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Insurance against reproductive failure in a semelparous plant: bulbil formation in *Agave macroacantha* flowering stalks

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Abstract Bulbils are small aerial rosettes that occur on the flowering stalks of semelparous *Agave* plants and in related families, and that are capable of acting as clones of the parent plant. We hypothesized that bulbil formation was inversely related to fruiting success in the flowering stalk, and we explored this hypothesis in *A. macroacantha*, a species from South-Central Mexico. Forty randomly chosen plants were divided amongst three treatments: (a) elimination of all floral buds, (b) exclusion of pollinators, and (c) control. We also studied 22 plants in which the flowering stalk had been felled by goat grazing. Between September and November 1991 we kept a record of the numbers of bulbils and capsules produced in each flowering stalk. Significant ($P < 0.0001$) differences between treatments were found in the proportion of plants bearing capsules and bearing bulbils. The control treatment had the highest proportion of plants producing capsules, treatment *a* had the highest proportion of individuals bearing bulbils, while treatment *b* showed an intermediate response. In the goat-grazed group, 45% of the plants failed to produce any propagative structure after the stalk was cut, and half of all plants produced bulbils on the remaining stump. A significant inverse relationship between the numbers of capsules and the numbers of bulbils per plant was found for the three randomly assigned treatments. Our results suggest that once the production of the flowering stalk has been triggered and the death of the rosette is irreversible, bulbils may act as an insurance mechanism that increases the probability of successful reproduction of the genet.

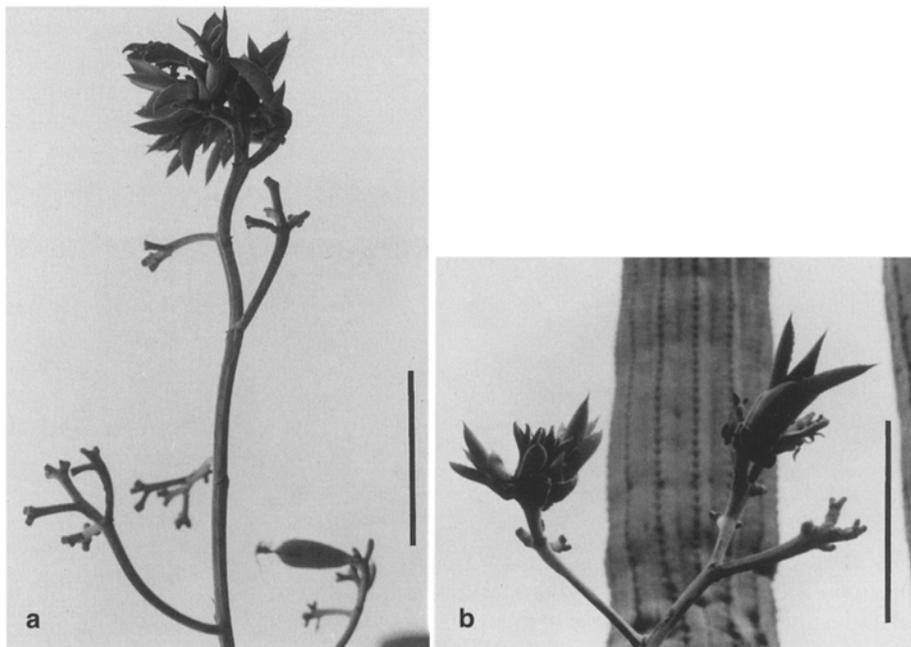
Key words Semelparity · Vegetative reproduction
Bulbil · *Agave*

Introduction

The production of small aerial rosettes (known as bulbils) on the tall flowering stalks of semelparous *Agave* plants is frequently observed in North American drylands. The adaptive importance of these structures, if any, has been unclear. It is well known that agaves can propagate vegetatively through basal shoots and rhizomes, and it seems self-evident that shoots rooted in the ground should have a greater chance of survival than unrooted rosettes exposed to the dry desert environment 1–5 m above the ground. In this paper we report data on the mechanisms that trigger bulbil formation in *Agave macroacantha* in southern Mexico, as part of a longer-term study on the reproductive and cloning mechanisms of *Agave* spp.

The genus *Agave* (Agavaceae) consists of succulent monocotyledonous plants with leaves arranged in basal rosettes. Agaves are native to the American continent and show their maximum diversity in Mexico, mostly in the dry regions. The capacity to accumulate water in the thick succulent leaves makes the genus especially adapted to aridity (Gentry 1982). These plants can propagate by two mechanisms: (a) the production of seeds through sexual reproduction of the semelparous rosettes, and (b) vegetative multiplication, or cloning; cloning is achieved in three different ways, by forming (i) bulbils, (ii) basal shoots, or (iii) rhizomatous suckers (Gentry 1982, 1985). Bulbils are small aerial shoots forming little rosettes on the meristems of the inflorescence (Gentry 1982; Robert and García 1985; Lock 1985; Nobel 1988). These rosettes are frequently shed through abscission as the stalk dries out, or fall to the ground with the dead stalk if it is mechanically damaged (Fig. 1). Basal shoots are ramifications from the lower axillary meristems of the rosette, forming new rosettes that emerge on the periphery of the parent plant and produce adventitious roots which allow their independent growth (Gómez-Pompa 1963; Gentry 1982; Lock 1985). Finally, suckers are shoots produced from rhizomes (i.e., subterranean stems generated from the base of the rosette) and emerge at a distance from the

Fig. 1 Bulbils of *Agave macroacantha* at the top of a flowering stalk, around 3 m above the ground. A capsule is also seen in the lower right corner of the plate. The vertical scale is 10 cm



parent plant (Nobel 1977, 1988; Gentry 1982; Barrientos et al. 1985).

Bulbils are sometimes planted to propagate cultivated species like *A. fourcroydes* (Gentry 1982), *A. tequilana* (Robert and García 1985) and *A. sisalana* (Barrientos et al. 1985; Lock 1985; Nobel 1988). The procedure allows clonal increase of a given genetic stock, although it also facilitates the propagation of viral diseases (Barrientos et al. 1985). Bulbil formation is not exclusive to the Agavaceae, but is present in other families, especially in other monocotyledons that are taxonomically related to the Agavaceae (Table 1). Because bulbils occur in flowering structures, they have been often confused with viviparous seedlings (Gómez-Pompa 1963; Bell 1991). In the context of this frequent confusion, Bell (1991) defined bulbil formation as “false vivipary”.

In many *Agave* species plants with the inflorescences covered with bulbils and with very few or no capsules with seed are frequently observed in the field (Table 1). On the other hand, plants that produce a high number of capsules usually have few or no bulbils. This pattern suggested to us that bulbil formation is, in some way, inversely related to fruiting success. This hypothesis has also been put forward by Hodgson et al. (1989) for *Agave murpheyi* in Arizona. These authors noted that when freezing temperatures occur during flowering, “flowers are produced but abort, and are replaced by vegetative bulbils”. Their published observations, however, are not supported by quantitative data. We explored this hypothesis in *A. macroacantha* Zucc., an endemic species from the Valley of Tehuacán-Cuicatlañ in south-central Mexico (Gentry 1982) that produces both capsules and bulbils in the flowering stalk, and also propagates by means of basal shoots and suckers.

Trade-offs between sexual reproduction and asexual propagation have been described in detail by many au-

thors (e.g., Sarukhán 1976; Willson and Price 1977; Widén 1992; for reviews see Abrahamson 1980; Fenner 1985; Bazzaz and Ackerly 1992; Stearns 1992). At a developmental level, van der Pijl (1972), Faegri and van der Pijl (1971), Solbrig (1976), and Widén and Widén (1990) have documented in detail the relationship between the process of fertilization and the formation of vegetative structures. In *Agave* the normal vegetative structures that propagate the individual ramet are the basal shoots and suckers. In this paper, however, we analyze a different phenomenon, occurring at a smaller scale than the whole ramet. Our study evaluates the relationship between flower and bulbil production, not within the whole plant, but specifically at the level of the flowering stalk and after the stored nutrients have been mobilized to the flowering (i.e., normally sexual) reproductive structures.

Methods

Our field observations were made between April and November 1991, at the Helia Bravo Botanical Gardens, 30 km south of the city of Tehuacán, Puebla. Mean precipitation is 400 mm (García 1981) and the prevailing vegetation type is a dry xerophytic scrub (Rzedowsky 1978) dominated by *Neobuxbaumia tetetzo*, a giant columnar cactus (Zavala-Hurtado 1982). The monsoon-type rainy season in this region starts in late May, and ends in late September. *A. macroacantha* produces flowering stalks in April and May. By September–November the capsules are ripe and start to open.

In April and May 1991, we randomly chose 50 plants from an area of approximately 2 ha, and divided them randomly amongst three treatment groups: (a) elimination of all floral buds from the inflorescence by clipping ($n=12$), (b) exclusion of pollinators with a gauze net ($n=12$; this treatment did not exclude the possibility of fertilization by airborne pollen), and (c) control ($n=26$). We also marked 12 plants in which the flowering stalk had been felled by goat grazing, randomly selected from a set of goat-grazed individuals (goats frequently nibble the stalks until they fall, and then eat

Table 1 Bulbiferous species from different plant families, taken from the literature

Family	Species	Reference
Monocotyledons		
Agavaceae	<i>Agave aktites</i>	Gentry 1982
	<i>A. angustifolia</i>	Gentry 1982
	<i>A. breedlovei</i>	Gentry 1982
	<i>A. cantala</i>	Gentry 1982
	<i>A. cantala</i> var. <i>acuispina</i>	Gentry 1982
	<i>A. chrysantha</i>	Gentry 1982
	<i>A. decipiens</i>	Gentry 1982
	<i>A. fourcroydes</i>	Gentry 1982
	<i>A. guingola</i>	Gentry 1982
	<i>A. macroacantha</i>	Gentry 1982
	<i>A. murpheyi</i>	Gentry 1982
	<i>A. neglecta</i>	Gentry 1982
	<i>A. parvidentata</i>	Gentry 1982
	<i>A. parviflora</i>	Gentry 1982
	<i>A. polyacantha</i>	Gentry 1982
	<i>A. sisalana</i>	Gentry 1982
	<i>A. toumeyana</i>	Gentry 1982
	<i>A. weberi</i>	Gentry 1982
	<i>A. werchlei</i>	Gentry 1982
	<i>A. arizonica</i>	Powers & Blackhaus 1989
	<i>A. karwinski</i>	Gómez-Pompa 1963
	<i>Furcraea andina</i>	Cave 1964
	<i>Furcraea gigantea</i>	Alvarez 1986
	<i>Furcraea hexapetala</i>	Alvarez 1986
	<i>Furcraea macrophylla</i>	Alvarez 1986
Araceae	<i>Amorphophallus bulbifer</i>	Mabberley 1987
	<i>Remusatia viviparum</i>	Mabberley 1987
Cyperaceae	<i>Cyperus alternifolius</i>	Bell 1991
Dioscoreaceae	<i>Dioscorea alata</i>	Passam et al. 1982
	<i>D. bulbifera</i>	Passam et al. 1982
Gramineae	<i>Dactylis glomerata</i>	Bell 1991
	<i>Deschampsia alpina</i>	Bell 1991
	<i>Festuca ovina</i> var. <i>vivipara</i>	Bell 1991
Iridaceae	<i>Homeria breyniana</i>	Mabberley 1987
Liliaceae	<i>Allium oschaninii</i>	Mabberley 1987
	<i>Allium cepa</i> var. <i>viviparum</i>	Bell 1991
	<i>Brimeura fastigiata</i>	Bibiloni et al. 1987
	<i>Lilium bulbiferum</i>	Bell 1991
	<i>Narcissus</i> spp.	Hanks 1987
Musaceae	<i>Heliconia</i> spp.	personal observation
Orchidaceae	<i>Cynorkis uncata</i>	Mabberley 1987
Zingiberaceae	<i>Costus spiralis</i>	Bell 1991
	<i>Globba propinqua</i>	Bell 1991
Dicotyledons		
Brassicaceae	<i>Dentaria bulbifera</i>	Mabberley 1987
Polygonaceae	<i>Polygonum viviparum</i>	Mabberley 1987
Ranunculaceae	<i>Ranunculus ficaria</i>	Mabberley 1987
	subsp. <i>bulbifer</i>	
Saxifragaceae	<i>Saxifraga cernua</i>	Mabberley 1987
	<i>S. granulata</i>	Mabberley 1987

the flowers). Although we also analyzed the results from this last group, for comparative purposes, it cannot be strictly considered a random sample of the flowering plants, as goat grazing may be non-random. During the experiment, goat grazing reduced our sample size in treatment *b* to 9 individuals, and in the control group to 19. Accordingly, the goat-grazed group increased to 22 plants. Between September and November 1991, we kept a record of the number of bulbils and the number of capsules with seed that were produced by each flowering stalk.

As our dependent variables were frequencies in all cases (i.e., counts of plants, capsules, or bulbils), log-linear models were used

to test the significance of differences between treatments (McCullagh and Nelder 1983). In these models, the measure of deviance (i.e., the squared differences between the observed values and the values expected under the null hypothesis) is the *G* statistic (Sokal and Rohlf 1981), which is distributed as χ^2 , and is the appropriate measure of dispersion for frequency data. To avoid the error introduced by low expected values, we lumped categories in which these values were too low by adding them to contiguous classes (Sokal and Rohlf 1981).

The relationship between production of seeds and production of bulbils was evaluated by a principal-axis analysis (Sokal and Rohlf 1981), as both variables were equally subject to random error and it was not possible to define which should be considered the dependent variable. The goat-grazed group was not included in this analysis for two reasons: (a) it was not a random treatment, and (b) an ANOVA of the residuals of the principal axis line (calculated as the second component axis) for all four groups together showed that the goat-grazed group differed very significantly from the rest ($P < 0.0001$), while the three random treatments did not differ significantly in the distribution of their residuals. Additionally, the inclusion of the goat-damaged group caused the residuals to fail the standard tests for constant variance (homocedasticity), and for lack of outliers and serial correlation (Draper and Smith 1981). Thus, the principal axis line was calculated only for the three randomly assigned treatments.

To analyze the possible effect of other unknown factors on the number of structures per plant, the variation within treatments was tested for randomness by calculating the probability of their residual χ^2 [$\sum(\text{observed frequency} - \text{treatment mean})^2 / \text{treatment mean}$] under the null hypothesis that the within-treatment variation was random. For simpler interpretation, the residual χ^2 was divided by the degrees of freedom of the treatment ($n-1$), to calculate the variance-to-mean ratio (V/m), an indicator of randomness. V/m approaches unity in random Poisson frequencies, and is higher than unity in clumped, non-random distributions (Greig-Smith 1983).

Results

Significant ($P < 0.0001$) differences between treatments were found in the proportion of plants bearing capsules, the proportion bearing bulbils and the proportion bearing no propagation structures (Fig. 2; the proportions do not necessarily add up to 100%, as some plants may produce both capsules and bulbils). The control treatment had the highest proportion of plants producing capsules and the lowest proportion of plants producing bulbils. Treatment

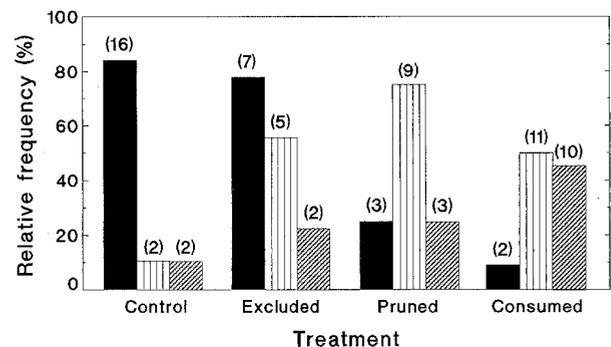


Fig. 2 Relative frequency of rosettes bearing capsules (solid bars), bulbils (vertically striped bars), and bearing no propagative structures (diagonally shaded bars) in their flowering stalks for the different treatments. The absolute frequencies are given in parentheses at the top of each bar. The proportion of plants bearing capsules, bulbils, and no structures varied significantly among treatments ($\chi^2=28.6$, $df=6$, $P < 0.0001$)

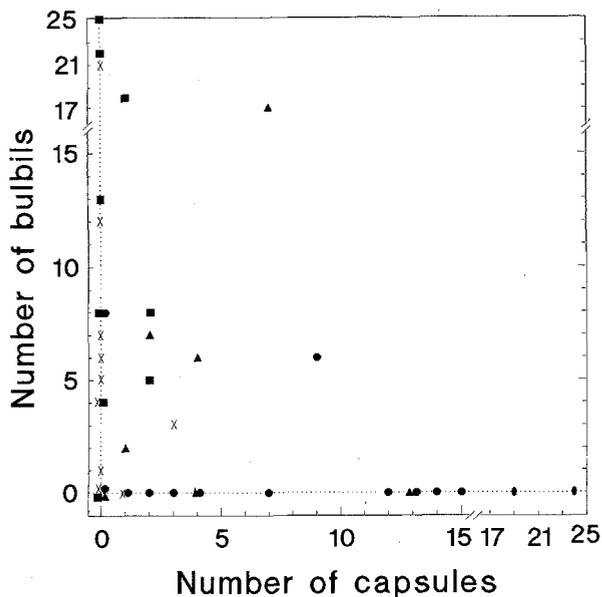


Fig. 3 Numbers of capsules plotted against numbers of bulbils in flowering stalks from the different treatments [circles control plants ($n=19$), triangles pollinator-excluded plants ($n=9$), squares plants where floral buds were pruned ($n=12$), crosses goat-felled plants ($n=22$)]. The treatments differed significantly both in the number of capsules ($\chi^2=34.8$, $df=6$, $P<0.0001$), and of bulbils ($\chi^2=14.0$, $df=6$, $P=0.03$)

a (elimination of flower buds) had the lowest proportion of individuals bearing capsules and the highest with bulbils, while treatment *b* (pollinator exclusion) showed an intermediate response. In the goat-felled plants, a large proportion (45%) failed to produce any propagation structure after the stalk was cut, a few individuals regenerated new branches and some capsules on the old stump, and half of all plants produced bulbils on the bracteal meristems of the remaining flowering stalk.

The same trend as that described in the previous paragraph for whole plants was observed for the number of structures per plant. On average, the highest number of capsules and the lowest number of bulbils were found in the control plants. Treatment *a* (elimination of flower buds) had the lowest numbers of capsules and the highest numbers of bulbils, and treatment *b* (pollinator exclusion) showed an intermediate response. Our current investigations of the reproductive system of *A. macroacantha* suggest that this species is strongly self-incompatible. The capsules formed in the pollinator-excluded treatment are probably the result of wind-pollination. These three treatments defined a significant ($P<0.0001$) principal axis line showing that these structures have some functional equivalence and can replace each other (Figs. 3 and 4). The analysis of the residuals showed that the goat-felled plants lie significantly below this line. Their joint production of capsules and bulbils was lower than in any other treatment, as the felling of the stalk eliminates a substantial amount of biomass and active meristems. With only one exception, the frequencies within all treatments were not randomly (Poisson) distributed around the treatment mean (Table 2). This indi-

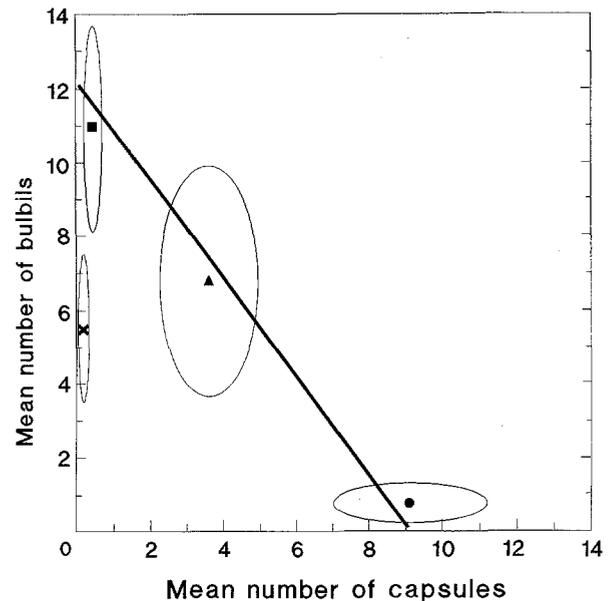


Fig. 4 Principal axis analysis of number of capsules against number of bulbils. Symbols as in Fig. 3. A significant negative correlation was found between the number of bulbils and the number of capsules for the three randomly assigned treatments ($r = -0.31$, $n=40$, $P=0.05$; in each treatment taken separately the two variables were uncorrelated). The slope of the axis line (bulbils=12.2 -1.3 capsules) was significantly different from zero ($P<0.05$). For clarity, only the mean of each treatment, and the ellipse corresponding to the bivariate standard error of that treatment, are given

Table 2 Variance-to-mean ratio (V/m) in the four treatments for both numbers of capsules and numbers of bulbils, and significance (P) under the null hypothesis of randomness of the within-treatment variation. With the exception of the numbers of capsules produced in plants which had the original flowers pruned, the within-treatment frequencies of all other treatments departed significantly from randomness

	Treatment			
	Control	Pollinator excluded	Flowers pruned	Goat-grazed
n	19	9	12	22
Capsules				
V/m	9.67	5.00	1.51	2.43
P	<0.0001	<0.0001	0.12	<0.0003
Bulbils				
V/m	6.41	14.86	9.37	16.37
P	<0.0001	<0.0001	<0.0001	<0.0001

icates that although the treatments accounted for a significant part of the observed variation, within treatments some individual plants produced a significantly higher number of structures than others, possibly as a result of other ecological factors not considered in our design.

Discussion

One of the main demographic risks in the life history of long-lived semelparous plants is the threat of total reproductive failure induced by random environmental events.

However, it can be seen that most long-lived plants usually cited as semelparous can, and often do, multiply vegetatively by suckers and basal shoots. Thus, the individual ramet may be semelparous, but the whole genet is often iteroparous. In this way, cloning may act as a way of bet-hedging against long-term reproductive failure.

At the level of the individual ramet, however, semelparity poses a special challenge to long-lived plants. In *Agave*, for example, the mobilization of metabolic reserves stored in the base of the rosette seems to be an irreversible physiological process. Once the development of the flowering shoot has been triggered and the basal reserves begin to be hydrolyzed and translocated, the final reproductive effort and the ensuing senescence of the rosette cannot be reversed (Howell and Roth 1981), although in some cases severe damage to the inflorescence may prolong the life of the plant for some time (Nobel 1988). This fact is the basis for the production of *pulque* (a fermented brew obtained from *Agave* sap), and is well known by Mexican peasants. If the apical meristem and the central core of the stem are carved out before flowering starts, the plant will continue mobilizing sugar-rich sap from the leaves into the hollow cavity thus formed in the center of the rosette until the plant dies (Gentry 1982; MNCP 1988). Pulque farmers can predict when a plant is going to flower by the thinning of the central leaves of the rosette and by a change in the color and aspect of the lateral leaves during the previous growing season (MNCP 1988). This suggests that the floral structures in *Agave* are preformed at least a year before flowering occurs.

Quite obviously, if successful reproduction fails (e.g., through unsuitable environmental conditions, lack of pollinators, or excessive flower predation), though the genet may still survive through basal shoots and suckers, a large amount of reserves and energy stored in the main rosette will be wasted in the formation of the flowering stalk. Bulbils seem to be an adaptive response to this problem: when seed production fails, the flowering stalk will at least harbor some cloned saplings that may further multiply the genet and rescue the individual ramet from a demographic collapse. We have followed the fate of bulbils in the field, and our preliminary (and still unpublished) results show that around 30% of the bulbils are shed from the flowering stalk, and that around 6% of those bulbils that are shed manage to establish successfully. In contrast, we have not yet observed successful establishment from seeds under natural conditions between 1991 and 1993. It is interesting to note that some *Agave* plants that are totally self-compatible do not produce bulbils when forced to auto-pollinate. In particular, we have observed that in *A. ghesbreghtii* Lem. ex Jacobi and in *A. polianthiflora* Gentry under greenhouse cultivation, ca. 70% of the flowers become fertilized under strict self-pollination without producing bulbils. Additionally, these two species have not been reported to produce bulbils in the field.

Plant-animal interactions can impede the successful reproduction of *Agaves* in a number of ways. Small her-

bivores (insects and rodents) often consume flower parts (Eguiarte y Búrquez 1987), while large herbivores can consume or break the whole flowering stalk. Introduced large grazers which did not evolve in interaction with the local flora often have an even greater effect than the native herbivores (Crawley 1983; Hart and Norton 1988; Tucker and Leininger 1990). This is clearly the case with goats in our study zone, which destroy whole flowering stalks and have been reported to be one of the main causes of environmental degradation in the region (Smith 1965; Meyrán 1980). Nectarivorous bats of the genus *Leptonycteris* (Glossophaginae), the main pollinators of *Agave* spp., are migratory and may fail to arrive in synchrony with the brief mast-flowering period of the flowering stalks (Howell 1979; Howell and Roth 1981; Arita and Humphrey 1988; Arita 1991). In any of the above cases, the result is the death of the rosette producing little or no viable seed. Our results suggest that once the production of the flowering stalk of *A. macroacantha* has been triggered and the subsequent death of the basal rosette is irreversible, the production of bulbils may act as an insurance mechanism that recovers metabolic resources that have been mobilized, and increases the probability of successful reproduction of the genet. We do not know how generalized this response is in other *Agave* species, but our field observations on other agaves suggest that the phenomenon may be common.

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