Aspects of the Reproductive Biology of Agave lechuguilla Torr.

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Figure 1. *Habit of* Agave lechuguilla *in El Paso County, Texas.*

Abstract

Agave lechuguilla Torr. is a small, widespread century plant characteristic of the Chihuahuan Desert growing from central Mexico to southern New Mexico. Most reproduction is vegetative. Flowering occurs primarily in May and June. The inflorescence shaft grows as rapidly as 2 dm/day, and reaches full height (about 2.6 m) in three to four weeks. Energy for flowering is stored almost entirely in the leaves. Flowers open in late afternoon, and last for approximately 96 hours. Anthers dehisce 24 hours after a flower opens and the stigma becomes receptive at approximately 66 hours. Nectar is produced during the second and third nights. The anatomy of the flower is of interest in that the pollen tubes do not penetrate tissue but have an unobstructed path to the ovules. The species is capable of self-pollination, but not apomixis.

Introduction

Agave lechuguilla Torr. (subgenus *Littaea*, Group Marginatae) is a rather small century plant characterized by rosettes composed of relatively few narrow leaves which have detachable margins with downward-pointing teeth (Figure 1). It is perhaps the best indicator species of the Chihuahuan Desert (Bailey, 1905; Benson and Darrow, 1954), which is noteworthy for its paucity of widespread endemic plant species. Lechuguilla occurs from the Valle de Mexico at about 19 degrees north (Sanchez, 1980; Gentry, 1982) to 33 degrees north in the Tularosa Basin of New Mexico (Freeman, 1973) as seen in Figure 2.

It is most commonly found on light-colored, limestone-derived soils on mountain slopes at elevations below 1500 m. On these sites Lechuguilla is sometimes a community dominant, where the rigid, spine-tipped leaves of the rosettes can make walking difficult. It also occasionally occurs in igneous and sandy substrates and above 1500 m. In these latter situations the populations are usually much less dense.

In spite of Lechuguilla having one of the most extensive ranges of the agaves and there probably being more rosettes of this species in nature than of any other agave (Gentry, 1982), very little is known about its reproductive biology. It has been observed that reproduction in nature is almost entirely asexual (rhizomatously derived offsets or "hijos") even though populations flower extensively in most years and produce large quantities of highly viable seeds per plant. We (Freeman, 1973b; Freeman et al., 1977) previously studied certain germination characteristics of Lechuguilla seeds. It was found that the seeds have no dormancy requirements, germinating quickly when moisture is available. However, germination was found to be suppressed by alternating temperature conditions which included exposure to 40°C for only four hours each day. These kinds of temperature conditions are common at the soil surface in the Chihuahuan Desert during the late summer rainy season when most of the annual precipitation occurs. Periods of cloudiness and rain which last continuously for several days are rare. Studies of the heat tolerance of Lechuguilla seedlings would be helpful in determining if seedlings are likely to survive the high temperatures found at the soil surface on hot, sunny days which invariably follow precipitation during the rainy season.

Little is known about other aspects of the sexual repro-

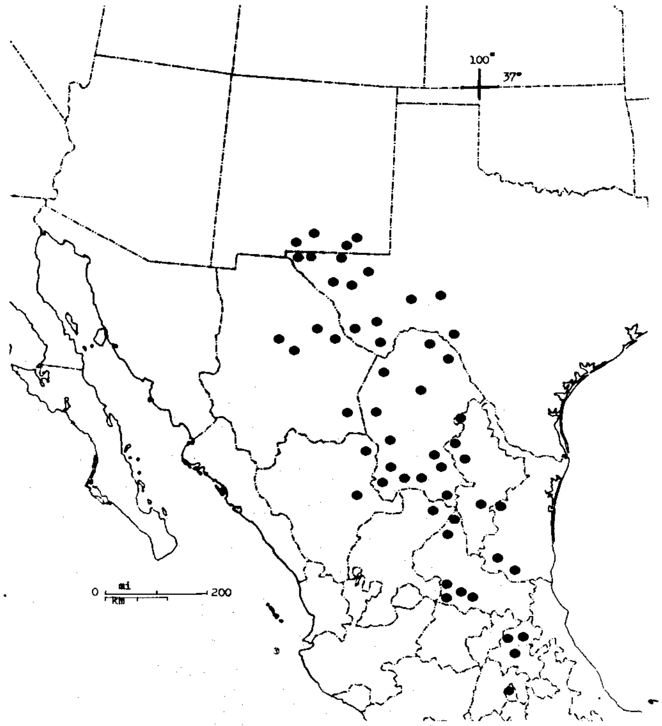

Figure 2. *Range of* Agave lechuguilla *in the United States and Mexico.*

duction in Lechuguilla. This paper brings together the results of a number of investigations on this subject conducted by us and a number of students during the last decade.

Methods

The populations sampled in these investigations were, unless otherwise stated, from Tom Mays Memorial Park on the northwest flank of the Franklin Mountains, El Paso County, Texas.

The number of leaves per individual was used as a measure of the maturity of plants. A randomly oriented compass line was located through a population. Lechuguilla plants for leaf counting were identified by modification of the point quarter method (Phillips, 1959). At 10-meter intervals a sampling point was located. The closest Lechuguilla to the point in each quarter was determined and the number of leaves counted. One hundred plants were sampled in this manner. No attempt was made to determine the clone from which each plant was derived.

A series of plants which were not flowering and others in various stages of the flowering process were selected in the field and brought into the laboratory. Plant parts were removed and placed in leaf, basal mass, and inflorescence categories. Tissues were then dried at 50°C for 48 hours or until dry and weighed.

A series of seven plants which were producing inflorescence shafts were arbitrarily selected and the heights of the shaft above the ground were measured at irregular intervals. Second order equations were calculated which best fit the heights and passed through zero. This was done because the beginning of the shaft growth was hidden by the rosette mass, and were not visible. The time required for full development was then estimated by the curve.

The sequence of development of individual flowers was followed on flowering plants which had been removed from the field to the greenhouse for ease of observation. Time 0 was considered to be the average dehiscence time of individual flowers. The lengths of filaments and styles were then measured during the lifetime of the flower. Other observations, such as time of nectar secretion and appearance of the stigma, were also made. The time of stigma receptivity was determined by dusting stigmas with pollen as the flowers opened and then sampling stigmas at ever-increasing ages until pollen tube development was observed.

Flowers were sectioned serially in order to determine the position of the nectaries and other morphological features. The floral nectar was analyzed for amino acid composition by a Beckman 121 MB amino acid analyzer. Identifications were based on retention times of amino acids in standard solutions. Amino acids which occurred in at least three of the four plants sampled were recorded.

Flower bagging experiments were used to determine the breeding system of a population on the campus of the University of Texas at El Paso. Some inflorescences were covered with one half gallon milk cartons which had the sides partially cut away to allow for air movement. Nylon stockings were then stretched over the cartons and tied to the shaft with wire to prevent insects and other potential

Table 1. Frequencies of different leaf counts for *Agave lechuguilla* in a typical population near El Paso, Texas.

Number of Leaves	Fraction of Population
1-10	0.12
11-20	0.38
21-30	0.36
31-40	0.08
41-50	0.04
51-60	0.02

Table 2. Distribution of biomass by dry weight among the shaft, leaves, and basal mass of eight *Agave lechuguilla* plants at various reproductive stages from a population near El Paso, Texas. Roots and rhizomes are not included.

Plant Description	Leaf Count	Leaves g (%)	Basal Mass g (%)	Shaft g (%)
1. No shaft	54	2,264 (84%)	434 (16%)	0 (0%)
2. Shaft intermediate, flower buds initiated.	43	1,065 (62%)	485 (28%)	175 (10%)
3. Shaft developed, flower buds developed but flowers closed.	47	852 (58%)	392 (27%)	228 (15%)
4. Shaft developed, flower buds developed but flowers closed.	42	536 (55%)	267 (27%)	181 (18%)
5. Shaft developed, first flowers open.	47	792 (55%)	322 (23%)	310 (22%)
6. Shaft developed, first flowers open.	54	771 (55%)	293 (21%)	345 (24%)
7. Shaft developed, about half of flowers open.	43	769 (68%)	94 (8%)	275 (24%)
8. Fruit and seeds well developed.	69	873 (48%)	173 (10%)	759 (42%)

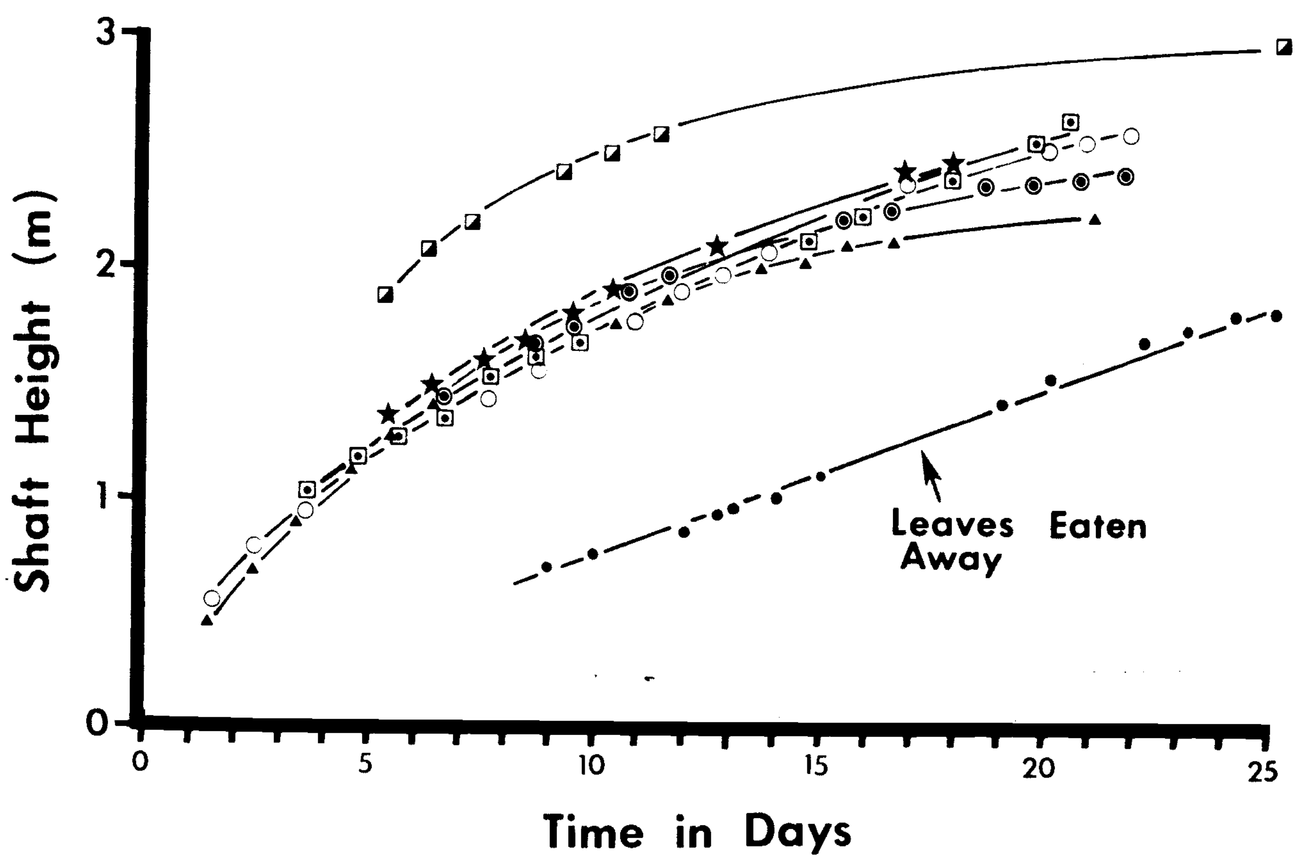

Figure 3. Agave lechuguilla *inflorescence shaft growth with time.*

pollinators from reaching the flowers. Other inflorescences were designated as controls and not bagged. Fruits (capsules) were collected when mature. The number of seeds per capsule was determined in each group per plant and these values were compared by the Kruskal-Wallis test (Sokal and Rohlf, 1969).

Results and Discussion

In most years, Lechuguilla flowers during May and June. However, in years with a very dry preceding rainy season and/or winter, flowering is infrequent and occurs over a protracted period ending as late as October.

Flowering is related to the number of leaves in the rosette. The number of leaves rarely exceeds 60 (Table 1), but on one occasion we found 69 (Table 2). The mean number of leaves of flowering plants is 51 (range 42 to 69). This range included 6% of the individuals counted. Data from another study (Reid et al., 1981), conducted in another year, showed that 5% of the plants at that locality flowered in that year. Assuming that the populations are stable, this suggests that plants are approximately 20 years old when they flower.

The growth rates of seven inflorescence shafts are shown in Figure 3. The maximum growth rate of about 2 dm/day occurs soon after the shaft emerges from the rosette. Growth rates then decline until full shaft height is achieved (mean of 2.6 m) between three and four weeks after estimated shaft initiation. Resources for this growth are drawn from the leaves, basal mass of the rosette, and perhaps the rhizomes and roots. Our experience in removing flowering plants from the field for laboratory study suggests that the roots and rhizomes begin to die as flowering is initiated. Table 2 shows that in a non-flowering individual almost 85% of the plant's total biomass is in the leaves while the rest is in the basal mass. This basal mass weight relative to the leaf biomass in Lechuguilla seems to be considerably less than is seen in some of the large species of the subgenus *Agave* which are utilized as a sugar source (e.g., in the manufacture of tequila). As the shaft develops, the resources for its growth are drawn principally from the leaves. Only when shaft development is well advanced does the basal mass begin to lose substantial amounts of biomass. As flowering nears completion, about 40% of the total plant biomass is invested in the inflorescence, about 50% remains in the leaves, and about 10% is in the basal mass. Occasionally in the field, plants are found which have had their leaves heavily damaged by what appears to be rodent foraging activity (presumably by woodrats of the genus *Neotoma*). One such plant which was flowering is shown in Figure 2. Note that the shaft elongation rate is slow and linear in comparison to the others. This perhaps substantiates the assertion that leaf resources are the major energy source during flowering.

Since floral development is indeterminate, flower maturation begins at the lowermost buds and proceeds upward. Grove (1941) provided much information on floral anatomy. Several features of floral development not disucssed by Grove are shown in Figure 4. Flower dehiscence is concentrated in late afternoon before dusk. As the flower opens, filament elongation is already underway and rapid with a maximum rate of almost 1 mm/hour. Anthers dehisce after about 24 hours, but maximum filament

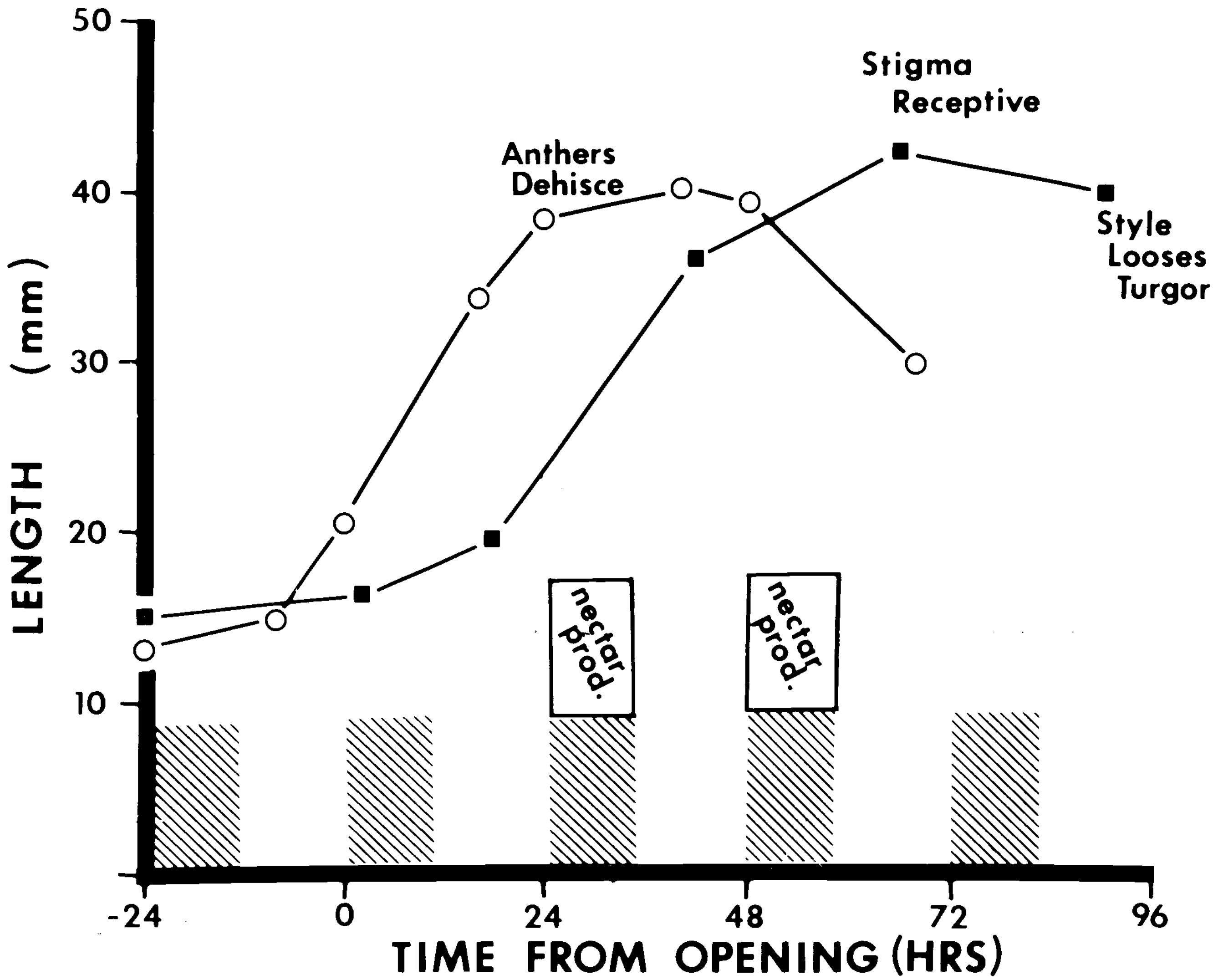

Figure 4. *Floral schedule of* Agave lechuguilla. *Symbols: open circles are the mean of filament length measurements, closed squares are the mean of style length measurements. Time zero represents the mean time of flower dehiscence (4 to 8 p.m. M.D.T.).*

length does not occur until approximately 40 hours after opening. Beyond 48 hours the filaments lose turgor and wilt. The style also shows marked elongation after flower opening. Style elongation begins more slowly, reaches a maximum rate of almost 1 mm/hour also, and reaches its maximum length about 66 hours after flower opening. At maximum length, the dry, papillate surface of the stigma becomes moist and receptive, and pollen germinates.

Examination of serial sections of flowers showed that, as seen in Figure 5A, the grooves between the stigma lobes are continuous with a triangular stylar canal (Figure 5B) mentioned by Gentry (1982). This canal traverses the length of the style and, just above the neck of the ovary, trifurcates (Figure 5C). These three canals enter the locules without obstruction. Thus, the ovary of this species is not fully enclosed. This sort of anatomy is apparently uncommon (K. Esau, pers. com.). Also seen in Figure 5C is a groove in the style base which marks the exit of the nectar duct.

The position of the nectaries is of a type described by Fahn (1979) as ovarial and septal. Septal nectaries occur only in monocots and are the most common nectary type in that group, making up 59% of the total species surveyed by Daumann (1970). The nectar ducts (Figure 5D) lead upward through the neck of the ovary and empty into the floral tube. Nectar is produced during the second and third nights after flower opening (rarely during the fourth night also) beginning shortly before dusk and ending at dawn. Most plants concentrate nectar production during the first half of the night. It is our impression that nectar is not produced on windy nights.

Nectar-sugar composition has been described by Freeman et al. (1983) as being hexose (fructose and glucose) dominated with sucrose being about 10% of the total sugars by mass. Individuals in populations surveyed to date range from no detectable sucrose to a maximum of about 20% sucrose (Freeman, unpubl. data). Nectars of this general composition type have been described as typical of plants pollinated by short-tongued bees, flies, bats, and passerine birds (Baker and Baker, 1983). However, Lechuguilla flowers attract large numbers of animals of many kinds during both the daylight and night hours and the principal pollinator(s) has not been established. Night visitors include large numbers of moths

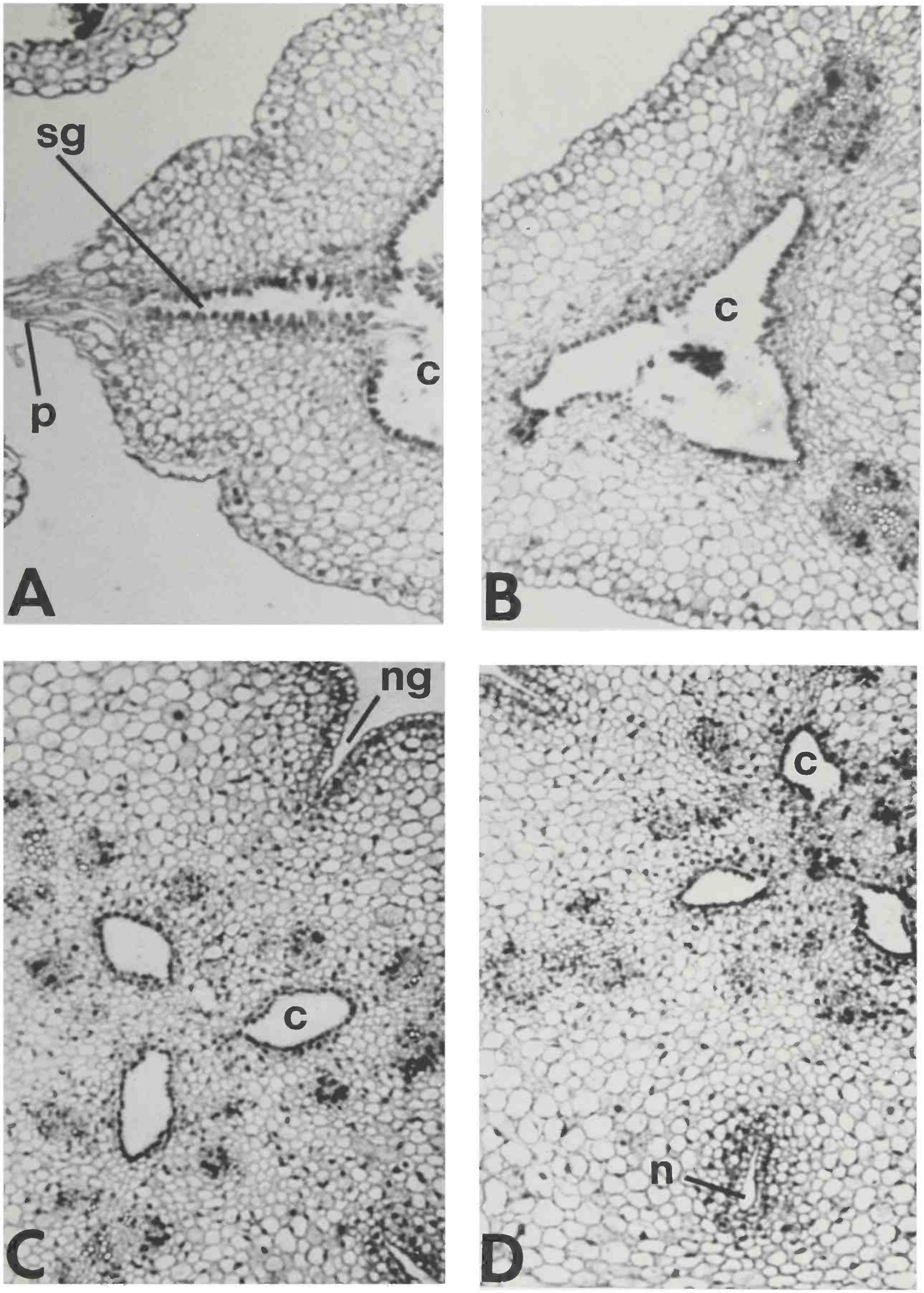

Figure 5. *Cross sections of* Agave lechuguilla *flowers.* **A:** *stigma region, showing one of the three stylar grooves (sg), papillae at the stigmatic surface (p), and the stylar canal (c).* **B:** *cross section of the style showing the triangular canal (c.).* **C:** *the base of the style near the floral tube showing the trifurcation of the stylar canal (c), and the nectar duct groove (ng) where the duct opens against the style.* **D:** *the neck of the ovary showing the trifurcated canal leading to the locules (c) and the nectary (n).*

(D. Howell, pers. comm.). The apparently promiscuous Lechuguilla flowers do not seem unusual within the genus. The flowers represent an exceptional source of both water and energy for animals during the height of the dry season (May-June) when these resources are in short supply. Thus, animals are probably opportunistic, consuming a nectar which may not conform to their taste preference.

Amino acids are also found in Lechuguilla nectar in low concentrations. Both protein and non-protein amino acids were detected. While several amino acids were found in only one or two of the four plants studied, several were found in three or all four of them. These were phosphoserine, phosphoethanolamine, aspartic acid, serine, glumatic acid and glutamine, glycine, alanine, histidine, and threonine. These amino acids have also been found in the nectars of other agaves (Freeman et al., 1983).

Flower predation is an important aspect of the species' biology in the El Paso area. When we brought entire plants to the laboratory for nectar studies, we observed moth larvae climbing the shaft each evening, leaving a characteristic scar on the shaft, and feeding on unopened flowers. Field observations revealed 90-95% aborted flowers on shafts with scars. Specimens were submitted to the U.S. Department of Agriculture for identification. Their report indicates they belong to an unknown genus in the family Noctuidae, subfamily Amphipyrinae (D. M. Weisman, pers. comm.).

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