



Agave Adaptation to Aridity

Item Type	Article
Authors	Burgess, Tony L.
Publisher	University of Arizona (Tucson, AZ)
Journal	Desert Plants
Rights	Copyright © Arizona Board of Regents. The University of Arizona.
Download date	13/12/2023 18:21:04
Link to Item	http://hdl.handle.net/10150/554187

Agave Adaptation to Aridity

Tony L. Burgess

Herbarium, University of Arizona, Tucson

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.

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 (Ehrlert, 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.

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 super-species 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 infre-

quent, 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.

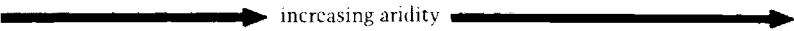
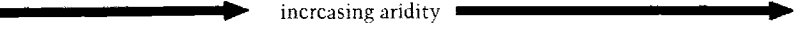
During the Pleistocene, pluvial conditions, postulated to have combined cooler summers and a longer duration of the winter rainy season (Van Devender and Spaulding, 1979), should have enabled *A. deserti* to survive at lower elevations, thereby expanding its range considerably. If conditions were too 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 LITTAEAE			
			
Striatae	<i>A. dasylirioides</i>	<i>A. striata</i> ssp. <i>falcata</i>	<i>A. striata</i> ssp. <i>striata</i> , Chihuahuan desert
Amolae	<i>A. pedunculifera</i>	<i>A. vilmoriniana</i>	<i>A. chrysoglossa</i> , Coastal Sonora
Filiferae	<i>A. multifilifera</i>	<i>A. schidigera</i>	<i>A. felgeri</i> , Coastal Sonora
	<i>A. colimana</i>	<i>A. ornithobroma</i>	
Parviflorae	<i>A. polianthiflora</i>	<i>A. parviflora</i>	<i>A. toumeyana</i>
			<i>A. schottii</i> , Central Arizona to Northern Sonora
Marginatae	<i>A. angustiarum</i>	<i>A. funkiana</i>	<i>A. lechuguilla</i> , Chihuahuan Desert
	<i>A. horrida</i>	<i>A. kerchovei</i>	<i>A. victoriae-reginae</i> , Chihuahuan Desert
		<i>A. lophantha</i>	<i>A. pelona</i> , Northwestern Sonora
		<i>A. obscura</i>	
		<i>A. potrerana</i>	
Urceolatae			<i>A. utahensis</i> , Mohave Desert
SUBGENUS EUAGAVE			
			
Rigidae	<i>A. rhodacantha</i>	<i>A. angustifolia</i>	<i>A. aktites</i> , Coastal Sonora
			<i>A. dasylio</i> , Baja California Sur
Marmoratae			<i>A. zebra</i> , Northwestern Sonora
Americanae		<i>A. americana</i>	<i>A. scabra</i> , Chihuahuan Desert
Ditepalae	<i>A. wocomahi</i>	<i>A. flexispina</i>	<i>A. colorata</i> , Coastal Sonora
	<i>A. shrevei</i>	<i>A. palmeri</i>	<i>A. fortiflora</i> , Northwestern Sonora
	<i>A. durangensis</i>	<i>A. chrysantha</i>	
Parryanae		<i>A. parryi</i>	<i>A. neomexicana</i>
			<i>A. havardiana</i> , Northern Chihuahuan Desert
Campaniflorae		<i>A. parrasana</i>	<i>A. gracilipes</i> , West Texas
	<i>A. promontorii</i>		<i>A. aurea</i>
			<i>A. capensis</i> , Baja California Sur
Deserticolae	<i>A. moranii</i>	<i>A. mckelveyana</i>	<i>A. deserti</i> , Sonoran Desert
	<i>A. gigantensis</i>	<i>A. sobria</i>	<i>A. cerulata</i> , Sonoran Desert
		<i>A. vizcainoensis</i>	<i>A. margaritae</i> , Baja California Sur
		<i>A. subsimplex</i>	
Umbelliflorae	<i>A. shawii</i> ssp. <i>shawii</i>	<i>A. sebastiana</i>	<i>A. shawii</i> ssp. <i>goldmaniana</i> , Baja California

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

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

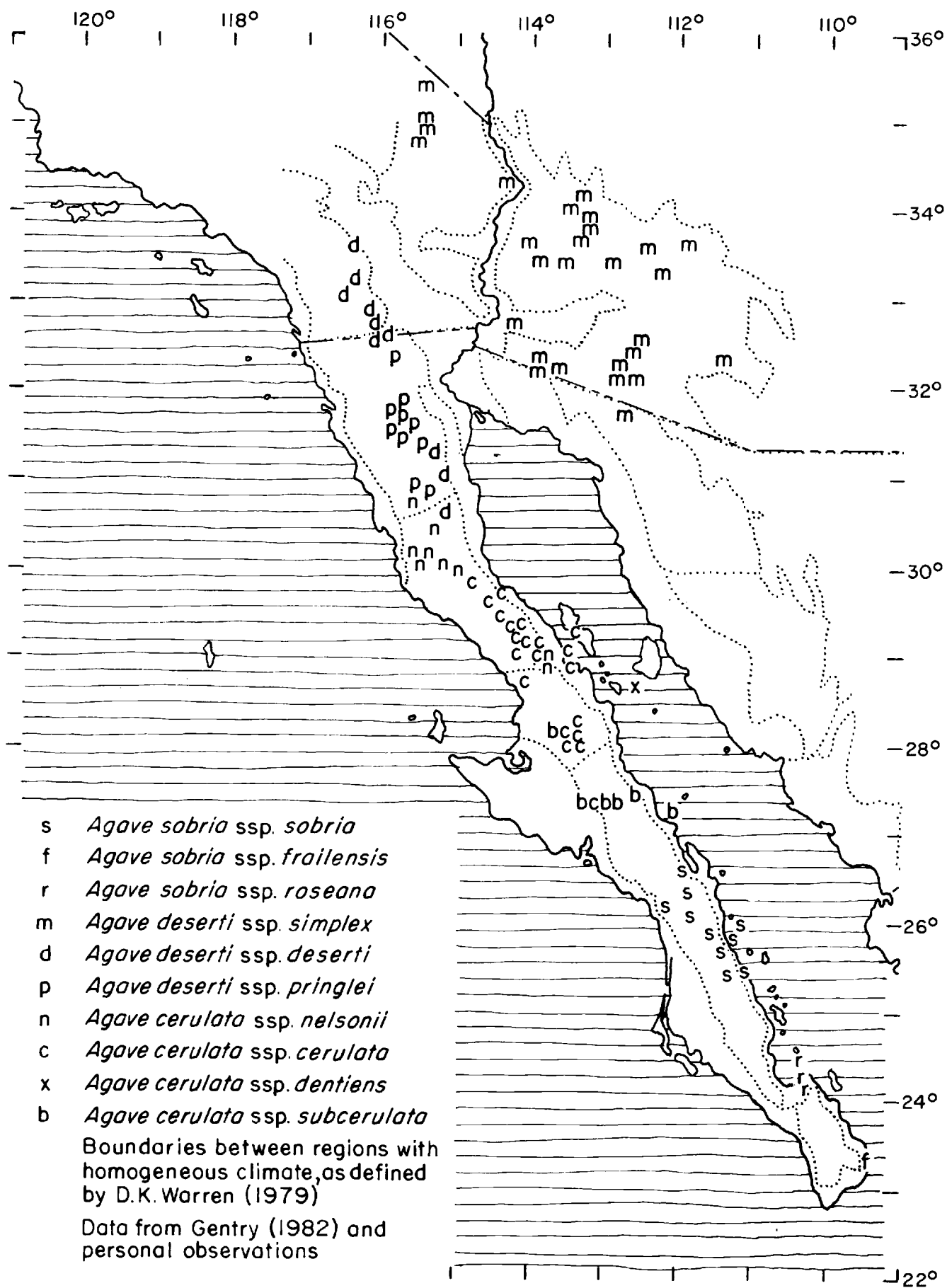


Figure 1. Distributions of selected taxa in Agave group *Deserticolae*.

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 19.0	22.3 22.4	28.5 28.1	26.1 26.5
Precipitation	38 55	2 0	58 65	83 149

(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. cerulata* and *A. sobria* Brandegees 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

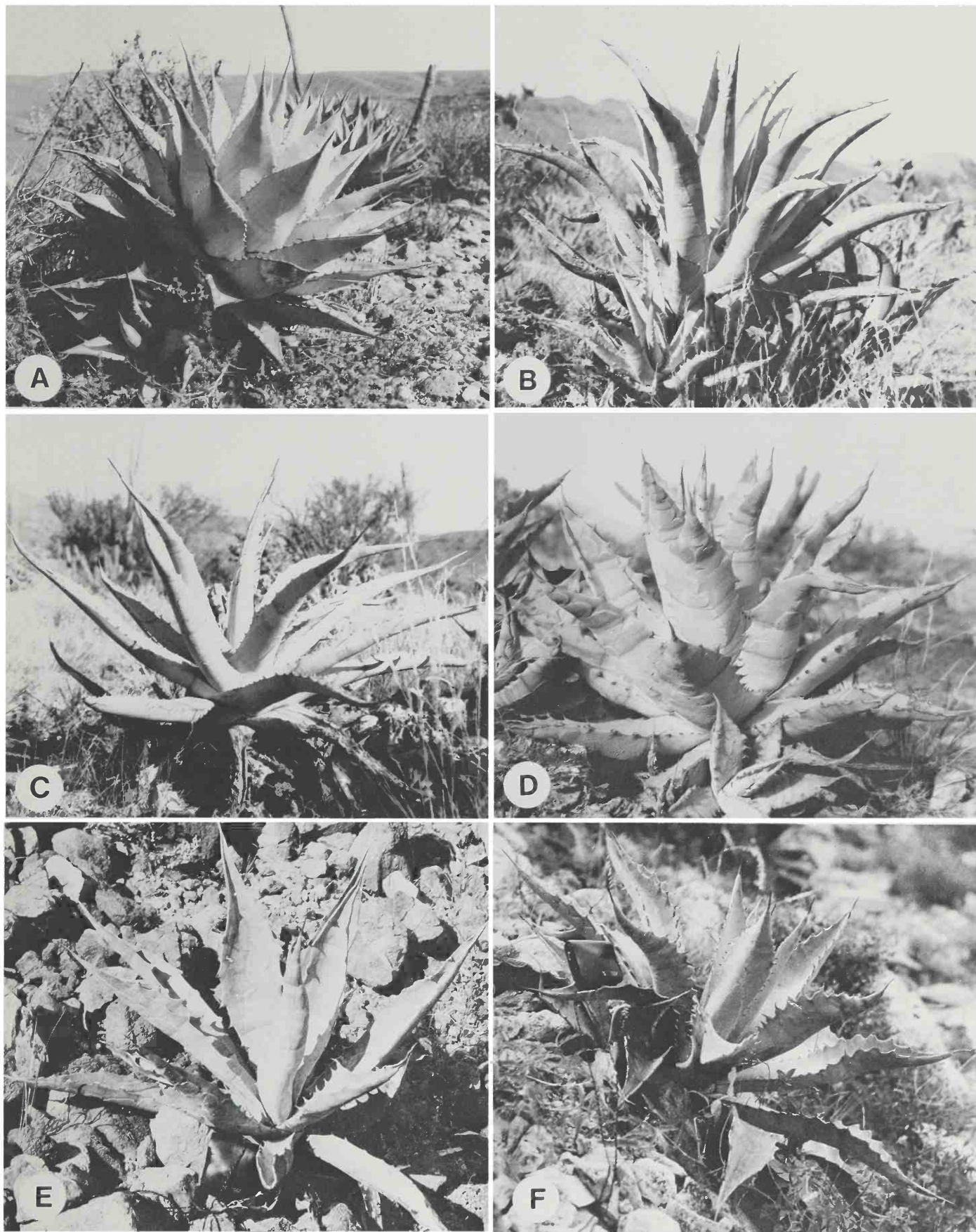


Figure 2. Rosettes of *Agave* along a transect in Baja California. **a:** *A. cerulata* ssp. *nelsonii*, east of El Rosario, BCN; **b, c:** *A. cerulata* ssp. *cerulata*, north of El Arco, BCN; **d:** *A. cerulata* ssp. *subcerulata*, near San Ignacio, BCS; **e:** *A. sobria* ssp. *roseana*, north of La Paz, BCS (photo by R.M. Turner); **f:** *A. sobria* ssp. *frailensis*, near Los Frailes, BCS (Photo by R.M. Turner).

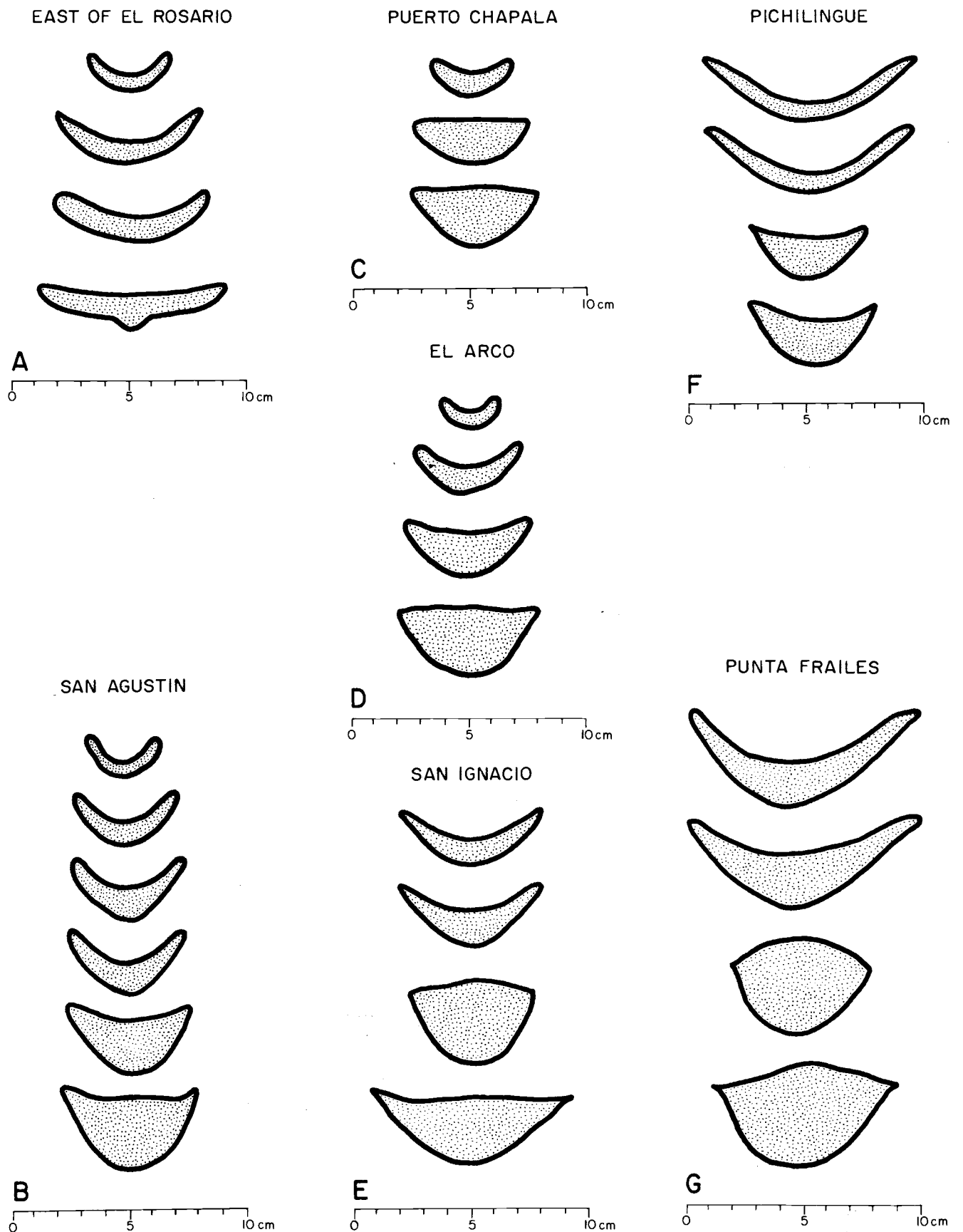


Figure 3. Transections of *Agave* leaves from Baja California. Within each series the sequence from bottom to top represents successive cross-sections from the proximal to the distal end of the same leaf. Locations are given above each sequence. **a:** *A. cerulata* ssp. *nelsonii*; **b, c, d:** *A. cerulata* ssp. *cerulata*; **e:** *A. cerulata* ssp. *subcerulata*; **f:** *A. sobria* ssp. *roseana*; **g:** *A. sobria* ssp. *frailensis*.

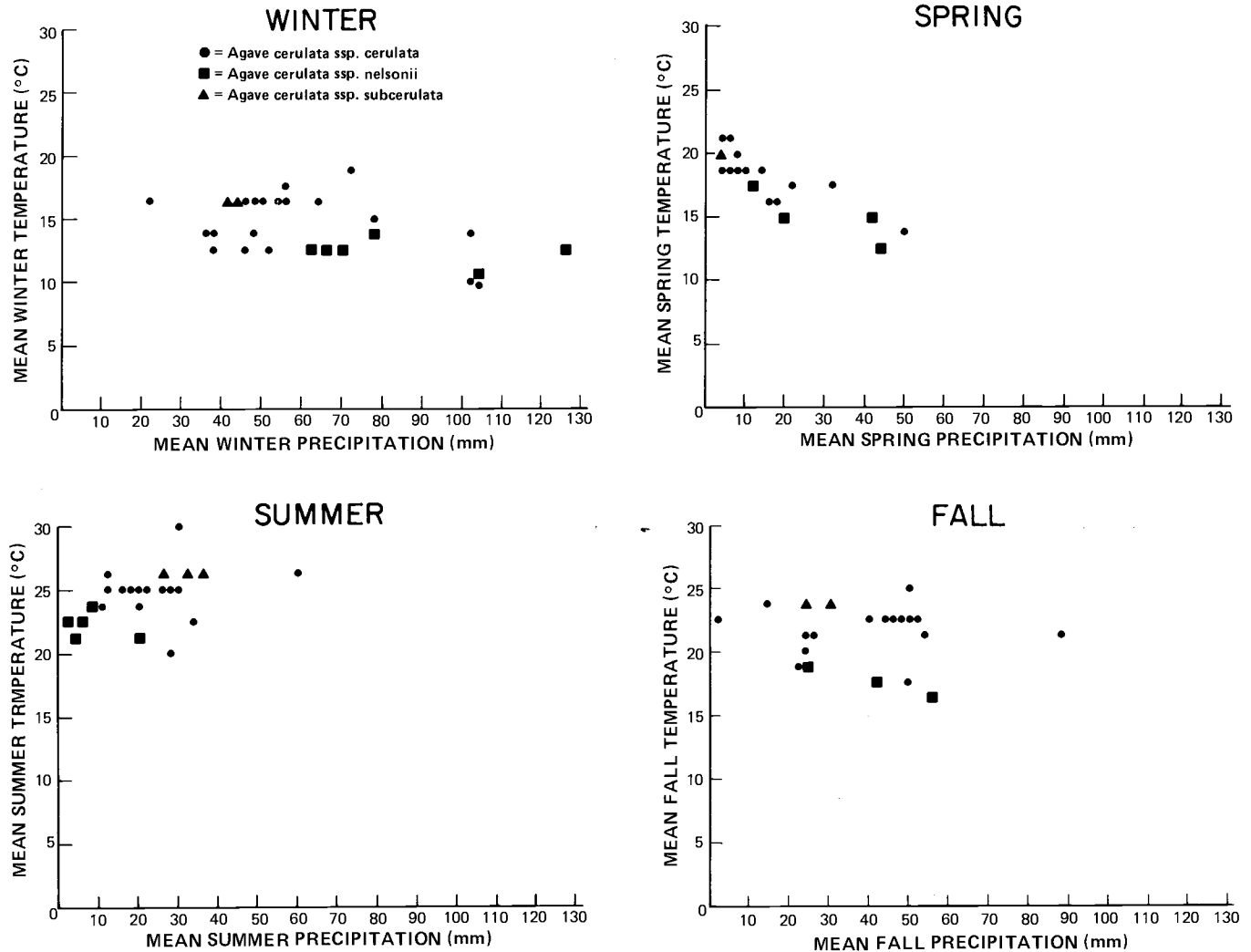


Figure 4. Mean seasonal temperature and precipitation relationships for *Agave cerulata* sites. Symbols: circles = *A. cerulata* ssp. *cerulata*; squares = *A. cerulata* ssp. *nelsonii*; triangles = *A. cerulata* ssp. *subcerulata*.

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 noted 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.

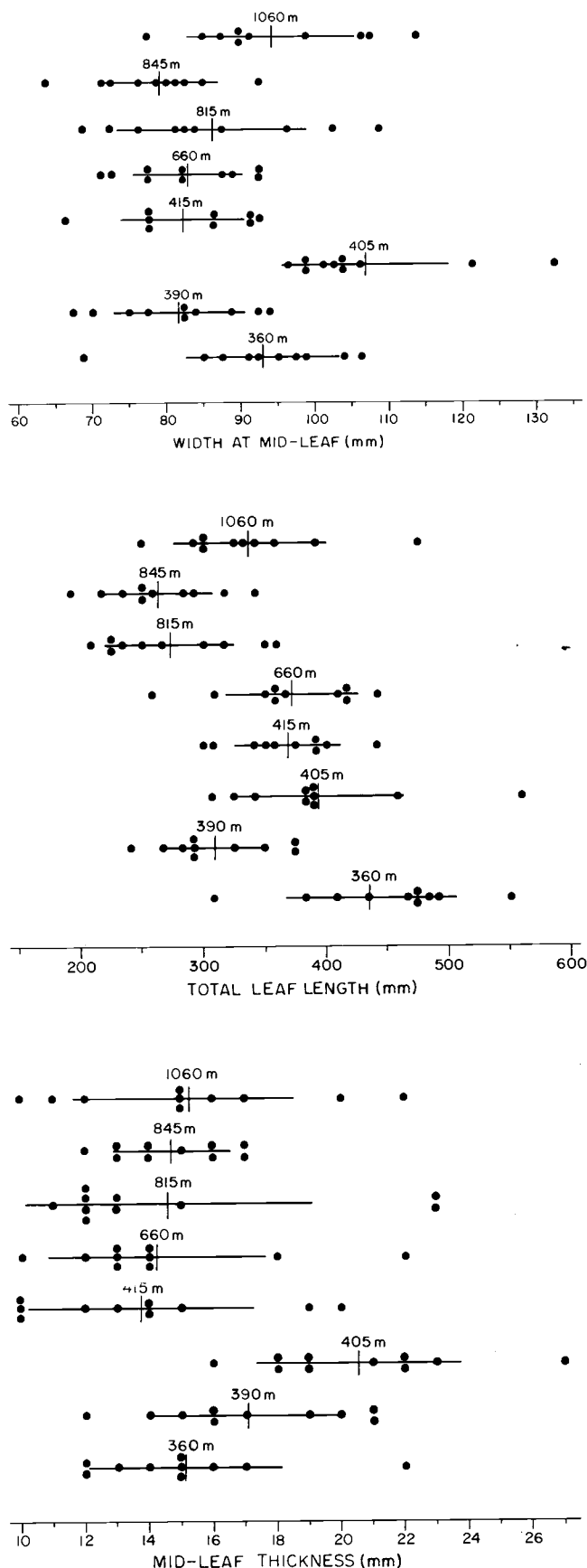


Figure 5. Leaf dimensions of *A. deserti* along an elevational gradient in San Diego County, California. The vertical line is at the mean value for each site, solid lines encompass one standard deviation on either side of the mean, and outlying values are represented by dots.

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.

Literature Cited

- Burgess, T.L. 1979. *Agave-complex of the Guadalupe Mountains National Park*; putative hybridization between members of different subgenera. Pp. 79-89. In: H.H. Genoways and R.J. Baker (eds.), *Biological Investigations in the Guadalupe Mountains National Park, Texas*. National Park Service Proceedings and Transactions Series No. 4. Washington, D.C.
- Ehrler, W.L. 1969. Daytime stomatal closure in *Agave americana* as related to enhanced water-use efficiency. Pp. 239-247. In: C.C. Hoff and M.L. Riedsel (eds.), *Physiological Systems in Semiarid Environments*. University of New Mexico Press, Albuquerque.
- Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton. 246 pp.
- Gates, D.M. 1980. *Biophysical Ecology*. Springer-Verlag, New York. 601 pp.
- Gentry H.S. 1967. Putative hybrids in *Agave*. *Journal of Heredity* 58:32-36.
- Gentry, H.S. 1972. *The Agave Family in Sonora*. U.S. Dept. Agric. Handbook 399. 195 pp.
- Gentry, H.S. 1982. *Agaves of Continental North America*. University of Arizona Press, Tucson. 670 pp.
- Gentry, H.S., and J.R. Sauck. 1978. The stomatal complex in *Agave*: Groups Deserticolae, Campaniflorae, Umbelliflorae. *Proceedings of the California Academy of Science* 41:371-387.
- Grant, V. 1971. *Plant Speciation*. Columbia University Press, New York. 435 pp.
- Hartsock, T.L., and P.S. Nobel. 1976. Watering converts a CAM plant to daytime CO₂ uptake. *Nature* 262:574-576.
- Hastings, J.R., and R.R. Humphrey (eds.) 1969. *Climatological Data and Statistics for Baja California*. Technical Report on Meteorology



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.

- and Climatology of Arid Regions No. 18. University of Arizona Institute of Atmospheric Physics. 96 pp.
- Hastings, J.R., and R.M. Turner. 1965. Seasonal precipitation regimes in Baja California, Mexico. *Geografiska Annaler* 47:204-223.
- Jordan, P.W., and P.S. Nobel. 1979. Infrequent establishment of seedlings in *Agave deserti* (Agavaceae) in the northwestern Sonoran Desert. *American Journal of Botany* 66:1079-1084.
- Nobel, P.S. 1974. *Introduction to Biophysical Plant Physiology*. W.H. Freeman and Co., San Francisco. 488 pp.
- Nobel, P.S. 1976. Water relations and photosynthesis of a desert CAM plant, *Agave deserti*. *Plant Physiology* 58:576-582.
- Nobel, P.S. 1977. Water relations of flowering of *Agave deserti*. *Botanical Gazette* 138:1-6.
- Nobel, P.S. 1984a. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia (Berlin)* 62:310-317.
- Nobel, P.S. 1984b. Productivity of *Agave deserti*: measurement by dry weight and monthly prediction using physiological responses to environmental parameters. *Oecologia (Berlin)* 64:1-7.
- Nobel, P.S. and T.L. Hartsock. 1978. Resistance analysis of nocturnal carbon dioxide uptake by a Crassulacean acid metabolism succulent, *Agave deserti*. *Plant Physiology* 61:510-514.
- Nobel, P.S., and S.D. Smith. 1983. High and low temperature tolerances and their relationships to distribution of agaves. *Plant, Cell and Environment* 6:711-719.
- Schaffer, W.M., and M.V. Schaffer. 1979. The adaptive significance of variations in reproductive habit in Agavaceae II: Pollinator foraging behavior and selection for increased reproductive expenditure. *Ecology* 60:1051-1069.
- Turrill, W.B. 1936. Contacts between plant classification and experimental botany. *Nature* 137:563-566.
- Van Devender, T.R., and W.G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204:701-710.
- Walter, H. 1979. *Vegetation of the Earth, and Ecological Systems of the Geo-biosphere*, Edition 2. Springer-Verlag, New York. 274 pp.
- Warren, D.K. 1979. Precipitation and temperature as climatic determinants of the distribution of *Fouquieria columnaris*. Ph.D. diss., Walden University, Naples, Florida. 133 pp.
- Wells, P.V., and D. Woodcock. 1985. Full-glacial vegetation of Death Valley, California: juniper woodland opening to yucca semidesert. *Madroño* 32:11-23.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton University Press, Princeton, New Jersey. 200 pp.
- Woodhouse, R.M., J.G. Williams, and P.S. Nobel. 1980. Leaf orientation, radiation interception, and nocturnal acidity increases by the CAM plant *Agave deserti* (Agavaceae). *American Journal of Botany* 67:1179-1185.
- Woodhouse, R.M., J.G. Williams, and P.S. Nobel. 1983. Simulation of plant temperature and water loss by the desert succulent, *Agave deserti*. *Oecologia (Berlin)* 57:291-297.

Agave and the Pre-Cortés Religion

Continued from page 115

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 Chalchihuatl 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 Chalchihuatl 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 Magüey. To understand the surging 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 MOTEZUMA 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