Desert Plants

Special Issue

Symposium on the Genus Agave

*Held at Desert Botanical Garden, Phoenix,
March 7-9, 1985, in honor of the Centennial
of Arizona State University, Tempe*

Edited and organized by
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ARIZONA STATE UNIVERSITY/1885-1985

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DESERT
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*Cover photograph for this issue: "Adelante Magueyeros!"—
H.S. Gentry in the fog atop Sierra de Parras, Coahuila,
Mexico. Dr. Marshall C. Johnston is behind the horse.
Photograph by Rodney Engard. See page 74 for dedication of
this issue to Dr. Gentry.*

The Bat, the Blossom - and the Biologist

a film by the
British Broadcasting Corporation

featuring
Donna J. Howell
Far Flung Adventures
Terlingua, Texas

Editor's Note

This educational film, featuring bat-pollination of *Agave*,
was screened at the Symposium during special sessions on
March 7 and March 9. Dr. Donna Howell, featured in the
film, kindly appeared to discuss the film and answer questions.

Synopsis

The film opens with a panorama of the Chiricahua
Mountains, Cochise County, Arizona, and explains that this
is the summer "stage" for a remarkable plant/pollinator
relationship between century plants (genus *Agave*) and nectar-
feeding bats. These bats migrate northward from central
Mexico following the sequential blooming of bat-adapted
plant species until they arrive in Arizona. The natural history
of the agaves and of the bats (genus *Leptonycteris*) is presented
using sequential shots of agave growth and death and slow
motion photography of the bats in flight drinking nectar and
transferring pollen.

It is explained that each partner must benefit as an
individual for the relationship to be evolutionarily stable.
Thus an examination of the energetic physiology of the bats
and the reproductive energetics and requirements of the
plants is undertaken. The film shows hand-pollination experi-
ments that demonstrate the need of the plants for outcrossing
and examines strategies of the agave for attracting bat flocks
and for maximizing pollen transfer.

The second emphasis of the film is the decline of bat
populations and plant reproduction. It is set in northern
Mexico where "moonshining" of agave liquor is a popular
industry. The *mescaleros,* as the moonshiners are called, cut
several species of paniculate agaves when they are "sweetest,"
immediately before blooming. The plants are neither managed
as a resource nor replaced. The one *mescalero* interviewed in
depth shows the liquor-making process from harvest through
baking and distillation in his primitive, hidden still. He
explains that he cuts 400 to 500 plants annually and now,
after three generations of family business, he has to go as far
as 70 kilometers to get his plants. He estimates that there are
fifteen other mescaleros in the region doing the same. Thus,
in one region, 7,500 plants may be destroyed each year.

In northern Mexico there are very few appropriate food
plants for the bats and Dr. Howell speculates that this swathe
of foodlessness is responsible for the well-documented decima-
tion of populations of nectar bats, especially over the last 35
years. She explains that agave seed set, as demonstrated by
herbarium specimens, has shown a parallel decline. In areas
of the southwestern United States where populations of
nectar bats have vanished or are severely reduced, agaves are
realizing only 1/300th of their sexual reproductive potential.

Figure 1. *A* Leptonycteris *bat darts in front of Dr. Donna J. Howell as she takes a nectar sample from an* Agave *inflorescence.*

Figure 2. *As* Leptonycteris *visits* Agave *flowers, the animal's head is buried among the anthers and styles and the tongue penetrates the flower tube. Cross-pollination occurs when pollen adhering to the bat's fur is pressed against the stigma of another plant in the local* Agave *population.*

Symposium on the Genus Agave

Edited and organized by

Donald J. Pinkava
Arizona State University

and Howard Scott Gentry
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Introduction to the Symposium

Howard Scott Gentry
Desert Botanical Garden

There is a Spanish saying—*"I speak two languages, I live two lives."* I have enjoyed living in two provinces. There are three other lives I can mention; the first is my pre-*Agave* period, the second, my *Agave* life, and thirdly my post-*Agave* life. It is proving hard to get free of agaves, as I had hoped to do when my *Agave* monograph was published. It seems that the mothering arms of Mayahuel will not release me. I am so old now that my birthdays seem to come several times a year. Last year, Manuel Puebla, a good steroid man (agaves are high in steroid precursors), gave me some pills to help me reach 140 years of age. Briefly, I looked forward to my third life, but ALAS! an inspector at the border took those pills away from me!!

You can imagine the great satisfaction I feel in seeing all you *Agave* students here. You can all carry on as I lay off, each in your own individual way, and you will collectively exceed my work. How fortunate that we can practice the greatest endowment given to man; the pleasure of learning and imparting that learning to fellow men; young and old alike. It can be a hunger that never distresses, it may be periodically allayed, but is a renewable personal resource, like the air we breathe, an ethereal nourishment better than a shot of tequila.

With this symposium I see some surcease from my *Agave* predicament. You are all going to write the next chapter, the chapter I intended to write, but never did—Current Research on Agaves, or some such title. It will be better than I could have done, because little of it existed when I laid down the *Agave* burden. New facts, perspectives, and I hope new ideas will appear with your endeavors. You will not only finish an unwritten chapter, but you are starting a new volume of Agaveology.

I find it very suitable that Mexico was first to put on an *Agave* symposium, because it has been the center of the *Agave* world since long-ago prehistoric times. We are fortunate that Dr. Manuel Robert is with us here, as he led the first *Agave* symposium in Mérida, Yucatán, in November of 1981. I must also mention Dr. Frank Crosswhite of the Boyce Thompson Southwestern Arboretum, who is playing a major role by publishing your contributions to this *Agave* Symposium in the excellent young journal *Desert Plants*. This journal is published at the Arboretum by the University of Arizona, which is also opening its own centennial celebration, even as our Arizona State University is soon closing its own. So, this delicate cooperation between our sister universities gives a fuller insight into the educational matrix than the rivalries engendered by athletic competition.

With the assistance of our fellow Mexican biologists, we reach out beyond our political borders and step forth into the world. My idealism might lead me to hope for a world led by scientists rather than by lawyer-politicians, who sadly are fated to deal with the contentions of men. Let us stick to our own last, the agaves, which, for all we know, may be better organisms than ourselves. I have met them and the only trouble they showed was with myself. *Adelante Magueyeros!!*
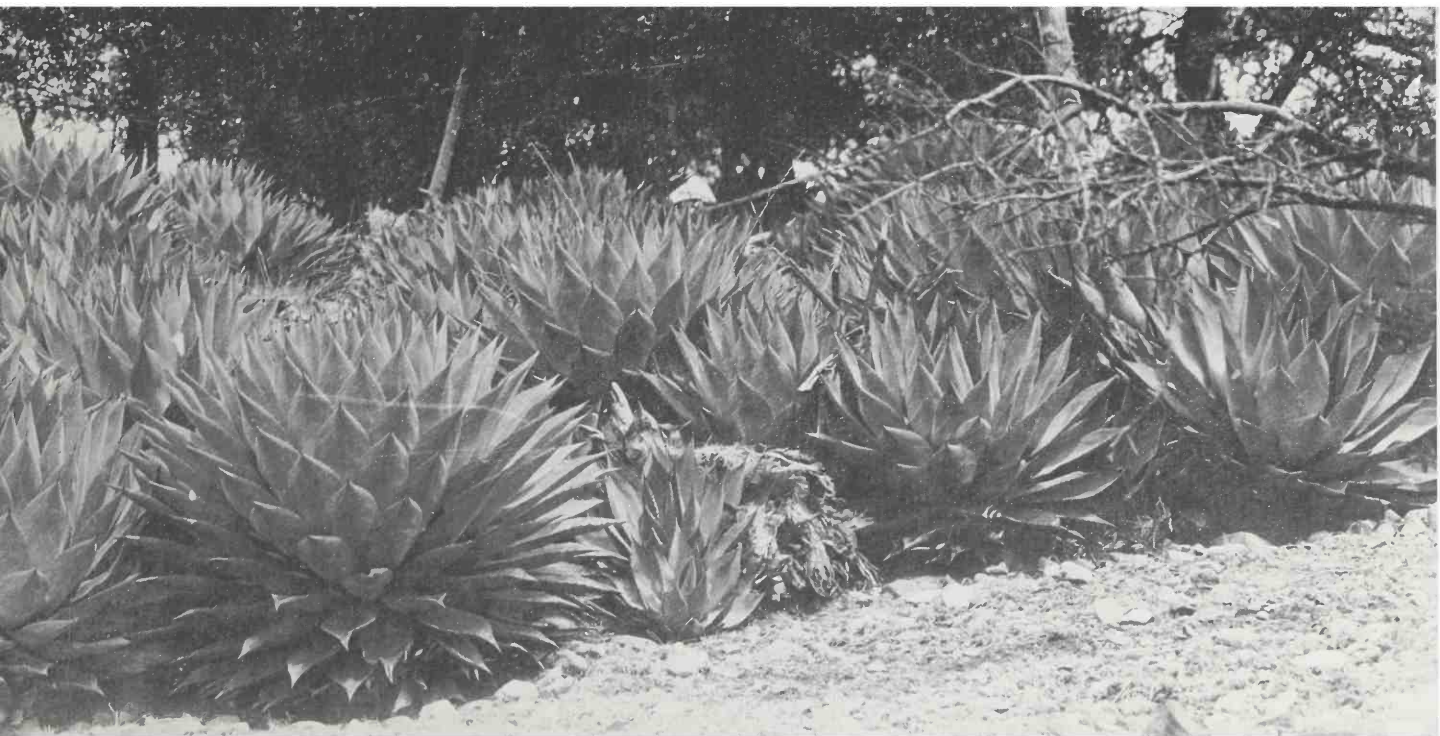
Frontispiece. Agave sebastiana on the island of San Benito del Oeste, Baja California Norte, has a rather low ratio of leaf length to width (see Table 2). In Agave, leaf shape and rosette configuration can be correlated with environmental factors. See text for explanation. Photo by Martha Ames Burgess.

Agave Adaptation to Aridity

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Introduction

It is fortunate that, coinciding with publication of Gentry's taxonomic monograph (1982), there has been a proliferation in research on *Agave* physiology. Integration of these two lines of research offers insight into the forces shaping *Agave* evolution, and promises to provide a valuable foundation for refining systematics of this group. In this paper I have focused on those aspects of morphology and ecology in respect to radiation of the genus into arid habitats. Ultimately it would be desirable to generate a set of "rules" summarizing the adaptive responses of individual organs to specific components of natural selection. To develop ideas concerning the adaptive significance of morphological features, a brief review of *Agave* physiology is necessary.

It has been established that normally *Agave* exhibit Crassulacean acid metabolism (CAM) with nocturnal carbon fixation (Ehrler, 1969; Nobel, 1976). At the seedling stage and after extended periods of moisture surplus, however, diurnal carbon dioxide uptake can be observed (Jordan and Nobel, 1979; Hartsock and Nobel, 1976). By assuming that most biomass production occurs in the CAM mode, several inferences can be drawn concerning relationships between leaf temperature and productivity. With atmospheric exchange occurring mainly at night, optimum nocturnal leaf temperature should reflect a compromise between maximizing carbon fixation and minimizing water vapor loss. At a given stomatal resistance, the rate of water vapor loss from the leaf will be a positive function of leaf temperature because saturation vapor pressure of water increases with heating, thereby increasing the concentration gradient between plant and atmosphere. The necessary relationship between carbon influx and nocturnal leaf temperature is less certain. Metabolic activity and diffusion through mesophyll air space will increase with temperature, whereas carbon dioxide solubility in aqueous solutions of the cell wall decreases at higher temperatures (Nobel 1974). Nobel and Hartsock (1978) found that internal resistance to carbon dioxide diffusion in *Agave deserti* is sensitive to temperature, increasing rapidly above an optimum of 16°C. They attributed this behavior to changes in biochemical activity involved in carbon dioxide fixation rather than to simple diffusion processes within the leaf. If the temperature responses of stomatal and mesophyll resistances are largely determined by biochemical reactions, they should be subject to change by natural selection. Temperature acclimation of carbon uptake has been observed in several *Agave* taxa (Nobel and Smith, 1983) and it seems reasonable that optimal leaf temperature for carbon dioxide fixation should also be flexible over evolutionary time. In contrast, cooler leaf temperatures will invariably minimize transpiration.

Stomatal closure during the day is characteristic of CAM; therefore diurnal leaf temperature will largely be controlled by radiant and convective heat exchange with the environment. It can be logically assumed that, as a result of natural selection, Calvin cycle enzymes should tend to have maximum activity at those diurnal leaf temperatures occurring when leaf water potential is favorable for nocturnal stomatal opening. In *A. deserti*, Nobel and Hartsock (1978) found that nocturnal carbon dioxide fixation was hardly affected by daytime leaf temperatures between 20° to 37°C, but decreased above and below this range.

Abstract

To show features of *Agave* taxa adapting to arid habitats, comparative studies at three taxonomic levels in the genus are presented. There is a brief review of *Agave* physiology and some aspects of recent evolution are discussed. Comparisons among species groups within the genus show several traits differentiating desert species from related taxa. Related taxa in the Deserticolae group are examined over a transect in Baja California, revealing patterns linking leaf shape to climate. In a comparison of leaves of *A. deserti* Engelm. along an elevational gradient, high intrapopulation variation obscures differences between the sites. Results are summarized as hypotheses to be tested.

As in other desert plants with CAM photosynthetic pathways, *Agave deserti* exhibits no stomatal opening once tissue water content drops below a certain threshold (Nobel, 1976). During periods of drought stress there is no carbon gain, but rather a slow loss of carbon and water due to metabolic activity and diffusion through the cuticle. Both processes increase their rate at higher leaf temperatures (Nobel, 1984b). The probability of rosette survival in a prolonged drought is a positive function of the volume of stored water and carbohydrates, and negatively related to leaf temperatures and cuticular conductance.

Survival with extended water deficits also depends upon the ability to maximize growth during favorable periods. Rapid growth is especially important during seedling establishment (Jordan and Nobel, 1979). With an increase in the proportion of storage tissue, there should be an initial increase in productivity per mass of plant tissue due to the greater amount of time internal water content will be favorable for stomatal opening. Above some threshold, higher ratios of storage parenchyma to productive chlorenchyma will result in a drop in productivity because there will be relatively large metabolic allocations to construction and maintenance of nonproductive tissue. Thus the optimum ratio of surficial chlorenchyma to total leaf volume will vary depending on the relative importance of survival during drought versus rapid growth during favorable periods.

Recent evolution

Many difficulties in *Agave* taxonomy arise from the group's tendency towards reticulate phylogeny (Turrill, 1936; Gentry, 1967; Burgess, 1979) resulting from an apparent lack of complete reproductive isolation among recognized taxa. The species groups used in Gentry's (1982) monograph often seem to correspond with Grant's (1971) syngameons of superspecies composed of semispecies capable of some degree of genetic interchange. In several instances closely related taxa are dispersed over large areas, presumably the result of a single phylad radiating into a variety of habitats. These radiation events may have been quite recent because southwestern North America has experienced profound changes in climate over the last 15,000 years.

Consider *Agave deserti* which seems poorly adapted for long-distance dispersal. The species extends from the east slope of the Peninsular Ranges in Southern California to the Waterman/Silverbell Mountains in South-central Arizona (Figure 1). Over most of its range populations are relatively small, disjunct stands on small mountains providing limited habitat where the plants maintain moderate to low densities. To attain their present distribution, populations should have been larger and more contiguous at some past time.

The greatest density of *A. deserti* is on the east slope of the Peninsular Ranges between the Mojave and Vizcaino desert-scrub formations, below chaparral communities, and above the lower desert where microphyllous shrubs dominate. Where winters aren't too cold, *A. deserti* can survive at higher elevations, but, in the denser vegetation typical of these sites, it doesn't do well as a shaded understory plant. Although shading can aid seedling establishment by buffering extreme temperatures (Nobel, 1984a), primary production in *A. deserti* is adversely affected by shade (Woodhouse *et al.*, 1980). Jordan and Nobel (1979) found that seedling establishment is infrequent, occurring only in years with good rains and with an amelioration of summer and fall drought. But if every year were good for general seedling survival, it is likely that *A. deserti* would be eliminated by competition with other species. Therefore an alternation between good and bad years should maintain maximal *A. deserti* populations, with enough good years for regular recruitment and enough bad years to reduce competitors. *Agave deserti* is adapted to exploit rainfall variance. Drought and herbivore predation probably account for most seedling mortality. Because internally stored reserves are depleted faster at higher temperatures, *A. deserti* should have trouble persisting where summers are extremely hot and dry.

During the Pleistocene, pluvial conditions, postulated to have combined cooler summers and a longer duration of the winter rainy season (Van Devender and Spaulding, 1979), should have enabled *A. deserti* to survive at lower elevations, thereby expanding its range considerably. If conditions were too mesic, allowing woodland, chaparral, and grassland to cover lower slopes, *A. deserti* would have decreased in numbers caught between unfavorable heavy soils and grasslands on lower bajadas and too much shade at higher elevations. In dry woodland it can persist on xeric microsites, and it may have been widely scattered on such sites during the more mesic periods of the Pleistocene. Given such responses, we could expect *A. deserti* populations to have been most extensive at the onset of a pluvial period [prior to the spread of woodland and again at the onset of an interglacial] after woodland began to retreat upward and northward and before excessive heat and drought eliminated it from lower slopes. These putative reactions of *A. deserti* were probably typical for a class of arid-adapted plants which require an open vegetation to persist, yet cannot tolerate the climatic extremes which generally prevail during some portion of a glacial-interglacial cycle. Wells and Woodcock (1985) have proposed a similar scenario for *Yucca whipplei* Torr. For such species the climatic fluctuations of the Pleistocene have probably induced relatively brief episodes of expansion and genetic interchange separated by periods during which the species has persisted as smaller disjunct populations in enclaves of favorable habitat. With this flux of populations and the attendant opportunities for genetic exchange, it is likely that existing patterns in the more northerly *Agave* species have only developed recently.
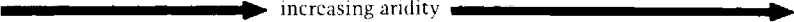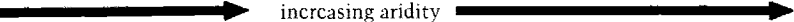
Trends in Desert-Dwelling Agave Phylads

Within a species group geographic trends can be viewed as interrupted clines maintained by local balances between infrequent gene flow and continuous selection (Endler, 1977). In determining those characteristics favored by aridity, a first step is to compare species in more xeric environments with related taxa from more mesic habitats. Table 1 shows those *Agave* species groups recognized by Gentry (1982) which enter the Sonoran or Chihuahuan Deserts. Included are species occupying the most arid habitats for the genus in the Colorado River watershed and the Vizcaino region of Baja California. Within each group I have selected taxa which seem to be related to the more arid-adapted species and merit consideration as a basis for comparative studies.

Crude phyletic comparisons of leaf dimensions and vegetative reproduction are presented in Table 2. Ranking by

Table 1. *Agave* phylads with members in the Sonoran and Chihuahuan Deserts. Within each group species are approximately arranged by the relative aridity of their habitats, with the most xeric-adapted taxa on the right. Data and taxonomy from Gentry (1972, 1978, 1982). Authors of binomials and subspecies are omitted so as not to interfere with spacing.

SUBGENUS LITTAEA

→ increasing aridity →

Striatae
A. dasylirioides — A. striata ssp. falcata — A. striata ssp. striata, Chihuahuan desert

Amolae
A. pedunculifera — A. vilmoriniana — A. chrysoglossa, Coastal Sonora

Filiferae
A. multifilifera, A. colimana — A. ornithobroma — A. schidigera — A. felgeri, Coastal Sonora

Parviflorae
A. polianthiflora — A. parviflora — A. toumeyana — A. schottii, Central Arizona to Northern Sonora

Marginatae
A. angustiarum, A. horrida — A. funkiana, A. kerchovei — A. lophantha, A. obscura, A. potrerana — A. lechuguilla, Chihuahuan Desert; A. victoriae-reginae, Chihuahuan Desert; A. pelona, Northwestern Sonora

Urceolatae
A. utahensis, Mohave Desert

SUBGENUS EUAGAVE

→ increasing aridity →

Rigidae
A. rhodacantha — A. angustifolia — A. aktites, Coastal Sonora; A. datylio, Baja California Sur

Marmoratae
A. zebra, Northwestern Sonora

Americanae
A. americana — A. scabra, Chihuahuan Desert

Ditepalae
A. wocomahi — A. shrevei A. durangensis — A. flexispina A. palmeri A. colorata, Coastal Sonora; A. chrysantha A. fortiflora, Northwestern Sonora

Parryanae
A. parryi — A. parrasana — A. neomexicana A. gracilipes, West Texas; A. havardiana, Northern Chihuahuan Desert

Campaniflorae
A. promontorii — A. aurea A. capensis, Baja California Sur

Deserticolae
A. moranii, A. gigantensis — A. mckelveyana, A. sobria, A. vizcainoensis — A. subsimplex — A. deserti, Sonoran Desert; A. cerulata, Sonoran Desert; A. margaritae, Baja California Sur

Umbelliflorae
A. shawii ssp. shawii — A. sebastiana — A. shawii ssp. goldmaniana, Baja California

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relative habitat aridity in this table is approximate because both temperature and precipitation regimes must be integrated to provide a scale for comparing relative moisture deficits in the various habitats. The most obvious trend is a general decrease in plant stature in arid environments, as evidenced by decreases in both leaf length and leaf area within each group. This corresponds well with the reduction in total plant biomass characteristic of gradients with decreasing rainfall (Walter, 1979). Using a sophisticated energy budget model for *A. deserti* rosettes, Woodhouse *et al.* (1983) have shown that water loss increases with rosette size, indicating a selective advantage for smaller rosettes under arid conditions.

In some groups a relative narrowing of the leaves is associated with greater aridity; in others the length/width ratios are relatively constant or show no consistent trend. Relative leaf width has important consequences in the thermal relationship between a leaf and its environment (Gates, 1980),

and the inconsistent length/width patterns among groups probably reflects the different thermal regimes under which they grow.

In some groups there is a tendency towards more vegetative reproduction in more xeric environments. Most of the desert-adapted taxa sucker freely or branch. Of those which don't, three—*A. chrysoglossa* I.M. Johnst., *A. ocahui* Gentry, and *A. pelona* Gentry—occur primarily in crevices of cliffs and rock outcrops, where limited substrate cancels the advantages of basal cloning. *Agave victoriae-reginae* T. Moore which inhabits limestone cliffs also seldom clones, unlike conspecific populations in other habitats. If *Agave* plants are to persist at a site, seed production must be inversely proportional to the probability of seedling establishment (Williams, 1975) which is lower in more arid habitats. In *Agave* the cost of flowering limits post-flowering survival of the rosette (Schaffer and Schaffer, 1979; Nobel, 1977). Extending the plant's life span

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Table 2. Leaf characteristics and vegetative reproduction of putative *Agave* phylads, approximately ranked by relative habitat aridity. Leaf area estimated as half the product of length and width. Length/width ratio is the mean of the ratios given by minimum and maximum leaf dimensions cited. Data and taxonomy from Gentry (1982).

Species	Length (cm)	Area (cm²)	Ratio l/w	Vegetative Reproduction	Species	Length (cm)	Area (cm²)	Ratio l/w	Vegetative Reproduction
Striatae					**Deserticolae**				
A. dasylirioides Jacobi & Bouche	40-60	40-90	20	none	A. gigantensis Gentry	40-75	220-600	4	none
A. striata Zucc. ssp. falcata (Engelm.) Gentry	30-60	12-54	35	axillary branching	A. moranii Gentry	70-120	280-720	9	none
A. striata ssp. striata	25-60	6-30	55	axillary branching	A. mckelveyana Gentry	20-35	30-88	7	var. suckering
Marginatae					A. vizcainoensis Gentry	25-40	75-200	4	var. suckering
A. angustiarum Trel.	50-80	150-280	10	none	A. avellanidens Trel.	40-70	180-490	5	none
A. horrida Lem. ex Jacobi	18-35	62-132	5	none	A. sobria Brandegee ssp. sobria	45-80	112-400	8½	suckering
A. kerchovei Lem.	40-100	100-600	8	var. suckering	A. sobria ssp. frailensis Gentry	20-35	60-140	4	weakly suckering
A. funkiana Koch & Bouche	60-80	105-220	16	suckering freely	A. sobria ssp. roseana (Trel.) Gentry	35-50	122-250	5	var. suckering
A. obscura Schiede	25-40	62-160	5	var. suckering	A. margaritae Brandegee	12-25	42-125	2	suckering
A. lophantha Schiede	30-70	45-175	12	var. suckering	A. subsimplex Trel.	12-35	18-88	5½	var. suckering
A. potrerana Trel.	40-80	120-280	9	none	A. deserti Engelm.	25-70	75-200	4	suckering
A. difformis Berger	50-80	100-240	13	suckering freely	A. cerulata Trel. ssp. nelsonii (Trel.) Gentry	20-35	60-140	4	suckering
A. victoriae-reginae T. Moore	15-20	30-60	4	var. suckering	A. cerulata ssp. subcerulata Gentry	15-30	18-105	5	suckering
A. lechuguilla Torr.	25-50	31-100	11	suckering freely	A. cerulata ssp. cerulata	25-50	50-175	7	suckering
A. pelona Gentry	35-50	52-125	11	none	**Amolae**				
Campaniflorae					A. pedunculifera Trel.	50-90	375-675	7	none
A. promontorii Trel.	100-150	550-1275	9	none	A. vilmoriniana Berger	90-180	315-900	16	bulbils frequent
A. aurea Brandegee	63-110	220-660	9	none	A. ocahui Gentry	25-50	18-63	18	none
A. capensis Gentry	30-60	60-210	8	axillary branching	A. chrysoglossa I.M. Johnst.	70-120	140-420	17	none
Umbelliflorae					**Rigidae**				
A. shawii Engelm. ssp. shawii	20-50	80-500	2-2½	branching stems	A. rhodacantha Trel.	140-250	560-1875	17	var. suckering
A. sebastiana Greene	25-45	100-540	2	branching stems	A. angustifolia Haw.	60-120	105-600	14	suckering, bulbils
A. shawii ssp. goldmaniana (Trel.) Gentry	40-70	200-625	4	branching stems	A. aktites Gentry	40-60	40-120	17	suckering
					A. datylio Simon ex Weber	30-80	45-160	16	suckering

and thereby increasing seed production through multiple flowering episodes can only be accomplished through production of more rosettes by means of rhizomes, axillary branching, or bulbils on the inflorescence. If conditions suitable for seedling establishment are rare, selection favors *Agave* plants which clone extensively and thereby expand the duration and amount of seed production from a given genotype (W. M. Schaffer, unpublished data). Bulbils represent a compromise between basal cloning and seeds, because they combine limited dispersal ability with a higher establishment probability. The resources available to a basal clone connected to the parent rosette are greater than those packaged with a bulbil and it seems unlikely that bulbils would be a reliable mode

of cloning in the more arid habitats where favorable sites for establishment are limited.

Banding of leaves with alternating lighter and darker segments is noticeable in some Sonoran Desert species, especially *A. zebra* Gentry, *A. colorata* Gentry, *A. deserti* Engelm. and *A. cerulata* Trelease. This is caused by variation in cuticle thickness, apparently arising from irregular, pulsed growth. Thicker cuticles could serve both to reflect excessive heat away from the interior of the leaf and to reduce the diffusion of water from the leaf; both desirable properties in warm, arid climates. The importance of leaf reflectance in regulation of both temperature and water loss in *A. deserti* has been demonstrated by Woodhouse *et al.*
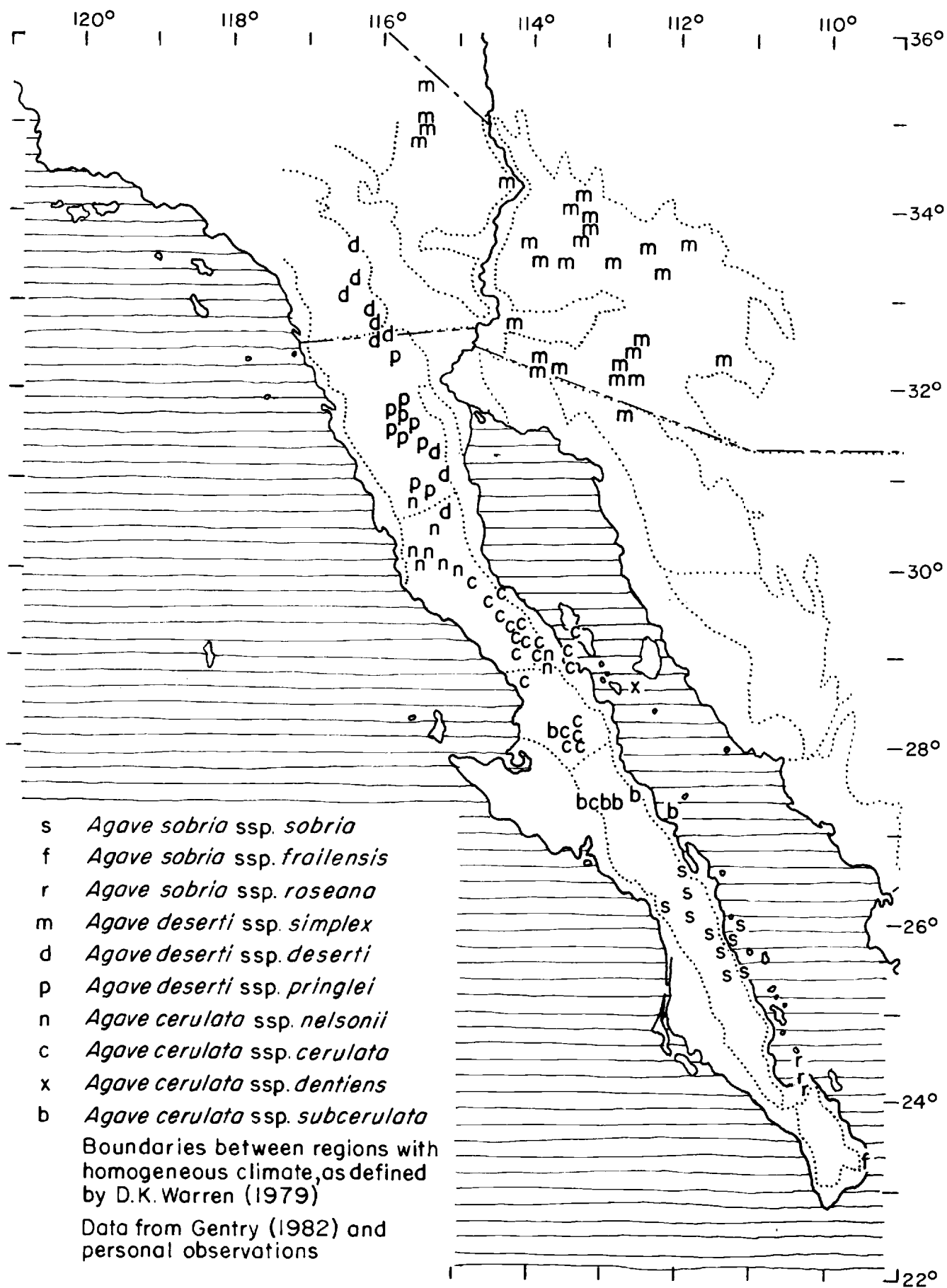
Figure 1. *Distributions of selected taxa in Agave group Deserticolae.*

Table 3. Mean seasonal temperature (°C) and rainfall (mm) for stations nearest populations of *Agave sobria* ssp. *roseana* from La Paz (shown above) and *A. sobria* ssp. *frailensis* from Boca del Salado (below). Data from Hastings and Humphrey (1969).

	Winter	Spring	Summer	Fall
Temperature	18.5	22.3	28.5	26.1
	19.0	22.4	28.1	26.5
Precipitation	38	2	58	83
	55	0	65	149

(1983) in their simulations of rosette energy budgets. In their survey of Sonoran Desert *Agave* cuticles, Gentry and Sauck (1978) found no consistent relationship between cuticle thickness and rainfall. Their data do show that some desert species, including those with leaf banding, have thicker cuticles, but this trend is not universal in the genus.

From this overview it is apparent that there are few gross features uniformly distinguishing the more arid-adapted *Agave* from related taxa. Smaller rosette size is the most widespread xerophytic characteristic. Other differences, such as narrower leaves and more cloning, are not equally developed in all phylads. This is not surprising, because desert-dwelling species exist in varied annual cycles of rainfall and temperature; their only common selection agent is periodic exposure to intense drought.

Clines in Baja California

Characteristics adapting *Agave* to specific climates can be revealed by examining variation within a group which has speciated under differing regimes of temperature and rainfall. The Group Deserticolae fulfills this requirement, because it contains taxa which occupy many different regions in the Sonoran Desert (Figure 1). A transect down the Baja California peninsula shows trends in leaf shape apparently reflecting the contrasting selection imposed by its varied climates. Figures 2 and 3 show rosettes and cross-sections of representative leaves respectively from *A. cerulate* and *A. sobria* Brandegee along this transect.

Starting in the north, *A. cerulata* ssp. *nelsonii* (Trel.) Gentry occupies an area just inland from the Pacific coastal vegetation, replacing coastal populations of *A. shawii* Engelm. ssp. *shawii*. Subspecies *nelsonii* also occurs farther inland at higher elevations. It is characterized by broad, relatively thin leaves forming compact-looking rosettes. The leaf transection from east of El Rosario is typical.

Farther south and inland the vegetation is more open and lower, evidence of greater drought, and *A. cerulata* ssp. *cerulata* is common over large areas. The leaves from a plant near San Agustin, near the northern limit of this taxon, are much longer than those from a plant from Puerto Chapala near the middle of its range. Longer leaves are also present in the southern populations around El Arco. Despite this variation in length all leaf samples from ssp. *cerulata* show lower surface/volume ratios than in ssp. *nelsonii*, but leaf samples from these two subspecies share a tendency to taper from base to tip.

Between El Arco and San Ignacio, just south of the 28th parallel, there is a major floristic change marking generally warmer temperatures and a shift from predominantly winter to biseasonal rainfall. Here *A. cerulata* ssp. *cerulata* is replaced by *A. cerulata* ssp. *subcerulata*. In contrast to the northern taxa, leaves of this subspecies are relatively broader in the middle and taper more abruptly at the tip. In the leaf sample from San Ignacio there is a noticeable difference in surface/volume ratios between the basal and distal parts of the leaf. The lowest transection was taken from near the leaf base, and the next section up is halfway between the base and the middle of the leaf, which is shown above it. This pattern is more fully developed in *A. sobria* farther south. The Pichilingue sample from just north of La Paz represents *A. sobria* ssp. *roseana* (Trel.) Gentry and the disjunct Los Frailes population is *A. sobria* ssp. *frailensis* Gentry, the southernmost taxon in the group Deserticolae.

Mean seasonal temperature and rainfall were estimated for *A. cerulata* sites (Figure 4) using equations developed by Warren (1979) from weather station data. After statistically delimiting regions of similar climate, regression equations for each region were derived using latitude, longitude, and elevation as independent variables and mean seasonal temperature or precipitation as the dependent variable. For most weather stations the estimated values were reasonably close to observed values, but the predictive utility of this technique is limited by the amount of climatic data available. Local microhabitat variation caused by topographic effects cannot be distinguished by these equations; they are most suitable for exposing general trends.

None of these subspecies of *Agave cerulata* is regularly exposed to subfreezing temperatures, and the necrotic leaf tips characterizing freeze-damaged plants (Nobel and Smith, 1983) were not observed. Even so, there should be strong selection in *A. cerulata* ssp. *nelsonii* for functioning efficiently under cool conditions. Sites occupied by this taxon are consistently among the coolest experienced by the species during all seasons and winter is the time when soil moisture is most likely to be available. Although most *A. cerulata* sites have their peak rainfall in winter and fall, they are generally warmer and often drier than *A. cerulata* ssp. *nelsonii* sites. The higher temperatures of *A. cerulata* ssp. *subcerulata* sites are apparent in Figure 4 as is their greater summer rainfall. Mean seasonal climate values for weather stations near *A. sobria* ssp. *roseana* and *A. sobria* ssp. *frailensis* are given in Table 3. These taxa grow at higher temperatures than *A. cerulata*, and their peak rainfall comes during the warm season. Over the transect, from *A cerulata* ssp. *nelsonii* in the north to *A. sobria* ssp. *frailensis* in the south, the gradient from cooler to warmer temperatures also shows a shift from cool-season to warm-season rainfall (Hastings and Turner, 1965).

I have not collected enough samples for a precise relationship between leaf shape and climate to be established, but general patterns are evident. In Baja California *Agave* leaves tend to be relatively broader and thinner in wetter habitats, but with lower surface/volume ratios on drier sites. This relationship has been predicted by the energy budget models of Woodhouse *et al.* (1983). Leaves from sites with predominantly cool-season rain are usually broadest at the base and thin gradually towards the tip, whereas leaves from warm-season rainfall areas tend to be as wide or wider at the middle as at the base, and often have a narrow, relatively thick, petiole-like portion between the
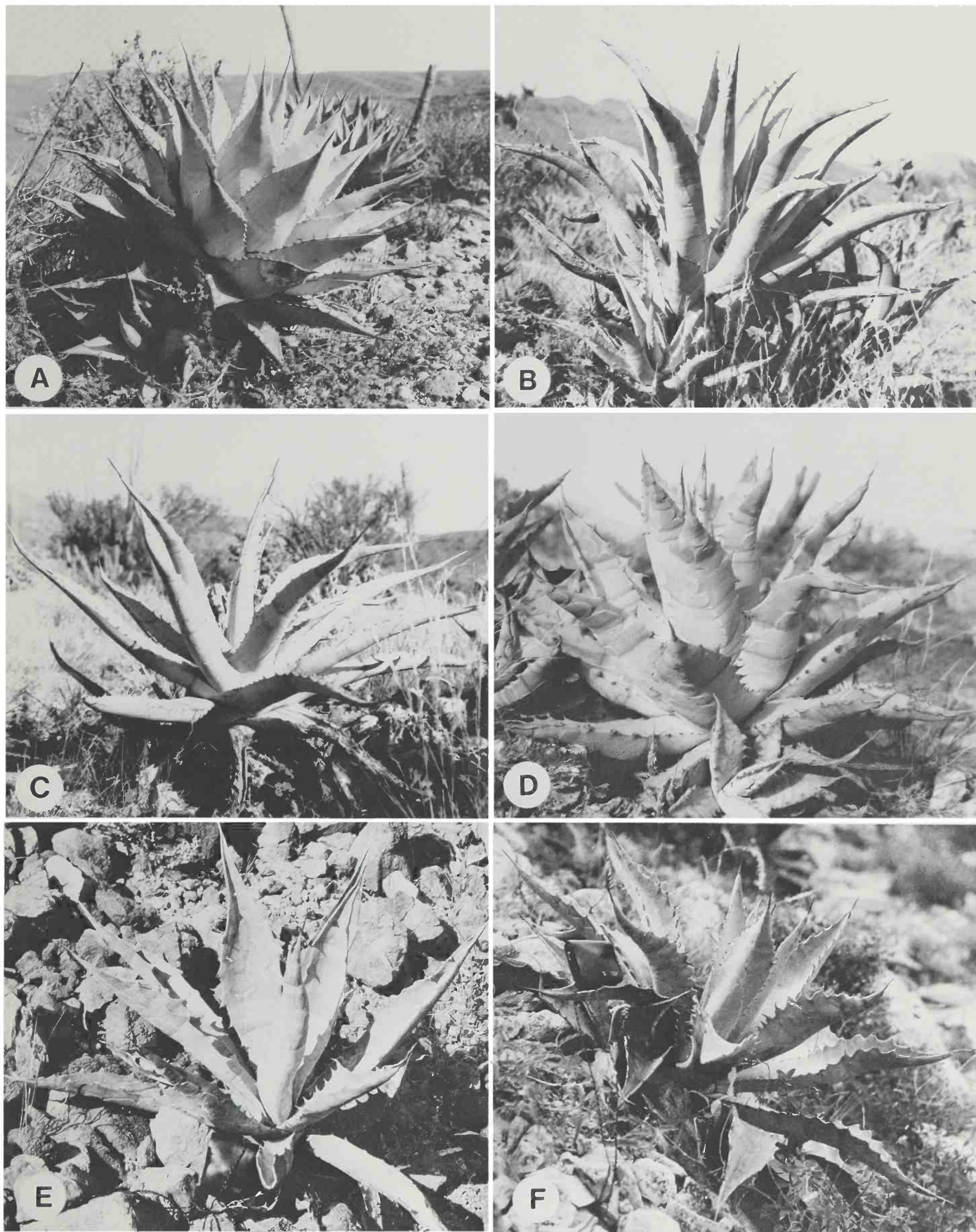
Figure 2. *Rosettes of* Agave *along a transect in Baja California.* **a:** A. cerulata *ssp.* nelsonii, *east of El Rosario, BCN;* **b, c:** A. cerulata *ssp.* cerulata, *north of El Arco, BCN;* **d:** A. cerulata *ssp.* subcerulata, *near San Ignacio, BCS;* **e:** A. sobria *ssp.* roseana, *north of La Paz, BCS (photo by R.M. Turner);* **f:** A. sobria *ssp.* frailensis, *near Los Frailes, BCS (Photo by R.M. Turner).*
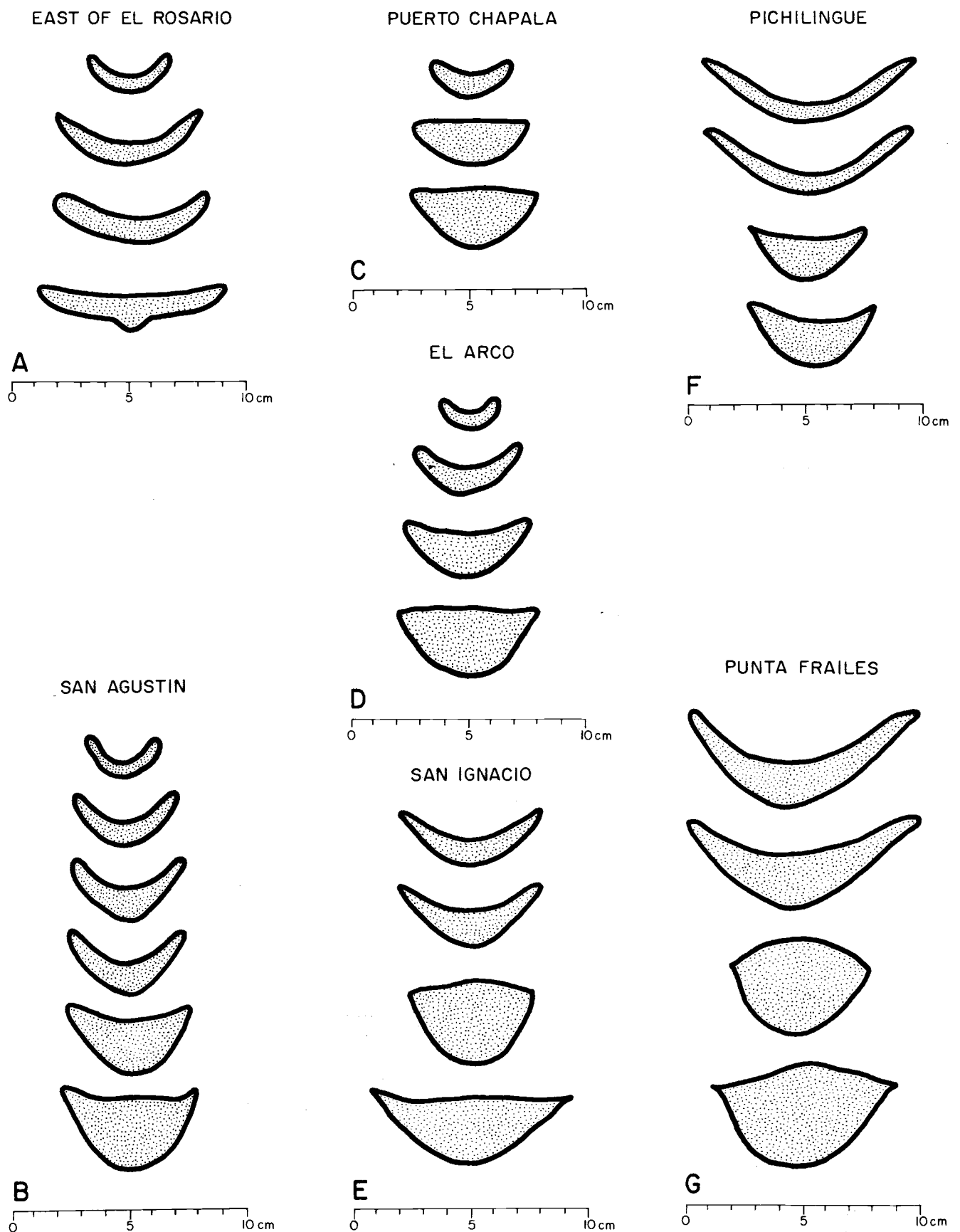
Figure 3. *Transections of* Agave *leaves from Baja California. Within each series the sequence from bottom to top represents successive cross-sections from the proximal to the distal end of the same leaf. Locations are given above each sequence.* **a:** A. cerulata *ssp.* nelsonii; **b, c, d:** A. cerulata *ssp.* cerulata; **e:** A. cerulata *ssp.* subcerulata; **f:** A. sobria *ssp.* roseana; **g:** A. sobria *ssp.* frailensis.
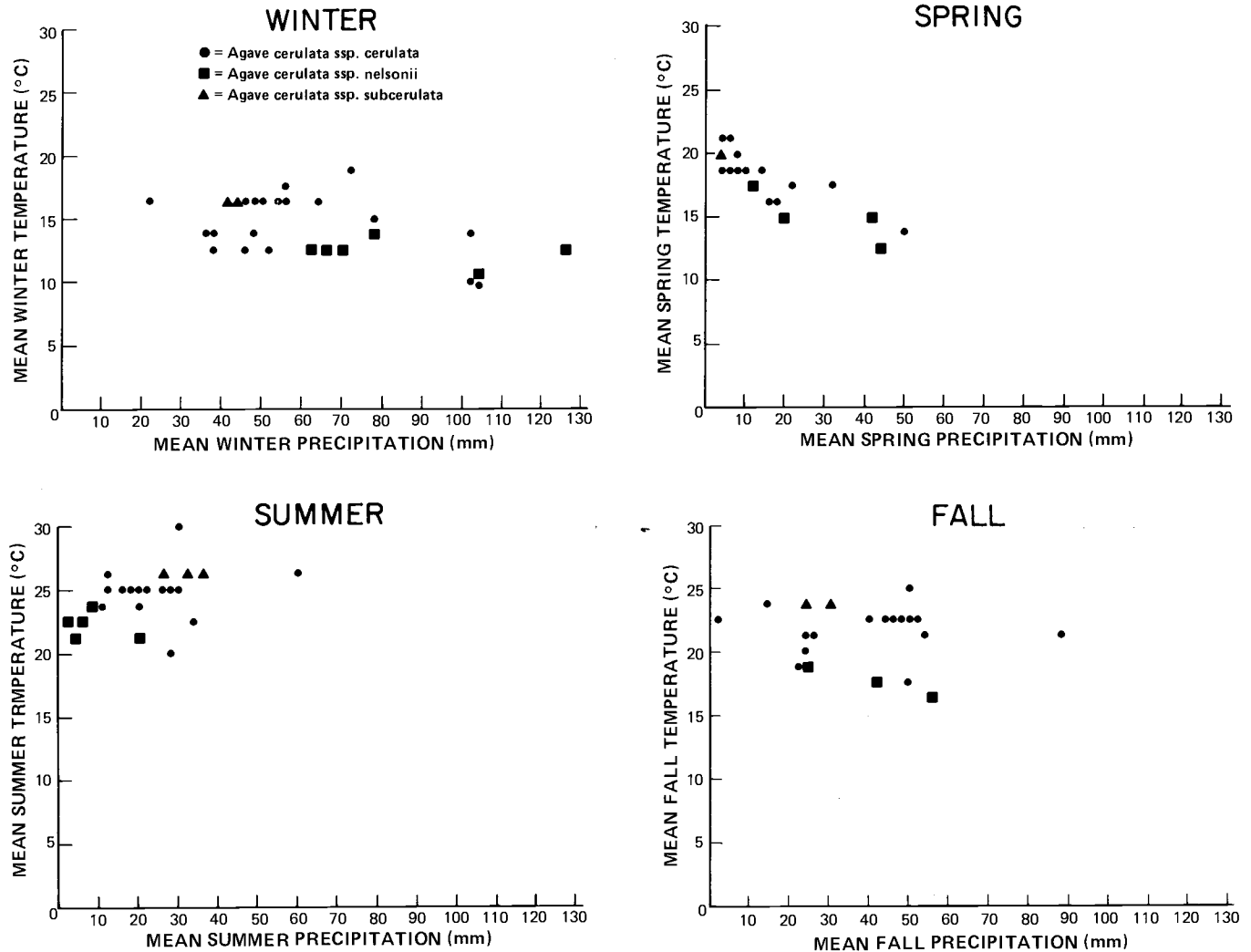
Figure 4. *Mean seasonal temperature and precipitation relationships for* Agave cerulata *sites. Symbols: circles* = A. cerulata *ssp.* cerulata; squares = A. cerulata *ssp.* nelsonii; *triangles* = A. cerulata *ssp.* subcerulata.

base and the flattened distal part. Taxa of the summer-wet regime seem to concentrate storage in the proximal part of the leaf and photosynthetic activity nearer the distal end. This shape produces rosettes which have a more open configuration and greater radiant exchange with their environment than do the more compact rosettes of *A. cerulata* ssp. *nelsonii*. These differences should be adaptive, assuming the thermal relationships between carbon fixation and transpiration n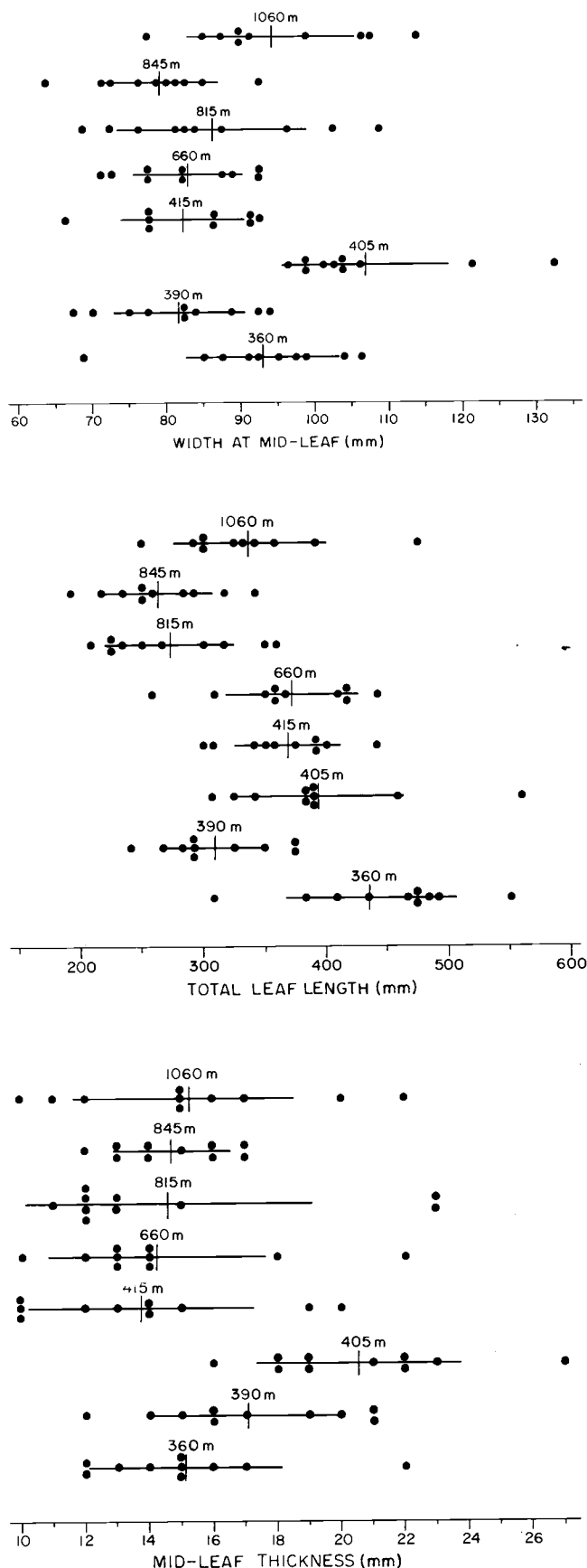oted above. In *A. cerulata* ssp. *nelsonii* nocturnal transpiration is unlikely to be high during wet winter periods because the water vapor concentration gradient from leaf to air is probably relatively low, but cool leaf temperatures may limit enzyme activity responsible for carbon uptake. If this is true, slowing the rate of rosette cooling during winter nights through buffering radiant and convective exchange would increase growth rates. In contrast *A. sobria* is probably performing most of its carbon fixation during the warm rainy season when metabolic activity is unlikely to be temperature limited.

Agave deserti in an Elevational Gradient

On a more local scale leaf characteristics of *Agave deserti* were measured from eight sites on the east slope of the Peninsular Ranges in San Diego County, California. In this area *A. deserti* occurs at elevations between 350 and 1100 m. At its upper limits it grows on the margin of chaparral with *Adenostoma fasciculatum* Hook. & Arnott and *Juniperus californica* Carr. The lower elevational limits are usually reached in washes, where nocturnal cold-air drainage off the mountains produces cooler microhabitats. Gentry (1982) shows evidence of considerable intrapopulation variation in *A. deserti* leaves, which seems understandable given the high microhabitat diversity on those mountain slopes. To control for differences in solar radiation, plants were sampled from the most level sites available. Throughout the area rain occurs mostly in winter, and there is an elevational increase in mean precipitation at all seasons. Not only is moisture input greater at higher sites, but its depletion from the soil is less rapid due to cooler temperatures.

WIDTH AT MID-LEAF (mm)

1060 m
845 m
815 m
660 m
415 m
405 m
390 m
360 m

60 70 80 90 100 110 120 130

TOTAL LEAF LENGTH (mm)

1060 m
845 m
815 m
660 m
415 m
405 m
390 m
360 m

200 300 400 500 600

MID-LEAF THICKNESS (mm)

1060 m
845 m
815 m
660 m
415 m
405 m
390 m
360 m

10 12 14 16 18 20 22 24 26

Figure 5. *Leaf dimensions of* A. deserti *along an elevational gradient in San Diego County, California. The vertical line is at the mean value for each site, solid lines encompass one standard deviation on either side of the mean, and outlying values are represented by dots.*

Measurements made were total leaf length, mid-leaf width measured along the adaxial curve, and mid-leaf thickness at the center of the leaf. The data are plotted in Figure 5. Nested analysis of variance for all three measurements showed that variation among leaves within a rosette is much less than variation among plants within a site, and variation within a site is much greater than variation among sites. Only leaf length shows statistically significant differences among sites. Regression analysis indicates that shorter leaves are more common at higher elevations. This confirms my impressions in the field that the higher sites had more plants with small, compact rosettes. Both leaf length and mid-leaf thickness are significantly correlated with mid-leaf width but not with each other, showing that these dimensions do not vary uniformly with leaf size. The weak trend in leaf length may represent an evolutionary response to low temperatures similar to that observed in *A. cerulata,* but it is obscured by the high variability of leaves within sites. Whether this is the result of greater gene flow or less uniform selection pressures is uncertain.

Conclusions

Comparative studies at different taxonomic levels indicate that certain features have adaptive significance for *Agave* in arid climates. The relationships discussed above need to be tested more thoroughly before they can be uncritically accepted, but some hypotheses about the characteristics of desert-dwelling *Agave* can be proposed: 1) as aridity increases rosette size decreases; 2) leaf surface/volume ratio decreases as the probable length of dry periods increases; 3) the temperature regime in which most carbon is fixed (i.e. the temperature during the rainy season) has a major influence on leaf shape and rosette configuration; and 4) if productivity is limited by low temperature, natural selection favors shorter leaves and more compact rosettes because they have less radiant and convective exchange with their environment.

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Figure 6. Agave deserti *from eastern San Diego County, showing variation in rosette configuration.* **6a, above:** *Cigarette Hills, elev. 840 m;* **6b, below:** *Near Vallecito, elev. 415 m.*

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Agave and the Pre-Cortés Religion

Huitzilopochtli himself and his corps of hummingbirds representing transformed warriors. Drinking by those not entitled (particularly rebellious youths), could and did result in the death penalty, particularly if the infraction was in public. There was one major exception: a person who had passed the age of 70, male or female, could drink pulque at any time in public or private. Such a person had earned the right to suck the fiery warmth of the Chalchíhuatl of the Jade Heart (of the Here and the Now and the Up and the Down and the Center) together with Huitzilopochtli!

After the coming of Cortés, Spanish-speaking people made peace with Mayahuel and taught the citizenry how the Chalchíhuatl nectar of *Agave* could be improved in octane to make MEZCAL and TEQUILA, subjects of articles in this issue of *Desert Plants.* These distilled products did not require the heart-rendering activity of old but nevertheless warmed the human spirit as in past revelries.

In reference to the *Agave* sandals given Huitzilopochtli by his poor mother, interestingly the eventual fall of the Aztec empire to Cortés did indeed radiate out from Tenochtitlán in a pattern similar to that when the empire had been formed. As this occurred, Nahua-speaking people did indeed become reduced to a down-to-earth existence and to wearing poor raiment of Maguey. To understand the surgings and ebbings of power in pre-Cortés Mexico, we have to realize that the nobility depended on religion to stay in power. There was an intentional confusing of the gods with people who merely bore the names of the gods. For example, several rulers actually bore the god's name Quetzalcóatl. People coming from Aztlán probably did indeed have a leader named Huitzilopochtli. Indeed, even the father of MOTECZUMA I was named HUITZILIHUITL. As shown by bearers of the name Quetzalcóatl, leaders were seen as incarnations of their deity namesakes. It is easy to see how accomplishments and innovations of the leader could be transferred in legend to the deity. But the reverse was true as well. Woe to the Quetzalcóatl in power at the time Venus would be eaten by the sun! Woe to followers of Tezcatlipoca or Huitzilopochtli when the astrology of Quetzalcóatl would again be in favor! Evidence now suggests that Malinche, the female companion and interpreter of Cortés, was thoroughly familiar with Aztec religion and helped Cortés play the role of Quetzalcóatl, probably even advising him on the date to land! Thus, Cortés became a player in a pre-existing political game. Throughout pre-Cortés Mexico, war, politics and religion did indeed follow astrology and the legends of the gods—because people made them do so!—F. S. Crosswhite

Water Relations and Carbon Dioxide Uptake of Agave deserti — Special Adaptations to Desert Climates

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Abstract

Agave deserti Engelm., a common agave of the Sonoran Desert, possesses Crassulacean acid metabolism. Thus, the main period for stomatal opening and net CO_2 uptake is at night, which leads to a high water-use efficiency. Seedling establishment occurs only when enough water-storage capacity can be generated following germination so that the young seedling can withstand the first drought. *Agave deserti* is only moderately tolerant of low tissue temperatures but extremely tolerant of high tissue temperatures, an important desert adaptation. Its rosette growth habit leads to a relatively uniform distribution of photosynthetically active radiation over the leaves, which contributes to its high productivity for a desert plant.

Introduction

Agave deserti Engelm. has become the most studied of all agaves from the ecophysiological point of view. As for other agaves, it exhibits Crassulacean acid metabolism, or CAM, which involves nocturnal stomatal opening and primarily nocturnal CO_2 uptake, a syndrome first clearly recognized in the Crassulaceae. The earliest reports that agaves open their stomates at night were published by Neales, Patterson, and Hartney (1968) and Ehler (1969) working on *Agave americana.* The CO_2 taken up at night is incorporated into 4-carbon organic acids, primarily malic acid, leading to a progressive acidification of the chlorenchyma during the night. CAM allows more CO_2 uptake per unit of water lost, as will be indicated shortly, and helps account for the substantial productivity of *A. deserti* and other agaves under arid conditions.

The studies reported here were conducted primarily in the northwestern Sonoran Desert at a site appropriately named "Agave Hill," which is in the University of California Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California (site at 33°38'N, 116°24'W, 850 m elevation). *Agave deserti* (Figure 1) is the dominant plant at Agave Hill, with 0.99 plant per m², which represents over 50% of the above-ground biomass and 29% of the ground cover (Nobel, 1976). Actually, *A. deserti* is fairly common in washes and rocky slopes below about 1700 m in southern California, western Arizona, northern Sonora, and northern Baja California (Shreve and Wiggins, 1964; Gentry, 1982). It is monocarpic, as are most agaves, with a basal rosette of up to about 70 leaves and an inflorescence about 4 m tall. The succulent leaves on a mature plant average about 35 cm in length, 500 g in wet weight when fully hydrated, and 80 g in dry weight.

Gas Exchange and CAM

As already indicated, *A deserti* exhibits CAM, a physiological pathway for which net CO_2 uptake occurs at night when there is no light and hence no photosynthesis. During the afternoon the water vapor conductance of the leaves is very low because the stomates are closed (Figure 2A). At dusk, stomatal opening begins and it is immediately accompanied by a net CO_2 uptake (Figure 2B). CO_2 uptake decreases through the night, in part due to partial stomatal closure. At dawn, the stomates reopen slightly and net CO_2 uptake increases for a brief period (Figure 2), which presumably reflects CO_2 metabolism by the conventional C_3 pathway (Nobel, 1976).

One might reasonably question the possible benefits of nocturnal CO_2 uptake. Because the CO_2 taken up at night must be incorporated into organic acids which are not further processed until light is available, the benefits are not metabolic. Indeed, chlorenchymatous cells of CAM plants must have large central vacuoles to store all the organic acids that accumulate during the night. To understand the benefits, one must turn to the water economy resulting from stomatal opening at night when air and tissue temperatures are lower than during the daytime. Next the consequences for water use will be considered quantitatively.

Transpiration (J_{wv}) is directly proportional to the leaf-to-air water vapor concentration drop (Δc_{wv}). It is also proportional to the water vapor conductance (g_{wv}), which is primarily determined by the degree of stomatal opening:

$$J_{wv} = g_{wv}\, \Delta c_{wv} \tag{1}$$
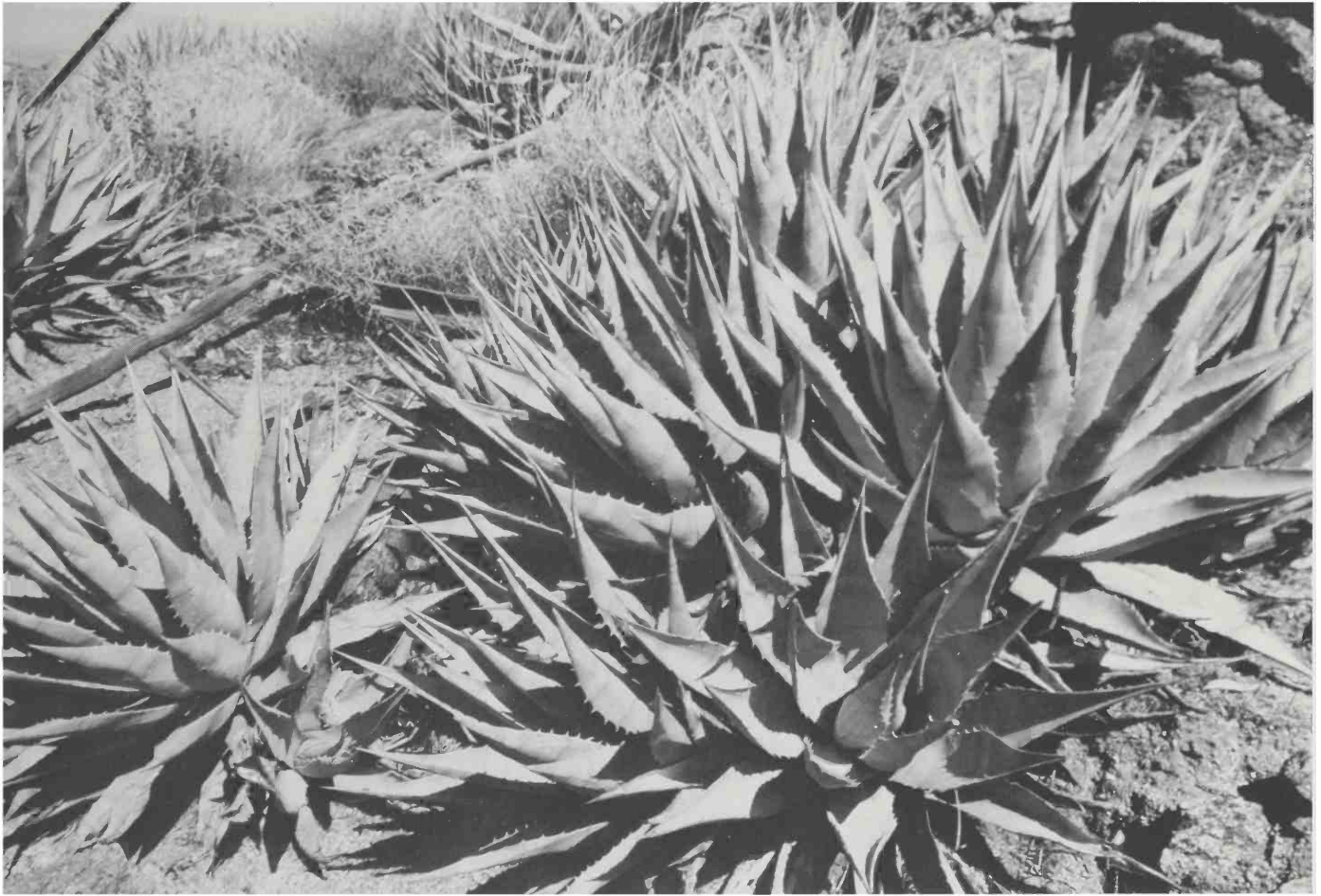
Figure 1. Agave deserti *at "Agave Hill", a site in the*
northwestern Sonoran Desert near Palm Desert, California.

For Figure 2, the leaf temperature during the daytime averaged 19°C and at night it averaged 4°C. Because air in the intercellular air spaces of leaves is essentially saturated with water vapor, such air averaged about 16.3 g water m^{-3} during the daytime and only 6.4 g m^{-3} at night. But the water vapor content of the ambient air was fairly constant during the 24-hour period at 3.6 g m^{-3}. This means that for a given amount of stomatal opening (i.e., a given g_{wv}), Δc_{wv} and hence the rate of water loss by transpiration would be five-fold higher during the daytime than the nighttime (see Equation 1). Such tremendous water savings is the essence of the advantage of CAM metabolism and underscores why agaves and other CAM plants can be successful in arid and semi-arid regions where water is limited.

The need for water economy justifies CAM, but what happens when water does not impose a limiation for *A. deserti*? After 12 weeks of daily watering in the laboratory, the normal nighttime stomatal opening of *A. deserti* was replaced by daytime stomatal opening and primarily daytime CO_2 uptake, presumably by the C_3 pathway (Hartsock and Nobel, 1976). Upon returning to a watering protocol more consistent with its habitat, *A. deserti* reverted back to the CAM pathway. However, such daytime stomatal opening and CO_2 uptake has not been observed in the field under natural conditions, although some stomatal opening can occur near

sunrise (Figure 2B). During the daytime a very high CO_2 level can build up behind closed stomates (30 times the external CO_2 concentration), which accounts for the small but detectable leakage of CO_2 out of *A. deserti* then (Figure 2B).

Seedling Establishment and Growth

Seedlings of *A. deserti* are hard to find in the field and indeed only rarely become established, at least in the northwestern Sonoran Desert. Laboratory studies have indicated that approximately 90% germination of seeds occurs at 21°C to 23°C, decreasing by 50% at temperatures 10°C higher or lower (Nobel, 1977a; Jordan and Nobel, 1979). Growth of roots and cotyledons of 10-day-old seedlings is optimal near 30°C (Jordan and Nobel, 1979). As seedlings grow, their volume increases more rapidly than their surface area, leading to a greater water reservoir per unit of transpiring area. For instance, shoot volume per unit shoot area, which represents the total depth from which water can be mobilized, is 0.07 cm at 10 days of seedling age, 0.18 cm at 120 days, 0.29 cm at 445 days (Jordan and Nobel, 1979), and about 0.91 cm for adult leaves (Nobel, 1976). The increase of water storage with age is a crucial aspect of drought survival.

Because *A. deserti* can tolerate leaf water potentials down to −1.6 MPa (about -16 atmospheres) and because the plant

must have a lower water potential than the soil for water movement into the plant to occur, drought can be defined as periods when the soil water potential in the root zone is below −1.6 MPa. As the seedlings become older and thus have more stored water per unit surface area, they can tolerate longer periods of such drought (Figure 3). For example, 30-day-old seedlings can tolerate only 10 days of drought while 100-day-old seedlings can tolerate 80 days of drought.

As the next step in the analysis of seedling establishment in the field, the wet periods available for initial seedling growth at Agave Hill were determined for each year beginning in 1961 and compared to the subsequent drought period that must be endured in that year (Figure 3). From 1961 to 1977, only 1967 had a long enough growing period for the seedlings to develop sufficient biomass to be able to survive the first drought. The favorable growing period began in late summer when temperatures were appropriate for seed germination as well as for root and shoot growth.

The year for successful seedling establishment was also estimated based on observations of the six smallest plants in an area containing over 1000 rosettes of *A. deserti* (Jordan and Nobel, 1979). By monitoring annual growth for a series of years in the late 1970's and extrapolating for leaf production in earlier years (dead leaves remained at the base of the plants and leaf scars were also visible), the average year for the establishment of these six plants was also found to be 1967. All six of these small plants occurred in protected habitats, an aspect that will be returned to when thermal tolerances are considered. The agreement between growth estimates in the field and microclimatic conditions serves to indicate that it is the first year which is most crucial for seedling survival (only the initial wet period and its subsequent drought are considered in Figure 3).

Since 1977, when the detailed study ended, the years 1982 and 1983 were judged to be suitable for seedling establishment (Figure 3). Indeed, three small seedlings of *A. deserti* about 3 cm tall with 3 or 4 living leaves were observed in June of 1983, a size consistent with germination near the beginning of the long wet period that commenced in July of 1982 and extended into 1983 (subsequent observations located more such seedlings). Observations in June of 1984 revealed no new seedlings from 1983, although such lack of evidence does not prove that no seedlings became established in 1983, bacause small seedlings are easily overlooked. However, the wet period that interrupted the first drought for such possible seedlings was short (30 days) and was followed by a long drought in 1984 (175 days), which the seedings should not have survived. Thus, this second drought may have proved lethal to the seedlings that one might otherwise expect from 1983 (Figure 3).

Water Relations

In addition to its influence on seed germination and seedling establishment, water also influences mature plants. For instance, appreciable stomatal opening with its accompanying CO_2 uptake (Figure 2) only occurs when the plants are hydrated. Because of water storage in the leaves and stem, nocturnal stomatal opening can continue for up to eight days after the soil becomes drier than the plant (Nobel, 1976). Indeed, the water potential of leaves of *A.*
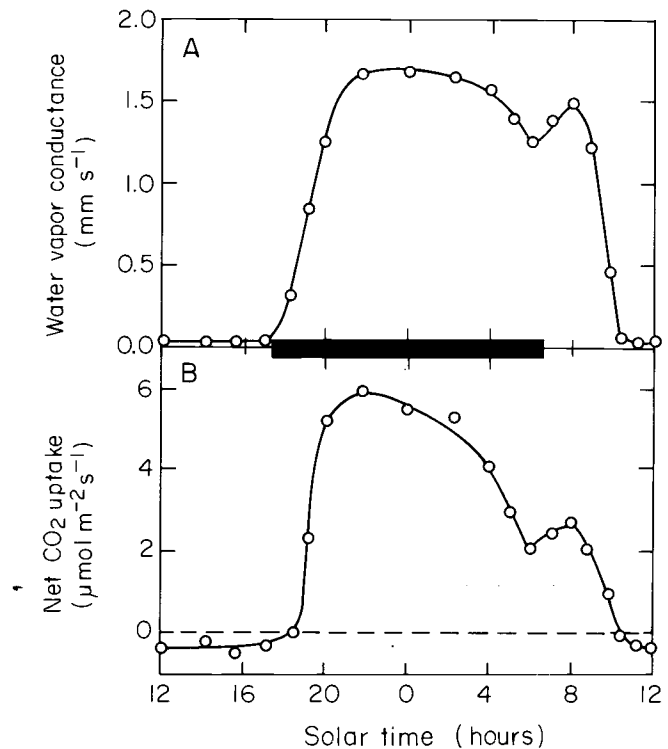

Figure 2. *Water vapor conductance (A) and net CO_2 uptake (B) for* A. deserti *on a clear day near the winter solstice. Maximum solar irradiance was 630 W m^{-2}, maximum/minimum air temperatures at 1 m above the ground were 19°C/7°C, maximum/miminum leaf temperatures at midleaf were 28°C/2°C, the air water vapor concentration averaged 3.6 g m^{-3}, and the soil was wet (soil water potential in the root zone above −0.5 MPa). Dark bar indicates night.*

deserti decreases only slightly (about 0.1 MPa) over a 24-h period even when they are supplying all of the transpired water, in marked contrast to thin-leaved plants (Nobel and Jordan, 1983). Taking into consideration this capacitance effect of stored water and the effect of rainfall on soil water potential (after a drought a rainfall of at least 7 mm is required to induce stomatal opening by *A. deserti*; Nobel, 1976), the times of the year favorable for growth can be determined. For the eight years from 1973 to 1980, these favorable periods averaged 4.0 months in the winter/early spring and 1.4 months in the summer, reflecting the bimodal pattern of seasonal rainfall in this part of the Sonoran Desert (Nobel, 1985).

Water relations also affect the reproductive phase of this monocarpic species. Water uptake by the roots of *A. deserti* cannot keep up with the needs of the inflorescence, part of whose 5½-month existence occurs in the generally dry late spring/early summer (Nobel, 1977a). Indeed, for mature plants at Agave Hill, a total of 18 kg of water was moved from the leaves to the inflorescence where 17% was stored in the main axis, 24% was transpired by the main axis, and 59% was lost by the lateral branches. The highest daily
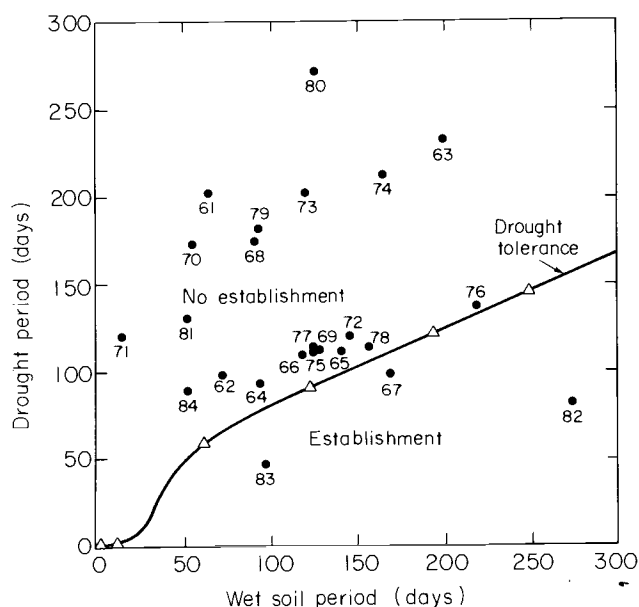
Figure 3. *Years possible for establishment of seedling of* A. deserti. *Seedlings were raised for various periods in the laboratory under conditions similar to those in the field and then subjected to various periods of drought (Ψ^{soil} below -1.6 MPa) to see what drought lengths could be tolerated (Δ). Weather records for Agave Hill together with field measurements of soil water potential (Nobel, 1977b) as well as simulations of soil water potential (Young and Nobel, 1985) were used to determine the longest wet period ($\psi^{soil} > -1.6$ MPa) beginning in the indicated year and the subsequent period of continuous drought ($\psi^{soil} < -1.6$ MPa; the wet period and/or the drought period could extend into the next year) for all years from 1961 ("61") to 1984 ("84").*

water loss (22 g/branch on inflorescences with 17 branches) occurred for the approximately eight days when flowers with their copious nectar were open (Nobel, 1977a). The fruit stage, which lasted about two months before viable seeds were developed, accounted for about half of the water lost by each lateral branch. The 18 mature fruit per lateral branch led to 66,000 seeds/plant. But because 95% of the propagation at Agave Hill is vegetative, only about 1 seed in 1.2 x 10⁶ leads to a mature flowering plant. We should also note that the dry weight of an inflorescence (1.3 kg) was about the same as the annual productivity of an entire mature plant (1.6 kg), and so dry weight must also be mobilized from the leaves to support reproduction (the leaves lost an average of 1.8 kg dry weight/plant from the time of inflorescence emergence to the production of viable seeds; Nobel, 1977a).

Nutrient Relations

So far relatively little is known about the nutrient responses of *A. deserti.* In terms of element stresses, its seedlings are quite sensitive to salinity, with 50 mM NaCl greatly reducing root elongation in hydroponic solution and watering with 25

mM NaCl preventing growth in sand culture (Nobel and Berry, 1985). Seedlings of *A. deserti* are rather insensitive to applied calcium concentrations from 0.2 to 5.0 mM and pH from pH 5 to 8. Also, they can tolerate high levels of boron and of the heavy metals copper and zinc, such high levels often occurring in the arid southwestern United States and north-western Mexico where *A. deserti* is found. Specific conclusions on the effects of edaphic factors on distribution must await future research.

Temperature Responses

Seasonal changes in temperature have relatively little effect on net CO_2 uptake by *A. deserti* over a 24-h period, although instantaneous nighttime values can markedly affect stomatal opening. For instance, the total nocturnal increase in acidity was reduced by only 30% for daytime leaf temperatures of 15°C or 40°C compared to the maximum uptake that occurred at daytime temperatures of 25°C to 30°C (Nobel and Hartsock, 1978). Nocturnal CO_2 uptake was optimal near a night temperature of 15°C. Actually, the optimum can shift some-what with mean nighttime temperature, from 15°C for a night-time temperature of 10°C to 18°C for a nighttime temperature of 30°C (Nobel and Hartsock, 1981). Although CO_2 uptake is maximal near 15°C, stomatal opening at night was actually greatest at the lowest temperature tested, 5°C. As the leaf chlorenchyma temperature was raised, stomatal opening de-creased as shown by a progressive decrease in the water vapor conductance, g_{wv} (Equation 1), e.g., g_{wv} decreased by 8% at 15°C, 53% at 25°C, and 92% at 35°C (Nobel, 1976; Nobel 1985; Nobel and Hartsock, 1979). Such stomatal closure at higher temperatures greatly restricts transpiration (Equation 1), which otherwise would increase substantially with tempera-ture because the water vapor concentration in the leaves rises essentially exponentially with temperature. Additionally, calculations using a computer model showed that transpira-tion does not reduce leaf temperature of the succulent leaves of *A. deserti* very much, as even full stomatal opening (a g_{wv} of 1.8 mm s⁻¹) decreased nocturnal leaf temperatures by only about 2°C compared to no transpiration at all (Woodhouse, Williams, and Nobel, 1983).

Besides effects on CO_2 uptake and transpiration, temp-erature—in particular, extreme temperatures—affects plant establishment and distribution. To study this, one can measure the fraction of the cells that take up a vital stain such as neutral red [3-amino-7-dimethylamino-2-methylphenazine (HCl)], which is only taken up by living cells (Nobel and Smith, 1983; Jordan and Nobel, 1984). Thus, whole plants or plant parts can be subjected to a particular extreme temperature for a given period (here chosen to be 1 hour, because the temperatures of agave organs are often fairly constant at an extreme temperature for this time period in the field), and then stain uptake by the cells determined microscopically using tissue slices 2- or 3-cells thick. Moreover, stain uptake is good predictor of lethal temperatures, because when stain uptake is reduced to 0% by an extreme temperature, the tissue will die. However, because it is experimentally difficult to determine the exact limiting temperatures for stain uptake, it is more convenient to determine where the high or low temperature stress reduces the number of cells taking up the stain by 50%. Based on studies on a series of agaves including *A.*

deserti, death occurs 3°C to 5°C above or below the temperature leading to a 50% decrease in stain uptake for high or low temperature treatments, respectively (Nobel and Smith, 1983).
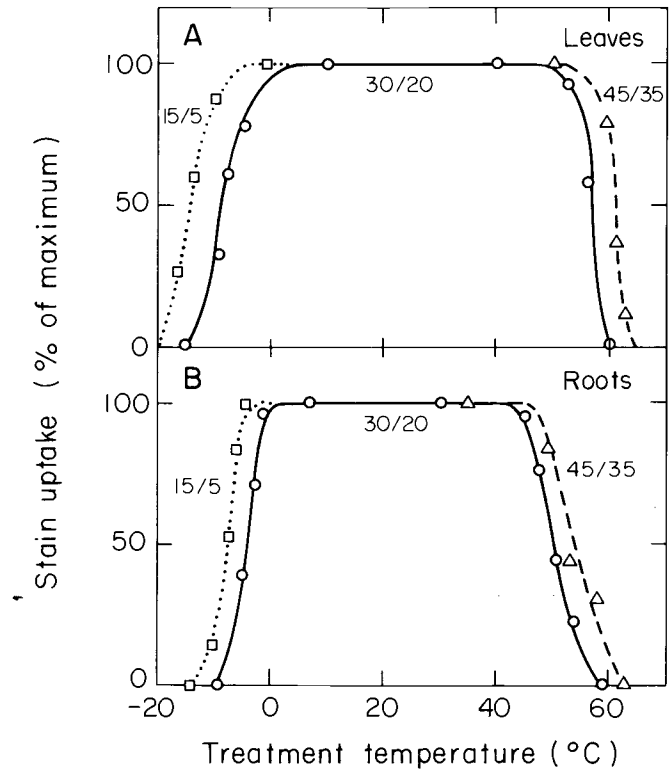
Figure 4 shows the thermal tolerances of leaves and roots of *A. deserti* as well as acclimation to high and low growth temperatures. For plants maintained in environmental growth chambers with day/night air temperatures of 30°C/20°C, stain uptake is reduced 50% at –9°C and 57°C for leaf chlorenchyma cells and –4°C and 50°C for root cortical cells. If the growth temperatures are lowered 15°C to 15°C/5°C, the 50% inhibition temperature was reduced 5°C for leaves and 3°C for roots (Figure 4). As growth temperatures were raised 15°C to 45°C/35°C, the high temperature for 50% inhibition of stain uptake icreased by 4°C for both leaves and roots (Figure 4). Such acclimation can help *A. deserti* adjust to seasonal changes in temperature.

Seedlings of *A. deserti* were slightly more sensitive to temperature extremes than mature plants. Specifically, 1–, 4–, and 12-month-old seedlings grown at 30°C/20°C had 50% inhibition of stain uptake by the leaves at –7°C and 56°C (Nobel, 1984a). Even after taking acclimation into consideration, the seedlings could not tolerate the 70°C that can occur at the exposed soil surface, and indeed all seedlings observed in the field occurred in protected microhabitats. Roots were 5°C to 7°C more sensitive than leaves to temperature extremes (Figure 4). This helps account for the absence of roots of *A. deserti* in the upper 3 cm of the soil, where soil temperatures can be extreme, except directly under a plant where temperature extremes are moderated (Jordan and Nobel, 1984). Even though roots were absent from the upper part of the soil, the mean root depth of *A. deserti* was only 8 cm (Nobel, 1976), which facilitates responses to the often light desert rainfalls.


Figure 4. *Temperature tolerance of leaves (A) and roots (B) of* A. deserti *as measured by cellular stain uptake. Data are from Nobel and Smith (1983), Jordan and Nobel (1984b), and unpublished observations. Day/night growth temperatures are indicated adjacent to the curves.*

PAR Responses

Despite the high radiation environment of deserts, net CO_2 uptake by unshaded plants of *A. deserti* is on the verge of being limited by the total daily photosynthetically active radiation (PAR) on clear days, i.e., more PAR would generally lead to greater growth. Also, because the leaves are opaque, the orientation of each surface must be considered in order to predict productivity. Actually, when totaled over a day near an equinox, average PAR on the leaves of an unshaded plant of *A. deserti* with 56 leaves is extremely similar for leaves radiating toward the upper, middle, or lower part of the canopy, about 15 mol photons m^{-2} (Figure 5). Variation is also slight (±7%) with compass direction. Again at an equinox, the abaxial (lower) surface receives 38% less PAR than the upper surface (Nobel, 1984b).

As the total daily PAR on the leaves increases, nocturnal CO_2 uptake and the accompanying acidity both increase. Ninety percent PAR saturation for *A. deserti* occurs at 19 to 23 mol m^{-2} (Nobel, 1984b: Nobel and Hartsock, 1978). The PAR level for the unshaded plant with 56 leaves on a clear day at the equinox leads to about 70% of the maximal CO_2 uptake. Near the summer solstice the higher PAR causes nearly 90% PAR saturation of net CO_2 uptake, while the lower trajectory of the sun near the winter solstice leads to less than 50% of the maximum net CO_2 uptake on clear days (Woodhouse et al., 1980; Nobel, 1984b, 1984c, 1985).

Productivity

All of the physical factors discussed above have an impact on productivity. However, the key factor for a desert plant like *A. deserti* is water, without which there is no stomatal opening or net CO_2 uptake. Indeed, a water status index has been developed (Figure 6A) that indicates month-by-month the fraction of maximal CO_2 uptake expected based on the soil water potential plus tissue water storage (Nobel, 1984c). This index ranged from 1.00 for a month with wet soil (soil water potential above –0.5 MPa) or when stomatal opening can be supplied by water stored in the succulent leaves and stem to 0.00 for a drought month in which water storage in the tissue has already been exhausted.

Indices for temperature and PAR have also been developed for *A. deserti,* which show the fraction of maximal CO_2 uptake expected for various values of these physical factors. The seasonal range for the PAR index on clear days has already been discussed. Clouds decreased the available PAR about 4% for a relatively clear June to 17% for a cloudy August during the period of interest (March 1983-October 1984), leading to corresponding reductions in the PAR index. Because of thermal acclimation of net CO_2 uptake and the moderate temperatures at Agave Hill, the temperature index ranged only from 0.67 to 0.97 over the period of interest, being lowest from July through September when even the nights were too warm for optimal CO_2 uptake.
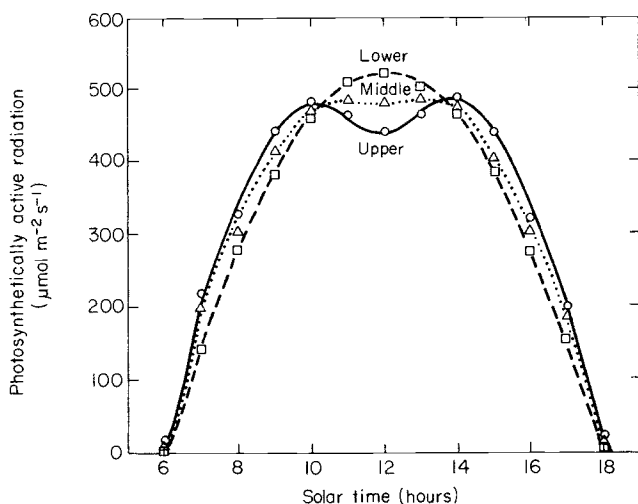
Figure 5. Diurnal course of PAR incident on various positions within the rosette. Data represent the averages for the entire adaxial and abaxial surfaces for 18 to 20 leaves radiating toward the upper, middle, or lower part of the canopy. Simulations were performed for 34°N on a clear day at the equinox using the computer model of Woodhouse et al. (1980).

Figure 6. Monthly values of the water status index (A), the environmental productivity index (B), and the total number of newly unfolding leaves on 50 plants (C).

The indices for water, PAR, and temperature can be multiplied together to obtain an overall "environmental productivity index" (Figure 6B). This latter index indicates month-by-month the fraction of maximal CO_2 uptake expected. Moreover, because CO_2 uptake is expressed on a leaf area basis (cf. Figure 2) and the leaf area per plant is known, the environmental productivity index can be used to calculate CO_2 uptake per plant. Assuming that CO_2 is incorporated into carbohydrate, correcting for root and stem respiration, and expressing the data on the basis of the ground area explored by the roots, productivity can be expressed per unit ground area. In this way, the annual productivity of A. deserti was predicted to be 0.60 kg m^{-2} y^{-1}, in excellent agreement with a measured productivity of 0.57 kg m^{-2} y^{-1} (Nobel, 1984c). Such a productivity is about six-fold higher than the average values for deserts (Noy-Meir, 1973; Leith and Whittaker, 1975).

Another interesting feature of the productivity studies with A. deserti relates to the unfolding of its leaves from the central spike of the rosette. In particular, the monthly unfolding of new leaves (Figure 6C) was highly correlated ($r^2 \geq 0.93$) with the environmental productivity index (Figure 6B) and the water status index (Figure 6A). Because monitoring such leaf unfolding is nondestructive and easily done in the field, the opportunity is available for new types of studies on the productivity of A. deserti and other agaves under a wide range of field conditions.

Future Research

Now that it has been shown to be a reliable estimate of productivity, the environmental productivity index should be used to assess the growth and productivity of A. deserti at other sites. It can also be applied to the study of nutrient relations, about which little is presently known. Moreover, this approach developed for A. deserti is being applied to productivity studies for other agaves, such as A. fourcroydes
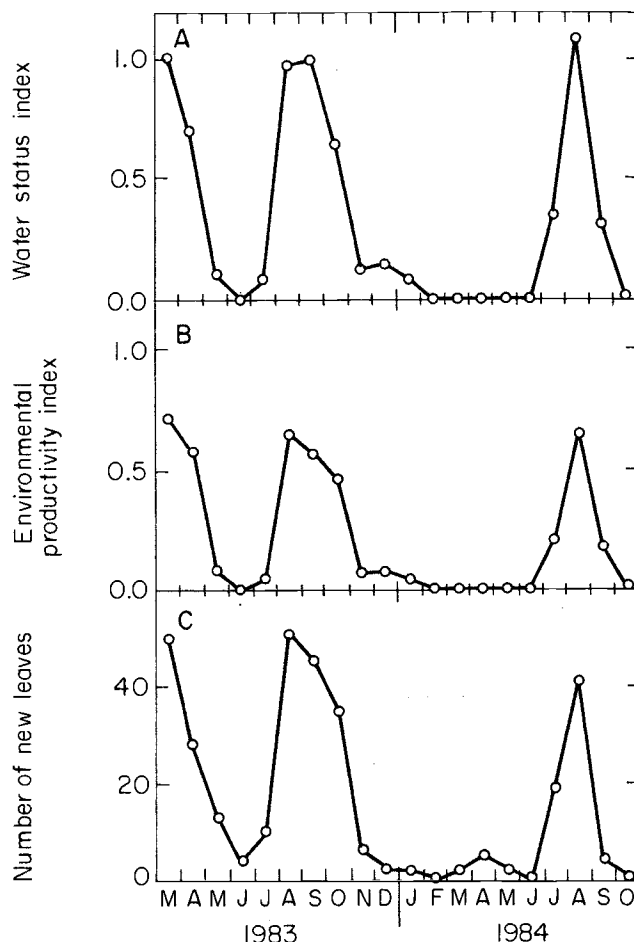
Lem. (Henequen) in the Yucatan and A. lechuguilla Torr. in the Chihuahuan Desert. Another area ripe for ecophysiological research is a comprehensive study of root properties of A. deserti and other agaves, embracing root growth, distribution in the soil, and consequences for competition with other plants. Such studies may well uncover other interesting adaptations to desert climates for this remarkable group of plants.

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Field Evaluations of Agave in Arizona

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Abstract

Four agave species *(Agave americana* L., *A. murpheyi* F. Gibson, *A. palmeri* Engelm., and A. *parryi Engelm.)* have been evaluated in a four-year study conducted at four Arizona field locations. Survival data, growth rates, approximate water requirements, and insect predation have been analyzed under Arizona field conditions. All species showed good survival at the Marana location, with *Agave americana* exhibiting the most rapid growth increment, averaging fresh weight gains of 70 to 110 kg per plant in the four-year period, with minimal supplemental irrigation. Analysis of carbohydrates in these plants showed an average 50% sugars on a dry weight basis. Projected growth parameters and biomass accumulation data are presented.

Introduction

Increasing economic pressures on the irrigated agriculture of the Southwest necessitate the evaluation of alternative agricultural technologies. One approach to dealing with the increasing cost of water, reduced availability of prime farm land, and depressed crop prices is to explore the usage of existing arid land crops which require minimum agriculture inputs, but which nevertheless produce an acceptable return to the farmer, and which keep agricultural land in production. One such potential crop is agave. Cultivated by man for many centuries, agave has proven to be an extremely adaptable crop plant, one which is presently grown in nearly every agricultural area of the world where climatic extremes are not limiting. A rather large compendium of information on the culture of agave for food, fiber, and pharmaceuticals now exists. Although Arizona has the largest number of native agave species of any state, with a single exception, this author can find no record of current agave cultivation in the state. In neighboring Sonora, Mexico, native stands of agave have been exploited for the production of alcoholic beverages for many years. Given the widespread occurrence of native populations of agave in Arizona, and their role as an economic crop in the adjacent northern states of Mexico, it seemed reasonable to investigate the potential of agave in Arizona agriculture.

Experimental Approach and Design

Four agave species were selected for the initial phases of this study, based upon three criteria: 1) the ready availability of planting stock; 2) the anticipated adaptation of the species to the climate of the farm sites available; and 3) a history of use of the species for alcohol production. Four locations were chosen based upon proximity to existing agricultural areas in the southern part of Arizona or to approximate rangeland conditions. Two sites were situated on University farms, where supplemental irrigation was available; two were dryland, desert locations. *Agave americana* was evaluated in a fifth location, at the Campus Agricultural Center in Tucson. Table 1 presents a summary of the locations, their elevation and the size of the present agave fields. These locations are fairly representative of the mid to high elevation agricultural areas in the southeastern Arizona counties.

An evaluation of the agave species grown at each location in the course of these studies and an overall assessment of their crop potential are given in Table 2. Six agave species, as well as the closely related *Dasylirion wheeleri* S. Wats. (Desert Spoon) have been evaluated as row crops. General evaluations to date rate *Agave americana* and its variants as the best adapted species, judged by survival and growth data. *Agave murpheyi* also looks extremely promising at some locales.

Table 3 illustrates the observed increase in fresh weights of *Agave americana* at three field locations. In a second planting at Tucson, *A. americana* plants averaging 20 kg or more each were lost when a section of the campus farm adjacent to the river was washed away. The effect of favorable climatic conditions as well as supplemental irrigation is clearly evident in the growth increments observed by comparing the Marana location to the Page Ranch environment. Both plots were established without irrigation, and
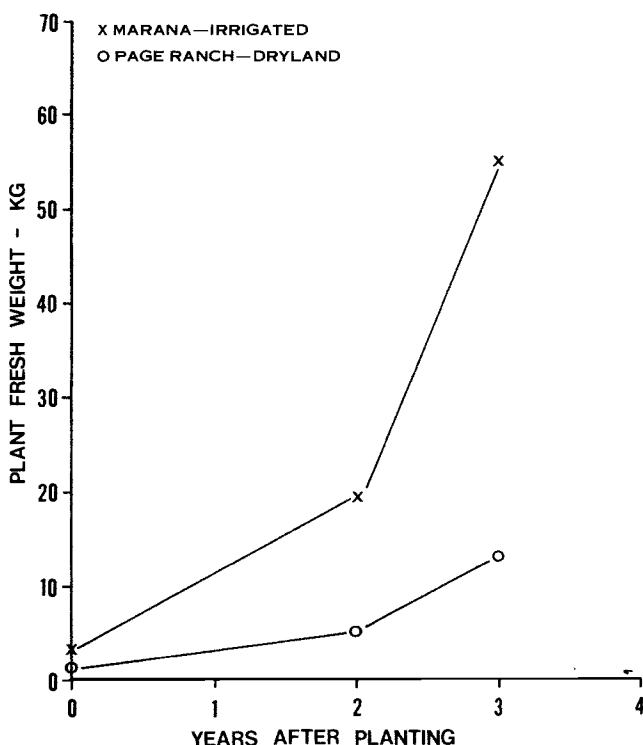
Figure 1. *Relative biomass accumulation of* Agave americana *cultivated at two Arizona locations, Marana and Page Ranch.*

the Marana plot received only infrequent unscheduled irrigation due to accidental overflow from adjacent borders. Figure 1 points out the rapid increase in agave biomass accumulation by the third year following transplanting at Marana. Nondestructive growth measurements made at the end of the fourth year of growth (November, 1984) indicate that many of these plants exceeded 90 kg. Figure 2 shows the recent appearance of a portion of this field.

Agaves were established by transplanting at the Page Ranch Agricultural Center in a grid pattern 4.3 meters apart with minimum disturbance to the desert surroundings. The purpose of this strategy was two-fold. First, it was important to evaluate the performance of these plants in a high elevation rangeland environment protected from grazing. Second, such a planting would allow testing the theory that the agave would offer a protected site for germination and establishment of native range grasses and other species. This premise was based upon observations by the author that the protected area around the base of the agaves encouraged the establishment of grasses in an otherwise unsuitable environment. Continued observations at Page Ranch following the introduction of cattle onto the ranch supported these observations, although no definitive data by a range specialist have been gathered yet. Clearly, the several agave species tested show promise as adaptable crop plants for several agricultural areas in southern Arizona. Figure 3 shows the recent appearance of part of this field.

Another principal agave test was initiated at the Safford Agricultural Center, with the plants established in three adjacent plots, each irrigated infrequently with water at three distinct salinity levels. Mortality data and growth data will be collected in November, 1985, but it is clear from viewing the fields that small (0.5 kg) transplants are markedly stunted by high salinity levels (approx. -18 bars).

Table 1. *Agave americana* L. evaluated under cultivation in Arizona.

Field Location	Elevation	Hectares Presently Cultivated	Original Planting Established
Marana Agricultural Center (I)	1900 Ft (580m)	0.9	1980
Avra Valley (D)	2000 Ft (610m)	0.7	1980
Tucson (2) (I)	2500 Ft (760m)	0.1	1979, 1983
Page Ranch Agricultural Center (D)3800 Ft (1160 m)		0.8	1981
Safford Agricultural Center (I)	2900 Ft (885m)	0.2	1980

I = irrigated farmland; D = desert, abandoned farmland or pasture.

Table 2. *Agave* species evaluated under cultivation in Arizona.

Field Location	Species	Evaluation
Marana (with supplemental irrigation)	Agave palmeri	Slow growth
	Agave murpheyi*	Rapid growth, prone to waterlogging
	Agave parryi	Extremely slow growth
	Agave weberi	Rapid growth, well adapted
	Agave fourcroydes	Failed to survive winter
	Agave americana	Rapid growth, well adapted, many off-shoots
Safford (two irrigations at each of three salinity levels	Agave americana	Rapid growth, some off-shoots
	Agave palmeri	Slow growth, high mortality at high salinity level
	Agave murpheyi	Slow growth and high mortality at high salinity level
	Dasylirion wheeleri	Very rapid growth, relatively little effect of high salinity
Page Ranch	Agave americana	Rapid growth, few off-shoots
	Agave palmeri	Slow growth, some mortality
	Agave murpheyi	Slow growth, high mortality

*Several plants already blooming at this location.

Table 3. Relative growth rate of *Agave americana* at three field locations.[1]

Location	Fresh Weight in Kilograms			
	At Planting	Year 1	Year 2	Year 3
Marana	1.2-5	— —	16-23	31-80[2]
Page Ranch	0.2-1.2	— —	4-5	11-14
Tucson	0.1	— —	1.2	3.7

[1]Final data are on a fresh weight basis, and include the majority of the root mass.
[2]These plants produced several dozen offshoots averaging over a kilogram each during the three-year period. Biomass of these offshoots was excluded from the calculated weights of these plants.

Table 4. Soluble solids in leaf homogenates of agave.

Species	Soluble Solids
Agave americana	7-9%
Agave palmeri	8-12%
Agave parryi	12-18%
Agave schottii	18-22%
Agave murpheyi	14-16%

Sections were cut from mature leaves of nonflowering specimens approximately 15 cm from the leaf base. Sap was expressed by crushing the leaf with a mallet. A series of sap samples were collected dropwise in micropipettes, and soluble solids (sugars, glycosides, amino acids, organic acids) were determined by refractometry. Specimens were collected in early March.
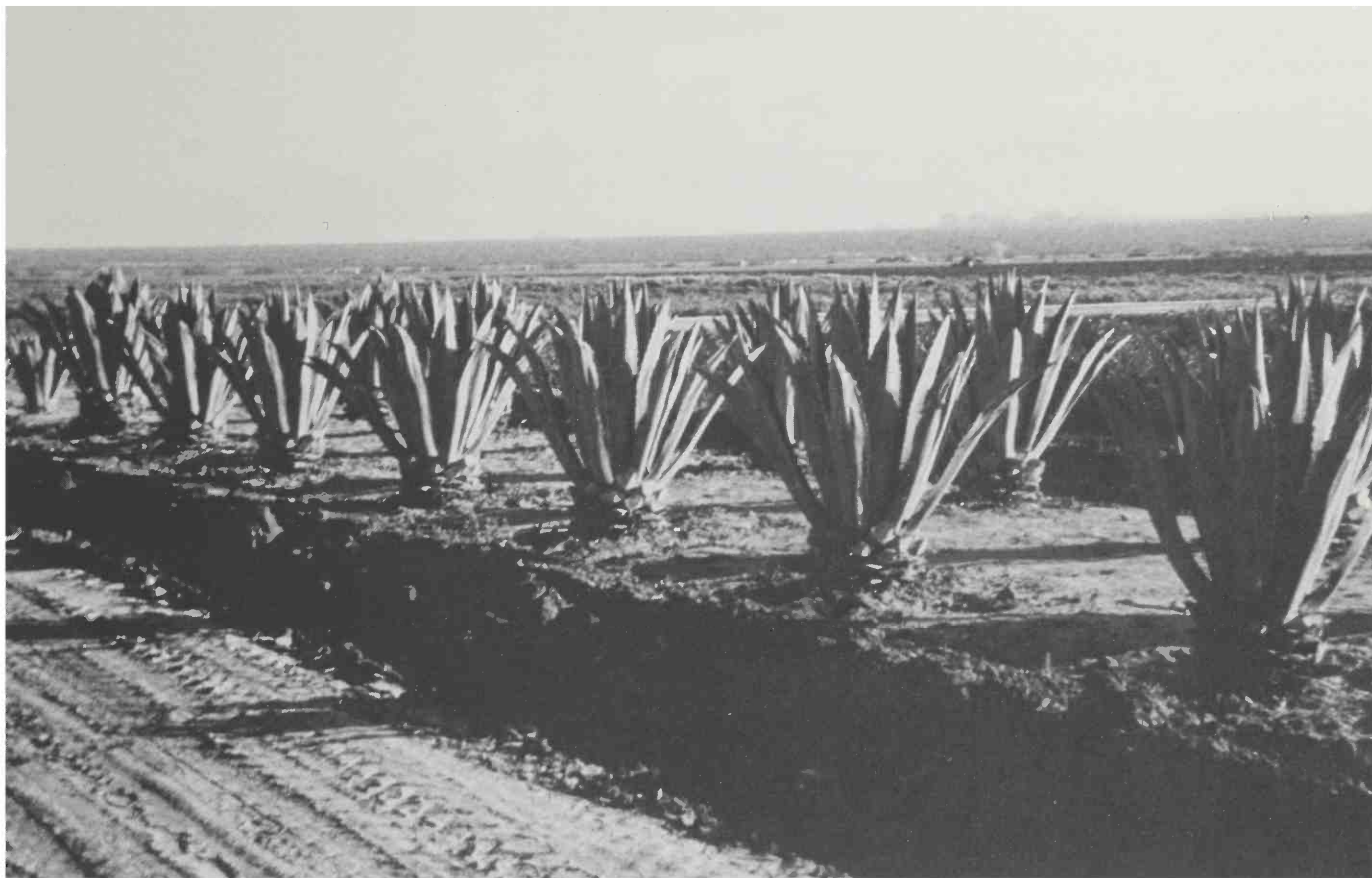
Figure 2. *A view of* Agave americana *four-year-old transplants at Marana, Arizona.*

Physiological Aspects of Field-grown Agave

Agaves occupy a rather unique ecological niche in that they are semi-succulents whose prime drought-avoidance strategy is Crassulacean acid metabolism (CAM). CAM plants avoid excessive transpirational water loss at high temperatures by stomatal closure. Additionally, they possess an extremely thick waxy cuticle (plants may average 0.2% wax on a dry weight basis). Winter (1974), Nobel and Hartsock (1979), and Ehrler (1982) have discussed these survival strategies of agave from the standpoint of water relations. The evident proliferation of agave species in the Arizona desert environment attests to the effective adaptation of agave (Gentry, 1982).

At the initiation of this study, emphasis was placed on the potential of agave for the production of ethanol for gasohol (Meckhof *et al.*, 1980). Ethanol production is a well-documented attribute of many agave species, and the literature of agave abounds with descriptions of the fermentative products of this plant (Gentry, 1972, 1982; De Barrios, 1971). Consequently one of the physiological traits of interest was the production of sugars by agaves under cultivation. Table 4 presents data illustrating the soluble solids in the leaves of several agave species. Refractometry provides a rapid, accurate, in the field analysis of agave sugar content, even though steroidal glycosides make a contribution to the reading. When compared to actual sugar percentages determined colorimetrically, shown in Table 5, the refractometer readings for *Agave americana* specimens fall within about 2 to 3% of actual sugar content. A sugar content of 50% on a dry weight basis is extremely high, and

commends agave as an alternative source of ethanol in a suitable economic situation.

Agaves represent a world-wide source of steroids which find a market in the pharmaceutical industry. As byproducts of sisal fiber production, agave steroidal sapogenins account for about 6% of the world supply of precursors for corticosteroid synthesis (Blunden *et al.*, 1975; Bokirko and Kintya, 1975). These chemicals also find use as animal feed supplements (Jones and Conner, 1918; McKeen and Haas, 1964); and even show promise as anti-cancer agents (Bianchi and Cole, 1969). A domestic industry presently exists whereby steroids extracted from native yucca stands in the Mohave desert supply a commercial steroidal sapogenin extract. Industrial tests of agave steroids indicate that they have considerable promise as a substitute for yucca harvested from the wild. Table 6 gives a projection of the economic potential of agaves cultivated in Arizona judged by their steroid content. As a minimal input crop on marginal farmland in the mid-elevation areas, with limited or poor quality water, agave looks opportune. Johnson (1977) has briefly discussed some of the potential uses of agave in arid land agriculture.

Pests and Predators

Although the prospects for a place for agave in Arizona agriculture seem favorable, especially if breeders can profit from incorporation of hybrid materials produced locally or obtained from breeding programs worldwide (Wienk and van S'chendellaan, 1976); and if mechanization can be adapted to agave culture and harvesting, several problems do exist. First among these is the predation by agave weevils (Vauri,

Figure 3. A view of Agave americana three-year-old transplants at Page Ranch, Arizona.

Table 5. Sugar content of leaves and underground stems of Agave americana.

	Moisture Content (%)	Sugar Content (%)	
		(dry weight basis)	(fresh weight basis)
Leaves	89.5	50.7	5.35
Stems	85.5	48.7	7.05

Data are means of duplicate determinations on each sample. Percent sugar analyzed by the anthrone test with glucose as standard and expressed on a plant weight basis. Analysis courtesy of Dr. Joseph Scheerens, Department of Plant Sciences.

Table 6. Projected biomass accumulation of Agave americana under supplemental irrigation at Marana, Arizona.

Average estimated biomass per plant in kg[1] (Four-year production cycle)	95
Plants per hectare (Plants spaced 2.2 meters apart on 3-meter-wide beds)	1,650
Total biomass accumulated per hectare in kg	156,750
Water use: Rainfall plus some supplemental irrigation[2] (in mm)	250
Value of crop (for steroidal sapogenins at $50/ton[3]	$3,500

[1]Assumes initial offshoot transplants averaged 5 kg or greater weight.

[2]In October, 1983, the Santa Cruz river flooded the Marana Agricultural Center, leaving standing water in the field for several days. The actual water "applied" was impossible to calculate, but undoubtedly contributed to the growth of plants before representative plants were harvested in November, 1983.

[3]Price at farm, calculated on the basis of 10% soluble solids. (Personal communication, R. C. Fudge and D. T. Williams, 1984.)

Table 7. Projected probable uses of agave cropped in Arizona.

1. Production of steroidal sapogenins (for corticosteroid synthesis and odor control)

2. Production of ethanol (following conversion and fermentation of sugars)

3. Fiber production

4. Animal ration supplements

5. Erosion control and soil stabilization

6. Plant micro-climate for range grass reestablishment under grazing pressure

7. Ornamental for landscape use (application of biotechnology via tissue culture to create favorable variants)

1971) which are endemic to the Tucson basin (Waring, 1981). These insects can rapidly destroy mature agaves; but can be readily controlled by systemic insecticides. Although the Avra Valley planting was infested by agave weevils introduced from a transplant with unnoticed grubs, complete biological control of the weevil was achieved by black widow spiders, which evidently moved to the spiral-leaved habitat of the agave field from an adjacent cotton gin. Gophers have also been found to kill agaves of high sugar content by burrowing from beneath the plant and chewing out the "heart" of the plant.

A Demographic Study of Maguey Verde (Agave salmiana ssp. crassispina) Under Conditions of Intensive Utilization

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Abstract

In western San Luis Potosi, Mexico, wild populations of Maguey Verde *(Agave Salmiana* Otto ex Salm-Dyck ssp. *crassispina* (Trel.) Gentry) are intensively utilized, especially as raw material for production of the distilled liquor mezcal. A demographic approach was used to investigate possible explanations for recent population decline. The effect of overgrazing on the survival of young plants (offsets) was found to be a major problem. Harvest of sexually mature plants for mezcal aggravates the problem by leaving both soil and offsets exposed. But, in itself, this harvest seems to constitute a reasonable long-term use for wild populations, even though seed production is halted.

Introduction

In the semi-arid steppe country of western San Luis Potosi, Mexico, maguey verde *(Agave salmiana* ssp. *crassispina* (Trel.) Gentry) is a common and conspicuous component of the natural vegetation. It is an economically important plant whose multiple uses include the commercial manufacture of the distilled liquor mezcal. Raw material for local mezcal manufacture comes exclusively from wild populations.

The Altiplano Potosino is only marginally suited for rainfed agriculture, with an average annual rainfall of 350-400 mm and marked year-to-year variation. As a consequence, the burden of supporting the growing rural population falls heavily on the natural vegetation, which is utilized both through direct collection and through grazing. With the intensification of land use in recent years, natural ecosystems are experiencing visible and possibly irreversible degradation. One result has been a decline in the supply of raw material from wild maguey populations. The object of this study was to try to understand why maguey populations are declining and how they could be managed for sustained long-term yield.

Maguey verde is one of the more spectacular agaves of semi-arid Mexico, reaching rosette heights of 1.8 m and fresh weights of over 250 kg. As mentioned by Gentry (1982), it propagates freely of offsets and also sets abundant seed. It is adapted to a variety of habitats, including rocky hillsides, but it reaches its maximum development, both in population and individual terms, on broad plains with reasonably deep soils. It often shares this habitat with grassland vegetation, occurring in clumps dispersed in a grassland matrix. The grassland today is composed mostly of species tolerant to grazing and trampling.

Tello-Balderas (1983) has described the local utilization of maguey verde. Use of the flowering stalk as human food and in construction prevents seed production, but the bulk of the rosette is left in place. Harvest for mezcal production (for details see Tello-Balderas and Garcia-Moya, this issue of *Desert Plants)* involves the removal of entire plants once they have initiated the process of sexual reproduction. This halts seed production and also implies removal of resources and of the protection offered by the dead post-flowering rosette. Harvest of submature plants for cattle forage, in addition to having the above effects, may also interfere with offset production. Any form of intensive exploitation effectively eliminates the option of reproduction from seed.

Methods and Materials

The La Tinaja Study Site is typical of much of the 'magueyera' of the region (Figure 1). It is located about 10 km ESE of the town of Salinas de Hidalgo, San Luis Potosi, at 22° 35' north latitude, 101° 38' west longitude, and at an altitude of about 2280 m (for regional map, see Tello-Balderas and Garcia-Moya, this issue of *Desert Plants).* The almost level plain supports extensive maguey-grassland vegetation. The soil, a neutral sandy clay loam with a calcareous hardpan at (0-) 30-90 cm, is rich in potassium but poor in phosphorus and iron (Lagunes-Espinosa, 1985). The land is managed under the 'ejido' system, a type of communal ownership, as open range with intensive grazing by all classes of livestock.

Table 1. Damage to offsets and soil compaction (measured as resistence to penetration in kg/cm², in relation to position with regard to other agaves, based on a sample of 200 randomly selected offsets. Contingency table analysis shows highly significant departures from expected values per position for each type of damage, for damage in general, and for degree of soil compaction (p < .005 in each case).

| | Offset Position | | | | | |
	Within-Clump Protected	Within-Clump Exposed	Clump Edge Semi-Protected	Clump Edge Exposed	Open Grassland	General
% Total Offsets	24	28	32	16	0	100
Damage (% Total Offsets)						
Overall	12	71	61	82	-	56
Trampling	0	11	9	21	-	9
Predation	4	27	29	36	-	24
Insects/Pathogens/Stress	8	55	35	36	-	34
Soil Compaction (kg/cm²)						
% ≤ 1	65	33	20	3	0	-
% 1.1-2.0	27	27	23	26	0	-
% 2.1-3.0	8	11	28	29	4	-
% 3.1-4.0	0	16	21	18	10	-
% > 4.0	0	13	8	24	86	-

Harvest for mezcal is carried out under contract with a local factory, while small-scale harvest for other uses is continual.

In designing the study, we took the clump as the basic population unit, and considered factors which might affect its size (area), its size-class structure, and its potential productivity. We proposed that, within an agave clump, there ought to exist a critical value for biomass/area, above which the effects of crowding might be expressed as reduced growth rate, smaller size at flowering, or the supression of offset production. At biomass/area below this critical value, the advantages of cohabiting with other agaves, such as protection from trampling and access to better soil microsites, should outweigh the disadvantages. We considered that, given time and environmental homogeneity, agave clumps should continue to expand and should eventually merge with each other. That this has not happened implies either heterogeneity in terms of soil or topographic factors or decreased survivorship at clump edges due to biotic interactions. We also considered that plant size at flowering in this monocarpic perennial should provide a good index of site quality, integrating biotic and abiotic factors.

To obtain accurate estimates of biomass/area, we excavated a series of eight individuals of different sizes and used regression analysis to relate field size parameters to dry weight. The size of an individual expressed as its height × diameter in square meters was related to its dry weight in kilograms by the following equation:

$$\text{dry weight} = 11.44 \, (\text{height} \times \text{diameter})^{1.32} \quad (R^2 = .98).$$

To estimate the former size of harvested plants, the stem diameter in meters was related to the product of height × diameter in square meters by the following equation:

$$(\text{height} \times \text{diameter}) = 67.4 \, (\text{stem diameter})^{2.03} \, (R^2 = .97).$$

Non-destructive sampling of 52 agave clumps was carried out in the most homogeneous and least degraded part of the general study area. Clump area, soil depth inside and immediately outside the clump, and size-class structure for living, dead, and harvested agaves were among the parameters. Size class categories used the height × diameter (square meters) criterion as follows:

Class	Size Range
1	0.01-0.05
2	0.06-0.10
3	0.11-0.20
4	0.21-0.40
5	0.41-0.60
6	0.61-0.80
7	0.81-1.00
8	1.01-1.20
9	1.21-1.40
10	1.41-1.60
11	1.61-1.80
12	1.81-2.00
13	2.01-3.00
14	>3.00

Offset production by size class was examined by excavating 150 potential parent plants. To look for plants propagated from seed, we excavated 150 small offsets; their rhizome connections were also traced.

We looked at damage to offsets by sampling 200 individuals, noting type and degree of damage, position with regard to other agaves, and degree of soil compaction (Soiltest pocket penetrometer). Types of damage noted were trampling, predation, and a combination of the effects of abiotic stress, pathogens, and boring insects. Offset position was recorded as within-clump and protected, within-clump but exposed, clump-edge and semi-protected, or clump-edge and exposed.

We carried out an extensive survey of 360 plants in flower in order to relate plant size at flowering to the living agave biomass within a 1.5 m radius of the center of each plant. Flowering plants were classified by the height × diameter criterion as small (<1.00 m²), medium (1.00-2.00 m²), or large (>2.00 m²), while agave neighbor dry weight biomass was defined as low (<20 kg), medium (20 to 40 kg), or high (>40 kg).
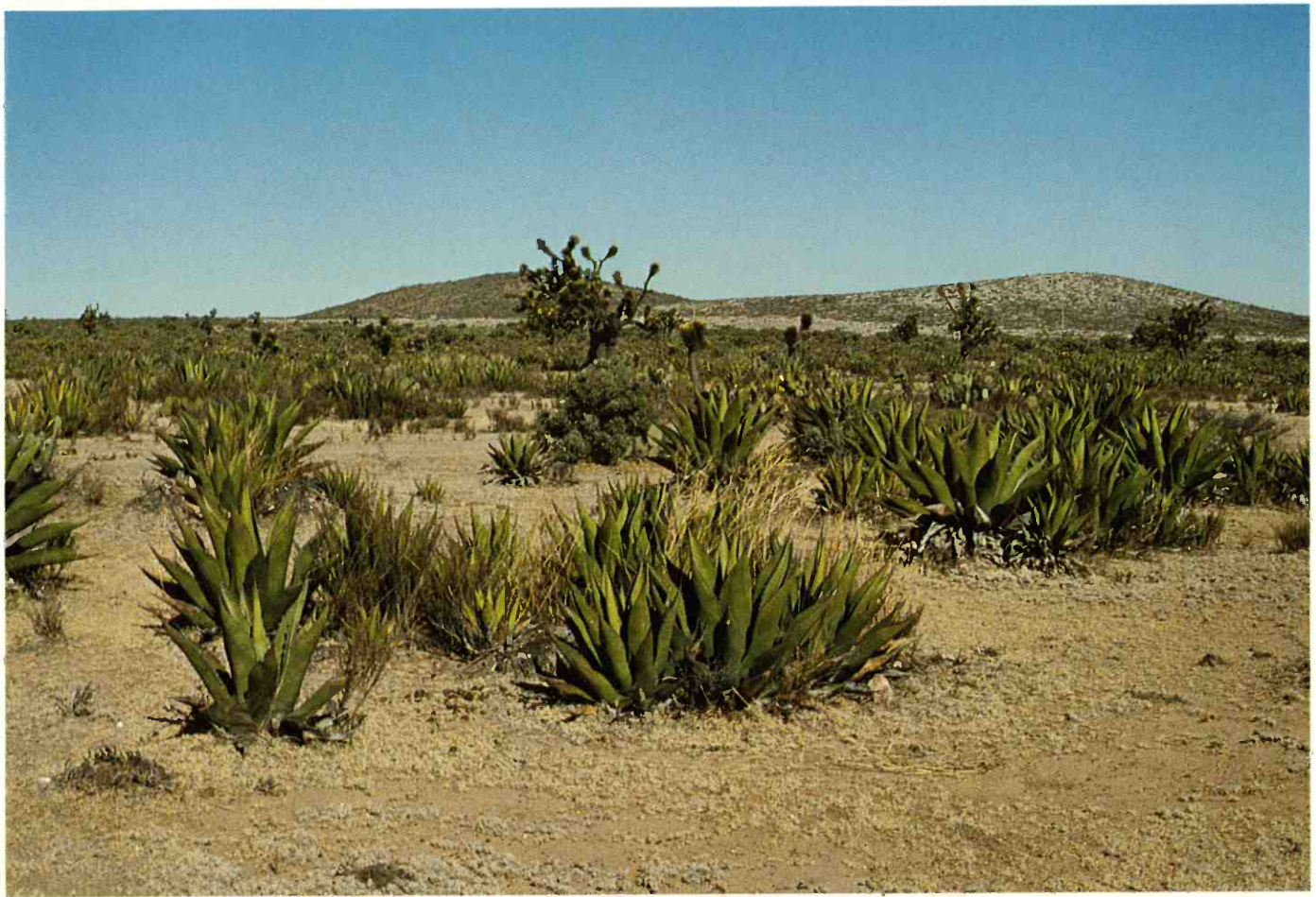
Figure 1. *View of the study site near Salinas de Hidalgo, San Luis Potosi, Mexico, showing maguey verde clumps in a matrix of degraded grassland vegetation. Offsets exterior to the clumps are subject to trampling and predation (see example at right) as well as soil compaction.*

The data were analyzed statistically using contingency table analysis. Further detail regarding the sampling methodology may be found in Martinez-Morales (1985).

Results and Discussion

A theoretical maximum value for biomass/area in this population of Maguey Verde is about 20 kg/m^2, based on a calculation for continuous cover by very large plants. Figure 2 shows how the 52 sampled clumps compared with this value. Over 90% of the clumps showed values equal to or less than 10 kg/m^2, while over two-thirds showed values equal to or less than 5 kg/m^2.

There was no correlation, either positive or negative, between offset density and biomass/area. Mean density was 0.4 offsets per square meter, and there was no great clump-to-clump variation. Thus there was little evidence either for the suppression of offset production or for enhanced offset survival in high biomass/area clumps. This may be because of lower survival rate in areas of higher production. Within-clump heterogeneity in terms of biomass distribution may also have obscured the results.

Results of the extensive sampling of sexually mature plants (Figure 3) show that most of the plants were surrounded by relatively little agave neighbor biomass, as
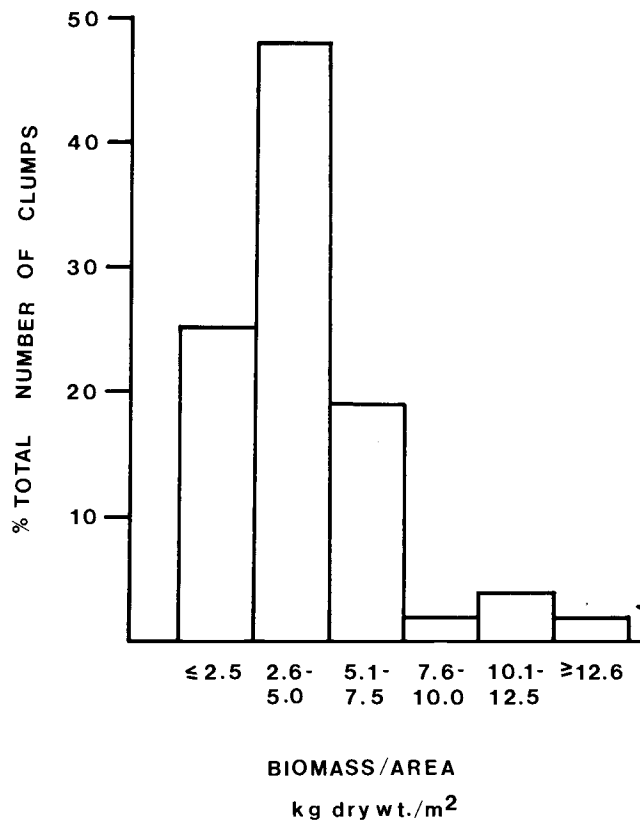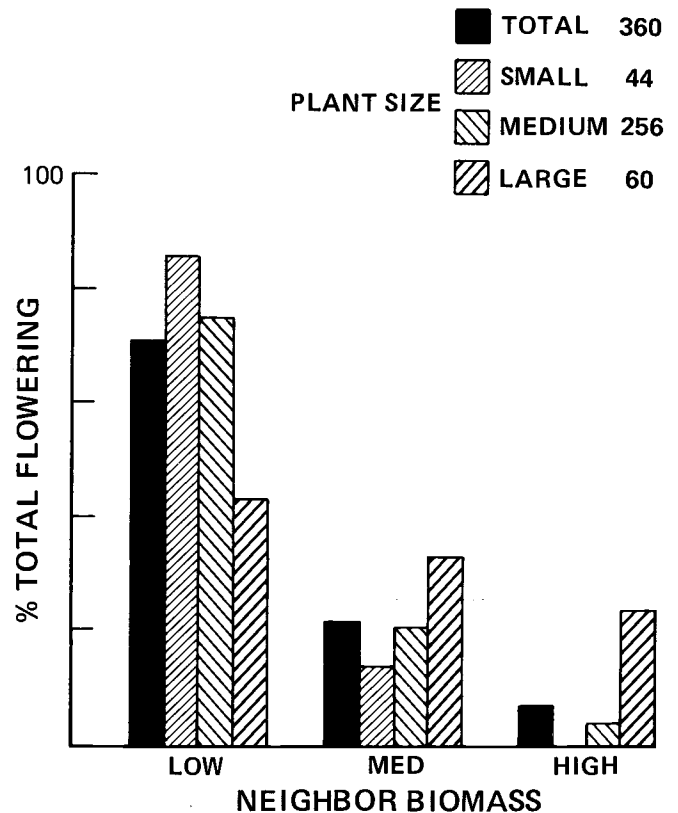
Figure 2. *Frequency distribution showing the proportion of nondestructively sampled clumps in each of six dry weight biomass/area categories.*

Figure 3. *The relationship between plant size at flowering and agave neighbor biomass, from an extensive sample of 360 sexually mature plants. Large flowering plants are significantly underrepresented in low neighbor biomass locations and overrepresented in medium and high neighbor biomass locations ($x^2 = 46.5$, $p < .005$).*

would be expected from the general biomass/area data. But in areas with medium or high neighbor biomass, large flowering plants were significantly overrepresented. This suggests not only a lack of competition but a positive intraspecific interaction. The growth advantage in dense groups seems to be related to improved soil conditions.

The biomass in an agave clump may be very unevenly distributed among its members, and the flowering and death of a large individual can lower the overall value considerably. Variation in time is therefore to be expected and different clumps would be at different stages in this cycle. But the low biomass/area in the groups with values less than 5 kg/m² is only partially explained by size class structure. Some other factor seems to be operating to keep the overall biomass/area low. The critical step may involve the production and survival of young plants.

We found no evidence of successful reproduction by seed, not a surprising result in view of the almost non-existent seed production under current management practices. Reproduction from seed could be important in the reestablishment of extinct clumps on a local scale as well as in the colonization of new areas and the maintenance of genetic diversity.

Vegetative reproduction by offsets seems to be a potentially adequate mechanism for the maintenance of already-established clumps. The mean density of 0.4 offsets/m²

was obtained in late summer, at the end of the main period of production. If there were no subsequent mortality and no further recruitment, this value could ultimately result in nearly continuous cover by large flowering agaves. But the evidence suggests that both year-by-year recruitment levels and offset mortality levels are high under present conditions. The size-class distribution of the overall population (Figure 4a) shows that new offsets (Size Class 1) constituted over 25% of the individuals present, while the subsequent size class contributed only 10%. Given a time-stable size-class distribution, this suggests high mortality for offsets.

Plants of virtually all size classes are capable of producing offsets (Figure 4b). In practice, however, most offsets are produced by plants of intermediate size classes, in spite of the somewhat higher production per plant in larger individuals (Figure 4c). The functional rhizome connection with the parent plant is short-lived, rarely persisting in offsets with a fresh weight of over 1 kg.

Possible causes of offset mortality were examined indirectly by assessing offset damage (Table 1) six months after the end of the season of maximum production. Over

The Tequila Industry in Jalisco, Mexico

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Abstract

In Jalisco, several liquors are extracted from plants of the genus *Agave* L. Tequila is the most important of these, because of its large national and international market. It is a major Mexican export product. In order to produce the various tequilas, the juices of *Agave tequilana* Weber are fermented, distilled, and prepared in various forms. The principal plantations are located between 20°30′ and 21° north latitude and 102°30′ and 104° west longitude and cover 16,000 hectares of dry-farmed lands with a warm temperate, semi-arid climatic regime. Over 50% of the factories are located in the Tequila region of Jalisco; these account for 80% of the world production.

Introduction

The use of *Agave tequilana* for the production of fermented beverages dates from pre-colonial times. The fermented juices were consumed by priests and nobles as part of religious ceremonies. The beverage was highly nutritious, being rich in proteins, but it was only mildly alcoholic (6%). The production of the distilled liquor itself has a history of over three centuries.

It appears that the first tequila factory was established in 1621. It was a clandestine operation. The manufacture of tequila was illegal, because it was economically threatening to the importers of Spanish distilled liquors. A century later, its production was regularized and placed under government protection. It became a factor of prime importance in the economy of Nueva Galicia, as the Jalisco region was then called (Unidad Editorial del Gobierno de Jalisco, 1980).

Presently in Jalisco, over 16,000 hectares are planted with Maguey Azul, a cultivated variant of *Agave tequilana*. Approximately 50 factories are dedicated to tequila production. In this paper, the process of tequila production is explained step by step, with emphasis on the most essential aspects. The information is based on an extensive literature review, ten visits to plantations for interviews with growers, and visits to eight tequila factories in the Tequila region.

Distribution and Taxonomy

Agave tequilana is cultivated in the states of Nayarit, Michoacan, and southern Tamaulipas, but most of the production is from Jalisco, where there are two producing areas, the eastern highlands and the central area respectively (Figures 1, 3). Within these areas the most important municipios (counties) are: Amatitán, Tepatitlán, Atotonilco el Alto, Tototlán, Arandas, Tequila, Zapotlanejo, El Arenal, Hostotipaquillo, Jesús Maria, Magdalena and Zapopan. Ninety percent of the acreage planted with Maguey Azul in Jalisco is included within these areas. The main area of production is in the highlands of eastern Jalisco, while a smaller area is centered around Tequila, northwest of Guadalajara (Secretaria de Agricultura y Recursos Hidráulicos, 1984). Altitudes vary from 800 m to 2,100 m, while annual precipitation varies from 700 mm to 936 mm, most of which falls in the months of June through October. Annual mean temperatures vary from 16.9°C to 24.8°C. The highlands make up 55.5% of the surface occupied by cultivated agave and are characterized by ferralitic soils. The Tequila area is characterized by well drained soils formed over volcanic pumice.

In general, only one species is utilized in tequila production, although it is possible that different varieties or forms have been selected over time, giving rise to the idea that more than one species is involved. Gentry (1982: p. 582) listed the following binomials as synonyms of *A. tequilana*: *A palmaris* Trel., *A. pedrosana* Trel., *A. pes-mulae* Trel., *A pseudotequilana* Trel., and *A. subtilis* Trel. These names are sometimes used to designate different varieties.

Cultivation

Maguey Azul has been cultivated since pre-Columbian times, and the fund of practical, empirically based know-

Figure 1. *Plantation of Maguey Azul near Amatitan in the center of Jalisco.*

Figure 2. *Young plants of Maguey Azul growing in nursery beds. Notice the side dressing of chemical fertilizer.*

ledge is considerable. In spite of its importance, there has been little scientific research on this aspect of tequila production. There are a few key studies, however.

One pioneer study (Pérez, 1887) states that the plant requires a dry climate and a soil fairly high in clay content. Soils that are too sandy or too calcareous prevent good growth and also reduce the sugar content of the *"piña"*. Another early study (Blanco, 1906) concludes that when conditions are too moist the plant produces less sugar, but that watering young plants hastens sexual maturity. Irrigation should then be suspended some time before harvesting. Modern growers say that the best land has reddish, light-textured soils.

Propagation

Propagation is carried out by vegetative means, using the offsets which are produced by the mother plants every year. These are extracted and planted in nursery beds where they are irrigated, fertilized, and otherwise well cared for (Figure 2). Once the plants are established and reach a fresh weight of at least 750g they can be transplanted to the commercial plantations.

Preparation of the Land

This operation varies according to whether or not other crops are to be interplanted. If interplanting with maize, beans, peanuts, or other annual crops is planned, the land must be prepared by plowing, disking, furrowing, and the excavation of pits, in order to create good conditions for
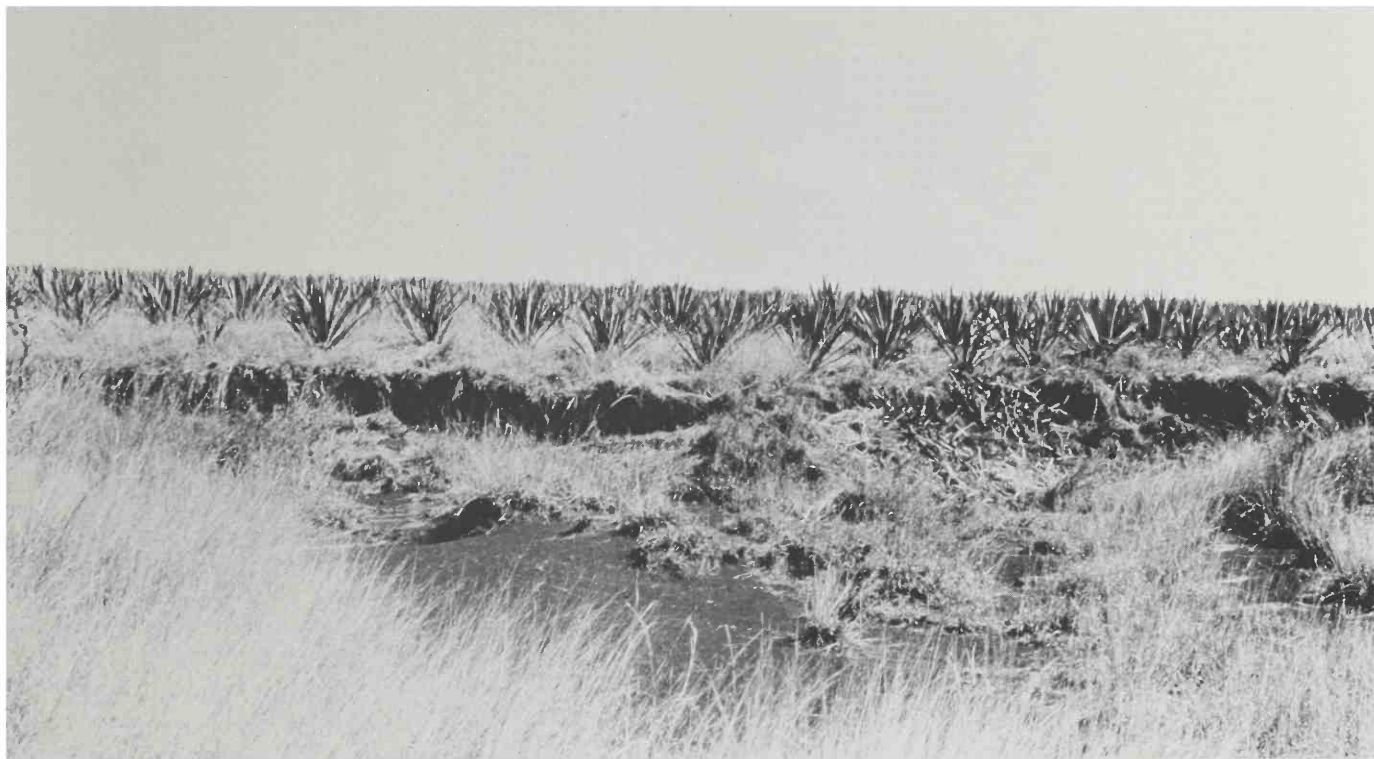
Figure 3. *Plantation of Maguey Azul in the highlands (Los Altos) of Jalisco.*

both the maguey and the annual crop. If the land is sloping, the initial preparation involves only clearing and pit excavation. When this is carried out along contour lines, it favors the formation of terraces where annual crops can later be planted. The topography also influences the sowing density. On steep slopes densities vary from 2500 to 3000 plants/hectare while on flat lands they vary from 3000 to 4500 plants (Sierra; 1973; Gómez, 1984).

Planting

The roots of the offset are almost always treated with a formol-water mixture and left to callus over for a month before planting, in order to prevent rot. Since maguey cultivation is a dry-farming operation (i.e., without artificial irrigation), the planting takes place during the rainy season. The offsets are placed in furrows 30 cm deep. The space between plants in a row is about 1.8 m, while the space between rows depends on the interplanted crop. In agave monoculture this distance is about 3 m.

Practices carried out in commercial plantations include chemical, mechanical, or manual control of weeds (Serrano, 1976), application of chemical or organic fertilizers and soil conditioners, and disease and pest control.

Inflorescence Removal and Pruning

The age at flowering is variable; the inflorescence bud may appear at any time after the fourth year. In order to prevent flowering, the young inflorescence *(quiote)* is cut off, a process called *"desquiote"*. This forces the plant to store its carbohydrates in the stem, which increases in size and becomes the *"piña"* which is eventually harvested.

Every year during the growth period the older leaves are cut off, and a few months before harvesting the tips of all the

leaves are removed. This is said to stimulate the concentration of sugars in the stem (Bustamante, 1984).

Harvesting

Harvesting is carried out when the leaf bases begin to shrink and become chlorotic and when a transverse cut through the inflorescene base reveals dense, close-packed tissue. All the leaves are cut off at the base, leaving behind the almost spherical stem *("piña"* or *"cabeza"*). This is pried out of the ground and delivered to the processing plant (Figure 4).

Industrial Process

The industrial process for the production of tequila is basically the same in all the factories, but relatively minor differences result in tequilas with slightly different flavors.

The constant aspects begin with the cooking of the *"piña"*, which converts the stored polysaccharides (inulins) to fructose and glucose. These are then extracted by milling and pressing the cooked material.

The sugars are fermented, usually in a mixture with 49% sugar from other sources (cane and sorghum), although tequilas made of 100% maguey sugar do exist. These are the tequilas most prized by connoisseurs. The fermented mash is then doubled-distilled, and the resulting liquor is subject to quality control analysis prior to its sale.

Cooking and Syrup Extraction

Cooking is carried out with steam heat, in traditional ovens or in stainless steel pressure cookers with cooking times of 48 and 12 hours, respectively. The cooked material is transported on conveyer belts to a mill where it is shredded with rotary knives and washed with potable water under

Figure 4. *Agave hearts from which most of the leaf material has been removed are referred to as* cabezas *or* piñas. *In this photo they are stacked in front of the* hornos *(ovens) just prior to heating. The treatment in the ovens converts complex polysaccharides to simple sugars: fructose and glucose.*
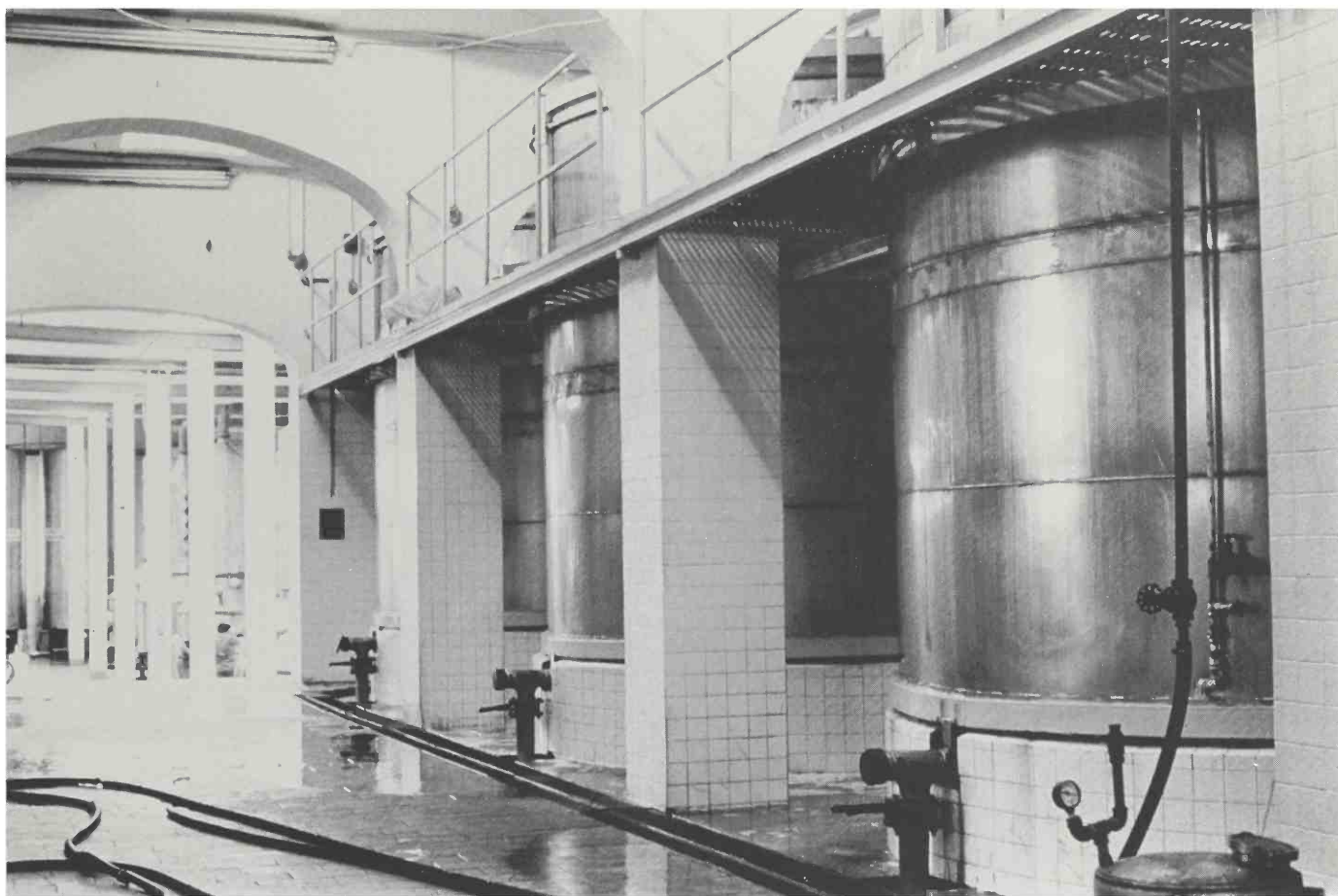
pressure to dissolve the sugars. Finally, the material enters a press where the syrup is extracted, leaving behind the fiber.

The fiber, or *"bagazo"*, is the first waste product of the industrial process (Figure 5). It is currently used as fuel, furniture stuffing, fodder for livestock, organic fertilizer, and in brick manufacture. The University of Guadalajara has experimented with other uses for this waste fiber, including silage, fiberboard (Nava, 1978), paper (Salcedo, 1961), livestock nutrient supplements (Guzmán, 1977), and cellulose (Daza, 1974). The results indicate that it has many potentially profitable uses.

Fermentation

This is the most important phase in the production of tequila (Correa, 1978; Avalos, 1982; Mendoza, 1977; Terrazas, 1976). The sugars are converted to alcohols, and other compounds, such as esters and aldehydes are formed. The yeast strains belong to the genus *Saccharomyces; S. cerevesiae* is the most commonly used species. The fermentation is carried out in vats, generally of stainless steel (Figure 6). The adjusted yeast culture and nitrogen and phosphorus nutrient salts are added to the sugary juices which have come from the press. In order to insure that fermentation is effective, factors such as temperature, pH, yeast strain and adjustment, type and concentration of nutrient salts and enzymes, and

Figure 5. *After milling to mechanically break up the heated* cabezas, *a press separates syrup from waste fiber,* bagazo. *Here a conveyor belt deposits the* bagazo *away from the press.*

Figure 6. In the fermentation tanks yeasts of the species Saccharomyces cerevesiae feed on the sugary juices from the press. Chemical fertilizers are added to the liquid to provide nitrogen and phosphorus to improve yeast action. The stainless steel vats pictured here are in the Cuervo distillery.

fermentation time are controlled. Each factory has developed a slightly different version of the process. The alcohol content at the end of this stage is 4-6%.

Distillation

As was mentioned earlier, two distillations are performed in the production of tequila. The first is called "breaking" and it consists of distilling the fermented mash (Figure 7). "Tequila ordinario" and "vinaza" are the products. The latter is considered a waste product, but has potential uses in human and animal nutrition and as fertilizer (J. Reza, personal communication).

The second distillation is called "rectification" and it consists of distilling the "tequila ordinario" to obtain "tequila rectificado", which has a higher alcohol content. The first and last volumes of this process, called "heads" and "tails", constitute another waste product, which is currently used as a solvent for paints. The primary product of the second distillation is sold as "tequila blanco". It may be exported in bulk or diluted to 90 proof and sold in the national market. It may also be subjected to additional treatments such as resting in oak casks (which yields golden tequila) or in containers which do not substantially change the flavor.

Before the tequila is sold it is subjected to quality control analysis to determine its proof and its content of methanol, higher alcolols, and other impurities (Sánchez, 1980).
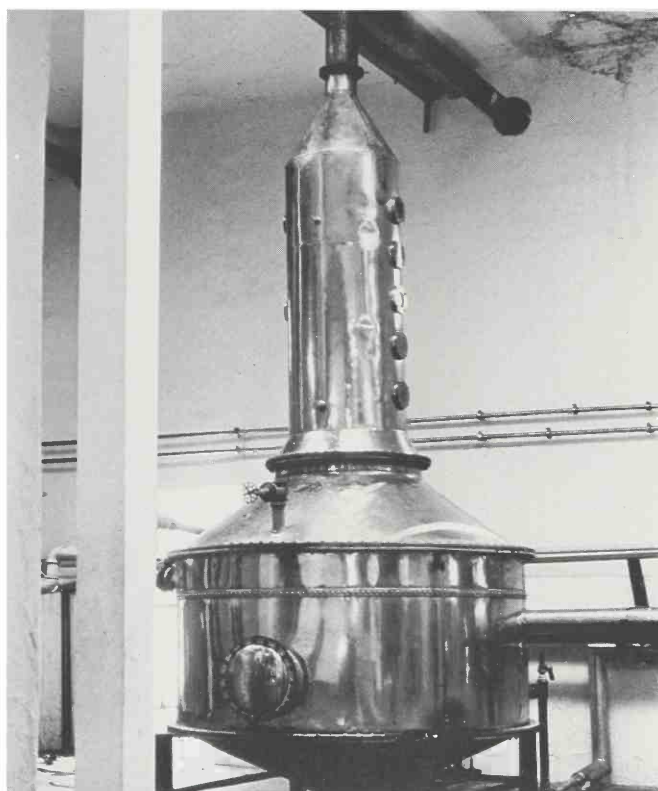
Figure 7. In this copper "breaking" still, tequila ordinario is separated from vinaza, the waste. A second distillation (termed "rectification") yields tequila rectificado of higher alcohol content and with fewer impurities. The beginning and ending fractions of the retification process, called "heads" and "tails" are used as a solvent for paints.

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Agave Research Progress in Yucatan

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Introduction

From the second half of the 19th century the northern part of the Yucatan Peninsula became a major producer of hard fiber from the cultivation of Henequen *(Agave fourcroydes* Lem.). This industry reached its peak in terms of production and economic wealth during the early years of this century. The advent of synthetic fibers during the 1940's inverted this pattern, however, to one of poverty and social problems that have weighed heavily on the area ever since.

Because of its very poor soil conditions and its socio-economic problems (which are beyond the scope of this paper), it has not been easy to find a substitute for Henequen in the *zona henequenera.* The industry therefore persists, in spite of the fact that low market prices and demand give a low added value to the fiber and that Federal Government subsidies are needed to keep it going. The Henequen industry, which represents the only source of subsistance for some 60,000 families could, however, become far more prosperous than it is at present if production could be increased and alternative uses found for its fiber and wastes, the latter representing 96% of the total biomass of the leaf.

The Center for Scientific Research of Yucatan was created by the National Council for Science and Technology (CONACYT) in 1979 with the mandate to carry out basic reasearch on a number of topics centered around the local flora and to propose alternative uses for some of the main plants. Because of their importance in Yucatan, the hard fiber-producing agaves were the first group of plants to be singled out for close study and continue to play a major part in our research.
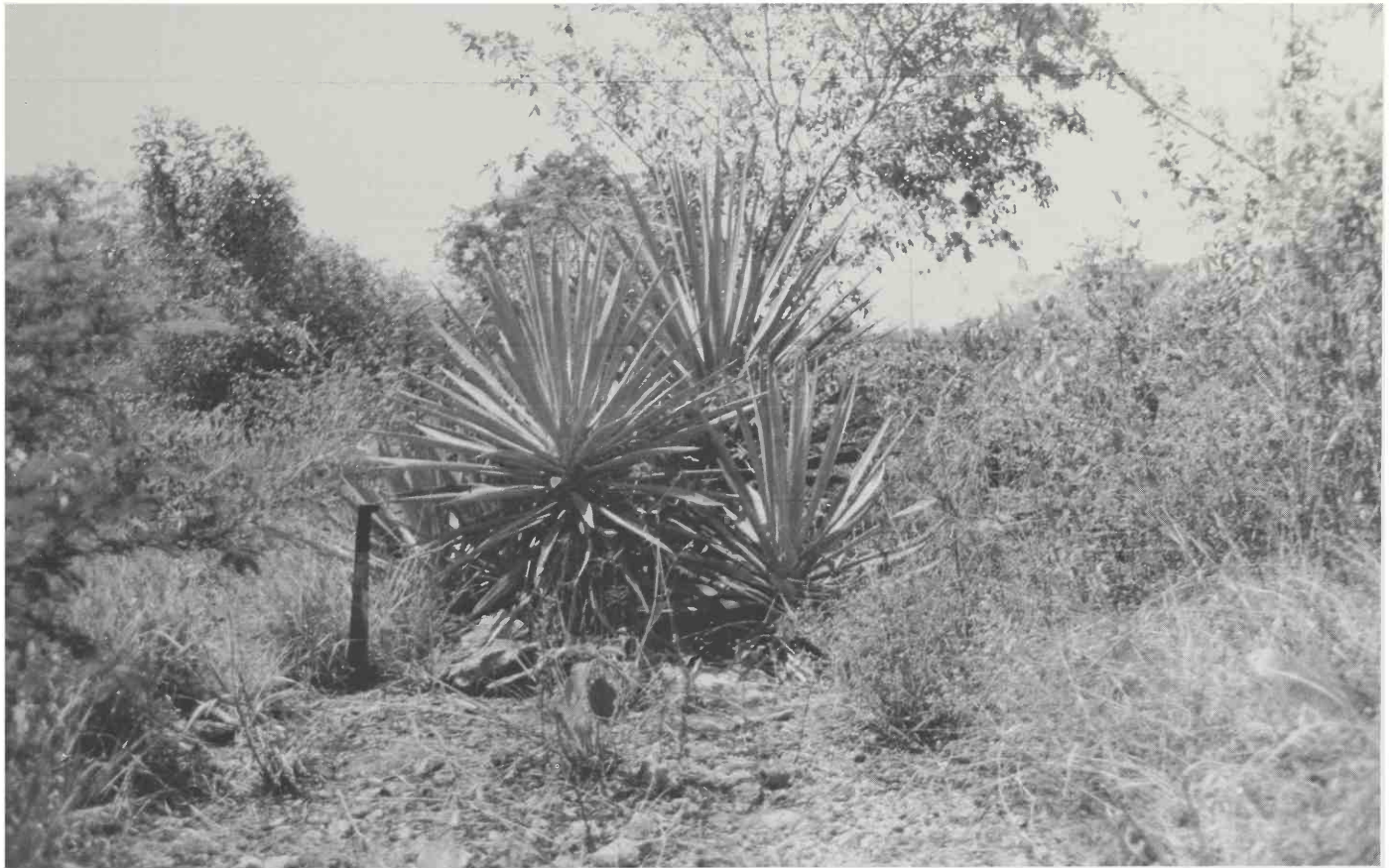
CICY is divided into four groups, namely Ecology, Applied Chemistry, Biotechnology and Genetics and Physiology which are doing research in the following areas: 1) biological studies, 2) alternative uses for fiber and agricultural wastes, and 3) genetic improvement.

In this paper we shall briefly discribe some of the work we have done at CICY concerning the Henequen problem and analyze the difficulties and perspectives which have emerged from it.

Discussion

Biological Studies. The Department of Ecology began studying the agaves of Yucatan in 1981, looking initially at their taxonomy. This group of plants has always posed problems for taxonomists because, according to Gómez-Pompa (1963), the genotype expresses itself in a wide range of phenotypic variants even within a single population, making it extremely difficult to distinguish between different species. Gómez-Pompa cites the following factors as causes of this variation: 1) high chromosome numbers, 2) polyploidy, 3) easy hybridization, and 4) efficient vegetative propagation.

The agaves of the Peninsula of Yucatan are no exception to this situation. The literature review brought to light wide discrepancies in the number of species reported for the region by different authors: the Maya nomenclature distinguishes 10 species; Roys (1931) reports five; Souza-Novelo (1945), eight, and Standley (1945) six. Amongst them there are two whose existence cannot be doubted: *Agave fourcroydes* Lem. and *A. sisalana* Perrine. However, there

Abstract

The Center for Scientific Research of Yucatan carries out research aimed at solving some of the problems posed by the henequen industry in northern Yucatan. This paper briefly describes CICY's main research lines related to the hard fiber-producing agaves: a) taxonomic studies are being pursued to obtain a better understanding of the flora of the region; b) tissue culture techniques are used for the genetic improvement of agaves, and c) studies of composite materials and chemical substances derived from Henequen wastes are being carried out as possible alternatives to cordage production.

Figure 1. *Differences in the morphological expression of the complex* Agave angustifolia *in the peninsula of Yucatan are apparently related to the climate and type of vegetation:* **Above:** *A population in the semiarid zone of the northern coast near Rio Lagartos.* **Below:** *Part of a population of low deciduous secondary tropical forest in the central part of the peninsula near Carrillo Puerto. A wide range of intermediate forms has been found which makes it impossible to fit them into useful taxonomic groups.*
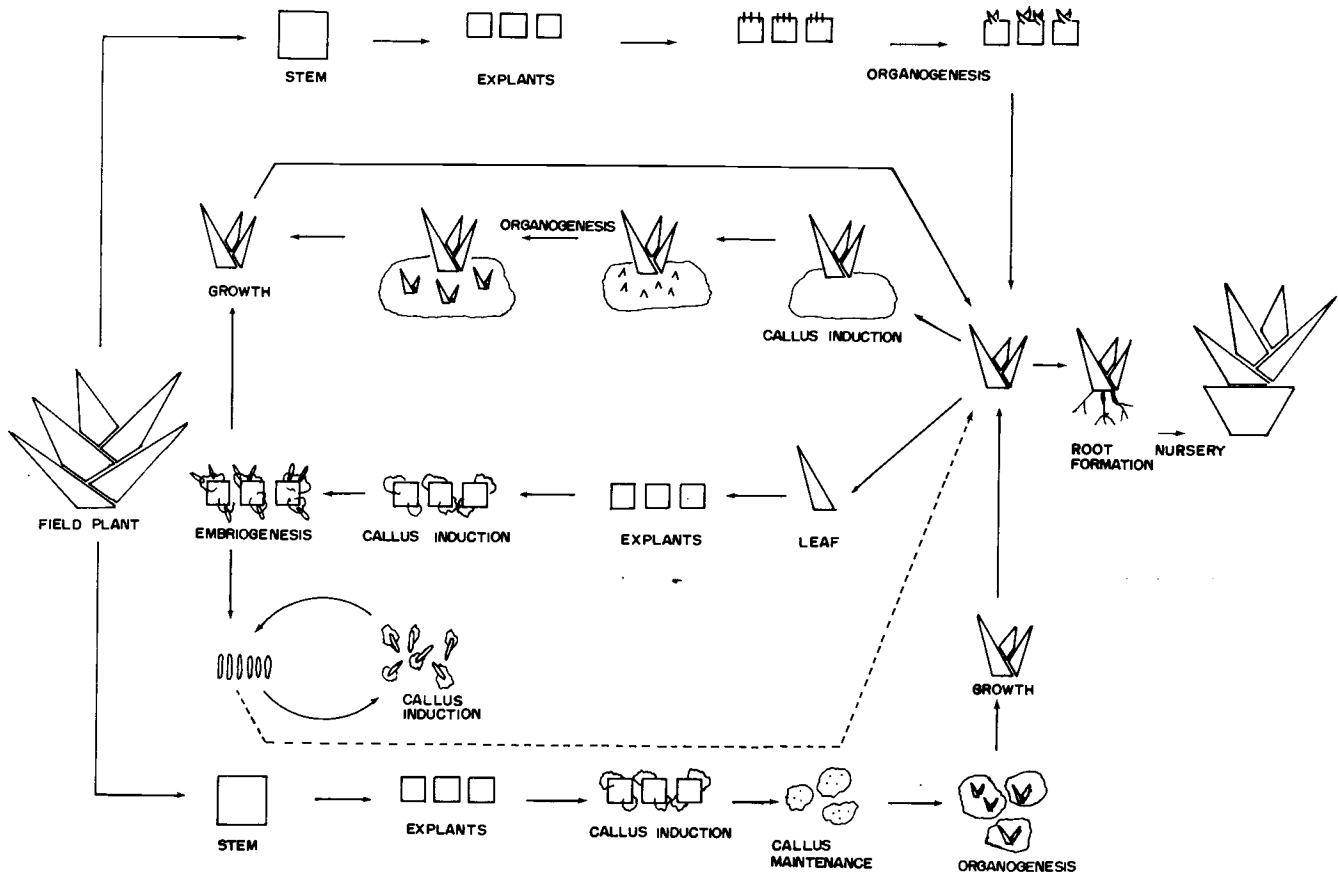
Figure 2. *Tissue culture of Henequen* (Agave fourcroydes).

are a great number of wild forms which do not fit the descriptions of either of these two species. Gentry (1982) has classified all of them as *A. angustifolia* Haw.

Originally, all the taxonomic studies were based on the morphological characteristics of the vegetative parts of the plants because, although they show the greatest degree of variation, they provide the basis for useful ecological descriptions. Orellana *et al.* (1981) found a wide range of phenotypic variation which seems to be largely caused by differences in the environment. For example, there is a direct relationship between the size of the plant and the climate and surrounding type of vegetation. The smaller forms are found in the semiarid zone along the northern coast of Yucatan, while the larger ones occur in the humid central and southern areas. In addition, microenvironments such as small outcrops of calcareous rock or areas which can be flooded modify the general pattern of variation.

The study of pollen grains has shown the same variation noted in the vegetative parts. Ludlow-Wiechers and Ojeda (1983) found that even when the ornamentation is constant there are five types of apertures, with as many as four different types being present in the same sample. The authors suggest that this variation is intimately linked to vegetative propagation and decrease in importance of sexual reproduction.

In his book *Agaves of Continental North America,* Gentry (1982) classifies all the wild forms of Yucatan as varieties of *Agave angustifolia.* Following Gentry's classification Orellana (1984) found two varieties of *A. angustifolia* in Yucatan *A. angustifolia* var. *marginata* Hort. and *A. angustifolia* var. *sargentii* Trel. He also mentions the existence of a third group which requires further study in order to decide whether it should be classified as an existing variety or should form a new one.

Orellana (1984) has also made a complete inventory of the species of the family Agavaceae found in the Peninsula of Yucatan. Following Hutchinson (1934), he reports the existence of 21 species belonging to nine genera and five tribes of which nine are native and 12 are introduced.

Ojeda *et al.* (1984) carried out the pollen analysis of the same species but their results correspond more closely with the classification proposed by Takhtajan (1980). They, however, recommend further studies of different genera of the same family and comparisons with genera from the Amaryllidaceae and Liliaceae before any definite conclusions are made.

Genetic Improvement Through Tissue Culture.
Plant tissue culture techniques offer an alternative for those species which, because of their biological characteristics, are

Dedication—
This issue of Desert Plants is dedicated to Dr. Howard Scott Gentry, high priest of Mayahuel and Agave scholar extraordinary.

Right. *On the trail, Sierra de las Palmas, southwest of San Bruno, Baja California Sur, June, 1973.* Nolina beldingii *(Agavaceae) is in the background. Dr. Gentry's search for Agave taxa has taken him to remote regions of Mexico. Photo by John McClure.*

This group of participants at the 1985 Symposium on the Genus Agave *had been talking in the patio of Desert Botanical Garden between the herbarium, library, and auditorium when they were asked to face the camera. Left to right, R. Martinez M.; J. Tello B.; S.E. Meyer; T.L. Burgess; M.L. Robert; R.G. McDaniel; H.S. Gentry; D.J. Pinkava.*

Aspects of the Reproductive Biology of Agave lechuguilla Torr.

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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.
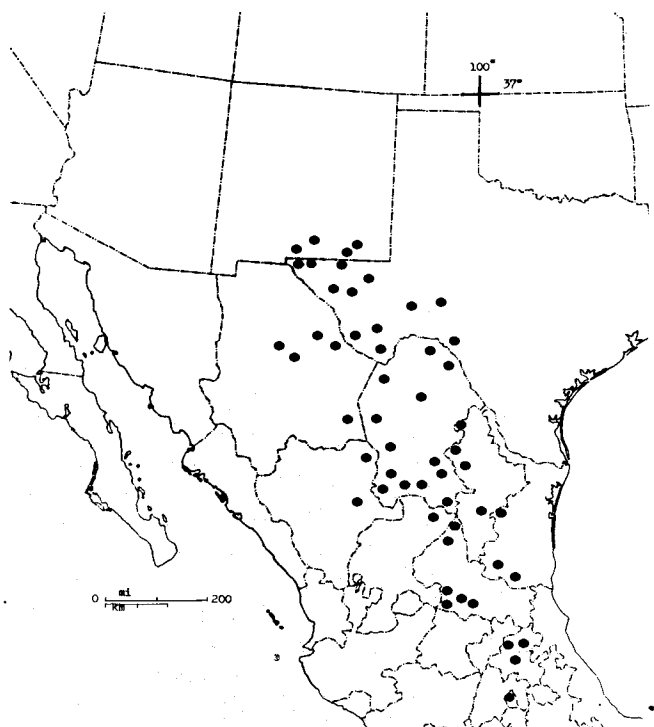
Introduction

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

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

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%)

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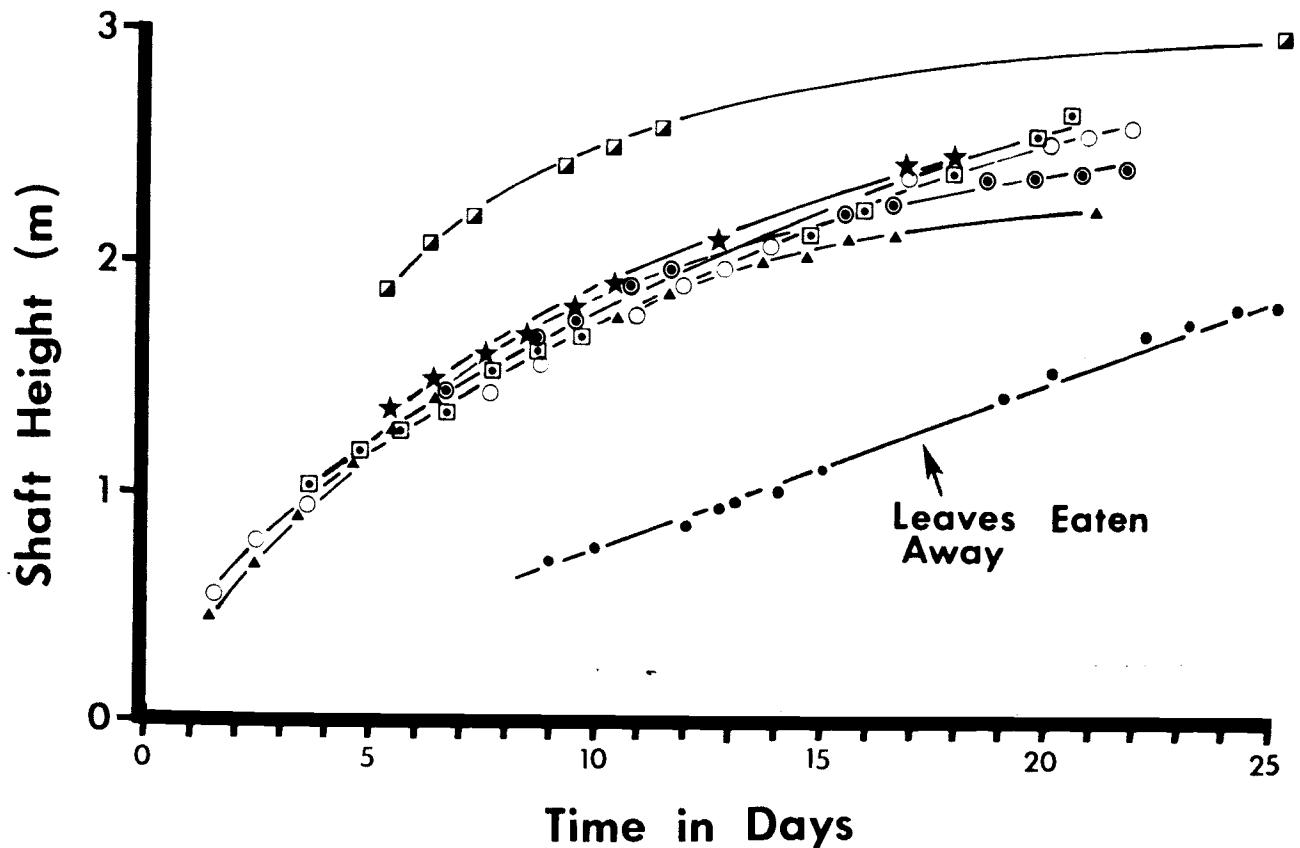
Figure 3. Agave lechuguilla *inflorescence shaft growth with time.*

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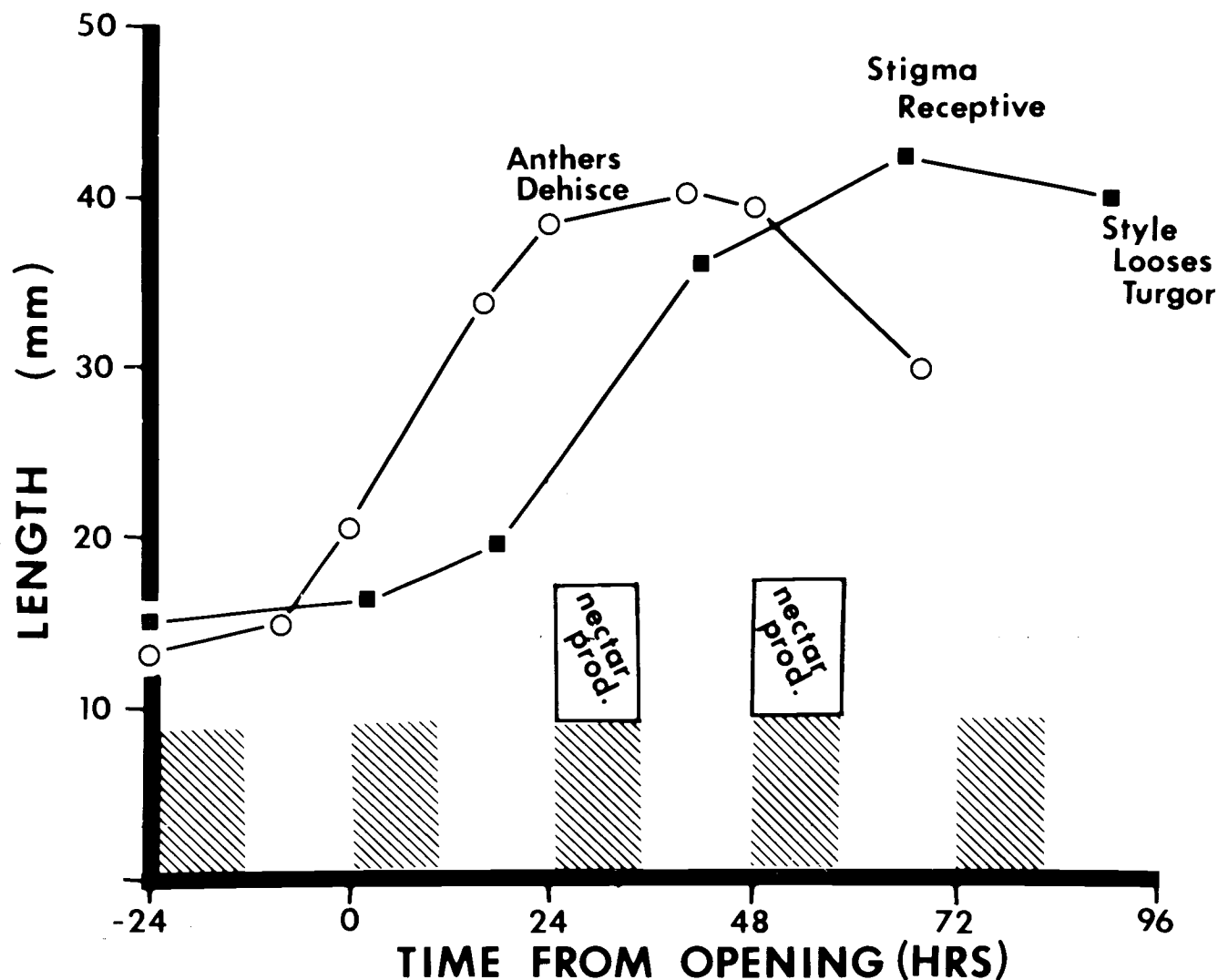
Figure 4. *Floral schedule of* Agave lechuguilla. *Symbols: open circles are the mean of filament length measurements, closed squares are the mean of style length measurements. Time zero represents the mean time of flower dehiscence (4 to 8 p.m. M.D.T.).*

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
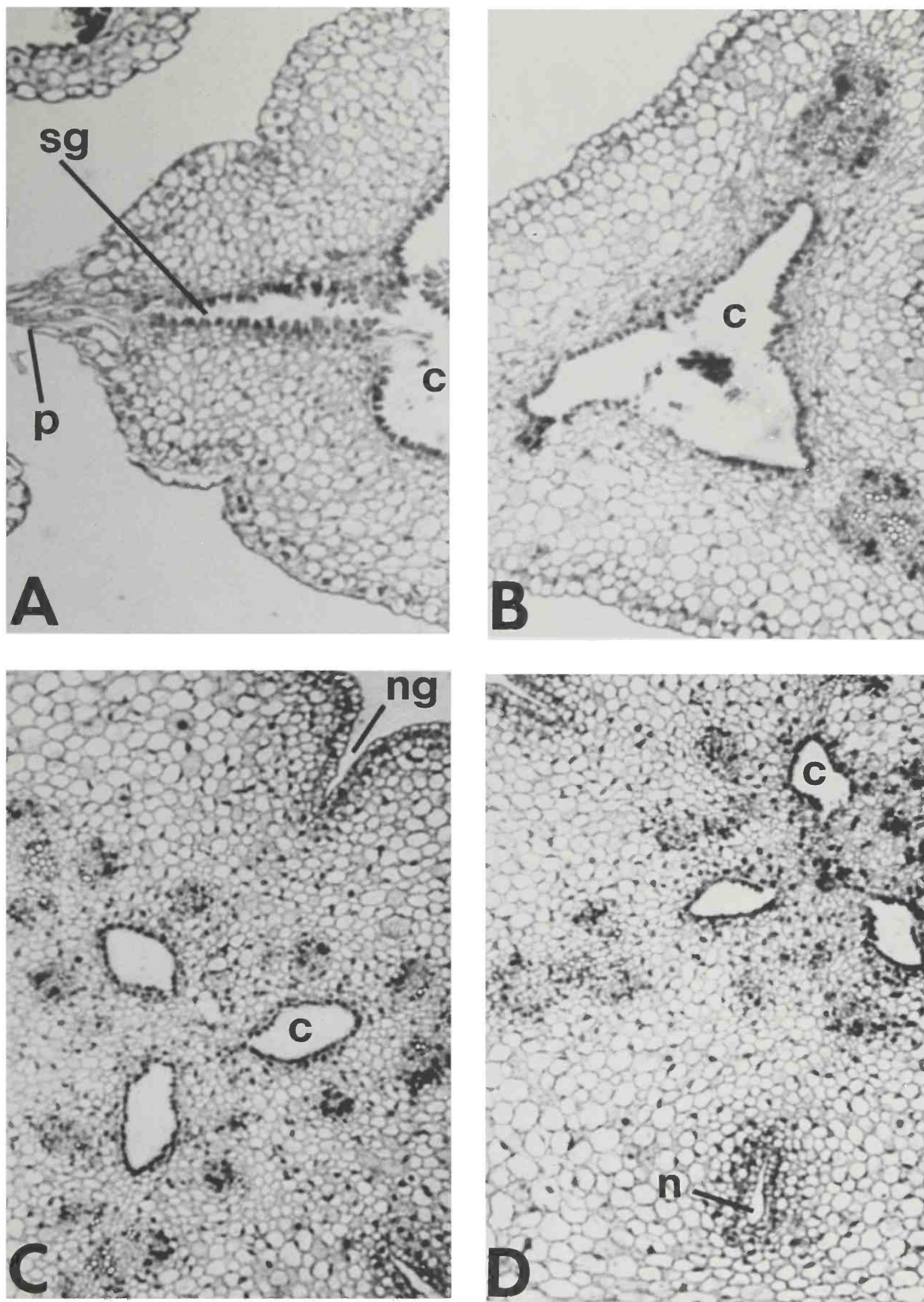
Figure 5. *Cross sections of* Agave lechuguilla *flowers.* **A:** *stigma region, showing one of the three stylar grooves (sg), papillae at the stigmatic surface (p), and the stylar canal (c).* **B:** *cross section of the style showing the triangular canal (c.).* **C:** *the base of the style near the 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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The Mezcal Industry in the Altiplano Potosino-Zacatecano of North-Central Mexico

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Abstract

Agaves play an important role both ecologically and economically in the San Luis Potosi-Zacatecas region. This study describes the principal use of one of the wild species, the manufacture of the distilled liquor *mezcal*. The resource is currently overexploited, resulting in dwindling supplies of raw material. This is in turn sub-utilized, since harvest practices are not carried out in an organized manner and the technology used in *mezcal* manufacture is antiquated and inefficient.

Introduction

Pulque and Mezcal were consumed in great quantities by the indigenous people during colonial times (Cué, 1979; Guerrero, 1980). The latter was developed in Mexico after the introduction of distilling technology by the Spaniards and Filipinos during the Sixteenth Century (Bruman, 1935, 1940, as cited by Bahre and Bradbury, 1980; Guerrero, 1980). During the era of the viceroyalty a flourishing agro-industry based on mezcal liquor was established, with countless haciendas dedicated to its production and, since large profits could be gained, considerable areas were devoted to maguey cultivation (Bazant, 1975; Cabrera and Cabrera, 1978).

The mezcal industry continues to provide great economic benefits to the present day, in spite of the fact that mezcal production has diminished due to lack of raw material because of over-exploitation of wild populations and due to socioeconomic problems (Gonzalez and Scheffey, 1964).

With respect to the mezcal manufacturing techniques which were used in earlier times (Payno, 1864, as cited by Segura, 1901), the processes of cooking, milling, fermentation, and distillation were different from those used today, although the principles remain the same. The old-fashioned still was of the "drip" or "bell" type and its form determined the name of the mezcal produced, "vino de chorrera" or "vino de campanilla." Bye (1979) also gives an account of these processes, while Tello (1983) does the same for the production of "mezcal campanilla." The bell-type still is analogous to the stills used by the Huichol and Cora Indians of Nayarit and Jalisco (Bahre and Bradbury, 1980), which are of the Asiatic type with an internal receptacle. It is also similar to the modified form used in Sonora in the elaboration of mezcal "bacanora." These forms of distillation are still practiced as part of moonshine operations (Bahre and Bradbury, 1980; Tello, 1983).

Materials and Methods

The object of the present study was to describe mezcal production as it takes place today in the Altiplano Potosino-Zacatecano (Figure 4).

In order to obtain information, the general method selected was direct interview with emphasis on concrete knowledge with informants selected by judgement, as proposed by Hernandez and Ramos (1977) and modified by Aguirre (1979).

The method was applied in five of the six local mezcal factories within the study area. The information was organized according to the following sequence: (a) the descriptions and explanations were registered in a field notebook, (b) the field information was reorganized into field data files, (c) the field data files were organized by cross-reference according to practice and locality. In this
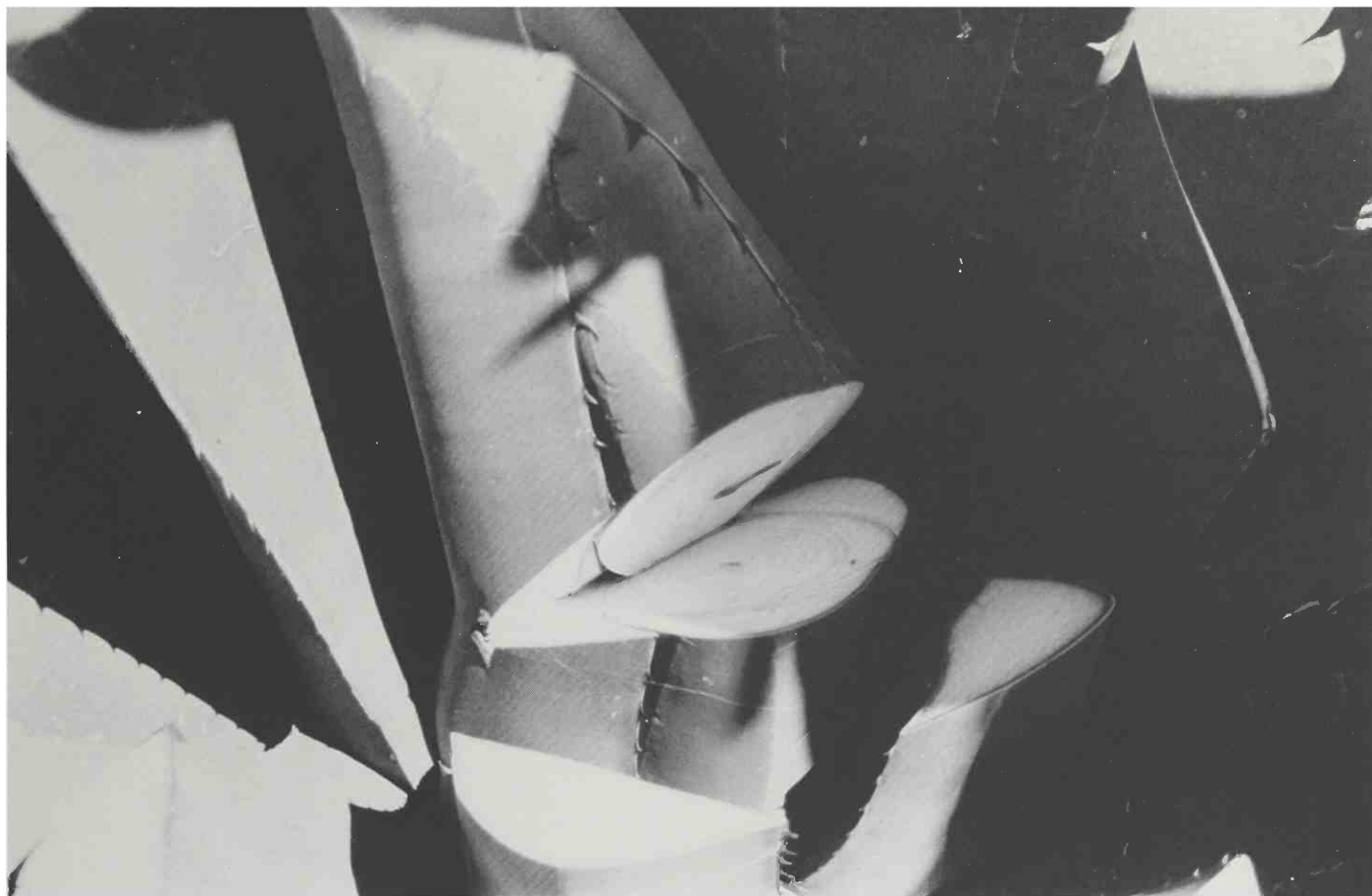
Figure 1. *A worker referred to as the* picador *searches for plants of Maguey Verde suspected of being ready to flower. He verifies that reproductive processes have been set into motion by cutting the bud and looking for a central orifice (dark spot in photo). If this is found, the physiological chain of events has begun which will translocate polysaccharides from the extremities of the leaves into the plant base to be used in producing the massive flower stalk. After verifying that the central orifice is present, the worker then "castrates" the plant by prying out the embryonic reproductive structures to prevent flowering.*

way it was possible to refer easily to the information in the preparation of the final report.

Results and Discussion

The principal zone of mezcal production in the study area is located to the northwest of San Luis Potosi, between 22°20′ and 22°38′ north latitude and 101°15′ and 101°42′ west longitude. Another small area is located to the northeast of Charcas, San Luis Potosi, at 23°08′ north latitude and between 100°45′ and 101°00′ west longitude.

The plant used as raw material for mezcal manufacture is commonly called Maguey Verde and belongs to the taxon *Agave salmiana* Otto ex Salm, ssp. *crassispina* (Trel.) Gentry. It occurs in the wild state at densities between 1138 (González, 1982), 1584 (Tello and García unpublished), and 2775 (López *et al.*, 1979) plants/hectare. It is also used intensively for livestock forage, construction, and as human food ("*aguamiel*" and "*golosina*"). It is planted as an ornamental and hedge plant.

Presently almost all the extensive wild populations of Maguey Verde are found on communally held (ejidal) land. The mezcal factories are mostly private companies which contract with the ejidos for the supply of the raw material, since these companies are staffed only with the workers needed for the actual manufacture.

Maguey Cultivation Practices

Replanting. Replanting activities are carried out only minimally. Government programs involve contour-planting in rows, while the mezcal factory programs involve planting in mounds. Offsets for planting come from nearby wild populations and vary from 30 to 60 cm in height. In row planting the distance between plants is 2 m and between rows approximately 8 m, with a density of 650-700 plants/hectare. In mound or pit planting the plant-to-plant distance is 1.5 m and the distance between strings of mounds varies from 1.5 to 4 m.

Figure 2. *The* hombre *wielding this extremely sharp* fierro desvirador *locates plants of Maguey Verde which have been "castrated" for about twelve months. By this time many of the polysaccharides which would have gone into forming the flower stalk engorge the base of the plant. Using the* fierro desvirador *and a machete, the worker removes the projecting portions of the leaves which now have been drained of much of their energy.*

Figure 3. *The* cabeza *(also termed* piña *because of its pineapple appearance) is obtained by means of a* barra tumbadora *which is used to strike at the base of the plant until the necessary leverage is gained to break it free from the soil. Usually two men, the* tumbadores, *remove the* cabezas *cut by a single* desvirador. *Together the three* hombres *constitute the team of workers known as the* rajadores.
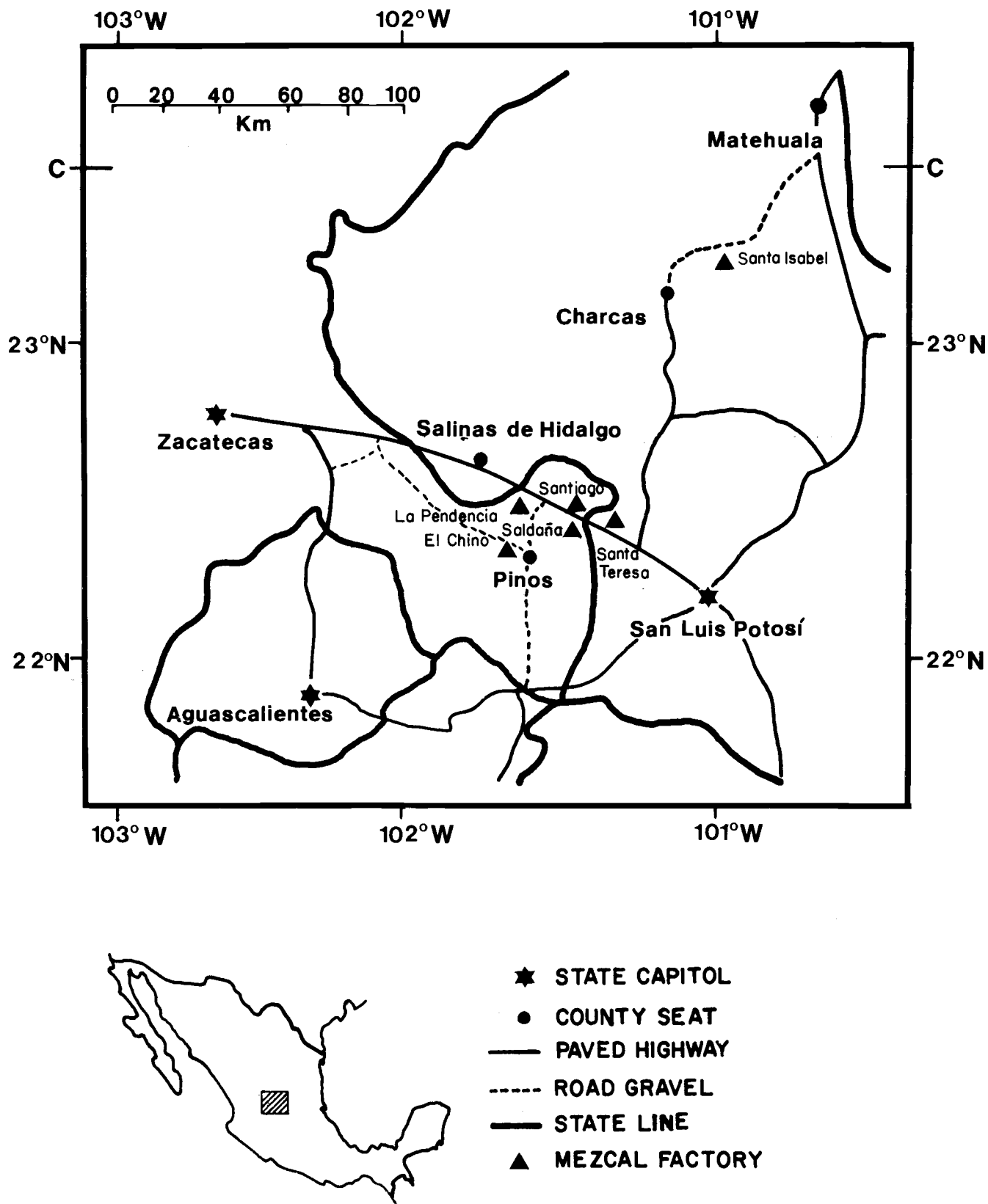
Figure 4. *Location of mezcal factories in the Mexican states of San Luis Potosi and Zacatecas.*

Castration. The castration or *"picazon"* of the maguey is a fundamental activity for obtaining raw material of top quality and consists of removing the inflorescence bud. The object is to halt the flowering process while still encouraging the transport and storage of nutrients in the *"piña"* (stem and leaf bases) of the maguey.

The job of the *"picadores"* (the people in charge of the castration) is to locate the plants which are ready to be castrated by considering certain morphological characteristics of the plant. The best indicator is that the terminal spine or *"pua"* of the central bud should be small, slender, and black. A plant with this characteristic is called *"maguey acarrillado"* and is eight to eleven years old, depending on site conditions.

Once the plant is identified as ready, a knife is used to remove enough leaves from one side to provide the necessary work space for removing the central bud, which is cut off transversely as close to the base as possible, revealing in its central portion a hollow circular orifice (Figure 1). This orifice is proof of the readiness of the plant. Castration without it simply damages the vegetative meristem and results in the premature death of the plant. Noting the orifice, the *"picadores"* proceed to force back the white leaves of the bud base with a prybar (*"palanca"*) until they are able to extract the nascent inflorescence.

The period during which the plants remain castrated prior to their harvest (*rajado*) is variable, depending on the policy of the particular mezcal factory. The minimum recommended period is 18 months, which provides time for the full "seasoning" or "fattening" of the *piña* with the carbohydrates which would have been destined for the inflorescence. The common practice is for a period from six to twelve months. Castration may be carried out at any time during the year.

Collection and Transport

The people in charge of collection are called *rajadores* and usually work in teams of three. The *desvirador* is in charge of locating the castrated plants and removing the majority of the leaf tips with the aid of a *fierro desvirador* and a machete. The two *tumbadores* are in charge of extracting the *piña* from the soil by means of a *barra tumbadora* which is used to strike at the base of the plant until the necessary leverage is gained to break it free from the soil. After this the *piña* is trimmed of excess leaves and otherwise prepared for transport (Figures 2-3).

Some mezcal factories do not practice castration, utilizing plants with young inflorescences or plants which were castrated after the emergence of the inflorescence. These practices represent poor utilization of the raw material.

The monthly extraction of wild maguey plants for the production of mezcal is estimated at 50,000. Table 1 shows some characteristics of the components of harvested castrated plants.

Industrial Processes

Baking or Cooking of the *Piña*. Once the *piñas* which contain starchy reserve carbohydrates are subjected to long cooking, the more complex substances are broken down to simple mannose sugars. In this state, the *piña* is known as *mezcal.*

The cooking ovens are made of stone (Figure 5) generally with vaulted interiors and a basal grillwork of concrete or

Table 1. Characteristics of magueys harvested after 12 months of post-castration seasoning in the ejido of Caballerias, Villa Hidalgo, Zacatecas (n = 50).

Variable	Mean (Kg)	Standard Deviation (Kg)	Minimum (Kg)	Maximum (Kg)
Plant weight	111.2	51.4	36.0	247.5
Piña weight	65.8	31.9	21.0	166.0
Total leaf weight	45.0	23.4	8.0	110.0
Leaf number	25.3	7.0	10.0	42.0
Offsets < 60 cm	2.2	2.0	0.0	0.0
Offsets > 60 cm	0.8	1.2	0.0	0.0

wooden beams. Beneath the grill are the burner or the steam discharge tube and the catchment basins for run-off. The ovens have a front door for loading and unloading (or sometimes a front door for unloading and back door for loading) and they are provided with a circular hole above which is used to stuff in more *piñas* once the first installment has settled in cooking. Stone ladders or earth ramps are used to lift up the *piñas*. Oven capacity varies from 20-60 metric tons.

There are two types of cooking. The more rustic method uses direct flame in the lower part of the oven while the other method uses steam. The *piñas* cook from three to five days. In this period they produce run-off juices called *guixi*. Those produced during steamheating are collected and purified by boiling, while those produced by flame heat, which are limited in any case, are discarded, since they are contaminated.

The people in charge of cooking are called *faineros* and those in charge of removing the mezcal are called *hechadores fuera* (Figure 6).

Milling. The mezcal is broken into pieces with axes in order to facilitate the milling process. There are two milling techniques. The more traditional is the stone mill (Figure 7), which consists of a "ring" or circular base of stone and cement with a slightly inclined peripheral groove in which the syrup collects and of a circular stone above, 1.7 m in diameter and 0.5 m thick, which has passing through its center a bar. One end of the bar rotates in a fixed point at the center of the ring while the other is attached to a traction source, which may be a team of oxen (Figure 8) or a tractor. The mezcal is placed in the ring; the syrup is extracted through rotary motion of the stone and is conducted by channels to the fermentation tanks. The *bagazo* (solid material) is washed in order to extract the maximum amount of syrup. The simplest but least adequate method is to wash the material *in situ* on the millstone; another method involves rinsing in vats followed by extraction in a steam-driven press. The other milling technique uses an electric press (Figures 9-10) with two conveyer belts, a shredder, and two sets of press rollers. The syrup extracted the first time through goes to the storage tanks, while the *bagazo* is given three more passes, adding water each time. The concentration of the combined syrup as measured by a Baume density meter is 6-8 degrees.

The *bagazo* is accumulated in the courtyard of the mezcal factory. It is burned or used for livestock forage. The people in charge of the milling process are called *molineros*.

Figure 5. *The ovens (los hornos) used for processing the Maguey Verde occupy this stone structure. The cabezas are fed in through the arched entryways.*

Figure 8. *Bovine power has traditionally been harnessed to power the stone mezcal mill. Sometimes nowadays a tractor will be hooked to the stone wheel instead.*

Figure 6. *The hombres in charge of cooking the cabezas are termed faineros. Others who remove the cooked product are referred to as hechadores fuera.*

Figure 9. *Some mezcal factories now use electric presses in place of the traditional stone mill. The bagazo (fiber) is washed three times.*

Figure 7. *The cooked mezcal is hacked into pieces with axes and crushed with a large stone wheel. Those in charge of this milling process are termed molineros.*

Figure 10. *This electric press consists of a large conveyor belt, a shredder, a small conveyor belt, and two sets of press rollers.*

Fermentation. The syrups obtained from the oven run-off, the milling and the washing are pooled for fermentation in vats, which may be of stone or cement but which are most commonly lined with wood in order to isolate the corrosive effects of the fermenting syrup, in addition to maintaining a more constant temperature. There are two types of fermentation, natural and accelerated. In the first type, the syrup is fermented without the introduction of seed or starter; fermentation time is three days. In the accelerated type, a seed liquor or *xinantli* and a *puño* (handful) of ammonium sulfate are added to the syrup, which shorten the fermentation time to 12-24 hours.

Distillation. The fermented syrup is conducted in several loads to the copper still (Figure 11). This consists of a boiler in which is placed the fermented mash, above which is located the receptacle which collects the vapors and conducts them to the refining plates and later to the water-submerged coil in which they cool and liquify. There are two methods for evaporating the syrup, direct flame using pressurized kerosene and steam-heating by means of a coil within the boiler.

Not all the mezcal factories carry out quality control in the distilling process. When it is carried out, the following method is used. The first flow from the still is called the "head"; when this "breaks" (arrives at some 80°GL or 160 proof), the *alambiquero* (distiller) sets aside the first ten liters, as these contain high levels of methanol. This contaminated liquor as well as the "tail" of each run, which is of too low proof, is reincorporated in order to be redistilled in the next run. The usable fraction is maintained at 45°GL (90 proof).

Total mean daily mezcal production is about 800 liters. It is sold bottled and in bulk locally and in certain large cities in various parts of Mexico. Demand for the product varies considerably with the season of the year, increasing in winter and decreasing considerably in the warmer months of April, May, and June.

Conclusions

The present practices represent a form of natural resource utilization which dates from much earlier times and which employs a technology best described as inefficient and antiquated. But the resource has considerable potential. It provides income for the people in control, but with the danger that the very source of the income could itself disappear. A planned use of this resource, based on the biology of the plant in combination with the empirical knowledge which already exists, could result in integrated long-term utilization.


Figure 11. *The* alambiquero *(distiller) who operates this still produces about 800 liters per day. He sets aside the first ten liters (the "head") because of the high methanol level and the last few liters (the "tail") because of the low proof. Often the head and tail are mixed back into the next run, however, until the methanol level becomes excessive, as judged by how a sample purses the lips of the* alambiquero.

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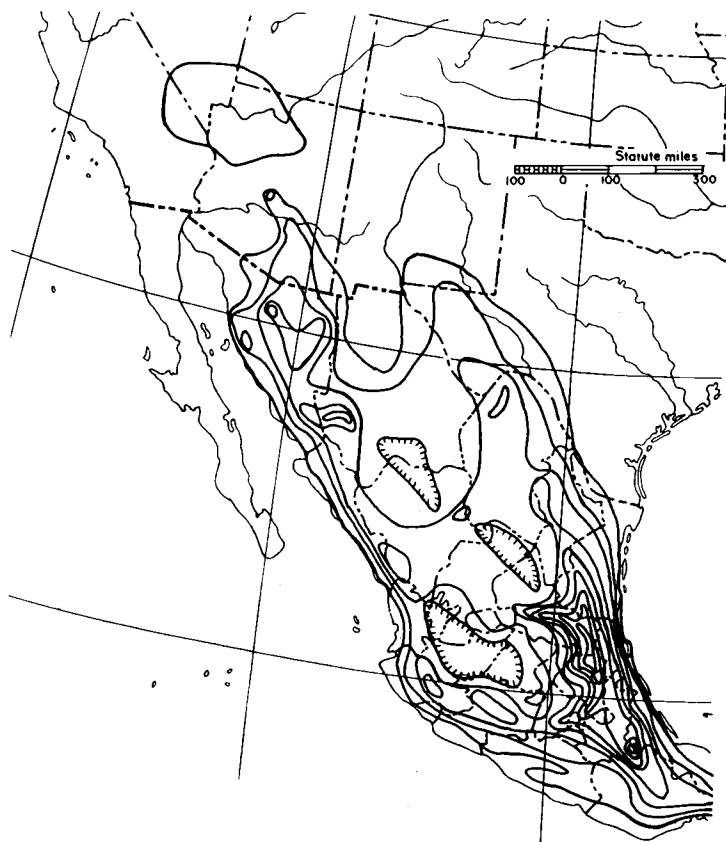
Figure 3. *Species abundance contour map of* Agave *subgenus* Littaea. *Contour interval equals one species.*
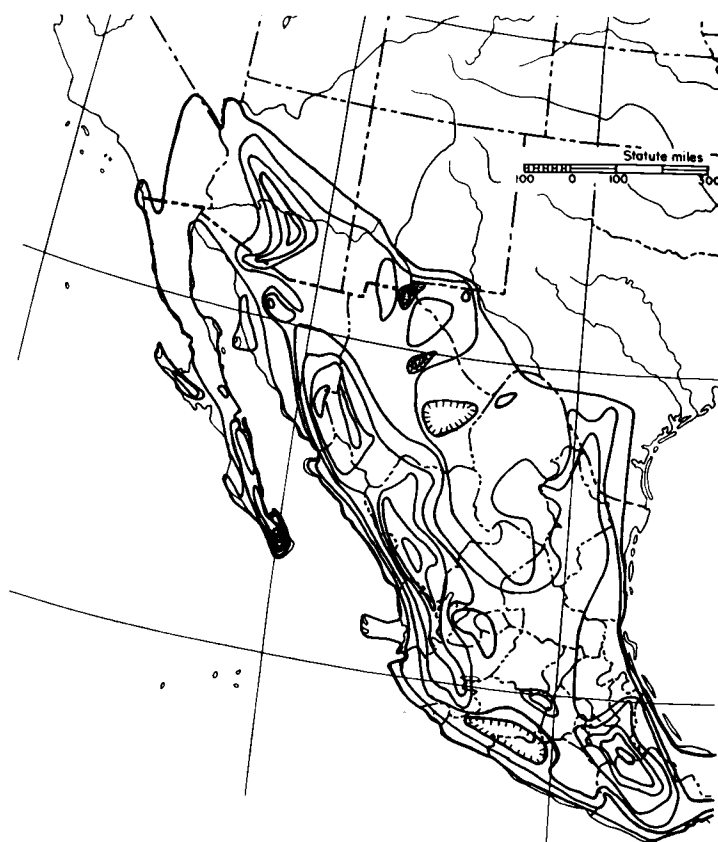
Figure 4. *Species abundance contour map of* Agave *subgenus* Agave *(excluding group Salmianae). Contour interval equals one species.*

# Conservation of Southwestern Agaves

Littaea) is "a remarkably distinct plant with no close relatives" and speculates that it may be a viable hybrid of *A. kerchovei* Lem. (subgenus *Littaea*) and *A. marmorata* Roezl (subgenus *Agave*). This would be one of the reticulations in the higher-order phylogenies Burgess and I envision; where two diverging but related groups of species cross reproductive barriers and exchange genetic information. It could also be an intermediate link between the two subgenera. In either case, it would make an ideal subject for further documentation and, if necessary, for recognition and preservation through the Endangered Species Act. Similarly, *Agave arizonica* represents another exchange of genetic information between the two subgenera; another "reticulation" in the evolutionary web. On the other hand, *Agave schottii* var. *treleasei* is more likely to be a single inviable hybrid or polyploid clone not involving an important evolutionary event.

The overwhelming array of species, subspecies, and varieties in complex groups makes application of the Endangered Species Act unavoidably arbitrary in some cases but some very useful perspectives can be achieved by assessing the group as a whole, sorting out the significant from the insignificant. My species abundance mapping approach and emphasis on reticulate evolution is one way of setting priorities and targeting potentially important taxa for conservation efforts. Others may be equally valid, or even better, with other groups. In the Southwest, genera such as *Astragalus* and *Eriogonum* and even whole families such as the Cactaceae lend themselves to this sort of approach.

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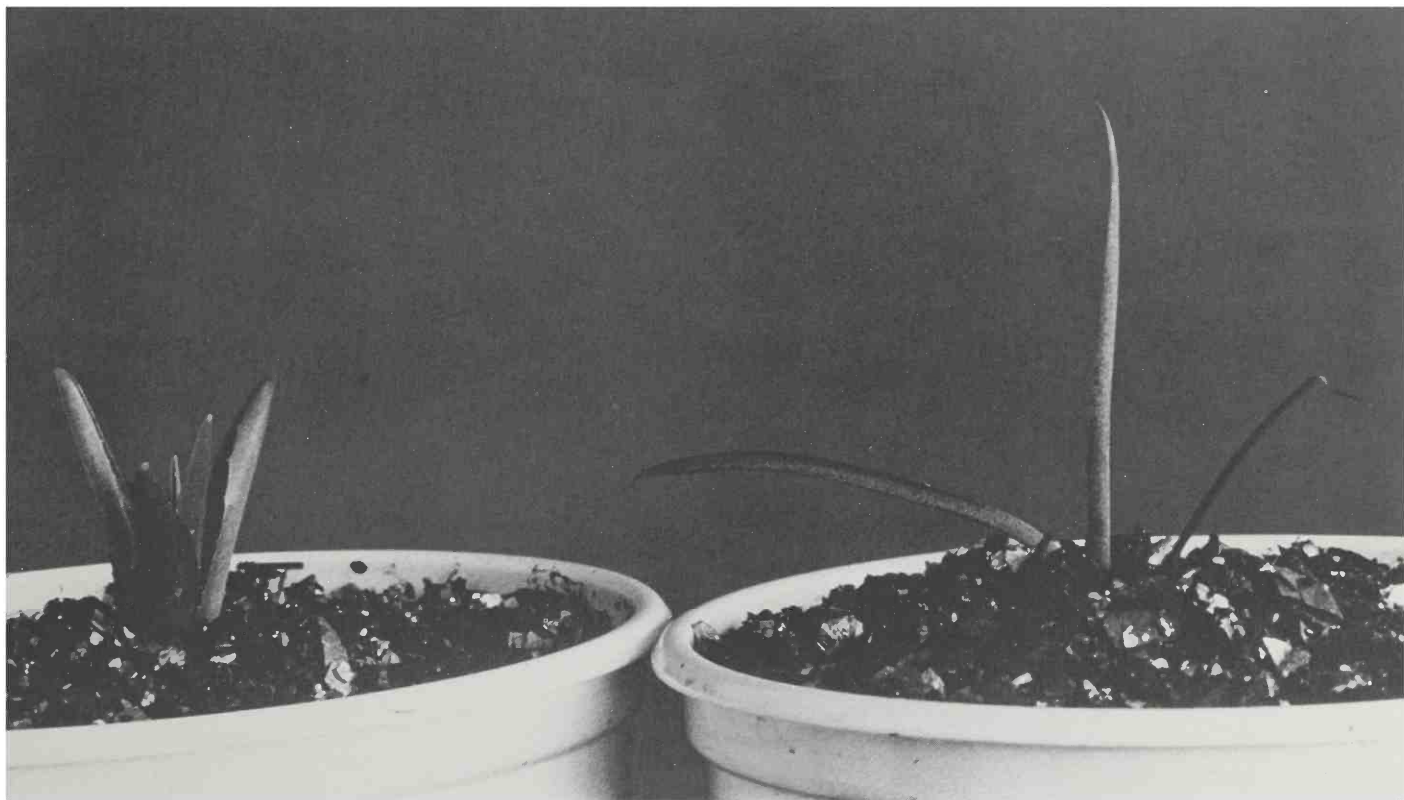
Figure 3. *Broad leaf morphological variant isolated from cultured cells of* Agave fourcroydes *compared with a typical regenerate from the same species.*

Agave Research Progress in Yucatan

difficult to study from a genetic point of view. Henequen, which only reaches sexual maturity after a period of 14 years and whose seeds have very low viability, is one such plant. Moreover, Henequen is far from being the ideal fiber producer; its 4% fiber content, low yield and late harvesting compare poorly with the characteristics of *A. sisalana* and the hybrid 11648 (*A. angustifolia* × *A. amaniensis* Trel. & Nowell back-crossed with *A. amaniensis*) grown in Tanzania (Lock, 1969). However, in spite of its poor showing, no one has ever attempted to genetically improve *A. fourcroydes*, probably because of the difficulties mentioned above.

Tissue culture studies started at CICY four years ago with the aim of improving the genetic variability of the hard fiber-producing agaves mainly through the fusion of somatic protoplasts.

We worked on all possible methods to culture and clone somatic cells and tried a wide range of nutritional, chemical and physical conditions without achieving much efficiency, though plants could be redifferentiated from callus induced from different explants such as meristems, leaves, rhizomes, etc. Finally, we discovered that the key factor for the success-ful culture of Henequen *in vitro* was the nature of the mother

plant. If seedlings are induced directly from meristematic tissues and are grown on defined media under controlled environmental conditions (low light intensity), the cuttings obtained from the young leaves produce a highly morphogenic and embryogenic callus which rapidly gives rise to several dozen new plantlets. These are easily rooted and are trans-ferred to pots with vermiculite before being transplanted to the nurseries.

Since protoplast work has been hindered by the very low efficiency of cell wall regeneration and division in our cultures, we have used the above material to evaluate the spontaneous variabliliy that arises in cultured cells.

In 1981 Larkin and Scowcroft found an enormous amount of variability in plants regenerated from cultured cells. This phenomenon, called somaclonal variation, has since then been confirmed in a wide range of species of both mono-cotyledonous and dicotyledonous plants.

The morphological variability of the plants, now readily produced by the micropropagation of tender leaf tissues, is being evaluated for the number of leaves, leaf size, rapidity of growth, number of marginal thorns, chromosome numbers, and odd phenotypes. These characteristics will be assessed for a period of two years since it appears that the enormous differences that emerge during the first three months in culture tend to homogenize at later stages. With regard to odd phenotypes only one such example with very broad and more numerous leaves has been isolated.

In order to increase the variability we have observed so far, we shall attempt this year to culture reproductive structures (anthers, pollen and ovaries) and will try to clone lines with

Table 1. Present CICY projects relating to *Agave fourcroydes.*

Composite Materials From Henequen Fiber
Physico-Mechanical Properties of Agave Fibers
   unsaturated polyester

Felt-Polyester
   felt-polyester-sand laminates

Gypsum (Fibrous Plaster)
   short fiber-gypsum
   pulp-gypsum

Hot Tops
   Henequen fiber-coir fines/sand/synthetic resins

Cellulosic Derivatives
Chemical Pulp
   cellulose triacetate
   cellulose ethers
   cellulose nitrate

Steroid Synthesis
Glucocorticoids From Industrial-Grade Hecogenin

Anti-fouling Agents
Descalants From Liquid Residues

Table 2. Comparative mechanical properties of different composites.

Property (kg/cm^2)	Henequen-Polyester-Sand	Fiberglass	Concrete
Tensile strength	150	812	17.1
Compressive strength	721	1,183	171.
Flexural strength	370	1,400	15.
Tensile modulus	10,175	34,000	204,082
Compressive modulus	114,230	65,000	—
Flexural modulus	130,346	59,500	—

gametic chromosome numbers for mutagenesis and polyploidization studies.

We are also engaged in the micropropagation of other agaves such as a variety of *A. letonae* Taylor ex Trel. from Guatemala which, under the conditions of cultivation in Yucatan, produces longer and more numerous leaves than *A. fourcroydes,* and the hybrid 11648 whose cultivation in Yucatan is prevented due to its sensitivity to *Phytophthora infestans.*

Alternative Uses for the Fiber and Waste Products. The Department of Applied Chemistry is actively working in two areas, polymeric materials and organic chemistry. An important part of the final objectives in each area is to develop technological alternatives that will make full and profitable use of the Henequen plant, through an intimate knowledge of its components.

Figure 5 describes the approximate composition of a Henequen leaf and some of the present and potential applica-tions of the fiber and its byproducts. As in other agaves, a whole industry is dedicated to the transformation of the fiber into cordage goods, whose economics was severely affected by the appearance of the synthetic polymeric fibers on the market. In addition to this problem, it has been recognized (Lock, 1969) that only a small portion of the leaf is being exploited, while the rest is wasted. An exception to this in the Mexican Henequen industry is the utilization, albeit questionable, of part of the bagasse produced as forage for cattle, after mixing it with other ingredients. However, no other commercial processes are in operation at the present time and, moreover, not all of the fiber extracted goes into textile processing; at least 10% lacks the minimum length required to form twine. This residue is generally woven into low cost felt.

Several noteworthy efforts have been made to take advantage of the chemical structures present in the plant, which closely follow previous experiments carried out on sisal (Lock, 1969). Thus paper production from Henequen fiber has been examined in recent times as an alternative use that might meet the growing demand for paper in this country (Villalvazo, 1985), but the large industrial facilities required, and the potential pollution problems have caused the project to be temporarily shelved.

Based on the above premises, our Applied Chemistry Department has pursued four main projects, two on the fiber and two more on the liquid residues, or Henequen "juice." Table 1 lists an overview of these activities.

The fiber has excellent physico-mechanical characteristics (Cruz-Ramos, 1984), which makes it possible to obtain structural composite materials by embedding it into suitable matrices. Gypsum (plaster of Paris) and unsaturated polyester have been successfully reinforced by short fiber or felt, thus producing materials with improved mechanical properties. Polyester fiber composites, laminated on both sides with a sand coating, can withstand weather exposure and are apparently resistant to biological attack and are non-flammable making them potentially useful for a variety of building applications (Belmares *et al.,* 1981; Marchand *et al.,* 1985). Some of the mechanical properties of these materials are compared with those of fiberglass and concrete in Table 2. In addition to showing good mechanical characteristics, gypsum-fiber composites appear to be outstanding acoustic insulators, both absorbing and reflecting sound waves.

After several tests supervised by CICY, hot tops for steel ingot production, based on sand and natural fibers, to replace asbestos and glass fibers are already being used by a steel-making company. Finally, polyurethane-Henequen composites are in the initial stages of a longer term development.

Regarding the use of Henequen fiber as a raw material for polymers, we have carried out chemical treatment tests on the short fiber and produced dissolving-grade pulps. This operation is possible because of the high alpha-cellulose content of the fiber (ca. 60% by weight) and its low percentage of lignin (ca. 13%). Although large amounts of hemicelluloses are present (ca. 16%), only minor processing difficulties occur as a result. The size of the manufacturing plant that would be required for this process is considerably smaller than that for papermaking.

The dissolving pulps can be transformed into a number of useful cellulose products, such as cellulose acetate and tri-
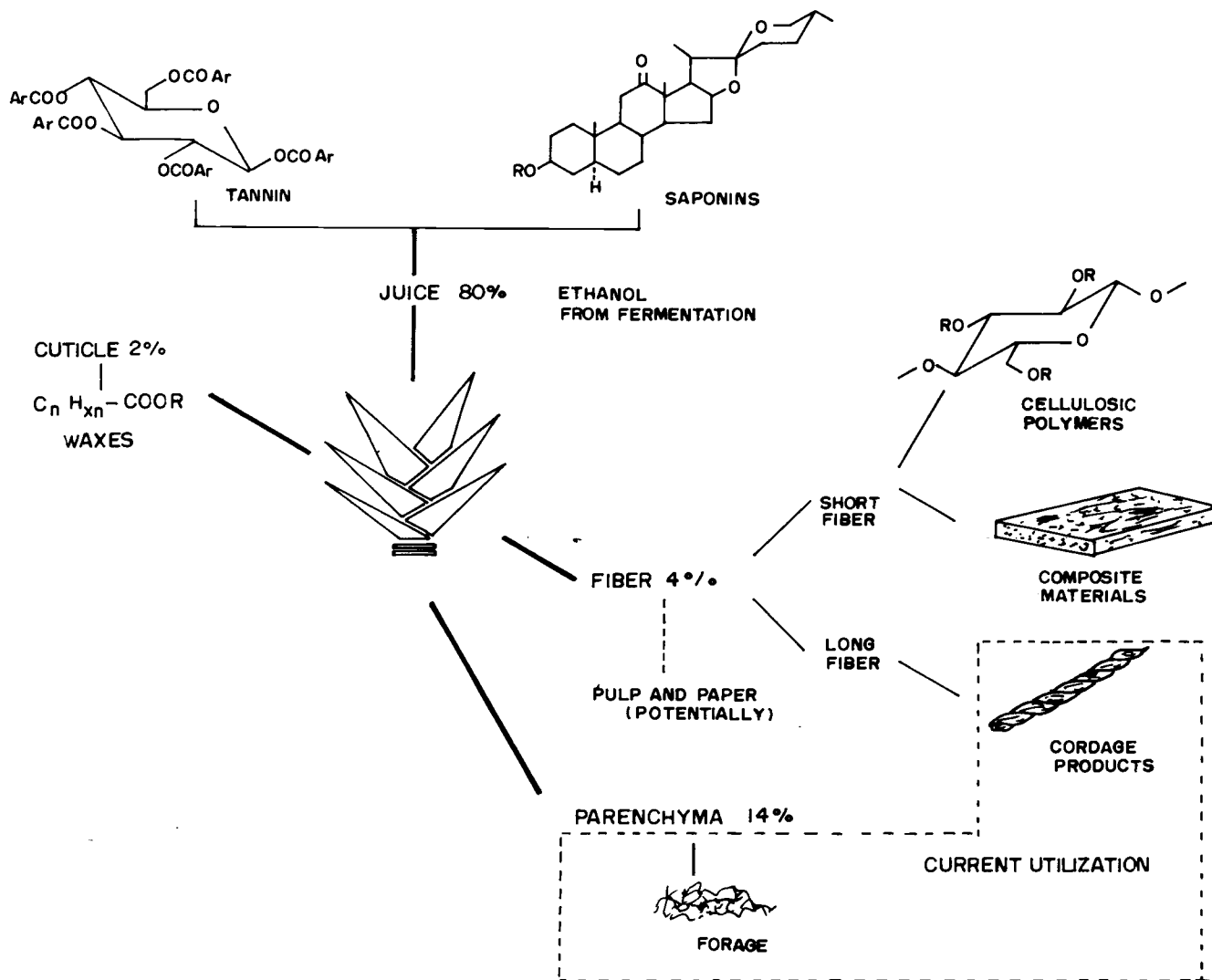
FIBER (4%)

DEFIBRATION → OTHER WASTES (12%)

LIQUID RESIDUES (84%)

SAPONIN MIXTURE → SEPARATION

TIGOGENIN

HECOGENIN

PURIFICATION

CHEMICAL TRANSFORMATION

PREGNADIENOLONE

PREDNISOLONE

TRIAMCINOLONE

PREDNISONE

DEXAMETHASONE

BETAMETHASONE

Figure 4. *Overall scheme of the advanced steroids produced using hecogenin as a raw material.*

Figure 5. *Present and potential uses of the components of Henequen leaves.*

acetate, cellulose nitrate, carboxymethyl cellulose, and butyl cellulose, all of which are under study in our laboratory.

Advanced steroid synthesis from hecogenin (Azolkar *et al.*, 1979), has become a major target for the Henequen industry as an alternative with high added value for part of its liquid wastes. The process, as depicted in Figure 4 involves an initial step separating hecogenin from tigogenin, which are present on a 1:1 ratio in the leaf, along with small amounts of other saponins. Each of the outcoming fractions is enriched with one of the two main steroids, and chemical synthesis can then take place. CICY's Organic Chemistry Group is carrying out the study of different chemical paths to convert hecogenin into pregnadienone, which then becomes the key to the more advanced steroids, as shown in Figure 4.

The production of advanced steroids is attractive for several reasons, chiefly because of their potential use in highly active pharmaceuticals. For example, the anti-inflam-

matory activity of betamethasone and dexamethasone is 25 times that of hydrocortisone, whereas cortisone itself is only 0.8 times as active. Most significantly, few of the cortisone side effects have been detected when testing these products in humans.

Another possible use of the liquid residue or "juice" is a source of anti-fouling agents. At least one patent in the literature describes how to obtain anti-fouling formulations from sisal wastes after moderate chemical treatments and the addition of small amounts of metal complexing agents (Hughes, 1941; Rubin, 1963). The chemical moieties responsible for this apparent synergism have not been identified as yet; hence, a thorough chemical analysis and physico-chemical studies are under way to help understand the process and provide the basis for the formulation of anti-scalants.

Chromosome and Hybridization Studies of Agaves

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Introduction

In 1933, McKelvey and Sax demonstrated that *Yucca* and *Agave* had the same configuration of chromosomes (5 large plus 25 small) even though these genera were considered as belonging to different families, Liliaceae and Amaryllidaceae respectively. *Nolina* and *Dasylirion*, long associated with *Yucca* in the Liliaceae, have a very different karyotype of 18-19 chromosomes (see summary by Gómez-Pompa et al., 1971). The first chromosome count for an *Agave*, $2n = 20$ by Müller (1912) for *A. americana*, is interpreted by Satô (1938) as representing the 20 large chromosomes in a tetraploid individual $(2n = 120)$ while overlooking the 100 small chromosomes. Most investigators of *Agave* chromosomes (e.g., Cave, 1964; Doughty, 1936; Gómez-Pompa et al., 1971; Granick, 1944; McKelvey and Sax, 1933; and Satô, 1935, 1938, 1942) interpreted their exact or approximate counts to represent $n = 30$ or multiples thereof. Sharma and Bhattacharyya (1962) report not only the "normal" number, mostly at or approximating $n = 30$ or multiples thereof, but also a wide variance in numbers for additional cells. These variant numbers are difficult to interpret but perhaps represent counts from cells of chimaeric tissues. In all cases, however, we assumed all approximate counts (or "normal" numbers) as representing the next higher ploidal level for ease of interpretation.

Herein, we shall not only report chromosome counts of *Agave* and related genera but attempt to utilize chromosome numbers in interpreting putative hybrids and in understanding evolutionary strategies, particularly polyploidy.

Materials and Methods

Flower buds were collected in developmental series from individuals growing in their native habitats or in cultivation at the Desert Botanical Garden (Phoenix) or on the campus of Arizona State University. Buds were trimmed of excess ovary material, then killed and fixed in chloroform, 95% ethanol, and glacial acetic acid (3:3:1), transferred to 70% ethanol after 24 hours, and refrigerated. Anthers were squashed and stained in acetocarmine and mounted in Hoyer's medium according to method of Beeks (1955) with the following modifications. A very small amount of finely powdered ferric ammonium citrate was added to the drop of acetocarmine in which the anthers had been placed. After some maceration, the anthers were allowed to stain for five minutes, then blotted, and transferred to Hoyer's medium where maceration was completed. The coverslip was added, blotted, and covered with a thick strip of paper toweling and pressed in a smooth-jawed mechanic's vice. If air became trapped in the preparation, the coverslip was removed and two slides were made, one with the original coverslip, the other with the original slide. Chromosome counts and behavior were documented by camera lucida drawings and/or photomicrographs. Voucher specimens, microslides, drawings, and photographs are deposited in the ASU Herbarium. Nomenclature follows that of Gentry (1982a).

Pollen grains obtained from mature, fresh or dried, unopened anthers were stained in aniline blue in lactophenol according to method of Maneval (1936). Percent pollen stainability (p.s.), based on 500+-grain samples, was calculated for certain plants.

Abstract

Interspecific hybridization, paleopolyploidy, secondary polyploidy, and vegetative reproduction appear to play significant roles in the evolution of *Agave* and certain related genera. First chromosome counts are reported for *Hesperaloe funifera* and 10 taxa of *Agave* including two triploid and one diploid putative hybrids. All of our counts for *Yucca*, *Hesperaloe*, and *Agave* are in agreement with the base number, $x = 30$, which comprises a complement of five very large chromosomes and 25 medium to small chromosomes. All published chromosome counts of *Agave* have been tabulated and the roles of hybridization and polyploidy are assessed. Secondary polyploidy occurs in 26 of 48 (54.2%) reported taxa of *Agave*; as yet only one-fourth of the total taxa are chromosomally known.

Table 1. Chromosome numbers of certain North American Agavaceae. Symbols: * = first count; ** = new count; p.s. = percent pollen stainability.

Taxon	Chromosome number	Collection data
NOLINEAE		
Nolina microcarpa Watson		
**$2n = 19_{II}$		ARIZONA: Maricopa Co.: west side of Humboldt Mtn., 34°58′45″ N, 111°47′20″ W, *Baker 4698 & Mohlenbrock* (Fig. 1); Yavapai Co.: Rte I-17, Little Black Canyon opposite Sunset View Rest Area, *Pinkava 14064 & Drake*.
YUCCEAE		
Hesperaloe funifera (Koch) Trelease, non sensu Gómez-Pampa et al. (1971)		
*$2n = 30_{II}$		ARIZONA: Maricopa Co.: cultivated on Arizona State Univ. campus, *Pinkava 14044 & Baker* (Fig. 2).
Yucca elata Engelmann		
$2n = 30_{II}$		ARIZONA: Pinal Co.: Barkerville Rd., 37 km SE of Florence, *Baker 4703* (Fig. 3).
AGAVEAE		
Agave subgenus *Littaea*		
Group Filiferae		
Agave ornithobroma H. S. Gentry		
*$2n = 3x = 90_{I}$		MEXICO: Sinaloa: 15-16 mi SE of Escuinapa, along hwy to Acaponeta, *Gentry 18358* (type collection cultivated at Desert Botanical Gard.) (Fig. 4) (p.s. = 11.7%).
Group Parviflorae		
Agave toumeyana Trelease ssp. *bella* (Breitung) Gentry		
$2n = 30_{II}$		ARIZONA: Maricopa Co.: New River Mtns., Boulder Basin, *J. H. Weber s.n.* (Fig. 5). Previously published (*Pinkava et al.*, 1974) without figure.
Group Urceolatae		
Agave arizonica Gentry & Weber		
*$2n = 30_{II}$		ARIZONA: Maricopa Co.: New River Mtns., *H. H. Weber s.n.* (clone DBG 61-6732) (Fig. 6) (p.s. = 25.0%).
Agave cf. *arizonica* Gentry & Weber Cline's Agave		
*$2n = 3x = 30_{II} + 30_{I}$		ARIZONA: Gila Co.: 7-A Ranch, S of Star Valley, *Pinkava 14036, McGill & Ray Cline* (Fig. 7, a,b) (p.s. = 0.6%).
Agave subgenus *Agave*		
Group Campanuiflorae		
Agave capensis H. S. Gentry		
*$2n = 30_{II}$		ARIZONA: Maricopa Co.: cultivated, Desert Botanical Gard., *Hodgson s.n.* (Fig. 8) (p.s. = 92.6%).
Group Deserticolae		
Agave sobria Brandegee ssp. *sobria*		
*$2n = 30_{II}$		MEXICO: Baja California Sur: 24 km W of Rosarito, *Baker 4042 & Gallagher* (Fig. 9).
Group Dipetalae		
Agave chrynsantha Peebles		
*$2n = 30_{II}$		ARIZONA: Maricopa Co.: cultivated, Desert Botanical Gard., Bed #27, *Hodgson 2215*; Pinal Co.: Queen Creek Canyon, just E of Superior (topotype), T1S R12E S36, *Baker 4675*; 3 km SE of King's Crown Peak at N end of Oak Flat, T1S R13E S28 NE1/4, *Baker 4692*; foot of Peralta Canyon, Superstition Mtns., T1N R10E S29, *Baker 4693* (Fig. 10).
Agave murpheyi F. Gibson		
*$2n = 30_{II}$		ARIZONA: Maricopa Co.: 8 km S of Bartlett Dam and 3.2 km E of Verde River, *Engard s.n.* (cultivated, DBG 72-0035) (Fig. 11) (p.s. = 19.8%).
Agave palmeri Engelmann		
$2n = 30_{II}$		ARIZONA: Maricopa Co.: cultivated, Desert Botanical Gard., *Hodgson s.n.* (DBG 81-0184) (Fig. 12) (p.s. = 92.5%).
Group Parryanae		
Agave parryi Engelmann var. *couesii* (Engelmann ex Trelease) Kearney & Peebles		
*$2n = 4x = 60_{II}$		ARIZONA: Coconino Co.: Schnebly Hill Rd. between Foxboro Lake and Scenic Viewpoint of Red Rock Canyon (Sedona), T17N R6E S1-2, *Pinkava 14054 & Drake* (Fig. 13).
Group Umbelliflorae		
Agave shawii Engelmann ssp. *goldmaniana* (Trelease) H. S. Gentry		
*$2n = 30_{II}$		MEXICO: Baja California Norte: near San Andreas, *Lindsay s.n.*, cultivated clone, Desert Botanical Gard. (DES 42) (Fig. 14)
Agave shawii Engelmann ssp. *shawii*		
$2n = 30_{II}$		MEXICO: Baja California Norte, 8 km E of Hwy 1, road to San Pedro Martir Observatory, *Baker 4021* (Fig. 15).

Results

In this study 19 counts are reported for four genera, 14 species (three of which are interpreted as interspecific hybrids), and one additional infraspecific taxon (Table 1, Figures 1-15); counts for all but four of these are first reports. Our count of $2n = 19_{II}$ for *Nolina microcarpa* is a new count, previously reported as $2n = 36$ by Satô (1942, 1953). Previously published counts consistent with ours are for *Yucca elata* by McKelvey and Sax (1933), *Agave shawii* by Lenz (1950), and *A. toumeyana* ssp. *bella* by Pinkava *et al.* (1974; same count but without chromosome drawing) and by Spellenberg (1979).

Discussion

Polyploidy. In the genus *Agave*, Gentry (1982a) recognized 195 taxa belonging to 140 species. From compiled chromosome data (Pinkava, unpublished), 48 of these taxa (24.6%) have known chromosome numbers; 26 of the 48 taxa (54.2%) are intrageneric polyploids or have polyploid members, with numbers ranging from $2n = 60$ (2x) to 240 (8x). Polyploidy occurs in 8 of 20 reported taxa (40.0%). in subgenus *Littaea*, and in 18 of 28 reported taxa (64.3%) in subgenus *Agave*. Goldblatt (1980) found one-half the species of *Agave* to be polyploid. He also reported that of the 300
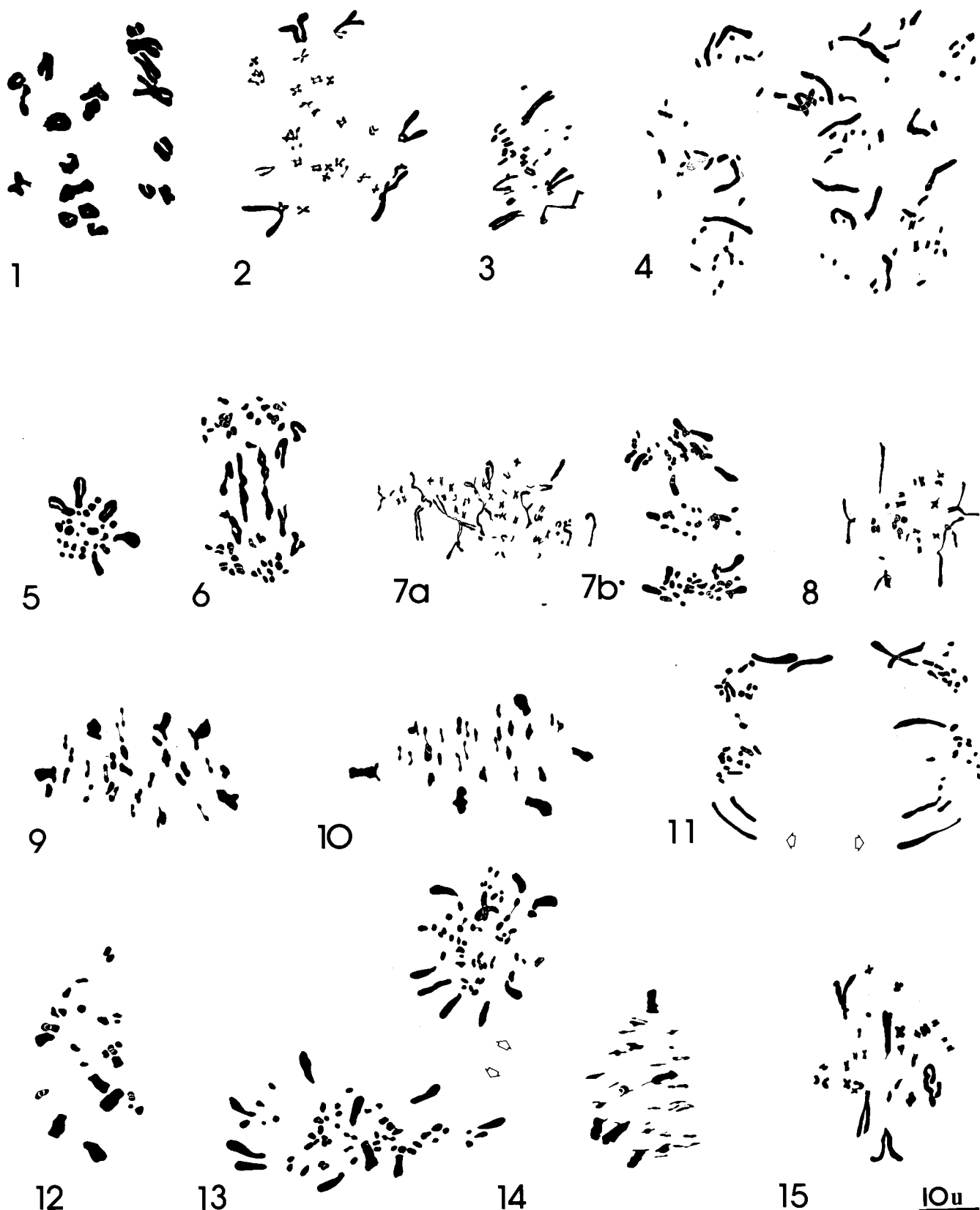
Figures 1-15. *Camera lucida drawings of meiotic chromosomes of certain Agavaceae. Voucher specimens are cited in Table 1. Spacing of chromosome groups adjusted in Fig. 11.* **1:** Nolina microcarpa, *diakinesis,* n = 19. **2:** Hesperaloe funifera *metaphase I,* n = 30. **3:** Yucca elata, *metaphase I,* n = 30. **4:** Agave ornithobroma, *metaphase I,* 2n = 3x = 90ₗ. **5:** A. toumeyana *ssp.* bella, *metaphase I,* n = 30. **6:** A. arizonica, *anaphase I,* n = 30. **7:** A. *cf.* arizonica: *a. metaphase I,* 2n = 3x = 30ₗₗ + 30ₗ; *b. anaphase I, irregular disjunction of 90 chromosomes.* **8:** A. capensis, *metaphase I,* n = 30. **9:** A. sobria *ssp.* sobria, *metaphase I,* n = 30. **10:** A. chrysantha, *metaphase I,* n = 30. **11:** A. murpheyi, *early telophase I,* n = 30. **12:** A. palmeri, *metaphase I,* n = 30. **13:** A. parryi *ssp.* couesii, *early telophase I,* n = 60. **14:** A. shawii *ssp.* goldmaniana, *metaphase I,* n = 30. **15:** A. shawii *ssp.* shawii, *metaphase I,* n = 30.

Table 2. Comparison of morphological characters of *Agave chrysantha*, *A. toumeyana*, and putative hybrids. Data, except for triploid hybrid, modified from Gentry (1982a).

Character	A. chrysantha	A. arizonica	A. cf. arizonica	A. toumeyana ssp. toumeyana	ssp. bella
Rosette	solitary or rarely suckers	solitary or with suckers	one sucker	clonal	clonal
Leaves					
length (cm)	40-75	17-24	18-20	20-30	9-20
width (cm)	8-10	2-4	1.6-2	1.5-2	0.5-0.7
teeth (margins)					
length (mm)	5-10	2-5	ca.1	denticles	denticles
spacing (cm)	1-3	to 1.5-2	close	close	close
orientation	straight or deflexed	mostly deflexed	straight	straight	straight
distribution	even along margin	variable along margin	basal	basal	basal
margin (corneous)	discontinuous	continuous	continuous	continuous	continuous
width (mm)	—	1-2, intact	1, separating	1, fibrous	1, fibrous
surface (upper)	guttered	shallow concave	nearly flat	flat	flat
orientation	straight	straight	falcate	falcate	falcate
Chromosomes (2n)	60	60	90	polyploid	60
Inflorescence	upper 1/4-1/3	upper 1/4-1/2	upper 1/3	upper 1/3	upper 1/3
panicle (m)	4-7	3-4	ca. 1.5	1.5-2.5	1.5-2.5
flowers/"umbel"	numerous	10-20	6-8	2(-3)	2(-3)
no. of "umbels"	8-18	35-50	ca. 50	numerous	numerous
Flowers	straight	straight	slightly reflexed	reflexed	reflexed
color	yellow	pale yellow	dull white	greenish white	greenish white
length (mm)	44-56	25-57(-31)	28-31	(21-)23-25(-28)	18-21
ovary length (mm)	23-27(-30)	13-15	10-12.5	(10-)11-14(-16)	8-12
tube l/w (mm)	9-13/10-13	4-5(-6)/7-8	3-3.5/6.8	3-4/6-10	3-4/6-7
tepal l/w (mm)	10-15/5-6,11-13	8-11/3-4.5,7-10	8.5-10/3.5-4,4-5.5	7-9/3-4,6-7	6(-7.5)/2.5-3
filament l (mm)	35-48	18-20(-26)	14-16	13-17	11-13
filament insert. above base (mm)	4-9 & 5-7	3-4	2-2.5	2-3	2(-3)
anther length (mm)	(11-)17-21	9-12	8-9	9(10)	7(-9)
anther color	yellow	dull yellow	dull white	dun	dun
Capsule l/w (mm)	35-50 x 13-15	15-20 x 8-9	unknown	12-15 x 8-10	12-15 x 8-10

Table 3. Putative intersubgeneric hybrids in *Agave*.

Subgenus *Littaea* putative parent	Subgenus *Agave* putative parent	Proposed hybrid	Subgenus *Littaea* putative parent	Subgenus *Agave* putative parent	Proposed hybrid
A. lechuguilla Torr. Marginatae; 4x (Cave, 1964, Granick, 1944)	*A. neomexicana* Woot. & Standl. Parryanae; 4x (Granick, 1944)	*A. gracilipes* Trel. ?x; Gentry (1982a,b); Burgess, 1977; C. E. Freeman, pers. comm.	*A. kerchovei* Lemaire. Marginatae; 4x (Sharma & Bhattacharyya, 1962)	*A. marmorata* Roezl. Marmoratae; ?x 1982a	*A. peacockii* Croucher. ?x; Gentry, 1967, 1982a
A. lechuguilla Torr. Marginatae; 4x	*A. havardiana* Trel. or *A. gracilipes* (a backcross) or *A. neomexicana*. Parryanae; ?x, ?x, 4x	*A. glomeruliflora* (Engelm.) Berger. ?x; Gentry, 1982a	*A. toumeyana* Trel. ssp. *toumeyana* and/or ssp. *bella* (Breit.) Gentry. Parviflorae; px (Cave, 1964), 2x Pinkava et al. (1974)	*A. chrysantha* Peebles. Dipetalae; 2x (this study)	*A. arizonica* Gentry & Weber. 2x (this study)
A. lechuguilla Torr. Marginatae; 4x	*A. scabra* Salm-Dyck ssp. *scabra* or ssp. *maderensis* Gentry. Americanae; ca. 6x (Cave, 1964), ?x	Unnamed hybrid ?x; Pinkava this study	*A. toumeyana* Trel. ssp. *toumeyana*. Parviflorae; px (Cave, 1964)	*A. chrysantha* Peebles. Dipetalae; 2x	Cline's agave 3x (this study)
A. victoriae-reginae Moore. Marginatae; 2x (Cave, 1964), 4x (Granick, 1944)	*A. scabra* Salm-Dyck. Americanae; ca. 6x	Unnamed hybrid ?x; Gentry, 1982a			

Figure 16. Photograph of herbarium specimen (ASU) of
Agave chrysantha *(Baker 4693). Scale: herbarium sheet measures 29 × 42 cm.*

Figure 17. Photograph of herbarium specimen (ASU) of
Agave toumeyana *ssp.* bella *(Pinkava et al 14037b). Scale: herbarium sheet measures 29 × 42 cm.*

species in Agavaceae (sensu Cronquist, 1968), chromosome counts are known for 116, all of which are $n = >13$. Grant (1963) considered that species with haploid numbers above 13 would mainly be polyploid. Thus the genus *Agave* would be polyploid itself ($x = 30$), probably an ancient polyploid or a paleopolyploid. In turn, polyploid taxa based on $x = 30$ would be secondary polyploids or intrageneric polyploids.

According to deWet (1980) and Lewis (1980), most polyploids probably arise via fertilization of unreduced gamets in a stepwise process wherein a diploid's unreduced gamete ($2x$, most likely an egg) is fertilized by a haploid gamete ($1x$, most likely a sperm) producing a triploid ($3x$); the triploid in turn produces an unreduced gamete ($3x$) which is fertilized by a haploid gamete ($1x$) producing a tetraploid ($4x$); and so on. Triploids are the most common polyploid formed but the most successful are tetraploids which probably combine genomes of differently adapted but closely allied taxa (deWet, 1980). He further states that most individuals probably produce unreduced gametes. Thus polyploids, so common in *Agave*, may arise via unreduced gametes of one species fertilized by reduced gametes of another, hence interspecific hybridization. Unreduced gametes are often the only functional ones produced by interspecific hybrids (deWet, 1980).

Hybridization. *Agave arizonica* is a narrow endemic, restricted to the vicinity of the New River Mountains in

Arizona. It has always been found associated with two other endemic, central Arizona species, diploid *A. chrysantha* (Figure 16) and *A. toumeyana* ssp. *toumeyana* (probably polyploid with irregular meiosis according to a single report by Cave in 1964) and/or diploid ssp *bella* (Figure 17). We propose these two species as putative parents of *A. arizonica* because: (1) it occurs only where the ranges of the putative parents overlap and then in very wide and random scattering of individual plant clones (R. DeLamater, pers. comm.); (2) its putative parents have overlapping flowering periods; (3) it has those morphological characters that were analyzed mostly intermediate between the putative parents (Table 2); and (4) it appears subfertile producing pollen with low percent stainability (25.0% in *Weber s.n.* (Table 1) and 2.4% in paratype, *Weber s.n.*, DBG 61-6738 (ASU; Figure 18)).

Agave chrysantha belongs to the subgenus *Agave* group *Dipetalae*; the other putative parent, *Agave toumeyana*, belongs to the subgenus *Littaea* group *Parviflorae*. *Agave arizonica* is not the only intersubgeneric hybrid proposed for agaves. Perusal of Gentry's monograph (1982a) reveals at least four others (Table 3).

In 1982, the Cline family from Star Valley, Arizona, alerted us to a single hybrid plant (Figure 19) beginning to bloom. Similar to *A. arizonica*, it differed in having falcate leaves with only basal teeth and a separating corneous margin. In
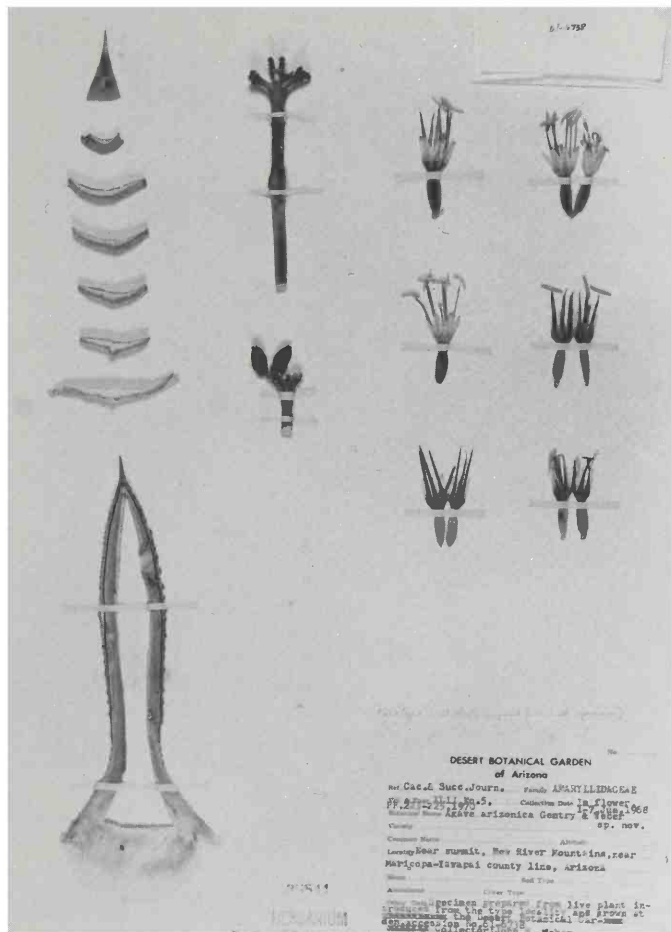
Figure 18. Photograph of herbarium specimen (ASU) of Agave arizonica (Weber s.n., paratype). Scale: herbarium sheet measures 29 × 42 cm.

Figure 19. Photograph of herbarium specimen (ASU) of Agave cf. arizonica (Pinkava et al. 14036). Scale: herbarium sheet measures 29 × 42 cm.

most characters it appears closer to *A. toumeyana* in morphology than does *A. arizonica*. Chromosome analysis revealed it to be a triploid having 30 bivalents and 30 univalents suggesting synaptic pairing of two sets of chromosomes from one parent and one set from the other parent remaining unpaired. Meiosis is irregular. Percent pollen stainability is only 0.6%. Capsule formation and seed set is not known. Growing in the immediate vicinity are *A. chrysantha*, *A. chrysantha* X *A. parryi*, and *A. parryi* in the subgenus *Agave* and *A. toumeyana* ssp. *bella* in the subgenus *Littaea*. Since the putative hybrid is closer to *A. toumeyana* ssp. *bella* than to any of the subgenus *Agave* taxa, we suggest that *A. chrysantha* (or *A. chrysantha* X *A. parryi*) contributed one set of chromosomes and *A. toumeyana* ssp. *bella* contributed two sets, either via an unreduced gamete or by a possible tetraploid individual's reduced 2x gamete. *Agave parryi* is a possible parent but its flowering time is not or but briefly overlapping that of *A. toumenyana* ssp. *bella*.

Two additional putative interspecific hybrids were found but not thoroughly analyzed. An individual from the type collection (*Gentry 18358*) of *Agave ornithobroma* is triploid (Table 1; Figures 3, 20), forming 90 univalents at diakinesis with resultant irregular meiosis and reduced percent pollen stainability of 11.7%. Although complete chromosome analyses were impossible, a cell at anaphase I had a 7-8
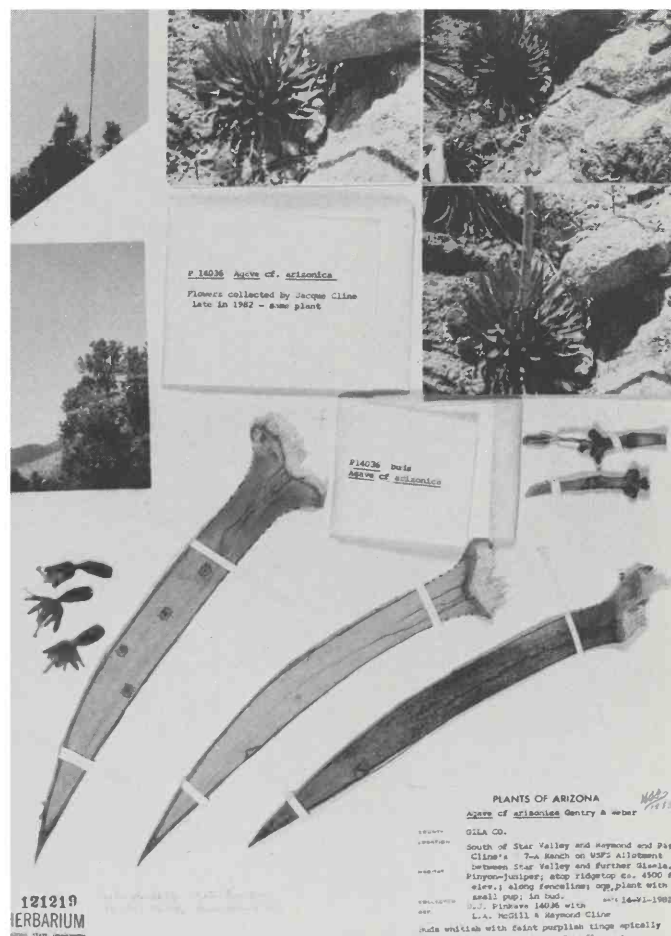
disjunction of the 15 large chromosomes and a mitotic cell was found with 15 large chromosomes, both cells indicating further the chromosome number to be $2n = 3x = 90$. We interpret this plant to be a trihybrid, combining one set of chromosomes from each of three parental stocks. One parent is very likely to be closely related *A. geminiflora* (Tabl.) Ker-Gawler.

The other putative hybrid is intersubgeneric, between *A. scabra* ssp. *scabra* or ssp. *maderensis* of subgenus *Agave* and *A. lechuguilla* of subgenus *Littaea* (Table 3). The collection (*Pinkava et al., 13603*; Figure 21) came from the lower slopes of the Sierra de la Madera northeast of Cuatro Cienegas, Coahuila, Mexico. The individual has leaves resembling somewhat those of *A. scabra* but the "umbel" stalks are much shorter and the fruits smaller as in *A. lechuguilla*. Fertility (pollen or seed) and chromosome number are unknown.

Agaves with odd-number ploidal levels (3x and 5x) should be further investigated for hybrid origins. Agaves known only as pentaploids (5x) are *A. mapisaga* Trel. (Gomez-Pompa et al., 1971), *A. fourcroydes* Lem. (Doughty, 1936), and *A. sisalana* Perrine (Doughty, 1936; Inariyama, 1937; Vignoli, 1937; Sato, 1935, 1938, 1942; Granick, 1944). Indeed, Gentry (1982a) considered the latter two, both important fiber species known as Henequen and Sisal respectively, to be sterile hybrids.
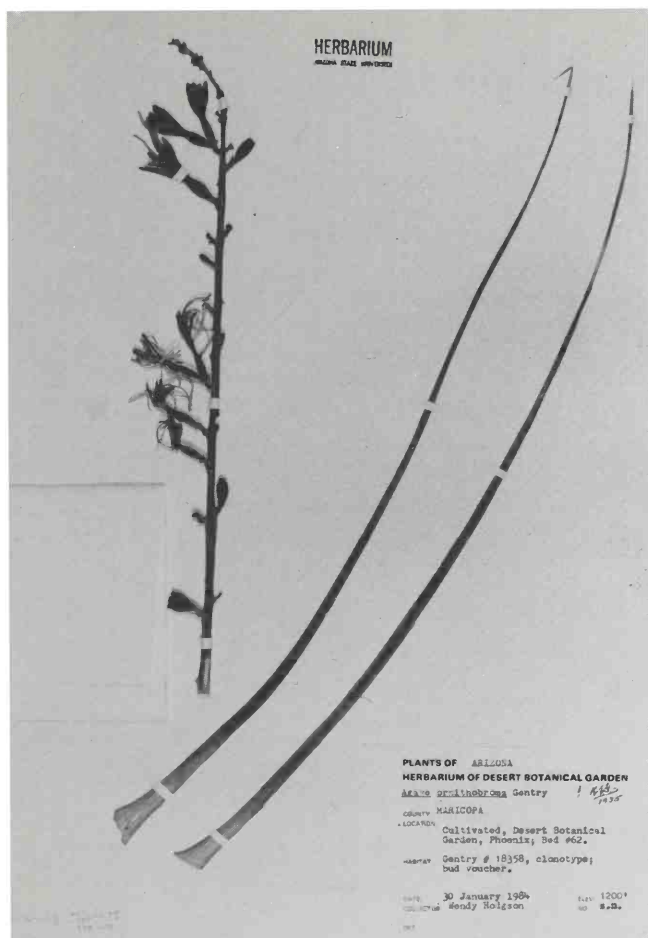
Figure 20. Photograph of herbarium specimen (ASU) of Agave ornithobroma *(Gentry 18358; from type collection). Scale: herbarium sheet measures 29 × 42 cm.*
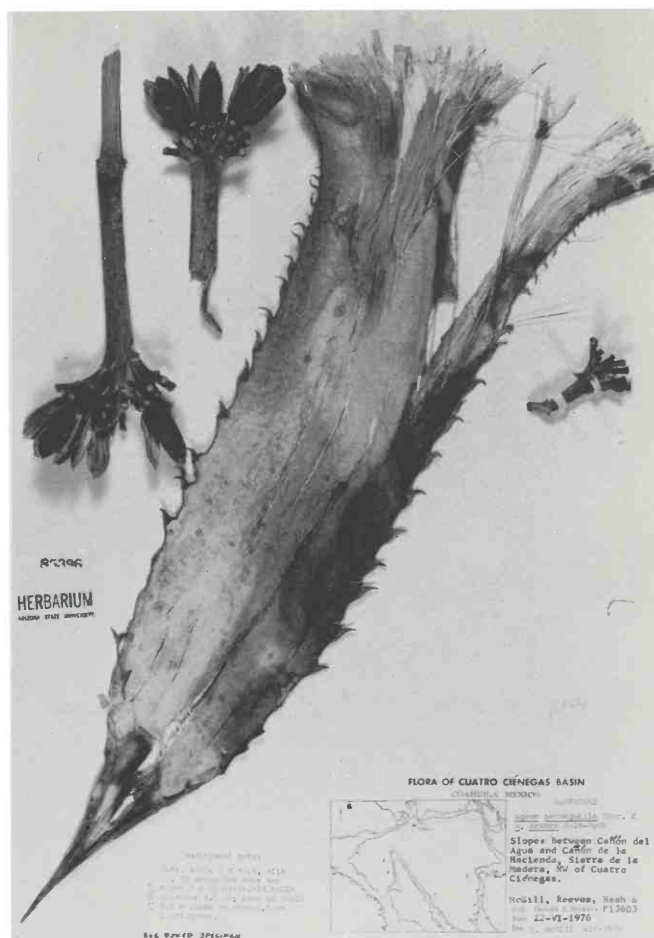

Figure 21. Photograph of herbarium specimen (ASU) of Agave *putataive hybrid between* A. lechuguilla *and* A. scabra *(Pinkava et al. 13603). Scale: herbarium sheet measures 29 × 42 cm.*

Conclusions

Several putative intraspecific and interspecific hybrids at both diploid and polyploid levels are known in *Agave*, three postulated herein. More than half the reported taxa are polyploid or have polyploid members. Most if not all successful, naturally occurring, polyploid taxa of vascular plants are of a hybrid nature ranging between similar and genetically compatible genomes to differentiated and genetically incompatible genomes (Stebbins, 1980). Polyploidization helps stabilize or balance the hybrid combinations by automatically increasing the number of alleles in polysomic inheritance and in buffering the vigor and heterozygosity. Ehrendorfer (1980) showed that diploids are more common in stable habitats of permanent or climax communities while recent polyploids are often found in liable or successional biotas. Their geographic ranges and ecological tolerances may be expanded via mutation, recombination, and additional hybridization (Stebbins, 1980). Polyploidy and hybridization promote apomixis in sexual polyploids since there is a greater probability of having gene combinations favoring a shift in reproductive cycles; apoximis, in turn, preserves highly adaptive and heterozygous gene combinations (Stebbins, 1980). Vegetative reproduction (offsets and bulbils) converts the agave monocarpic individual into a modified perennial allowing for prolonged sexual reproduction and probability of producing more adaptive gene combinations. Agaves apparently combine hybridity, polyploidy, and vegetative reproduction as their evolutionary strategy. Future studies in *Agave* need to incorporate ecological, cytological, and morphometric data with direct evidence from breeding studies.

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Prehistoric Agave Cultivation in Southern Arizona

Conclusions

The appearance of large middle bajada complexes, the expansion of total acreage in rockpile fields, and a concomitant emphasis on their yield have demographic correlates in the northern Tucson Basin. Site densities and population were at a peak in the early Classic Period. In an environment where aridity circumscribes agricultural activity, opportunities to expand irrigated or floodwater production were limited. Cultivation on marginal bajada slopes would have offered an optimal solution. Agaves are adapted to low and unreliable moisture to a greater degree than many annual crops. Poorer land could therefore be used to help satisfy growing needs for foodstuffs and craft supplies, as well as highly portable raw materials and finished products for trade.

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Field Evaluations of Agave in Arizona

Conclusions

Probably the greatest advantage of agave as a potential agricultural crop in Arizona is the multiplicity of uses for which it might be cultivated. A number of products from agave are illustrated in Table 7. At present the economic return from sale of steroidal sapogenins is sufficient to encourage establishment of plantations and the possibility of additional income from the remainder of the plant following extraction exists. Likewise, the climate in some agricultural areas of southern Arizona appears ideal for the cultivation of the Tequila Agave (*Agave tequilana* Weber) which would support the establishment of an industry for the distillation and sale of spirits derived from agave fermentation. The increasing sales of tequila worldwide suggest the success of such an enterprise.

With millions of acres in the Southwest suitable for agave plantations an enormous potential production is possible. Agave, by reason of its shallow root system and perennial growth habit, should act to stabilize desert soils and control erosion during the several years of growth before harvest. The agronomic attributes of agave make it a plant of choice for effective biological energy conversion in the arid Southwest.

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A Demographic Study of Maguey

half the offsets showed at least one type of damage. But only 12% of the within-clump protected offsets were damaged, compared with over 80% for clump-edge exposed offsets. Damages due to trampling, predation, and stress/pathogens/insects were all significantly lower for protected offsets. Offsets in within-clump exposed positions generally suffered damage similar to that suffered in clump-edge semi-protected positions.

Data on soil compaction (Table 1) show clearly that a major soil difference between protected positions in agave clumps and open degraded grassland is at least a fourfold increase in resistance to penetration in the open grassland soil. Resistance to penetration decreased progressively in the following order: open grassland, exposed edges, semi-protected edges, exposed within-clump positions, protected within-clump positions. This pattern helps to explain the increase in stress-related damage to offsets outside the immediate protection of other agaves. There was also a mean 10% decrease in soil depth in open grassland when compared to adjacent agave clumps, irrespective of absolute depth. These differences in soil depth and degree of compaction appear to be due to the differential effects of overgrazing on open grassland versus agave-protected soil. Clump area may be restricted both by direct biotic interactions (trampling and predation) at edges and by soil heterogeneity that itself seems to have been induced by overgrazing.

In order to evaluate plant size at flowering as an index of site deterioration, we examined three size class distributions. Figure 5a shows the distribution for plants in the nondestructively sampled clumps which reached sexual maturity during the study, while Figure 5b is based on the dead plants in the same clumps. Both show a preponderance of the largest size classes, and the two are statistically not distinguishable. This suggests that, at least in the relatively favorable environment of the nondestructively sampled area, there has been no major change in plant size at flowering within the last ten years (the estimated persistence period for dead plant remains). In contrast, Figure 5c shows the distribution for the more extensive sample of living plants, which included more obviously degraded areas with hardpan showing at the surface. Modal plant size in this sample was Size Class 10, while modal size in samples from the less-degraded area was Size Class 13. Plant size at flowering is clearly plastic and appears to
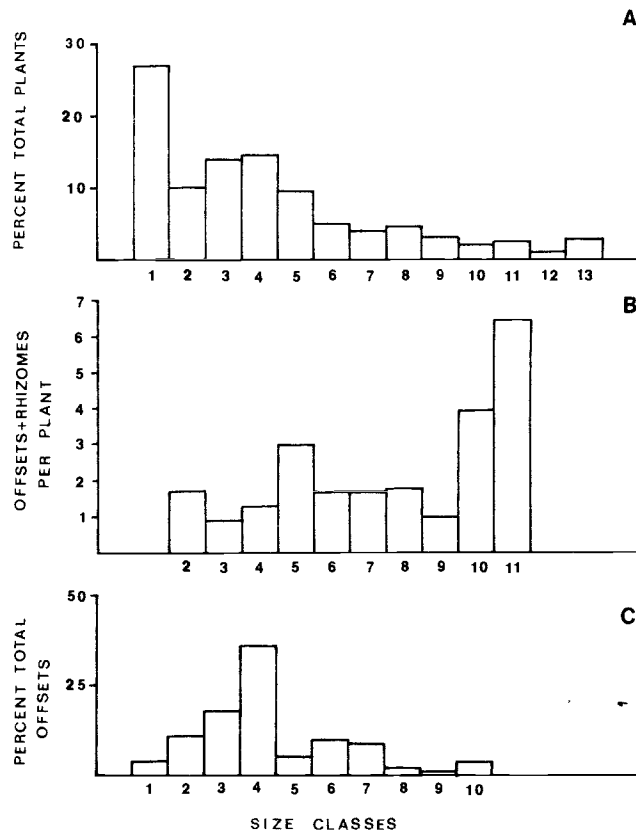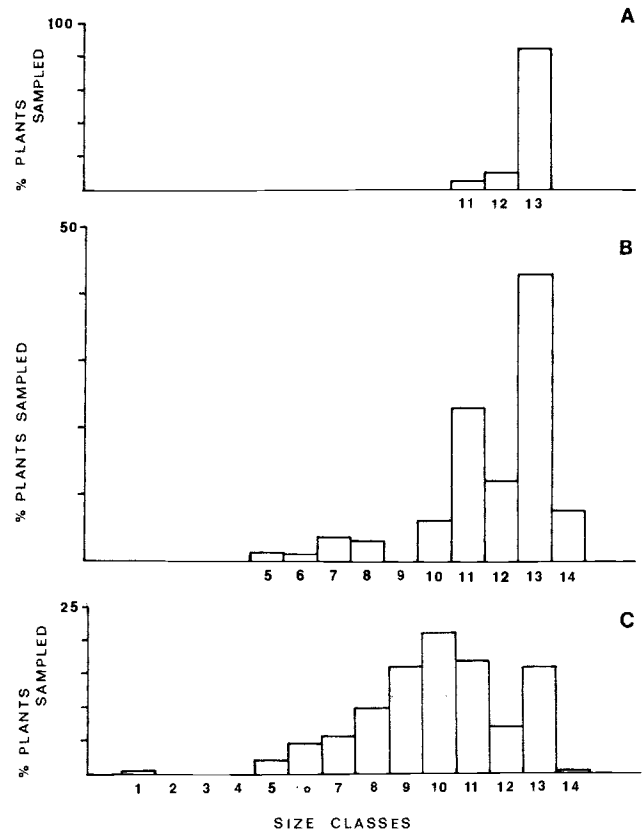
Figure 4. (a) Size class distribution for the overall population, based on data from the 52 nondestructively sampled clumps. (b) Mean potential offset production (current connected offsets + developing rhizomes) by plants of different size classes, based on the excavation of 150 potential parent plants. (c) Actual offset production by parent size class, based on the excavation of 150 randomly selected offsets. See text for class size details.

Figure 5. Size class distributions for sexually mature plants. (a) Living plants in nondestructively sampled clumps (n = 21). (b) Dead plants in nondestructively sampled clumps (n = 414). (c) Living plants in a more extensive sample which included more severely degraded habitat (n = 360). See text for class size details.

represent a direct response to integrated stress, making it a good potential parameter for site quality evaluations. In this case the abiotic stress related to soil conditions appears to be more important than the effects of crowding.

Conclusions

The evidence generated in this study suggests that under present conditions the agave biomass/area in clumps at the study site is often below the critical value. Evidence for the negative effect of crowding is weak, while the case for the positive effect of cohabiting with other agaves is quite strong, in terms of both apparent offset survival and improved conditions for the growth of large plants. Agave clumps offer protection against the direct negative effects of grazing and also have deeper, less-compacted soils than areas outside clumps. Clump area may be restricted by negative biotic interactions at clump-edges and by soil heterogeneity which seems to be grazing-induced. Clumps appear to be contracting, as areas formerly occupied by large agaves are negatively impacted by grazing following the removal of plants for mezcal production. Under current conditions, offset production is high, but apparent offset mortality is also very high.

The harvest of sexually-mature plants per se does not seem to be the cause of the population decline, although it aggravates the effects of overgrazing by leaving both soil and offsets exposed. Harvest for mezcal could probably be considered a rational long-term use of the wild maguey verde resource, if it were carefully managed and if the problem of grazing could be brought under control.

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Conservation of Southwestern Agaves

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Abstract

The status of Southwestern agaves being considered for listing under the 1973 Endangered Species Act are summarized. Numerous Mexican agaves appear to merit consideration for listing as threatened or endangered species. An outline of action to accomplish this and achieve some much-needed communication between the United States and Mexico is presented. The agaves are clearly of Mexican origin. Species abundance contour maps are used to locate areas and species of special significance in the study of the evolution of the genus and to map out a conservation plan for the genus.

Introduction

Although the Endangered Species Act became law in 1973, a reliable list of plant taxa which merited consideration for listing under the act was not available until 1978. At this time the Smithsonian Institution published its list of endangered and threatened plants of the United States (Ayensu and DeFilipps, 1978). The Act required the Smithsonian Institution to prepare the list although the U.S. Department of Interior Fish and Wildlife Service was entrusted with the responsibility of implementing the Act. Subsequently, the U.S. Fish and Wildlife Service assumed responsibility for review and republication of the list. The U.S. Fish and Wildlife Service (1980) republished the list indicating which taxa had been dropped from consideration and those which had changed listing status. Recently the U.S. Fish and Wildlife Service (1983a) published a list of the 1980 plants which changed listing status.

In 1978, 1980, and 1983, lists are of candidate species only. The Act and its amendments specify a lengthy process of review for each of the candidate plants after which the U.S. Fish and Wildlife Service will determine whether to list it as federally endangered or threatened or to drop it from further consideration. The U.S. Fish and Wildlife Service (1984a) published the names of plants and animals determined to be endangered or threatened. In brief, a taxon may be determined to be endangered if it is shown to be "in danger of extinction throughout all or a significant portion of its range" and threatened if it "is likely to become an endangered species within the forseeable future throughout all or a significant portion of its range" (Sec. 3(6) and Sec. 3(20) respectively of the Endangered Species Act as amended by the Endangered Species Act amendments of 1982). Functionally, the Act specifies five principal criteria for such determination:

"(A) the present or threatened destruction, modification, or curtailment of its habitat or range;

(B) overutilization for commercial, recreational, scientific, or educational purposes;

(C) disease or predation;

(D) the inadequacy of existing regulatory mechanisms; or

(E) other natural or manmade factors affecting its continued existence" (Sec. 4(a) of the Endangered Species Act as amended by the Endangered Species Act Amendments of 1982).

Agaves and the Endangered Species Act

Nine agave taxa have appeared on candidate taxa lists at one time or another. They are summarized in Table 1 and their geographic distributions are mapped on Figure 1.

Note that several are infraspecific taxa (i.e., subspecies or varieties). The Endangered Species Act recognizes the need to preserve reasonably distinctive infraspecific taxa if other criteria are met.

***Agave glomeruliflora* (Engelm.) Berger.** This taxon is apparently of hybrid origin, involving *A. lechuguilla* Torr., *A. gracilipes* Trel., *A. havardiana* Trel., and *A. neomexicana* Woot & Standl. It has the largest distribution of any of the candidate agaves and includes most major mountain ranges in west Texas and northern Coahuila. It was recommended as threatened by the Smithsonian in 1978 and is currently demoted to a Category 2 candidate. Few if any significant threats have been identified and substantial populations in Big Bend and Guadalupe Mountains National

Figure 1. *Distribution of candidate and listed threatened and endangered Southwestern agaves.*

Table 1. Summarized history of Endangered Species Act listing status of Southwestern Agaves.

1978

Ayensu & DeFilipps, Smithsonian Inst. Report to the Secretary of the Interior (Ayensu and DeFillipps, 1978)

  Recommended Threatened
    Agave glomeruliflora (Engelm.) Berger
    Agave utahensis Engelm. var. *ebosporina* (Hester)
      Breitung
    Agave utahensis ssp. *kaibabensis* (McKelvey) Gentry
    Agave utahensis var. *nevadensis* Engelm.

  Recommended Endangered
    Agave mckelveyana Gentry
    Agave arizonica Gentry & Weber
    Agave schottii Engelm. var. *treleasei* (Toumey)
      Kearney & Peebles
    Agave toumeyana Trel., ssp. *bella* (Breitung) Gentry

1980

Fish & Wildlife Service, Review of Plant Taxa for Listing as Endangered or Threatened Species (U.S. Fish and Wildlife Serv., 1980)

  Category 1 (Probably merits listing as endangered or threatened)
    Agave arizonica
    Agave parviflora Torr.
    Agave toumeyana ssp. *bella*

  Category 2 (Possibly merits listing, more data needed)
    Agave glomeruliflora
    Agave schottii var. *treleasei*
    Agave utahensis var. *eborispina*
    Agave utahensis var. *nevadensis*

  Category 3 (Dropped from consideration for listing)
    Agave mckelveyana
    Agave utahensis ssp. *kaibabensis*

1983

Fish & Wildlife Service, Supplement to the 1980 Review (U.S. Fish and Wildlife Serv.,1983)

  Category 1 → Category 2
    Agave parviflora

  Category 1 → Category 3
    Agave toumeyana ssp. *bella*

  Category 2 → Category 3
    Agave utahensis var. *eborispina*
    Agave utahensis var. *nevadensis*

1984

Fish & Wildlife Service, Determination of Listing as a Federally Endangered Species (U.S. Fish and Wildlife Serv., 1984).

  Agave arizonica

Parks are already protected.

Agave utahensis Engelm. var. *eborispina* (Hester) Breitung. Four of the five taxa recognized by Gentry (1982) in the group Urceolatae have been or are now being considered for listing. This one has the distinction of being the most northwestern member of the genus. Like most other *A. utahensis*, it shows an affinity for limestone substrates. The taxon was recommended threatened by the Smithsonian in 1978, assigned to Category 2 by Fish and Wildlife in 1980, and finally dropped in the 1983 revision. It was found locally common in rugged inaccessible sections of southeastern California and southern Nevada where few if any threats have been identified.

Agave utahensis ssp. *kaibabensis* (McKelvey) Gentry. This subspecies is largely confined to the Grand Canyon and some of its major side canyons whereas ssp. *utahensis* generally occurs well away from the Grand Canyon. Subspecies *kaibabensis* was recommended for listing as threatened by the Smithsonian in 1978 and dropped from consideration in 1980. Although feral burros were apparently eating flowering stalks in some areas, the taxon is adequately protected by Grand Canyon National Park.

Agave utahensis var. *nevadensis* Engelm. This variety, another localized segregate of the *A. utahensis* complex, centers in southern Nevada and southeastern

California. It too was originally recommended for listing as threatened by the Smithsonian in 1978, retained in Category 2 in 1983, and dropped in 1983.

Agave mckelveyana Gentry. This species is endemic to northwestern Arizona. It was recommended as endangered by the Smithsonian in 1978 and dropped in 1980 after it was found to be relatively widespread with few if any threats.

Agave arizonica Gentry & Weber. This species was always considered to be very rare. Several field searches sponsored by the U.S. Fish and Wildlife Service, the U.S. Forest Service, and the Desert Botanical Garden of Phoenix

have yet to reveal any new major populations. Only 15 (possibly 16) populations, varying in size from one to several plants, have been identified to date. The low species number prompted the U.S. Fish and Wildlife Service to expedite the listing process. It was officially proposed as an endangered species by the U.S. Fish and Wildlife Service in May of 1983 and officially listed as an endangered species in 1984 (U.S. Fish and Wildlife Serv., 1983b and 1984b respectively).

The nearly paniculate inflorescence of *A. arizonica* suggests a hybrid origin possibly involving *A. toumeyana* Trel. of subgenus *Littaea* and perhaps with *A. parryi* Engelm. or *A. chrysantha* Peebles of subgenus *Agave*. Evidence indicates the hybridization event is very rare and that the hybrid progeny are sterile or nearly so. This proved the greatest stumbling block to its eventual listing as an endangered species and illustrates a problem common to many rapidly evolving groups such as *Agave*. A flexible species concept is unavoidable and even desirable in applying the Endangered Species Act to some taxa in the "gray area" between a full species and a minor variant. If the classical Mayrian species concept (Mayr, 1942) is too rigidly applied to these cases, important evolutionary advances may be unwittingly eradicated. Indeed, as Burgess (*Desert Plants*, this issue) advocates, alternative species concepts revolving around the "reticulate phylogeny" concept may be necessary in developing realistic taxonomies for groups such as *Agave*. However, the public is sensitive to abuses of the Act and inappropriate listing of inconsequential morphological variants will be perceived and reacted to negatively. The U.S. Fish and Wildlife Service must make some very difficult decisions.

Agave schottii Engelm. var. treleasei (Toumey) Kearney & Peebles. This taxon was recommended endangered by the Smithsonian in 1978 in spite of the fact that no wild populations have been observed since its discovery by J. W. Toumey in 1896 (with the doubtful exception of a population in the Ajo Mts., Pima Co., Arizona [Gentry, 1982]). It was listed as a Category 2 candidate in 1980 and was retained in that category through the 1983 revisions. I have searched the type locality (Table Mtn., Santa Catalina Mts., Pima Co., Arizona) and found nothing that resembled var. *treleasei*. Still the possibility that wild populations exist argues against prematurely dropping the taxon from further consideration. Although if wild populations are discovered it may turn out to be one of those minor variants which simply do not merit Endangered Species Act protection.

Agave toumeyana Trel. ssp. bella (Breitung) Gentry. Recommended endangered by the Smithsonian in 1978, Category 1 candidate in 1980, and finally dropped in 1983 by the U.S. Fish and Wildlife Service. This very attractive member of subgenus *Littaea*, group Parviflorae, turned out to be nearly as common as *Agave toumeyana* ssp. *toumeyana*. Its habitat is rugged mountain slopes in central Arizona.

Agave parviflora Torr. This species was listed as a Category 1 candidate in 1980 and dropped to Category 2 in 1983. Both subspecies, *A. parviflora* ssp. *parviflora* and *A. parviflora* subsp. *flexiflora* Gentry, are presumably included

in the candidate listing although only subsp. *parviflora* is known from the United States. Subspecies *parviflora* is found in the mountains of south-central Arizona and north-central and northeastern Sonora while ssp. *flexiflora* is restricted to northeastern Sonora. The two are apparently sympatric in parts of Sonora. Over-collection of wild populations in Arizona has been documented.

It is likely that two of the remaining candidate species, *A. glomeruliflora* and *A. parviflora* will eventually be dropped from consideration as research turns up more localities and fails to reveal any substantial threats. *Agave schottii* var. *treleasei* will probably also be dropped if no wild populations are found. Nearly all U.S. agaves are plants of rugged mountain areas where man's influences are relatively minimal. The most pervasive human activities affecting the biota of those habitats, livestock grazing and suppression of natural wildfires, may benefit some agaves by removing competition with perennial grasses.
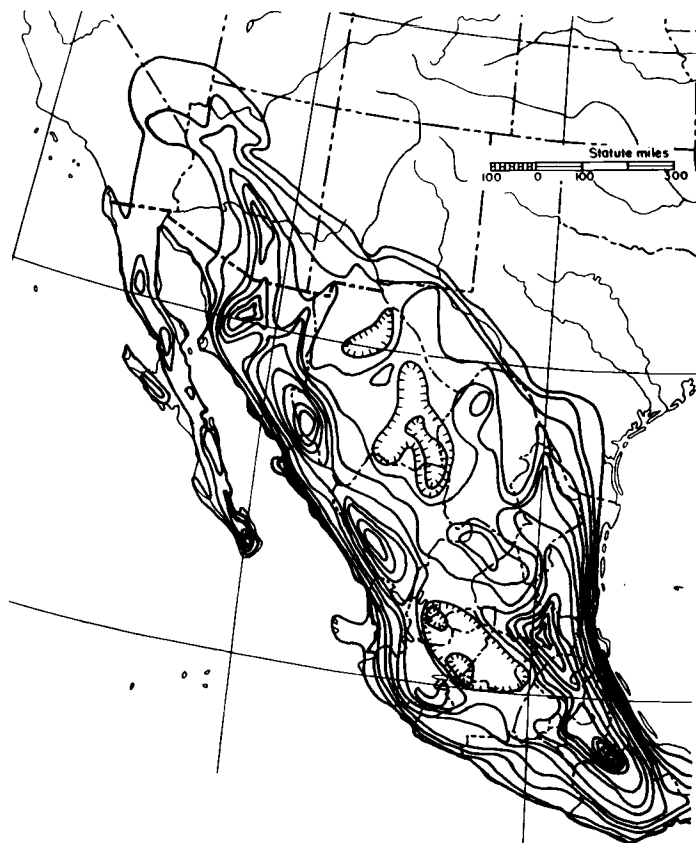
Conservation of Agaves in Mexico

Clearly the place to protect agaves is not in the United States at the northern edge of the genus' range. Rather, in Mexico a cursory examination of Dr. Gentry's monograph (Gentry, 1982) suggests many probably very rare species. Whole cultures have evolved through exploitation of agaves and the original wild populations of several species have succumbed to the spread of agriculture, wood cutting, and livestock grazing. I count at least 14 species never seen in the wild (approximately 10% of the genus). Table 2 shows a list of strictly Mexican agaves for which three or fewer localities appear on the distribution maps of Gentry (1982) or for which no native habitat can be identified.

The Endangered Species Act specifically directs the federal government to encourage conservation efforts of foreign governments by allowing endangered or threatened species in foreign countries to be listed if the foreign government is in agreement. It establishes a program and rules for cooperation with foreign governments which include the Convention on International Trade in Endangered Species of Wild Fauna and Flora and numerous other treaties and conventions.

Many of the species in Table 2 will turn out to be more common than previously thought, just like most of our American agaves. Still others may turn out to be extinct in the wild. Currently the only listed Mexican plant which does not also occur in the United States is *Abies guatemalensis* Rehder. Listing of some Mexican plants would substantially benefit conservation activities on both sides of the border. The strong cultural traditions and genuine rareness of some species makes the agaves an ideal starting point to apply the Endangered Species Act in Mexico.

I suggest that the only realistic approach to involving foreign governments in endangered species conservation hinges on their country's scientific communities. Governmental agencies of many so-called "Third World" countries are severely hampered by lack of funds and are largely unable, though not unwilling, to gather the necessary data. It seems incumbent on the scientists resident in those countries to assume at least part of that responsibility.

Figure 2. *Species abundance contour map of* Agave *subgenera* Agave *(excluding group Salmianae) and* Littaea. *Contour interval equals one species.*

Table 2. Mexican *Agave* species with three or fewer herbarium collections cited or for which no native habitat can be identified (see Gentry, 1982).

Baja California Sur
Agave margaritae Brandegee
A. vizcainoensis Gentry

Chiapas
A. pendula Schnitts.

Colima
A. gypsophila Gentry

Guerrero
A. gypsophila

Jalisco
A. attenuata Salm-Dyck
A. gypsophila
A. stringens Trel.

Mexico
A. attenuata

Michoacan
A. attenuata

Morelos
A. horrida Lem. ex Jacobi

Nayrit
A. geminiflora (Tagl.) Ker-Gawl.
A. nayaritensis Gentry
A. ornithobroma Gentry

Oaxaca
A. guiengola Gentry
A. lurida Aiton
A. oroensis Gentry

A. scaposa Gentry
A. titanota Gentry

Puebla
A. peacockii Croucher
A. triangularis Jacobi
A. stricta Salm-Dyck

Sinaloa
A. aktites Gentry
A. felgeri Gentry
A. fortiflora Gentry
A. jaiboli Gentry
A. zebra Gentry

Vera Cruz
A. attenuata
A. pendula

Unknown
A. albomarginata Gentry
A. bakeri Hook. f.
A. cantala Roxb.
A. desmettiana Jacobi
A. ellemeetiana Jacobi
A. ensifera Jacobi
A. franzosini Baker
A. pumila De Smet ex Baker
A. ragusae Terr.
A. sisalana Perrine
A. tecta Trel.
A. warelliana Baker
A. weberi Cels ex Poisson
A. yuccaefolia DC.

Biogeography and Conservation of Agaves

In the earlier discussion of *Agave arizonica*, I stressed the importance of flexible species concepts and alternative phylogenetic systems when dealing with endangered and threatened organisms and suggested the agaves are prime examples. In actual practice this is very difficult to apply because of the danger of abusing the Act's authority. In reviewing the distribution maps in Gentry (1982), some patterns became evident to me which may be pertinent to the problem.

Figure 2 is a species abundance contour map of the agaves prepared from the distribution maps in Gentry (1982). The confusing Salmianae group with its largely man-influenced artificial distributions was excluded. The greatest number of agave species occurs in southeastern Mexico in Puebla, Hidalgo, Queretaro, San Luis Potosi, and extreme southern Tamaulipas. Species abundance drops off quickly to the north and east where winter low temperatures fall below the tolerance of the genus. To the north and west agaves are abundant up the warmer west coast with several nodes of diversity. The diversity concentrations in Durango, Chihuahua, and Sonora roughly coincide with the two major trans-Sierra Madre Occidental travel routes and with Mexico Highway 15 but nonetheless probably indicate a real pattern of nature. The Cape region of the Baja penninsula supports another concentration. The concentrations of agave species range from five in the Cape region to 14 in the

Tehuacan Valley region of southeastern Puebla. The Tehuacan Valley concentration is significant in light of Axelrod's often criticized theory of the evolution of the North American Deserts (Axelrod, 1958). He postulated that the Tehuacan Valley was ultimately the place of origin for many of our desert taxa. The large number of *Agave* species in that region suggests the possibility it was likewise the place of origin, or at least of a substantial refugia, for the agaves.

The geographical abundance of the two *Agave* subgenera, *Littaea* and *Agave*, are plotted separately in Figures 3 and 4 respectively using the data in Gentry (1982) and excluding the group Salmianae. Several observations can be made:

(1) The presumably more primitive subgenus *Littaea* has a much more restricted distribution than subgenus *Agave*.

(2) Only subgenus *Agave* occurs on the Baja penninsula.

(3) Both subgenera share several concentrations along the west coast of Mexico.

(4) Both subgenera also share the same areas with few or no representatives in the dry central and northern plateau region.

(5) The only major area of low species diversity not shared by the two subgenera is the Sierra Madre Oriental. Subgenus *Agave* is conspicuously absent from this region while *Littaea* reaches its highest diversities there.

(6) The only major area of high species density shared by the two subgenera is again the Tehuacan Valley. The region could well be the center of origin of the paniculate infloresence which characterizes subgenus *Agave*. Gentry (1982) comments that *Agave peacockii* Croucher (subgenus

Prehistoric Agave Cultivation in Southern Arizona

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Abstract

Gathering of wild agave for food and fiber is widely recognized in ethnographic accounts of Southwestern Indians. Historically documented cultivation is limited to small-scale plantings and has not established agave as a significant aboriginal cultigen. The apparent absence of agave as a cultivated staple among peoples of the Sonoran Desert contrasts with pre-Columbian and historic ubiquity of this crop further south. It is a major cultigen throughout the rest of highland Mexico, including areas in Durango and Zacatecas, often considered within the greater Southwestern cultural sphere. Current archaeological evidence suggests that agave figured more prominently in prehistoric South-western agriculture than in that of subsequent groups.

Acknowledgments

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Introduction

Agave species of the Sonoran Desert grow mainly on rocky slopes of hills and mountains rather than in the valleys (Gentry, 1972:1). Distributional associations of *Agave parryi* Engelm. (Minnis and Plog, 1976) and *Agave murpheyi* F. Gibson (Crosswhite, 1981:58-59) with archaeological sites indicate a potentially active role for prehistoric Indians in spreading indigenous species beyond their natural range (Ford, 1981:21). In recent investigations, charred plant materials separated by flotation from sediments of Hohokam archaeological sites have included impressive amounts of agave. These sites in southern Arizona river valleys coincide poorly with natural distributions (Figure 1), yet in each case, agave is among the more common kinds of botanical remains. Cultivation near the sites rather than acquisition through trade has been proposed on the basis of overall quantity and the variety of plant parts (Gasser and Miksicek, *in press*).

Results and Discussion

Archaeological remains in the northern part of the Tucson Basin reveal the context and technology of Hohokam agave production. Farming took place on valley slopes or bajadas between the Santa Cruz floodplain and the Tortolita Mountains to the east. Here, limited modern surface distur-bance has permitted preservation of unburied features left by prehistoric farmers. Small devices constructed from unmodified local cobbles and pebbles include short terraces, check dams across shallow drainages, and rockpiles. Rock-piles or rounded heaps (Figure 5) are the most common feature type, and the complexes of related agricultural features are called rockpile fields. Roasting pits filled with ash and fire-cracked rock are also present in most of the fields. Similar rockpile complexes have been recorded by archaeologists throughout the extent of Hohokam culture in southern and central Arizona (Figure 1), but have received little directed investigation until recently.

Charred plant remains recovered from roasting pits in the present study provide a consistent association between rockpile fields and agave. Sixteen excavated pits in 12 fields have yielded plentiful burned fragments of agave and, in rare instances, other economic plants. While a few Arizona agave species may occur at elevations comparable to the fields between 625 and 670 meters above sea level (Gentry, 1982), wild stands are absent today on bajadas in the 350-square kilometers of the Tucson Basin study area. If modern distributions are indicative, bulky agaves gathered at higher elevations in the Tortolita Mountains would have required transport down the slopes and up to 15 kilometers across the bajada. A more likely explanation of the strong correlation between agave-filled roasting pits and fields is cultivation or at least the tending of hypothetical and now extinct bajada stands.

Stone artifacts scattered widely across rockpile fields provide additional evidence for the immediacy of agaves. Broad, flat implements with edges sharpened by chipping and grinding constitute 19.2 percent of all chipped stone tools in systematic collections. These sorts of specialized tools, called agave or mescal knives, were used by Southwestern Indians (Castetter, Bell and Grove, 1938) to sever leaves from agave hearts in preparation for roasting. Broken knives are not simply concentrated near roasting pits, but occur
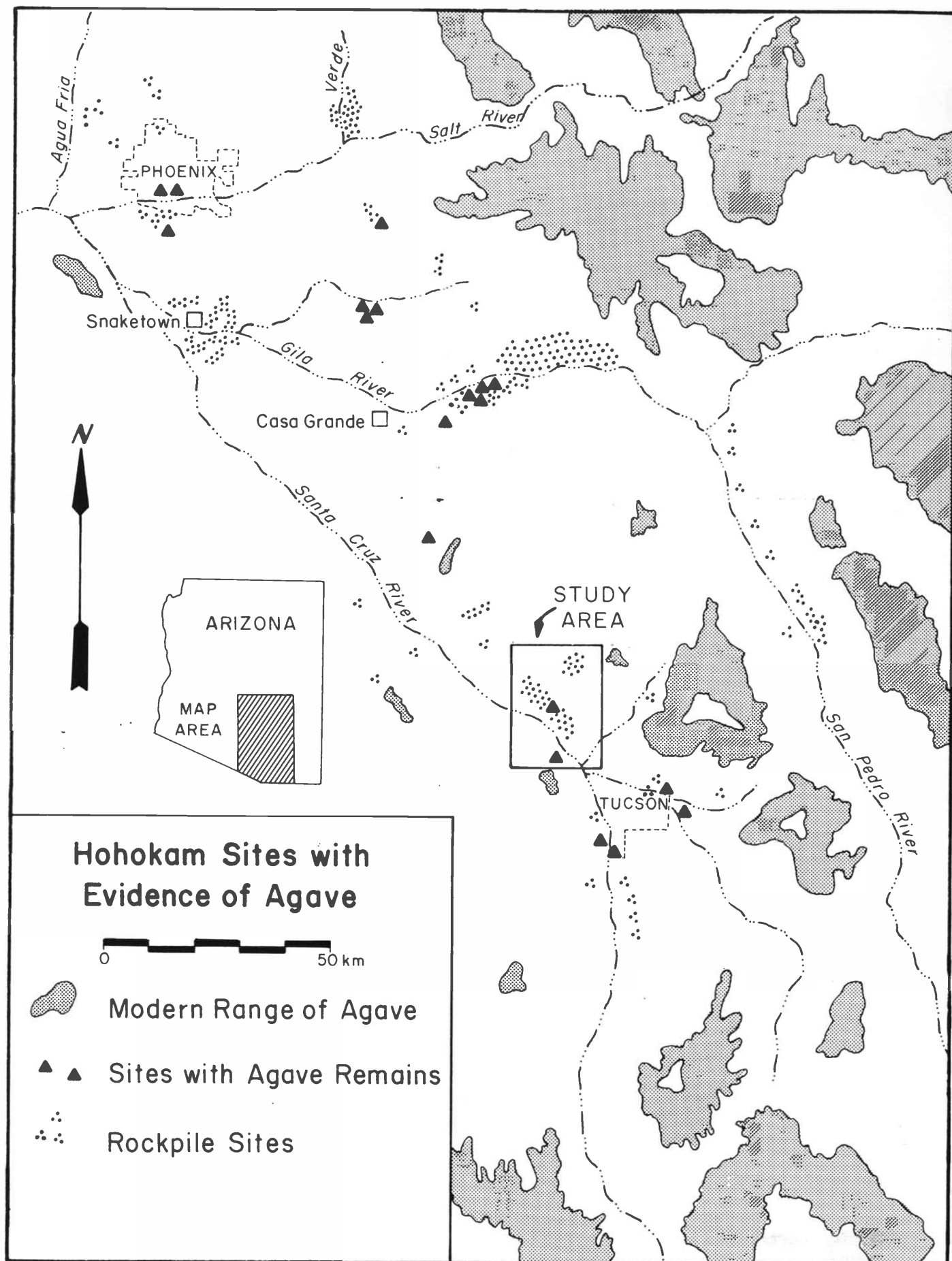
Figure 1. *The modern range of Agave is derived from Gentry (1982) and locations of elevations above 925 meters (3000 feet). Occurrences of rockpile loci have been compiled from site files at the University of Arizona, Arizona State University, and the Bureau of Land Management.*
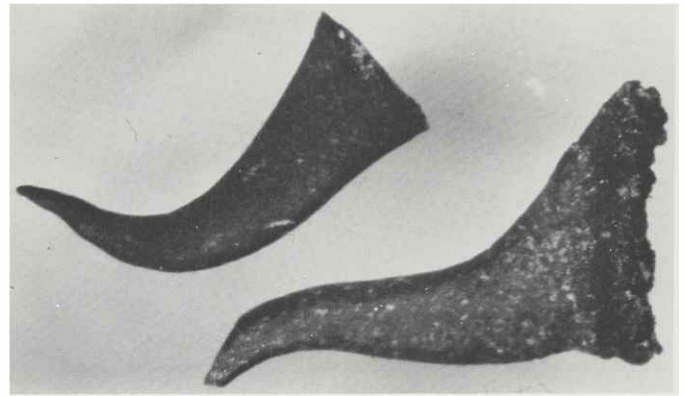
Figure 2. *Examples of different types of mescal knives from the Tucson study area.*

Figure 3. *Charred Agave prickles (marginal teeth) from a prehistoric roasting pit. The largest tooth is 6.0 mm long.*

throughout the field areas as though discarded after damage during harvest (Figure 2).

Species roasted at rockpile fields cannot yet be determined with certainty. Whether gathered or cultivated, agaves are usually harvested prior to maturation of the flowering stalk and concurrent dissipation of stored nutrients. Thus, it is not surprising that floral and fruiting parts are lacking among charred remains. Since the majority of Southwestern aboriginal crops were of ultimate Mesoamerican origin, Mexican cultivars are a possibility. However, size of vegetative materials discounts the upper ranges of large Mexican species. Historic ethnic groups of the Sonoran Desert such as the Papago (Gentry, 1982:442-443) and the Seri (Felger, 1985) are known to transplant local species, a practice which could have been used by the Hohokam to insure plants preadapted to local conditions.

Isolated fibers, leaf bases, and caudex (heart) fragments are the most common types of "macrofossils." One almost complete terminal spine compares most favorably with *Agave murpheyi*. Prickles or marginal teeth (Figure 3) recovered from several pits resemble both *Agave parryi* and *murpheyi*. Examination of the epidermal patterns on better preserved leaf bases suggests that at least two or three species are represented. It seems likely that several species, one of which was probably *Agave murpheyi*, were cultivated by the prehistoric inhabitants of southern Arizona.

Mexican cultivation practices relate agaves to stone devices in field systems where annual crops are also planted in better-watered field segments or in seasons of favorable rainfall (Wilken, 1976; Johnson, 1978; Messer, 1978; Sanders et al., 1979). Such mixed cropping may be indicated by corn pollen in several shallow subsurface samples from fields, and by single cotton seeds recovered from each of two roasting pits. Mexican farmers often plant agaves along check dam and terrace walls, aiding in stabilization and soil and runoff entrapment. Moisture-enhanced microhabitats created by these features would benefit agaves on low, exposed slopes. The agricultural role of rockpiles cannot be similarly illuminated by observed historic use.

Multiple lines of evidence indicate that rockpiles as well as terraces and check dams are facilities of agricultural production. They are improbable as residuals of rock removal for planting. Some occur in the midst of dense concentrations of surface rock and some appear to have necessitated importation of rock for construction. Origin in surface clearing to increase runoff to more arable land as suggested for Negev Desert piles (Evenari et al., 1971:127-146), also seems unlikely. Many Tucson rockpiles are topographically situated so as to receive optimal runoff. Also, diversion devices for directing water to other sectors are not present in any field.

Uneven, porous rockpile surfaces allow infiltration of rainfall in contrast to surrounding hard-packed and impermeable ground surfaces. Rocks then act as a mulch, slowing evaporation of soil moisture by blocking capillary action and preserving higher moisture levels beneath. This effect of rocks in desert soils has been established experimentally (Evenari et al., 1971:260).

A continuing response by modern plants to the microhabitats of prehistoric rockpiles is demonstrated by preferential growth of perennials, comparatively dense annuals, and the presence of lichens and moss. This response has been quantified in the current study by comparing root biomass in soil directly beneath rockpiles and adjacent controls (Figure 4). Root weight in rockpile soil averaged 2.7 times the weight of roots in controls. These observations further strengthen an interpretation of rockpiles as moisture-enhancing facilities for crop plants.

Experimental agave plantings in prehistoric Tucson fields illustrate the adaptability of agave to these settings and suggest an additional benefit of cobble features. Viable leaves on 39 offsets or suckers of *Agave americana* L. were counted at planting in the early spring of 1984 and were
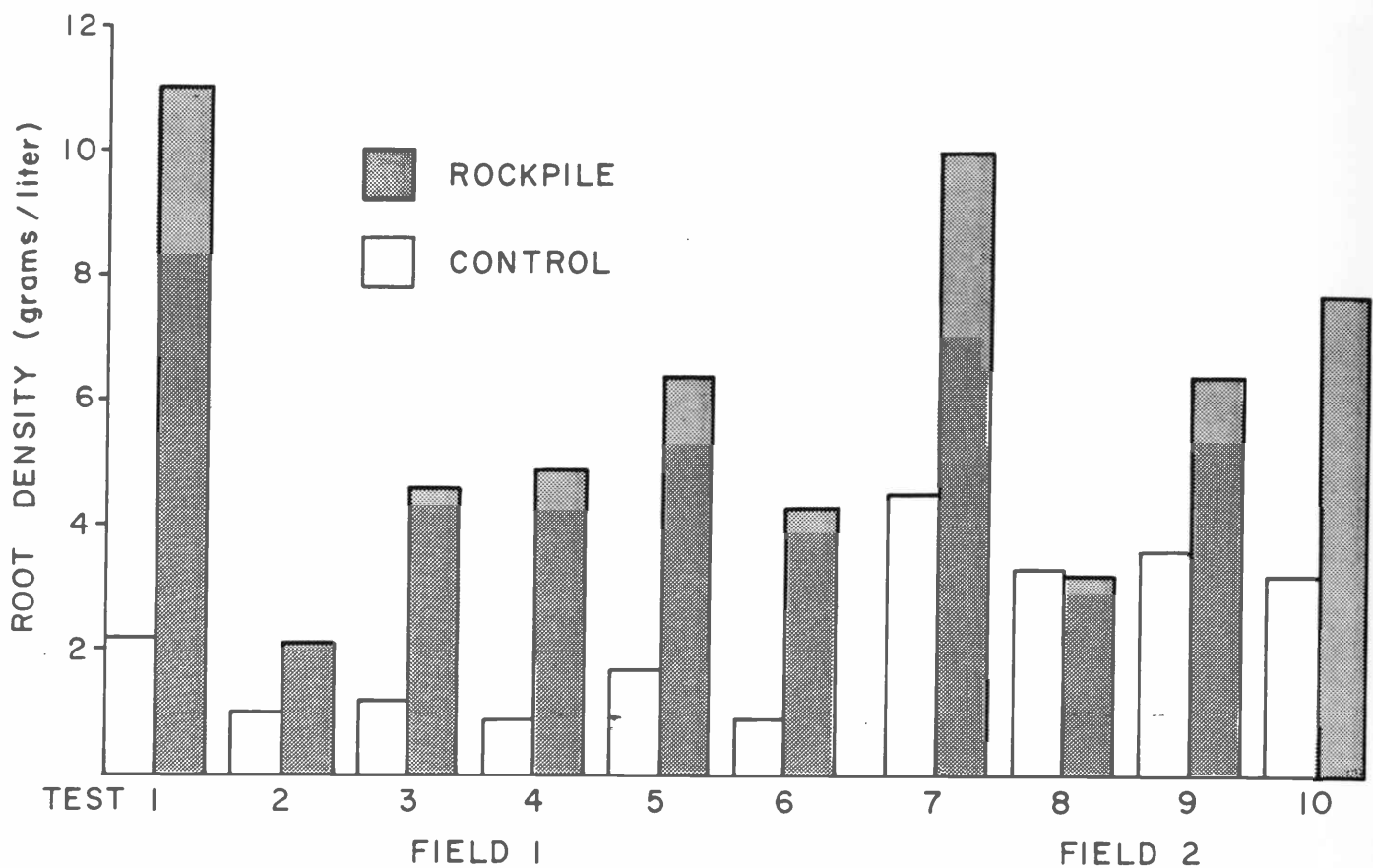
Figure 4: *Comparison of root biomass in rockpile soil samples and in adjacent control samples. Dry weight was determined after separation of roots from matrix by water flotation. Samples 1-6 are from one field and 7-10 from a second.*

tabulated again after the following summer rains. Average number of leaves increased 96 percent, from 3.0 to 5.9. Predation of leaves of all plants by rodents and possibly rabbits was heaviest after summer rains heightened succulence. Tunneling and occasional uprooting to procure roots and hearts occurred during the spring drought, when alternative food sources were low. Plants in rockpiles escaped this damage, unlike more vulnerable paired controls.

The nature and distributions of agricultural remains allow insight into the organization of Hohokam agave production. Archaeological survey of 350 square kilometers has been completed between the Tortolita Mountains and Tucson Mountains in the northern part of the Tucson Basin. Two preferred site locations for all periods parallel the flanks of the Tortolita Mountains and the Santa Cruz River. In the early Classical Period between about A.D. 1150 and 1300, population increased and a cluster of 320 interrelated sites covered 50 square kilometers (19 square miles) of bajada slopes between the floodplain and eastern foothills. A central site with a platform mound was located several miles from the present town of Marana. One of the unique aspects of this Classic Period settlement pattern was the elaboration of rockpile fields in general and the construction of very large ones in middle bajada locations.

The association of agave and roasting pits was not an innovation of the early Classic Period. A few small complexes of rockpiles, linear stone features, and roasting pits can be dated prior to A.D. 1000. While Classic Period field size was quite variable, differing combinations of these same feature types were used. With some larger and smaller exceptions, most rockpile diameters range near 1.5 meters, with heights no more than 75 centimeters. Checkdams across minor, shallow drainages and terraces trending across slopes are usually less than 10 meters long and composed of one to several cobble courses. Forty-one rockpile fields on the upper bajada cover less than two hectares each. Among 71 fields of the middle bajada, small ones are present as well as much larger complexes encompassing from 10 to 50 hectares. A portion of one such field is mapped in Figure 7.

The size and arrangement of fields have implications for farming labor and tenure. All upper bajada small fields are situated adjacent to habitation sites or include one or a few fieldhouse structures. In these cases, agricultural tenure seems linked to proximity. Both large and small fields of the middle bajada lack indications of nearby residence. Per unit of production, cultivators of these fields had to invest an added increment of travel time to and from their homes. Largescale complexes would have occupied many farmers, necessitating either some form of communal labor or commonly recognized intrafield boundaries. As among a number of Southwestern native peoples, kin-based or other corporate groups may have controlled arable land, with members assigned use rights to individual plots.

Figure 5. *Cross-section of a Tucson Basin rockpile.*

Figure 6. *A large roasting pit yielded charred Agave. The dark ashy surface stain marks a diameter of almost 30 meters. Pit roasting is the common ethnographic method for cooking edible Agave hearts and a means for facilitating fiber removal from leaves. Fuel species identified from prehistoric charcoal indicate vegetational communities like those of today.*
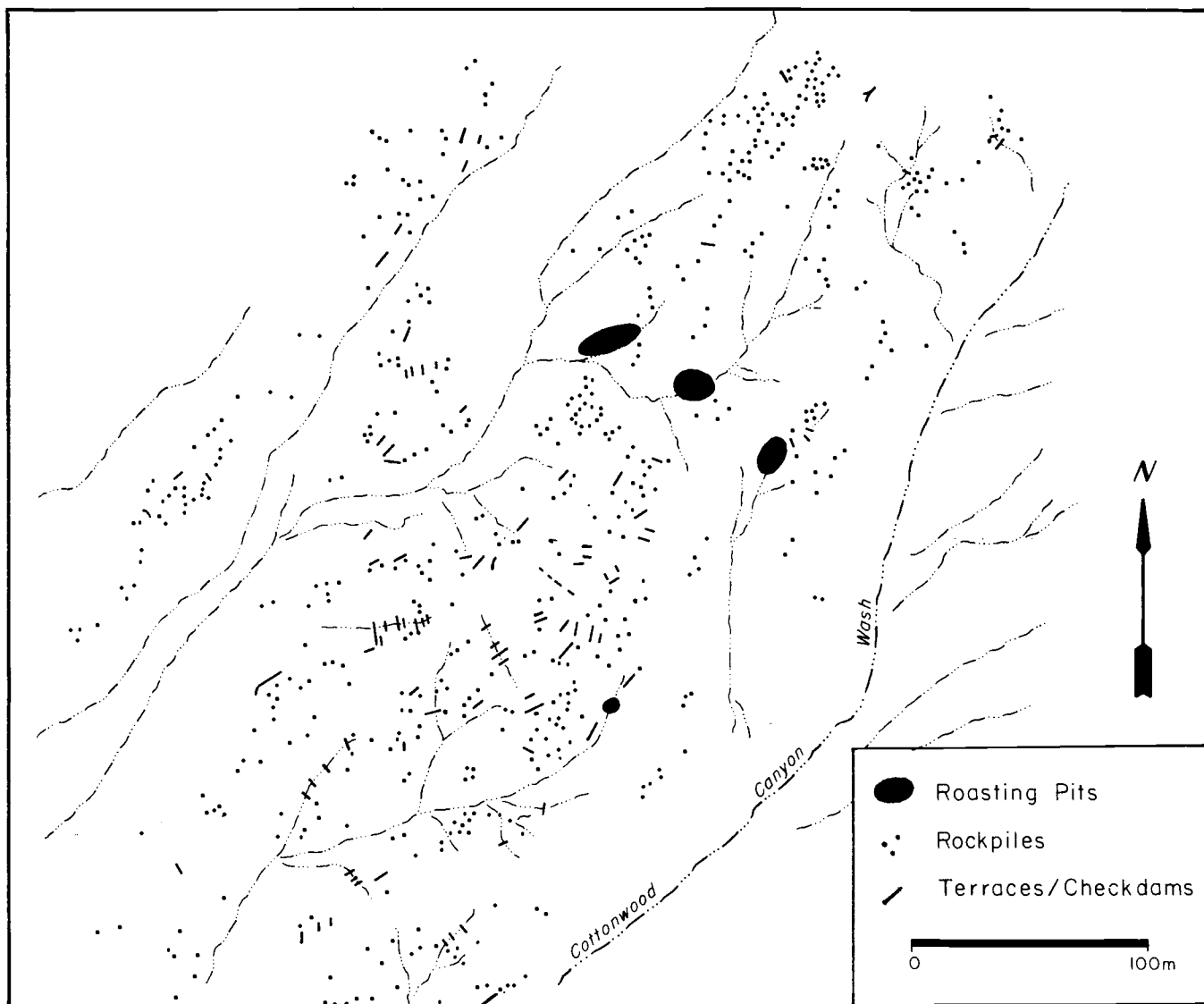
Figure 7. A portion of one large field of the middle bajada.

Roasting pit size tends to follow field size. Small pits about 3 meters in diameter are typical of small fields. Large fields are characterized by multiple huge features that might more properly be called roasting areas. Up to 35 meters in diameter (Figure 6), these features represent the accretion of repeated seasonal reuse, but show little evidence of small discrete firings. Cultivators would have had to coordinate harvesting and preparation of their plants. Collective roasting would have been an efficient use of desert woody fuels, revealed by charcoal to have consisted mainly of mesquite and ironwood. On the other hand, cultivators using the modest pits of small fields could have processed their harvests according to more individualized convenience.

The impressive scale of the large middle bajada rockpile fields is illustrated by the fact that they cover 485 hectares or over five square kilometers. Projecting numbers of rock-piles and meters of linear features from tabulated samples at representative fields, a total of 42,000 rockpiles and 120,000 meters of terraces and checkdams emerges. Experi-mental construction of features suggests that an initial expenditure of 50 man-years was required. Potential yields from the fields can be estimated by assuming one plant per rockpile and per two meters of linear feature, for a total of 102,000 plants at one time. With an average ten-year maturity for harvested plants, 10,200 agaves would have been available each year.

Agave hearts of small Southwestern species approximate four kilograms; at this rate, the large fields would have produced 40.8 metric tons of edible product. Furnishing 347 calories and 4.5 grams of protein per 100 grams (Ross, 1944), harvested agave could have supplied annual caloric requirements for 155 persons and protein requirements for 110 (FAO/WHO, 1973). Experimental fiber extraction in the present study suggests 365 grams of fiber per plant, for a 3.72 metric-ton annual crop. While all these estimates rely on modern analogy and experiment, they serve to demonstrate that agave production in rockpile fields could have added significantly to Hohokam diet and economy.

Discover traditional uses of desert plants
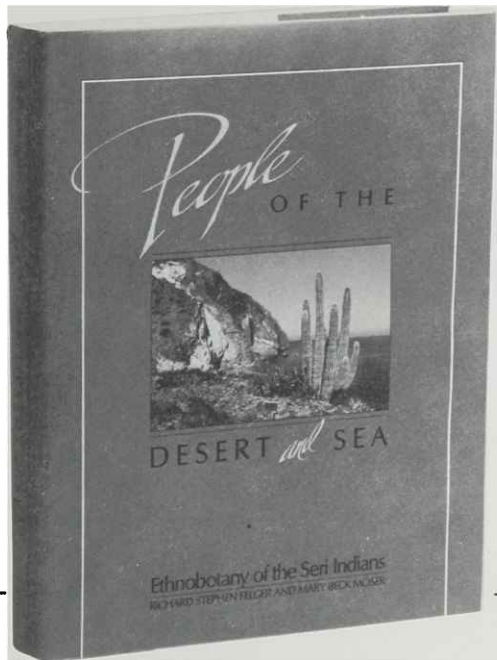
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*448 pages (8½ x 10½), illus. $65.00 cloth. June 1985.*

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288 pages, illus. $21.95 cloth. May 1985.
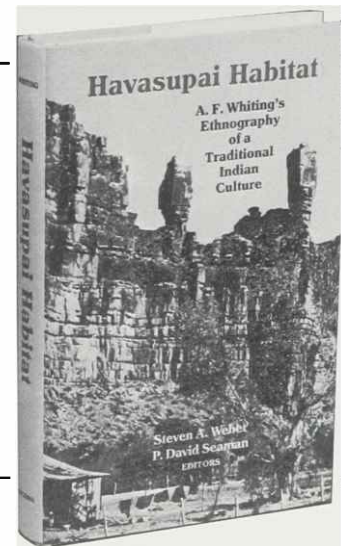
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Curtin recorded culinary, medicinal, and other uses of 76 desert plants in a book accessible to readers at all levels.

156 pp., illus. $6.95 paper. (1949) 1984.

This plant of Agave shawii in Baja California is a developmental monstrosity. As an addendum to the 1985 Symposium on the Genus Agave, Donald J. Pinkava announced that John R. Pasek had requested the photograph above to be projected on the screen. Some participants immediately thought of XÓLOTL, the pre-Columbian deity who changed himself into a monstrosity of an Agave. As the audience marvelled at the Agave monstrosity on the screen, the plenary session was declared closed.

Editorial

XÓLOTL and QUETZALCÓATL in Relation to Monstrosities of MAGUEY (Agave) and TEOCENTLI (Zea), With Notes on the Pre-Columbian Religion of Mexico. According to the Aztecs and their predecessors in pre-Columbian Mexico there were several creations and destructions of the world. We now theorize that each cycle ended with an eclipse of the sun. When the god TEZCATLIPOCA was ruling the world as the sun, his enemy QUETZALCÓATL knocked him from the sky, the former falling to become a Jaguar on earth. Tezcatlipoca now rules over the shadow kingdom of night as the god of darkness, the patron of youth and princes, but also of sorcerers and evil ones. He presides over feasts and banquets. As Tezcatlipoca tried to return from night to day one foot extended into day and was torn off by EARTH MONSTER to be replaced by a Smoking Mirror by which Tezcatlipoca detects events in his alter-universe of daytime. As soon as Tezcatlipoca had fallen from the sky, Quetzalcóatl became the sun, until he too was struck down in the next cycle of destruction to become the Plumed Serpent. Since a feathered snake is a monstrosity, he exists today as an incarnation of XÓLOTL, the god of monstrosities (see below).

Next came TLÁLOC and then CHALCHIUHTLICUE to become progressive suns. With each new cycle of creation and destruction of the world, men ate food plants which were progressively less wild and more refined, finally eating TEOCENTLI, the "Grain of the Gods" now considered the ancestor of modern corn. With each successive destructive cycle human beings were destroyed by converting them first to fish, then birds, then monkeys, finally giants. When the last world was destroyed, the gods killed the giants and all humanity. Unfortunately the sun was also lost in the battle. All the gods (the stars of the heavens) gathered at TEOTIHUACÁN so that one could volunteer to be sacrificed to the sun.

Not one but two gods volunteered, one rich and one poor. The rich god offered fine possessions in sacrifice as preparation. The poor god offered only spines of MAGUEY (Agave) stained with his own blood. To become the sun the god or gods had to leap into the flame of the sacred brazier to emerge pure so as to illuminate the world. The rich god tried three times to hurl himself into the fire but failed due to his inability to give up the realm of darkness. The poor god who had offered only *Agave* spines stained with his own blood succeeded. Before the new sun would move across the heavens from east to west, he demanded that the other gods (stars) be killed in sacrifice. This strong new sun of humble origin was HUITZILOPOCHTLI, the Blue Hummingbird on the Left, who became the alter-ego of Tezcatlipoca when the latter, the rich god, finally leaped into the brazier after the flames had weakened and (in something of a shadow sense) also became the sun, although he retained his alter-ego realm of the night. Venus, the Morning Star (Quetzalcóatl) shoots an arrow at the sun but is killed each morning as it is returned. Eventually all the gods are dead but Xólotl, the Evening Star (alter-ego of Quetzalcóatl). Xólotl, god of monstrosities and doubling, used sorcery to withstand the arrows of the sun. First, he changed into a doubled or monstrose Maguey, then into a doubled or monstrose Teocentli (*Zea*), eventually becoming the AXOLOTL, aquatic stage of the Tiger Salamander (*Ambystoma trigrinum*). The feathery gills of the Axolotl make it appear to be a plumed water serpent and at the same time a monster.

XÓLOTL-QUETZALCÓATL is a twin god, considered the god of all twins and monsters. [This pre-Columbian concept correctly recognizes that many monstrosities of growth are due to a doubling and re-doubling.] Interestingly, this god of monsters is the archetypically good god, indicating a belief by the ancients (probably the Toltecs) in the

potential good of novelties and inventions which might at first seem somewhat bizarre. As the Plumed Serpent, depicted as bird and snake, Quetzalcóatl is the beneficent god of all mankind. As the Axolotl this last remaining god seemed to be killed by the arrows of the sun but actually split into an ethereal EHÉCATL (plumed god of the wind) and a serpent-like (but often rather dog-faced) terrestrial CÓATL (perhaps originally the adult slithering form of *Ambystoma*, which may have been considered a monster because dog-faced and serpent-like but having legs). In any event the twin deity in his dog-faced serpent state penetrated the world of the dead and stole the bones of the dead humans of past destroyed worlds. Escaping with the bones but with the infernal demons of the dead in hot pursuit, the twin deity emerged Phoenix-like as the beautiful Quetzalcóatl. Taking *Agave* spines, he sacrificed some of his own blood, sprinkling it over the bones to bring to life the human beings of the present world. Quetzalcóatl is the god of resurrection, the "precious twin" who appears in the heavens as the Morning Star and again in the afternoon as the Evening Star (Xólotl). Being devoted to life, he resurrected the other gods as well. His earthly representation as TLAHUITZCALPANTECUHTLI has two faces, one of a living man, the other a skull.

Quetzalcóatl is the hero founder of agriculture and industry, the plumed serpent god of wind and life. As the wind of the storm clouds, he flies with plumed wings, but when he once again causes TLÁLOC and the rain of the storm to give life to the plants, his goodness slithers over the ground to become re-doubled in the crops. On July 16, AD 750, at the time of a solar eclipse, with Venus appearing extremely close to the sun, Quetzalcóatl, the good god of agriculture—as well as of science, industry and art—set off into the Caribbean on a raft of serpent skins, not to be seen again until a predicted return in the Nahuatl year CE ÁCATL. Quetzalcóatl's directional orientation among the gods made him the "white" god and he was often depicted having a beard. One can imagine the consternation of MOTECZUMA II when in the year Ce Ácatl (AD 1519) "giant winged canoes" of Cortés were cited off the coast of Mexico. The ships landed on Maundy Thursday of 1519 but Cortés did not disembark until the next day which was GOOD FRIDAY to the Spaniards but was, by strange coincidence, the birthday of Quetzalcóatl in the Aztec calendar! This was Year 1 of the new order, wherein the patron of agriculture, science, industry and art, who did not demand massive human sacrifice, had returned! Surely the white-faced and bearded Cortés with his strange hat and shining armor, coming as he did in a winged canoe, appeared every bit as monstrose as Quetzalcóatl, himself a monstrosity and alter-ego god of monstrosities. Interestingly, present-day Corn (*Zea mays*) is considered by many modern botanists to be a monstrose redoubled derivative of Teocentli (see *Desert Plants*, Volume 3, Number 4), and useful economic cultivars of *Agave* to be pentaploid or other ploidal monstrosities or re-doublings! One naturally wonders if the good of Quetzalcóatl did not indeed slither over the ground to become instilled in these crops as Xólotl stirred to miraculously produce these good monstrosities! —F. S. Crosswhite.

Agave and the Pre-Cortés Religion

Continued from back cover

hooks, then piercing the chests with a stone knife to rip the still-beating hearts out as an offering. But such sacrifice to Xiuhtecuhtli, whom they saw as the old god HUEHUETÉOTL, was merely calendric and became perfunctory. To be on the safe side all old fire was extinguished at the end of its lifetime (52 years) and a strong new fire created which was distributed to all the hearths. Sacrifice to the god of hunting involved shooting arrows into an *Agave*, since the Aztecs were no longer major hunters, then carrying bound victims (as if they were deer) to the tops of pyramids where their beating hearts were liberated from their chests. To the agricultural Aztecs, this sacrifice too seems to have been a token event.

The hallmark of the MÉXICA of TENOCHTITLÁN was sacrifice to Huitzilopochtli, their Hummingbird God of Sun and War. Making of the intoxicating drink PULQUE from *Agave* by the Méxica necessitated "castrating" the plant by removing the embryonic reproductive structures or flowering stalk so that flowers and seeds were not produced. The energy ebbed from the leaves and flowed into the central heart of the plant. Pulque was a liquid having a flame to warm the human spirit. Although Xiuhtecuhtli was god of the Center, the symbolic color of the Center and the Up and the Down was green rather than the red or yellow of flame. The preciousness of the center and the up and the down of the present is epitomized by the Jade, referred to as CHALCHÍHUITL. Aside from the green heart of the rosette of the *Agave*, another word, CHALCHÍHUATL ("Precious Liquid") refers to the nectar flowing from it. By castrating the *Agave* to make pulque, the Aztecs seem to have realized that they were depriving the pollinating hummingbird of his CHALCHÍHUATL. As children of Huitzilopochtli the Aztecs determined to remedy the deprivation and to regularly feed their chosen god. The word Chalchíhuatl also came to mean "Nectar Fed to the Gods" in the sense of human blood. The Méxica brought captives of war first directly to the temples at the tops of the pyramids, gave them pulque to drink and dedicated them to Huitzilopochtli. From that day on their bodies contained the Chalchíhuatl belonging to the hummingbird god. The captives lived peacefully as servants of their masters and were fattened for a good length of time. During famines and other occasions of religious need, including calendric ceremonies, the captives were again taken to the temples and for the second time willingly drank pulque, but this time the *Agave* nectar pulsating through their veins and vessels was liberated and offered to Huitzilopochtli as the beating heart was ripped from the chest. Then the flesh of the victims was cooked and eaten by the Méxica in a solemn communion. This vigorously prosecuted sacrifice largely superceded sacrifice to the "old, wrinkled" god of fire, just as harvest of polysaccharides to make pulque from turgid decapitated *Agave* replaced normal flowering which would have resulted in an old wrinkled monocarpic *Agave* (truly a HUEHUEMAGUEY) drained of its nourishment to nurture other life. One needs little imagination to see how the Aztecs must have compared this monocarpic wrinkling with the concept of fire being drained of its energy in supporting life (through domestic heating and cooking). The Aztecs simply came to prefer draining the energy of the Jade Heart (Chalchíhuitl) of the Maguey themselves before the Chalchihuatl became dissipated! But Huitzilopochtli had to receive his share. The powers and strengths of the cardinal directions were probably seen as instilled into the central Chalchíhuitl as the outstretched *Agave* leaves yielded their energy to the inner heart of the plant, just as Huitzilopochtli, in thankfulness to the Aztecs, ensured that tribute from conquered cities in all directions flowed incessantly to Tenochtitlán, the heart at the center of the empire.

The sacrifice of Chalchíhuatl to Huitzilopochtli in the temples legitimized the drinking of pulque by all celebrants in the sacrifice until the wee hours of the morning on a typical sacrificial night, until Quetzalcóatl, the Morning Star, again chased away Tezcatlipoca and the forces of night. The *Agave* goddess MAYAHUEL had 400 nipples to suckle the multitudes. To dedicate the Templo Mayor to Huitzilopochtli, the Tenochca sacrificed 20,000 captives, the entire male population of major districts of Oaxaca. The quantity of pulque involved must have decimated major *Agave* populations as well.

Drinking of pulque during the normal course of the day, rather than when sanctified by a religious occasion, was reserved to
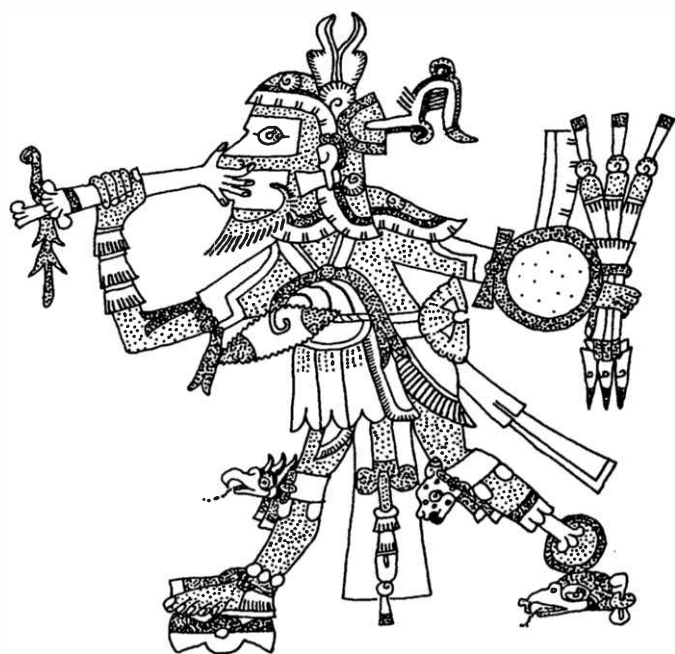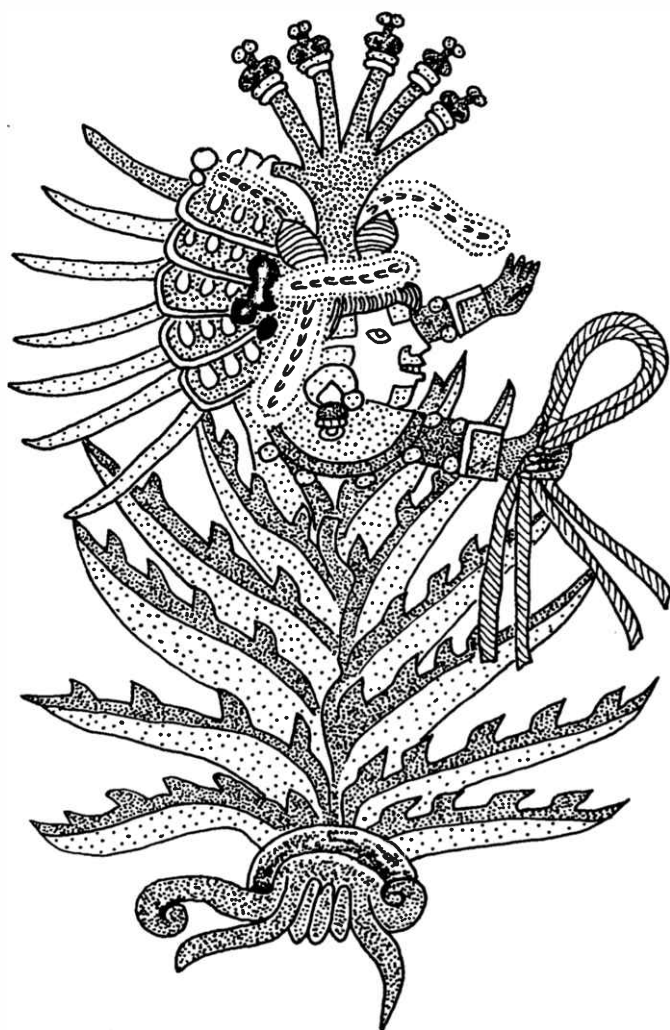
Left: MAYAHUEL, *goddess of Agave, holding a rope of Maguey and with foaming pulque in her head-dress. Drawn by Carol D. Crosswhite following the illustration in Codex Borbonicus, now in Paris.* **Right:** TEZCATLIPOCA, *god of darkness, eating the hand of a sacrificed prisoner. The god's left foot was severed by Earth Monster and is replaced by a Smoking Mirror. Drawn by Carol D. Crosswhite following the illustration in the Codex Fejervary-Mayer in the Liverpool City Museum, England.*

Agave and the Pre-Cortés Religion of the Mexican Altiplano Central. This issue of *Desert Plants* deals with *Agave*, a genus of plants so important in pre-Conquest Mexico that it became inextricably a part of the pre-contact religion. Just as John F. Kennedy claimed *"Ich bin ein Berliner,"* we all share a heritage from the Nahuatl people of the Valley of Mexico, now the Distrito Federál and surrounding regions. The Nahuatl COYOTL, OCELOTL, MESQUITL, CHOCOLATL, HUACOMOLI, METATL and HURAKÁN which are now our Coyote, Ocelot, Mesquite, Chocolate, Guacomole, Metate and Hurricane are superficial examples only. Occupation by Cortés and succeeding Spaniards created a melding of two strong peoples and the present Mexico City, indisputable hub of the Mexican subcontinent. Held in high esteem today in the Altiplano and elsewhere are the people who we now call AZTECS, those who came from AZTLÁN, the Seven Caves of the North, following HUITZILOPOCHTLI, the Hummingbird on the Left, and sucking with him the nectar of the *Agave* and the flowers of war! Huitzilopochtli's poor mother sent him off to the south with two sets of *Agave* sandals, one pair to wear while conquering each new city, the other to wear as he eventually lost each city in the same order. How stoic these Aztecs!

Human sacrifice to the god of fire, Xiuhtecuhtli, the god of the Center (and the Up and the Down) was ancient and well-known to the Aztecs. The fire of hearth and home was central but each major directional path from home was also important. The major deities of the cardinal directions were the black TEZCATLIPOCA (North), the white QUETZALCÓATL (West), the red XIPE TÓTEC (East, a red alter-ego of Tezcatlipoca), and the blue HUITZILOPOCHTLI (South, a blue alter-ego of Tezcatlipoca). Since Tezcatlipoca was the god of night, it was convenient for him (as Xipe) to hide in the red inner shade of another person's skin in order to go abroad in the daytime. The red color symbol of Xipe is appropriate because of the blood shed by the victim chosen for flaying. The blue color symbol of Huitzilopochtli was appropriate because the Aztecs saw him streaking across the blue sky as the god of the sun and across the blue sky of the local scene as the hummingbird. Huitzilopochtli flew fast and high but as an alter-ego of Tezcatlipoca could not be seen setting foot on earth in the day (unless as in the case of the *Agave* sandals it was in either ascending or descending to power). Huitzilopochtli defied (by rapid and high flight) being caught by man, beast or god, in contradistinction to the black alter-ego (Tezcatlipoca) whose foot had been torn off by Earth Monster. As the Aztecs devoted themselves to the Hummingbird God and moved south, they made him their god of war in inspiration from and in allusion to his powers. They believed that brave warriors fallen in battle went to TONATIUHICHAN, the House of the Sun, sipping nectar there from flowers and fighting mock battles. After four years the warriors fully transformed to hummingbirds and came back to earth.

As opposed to Quetzalcóatl, Tezcatlipoca and his alter-egos (sometimes called "disguises") demanded sacrifice of a portion of the population, as also did Xiuhtecuhtli and various minor deities. The Aztecs saw Xiuhtecuhtli as the "old god" with a wrinkled face and a brazier on his head like a barbecue grill. Sacrifice to him annually involved throwing victims onto hot searing coals, as if pumping adrenalin into the old god, pulling the living sizzling bodies out with grappling