of decreased genetic variation in those crops (Colunga-GarcíaMarín and May-Pat, 1993, 1997; Colunga-GarcíaMarín, Estrada-Loera, and May-Pat, 1996). When asked, agave farmers in the Tehuacán Valley failed consistently to recognize the seeds of their own plants.

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