Chromosome and Hybridization Studies of Agaves

Donald J. Pinkava
and Mark A. Baker
Department of Botany and Microbiology
Arizona State University

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.

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 Gômez-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; Gômez-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.

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

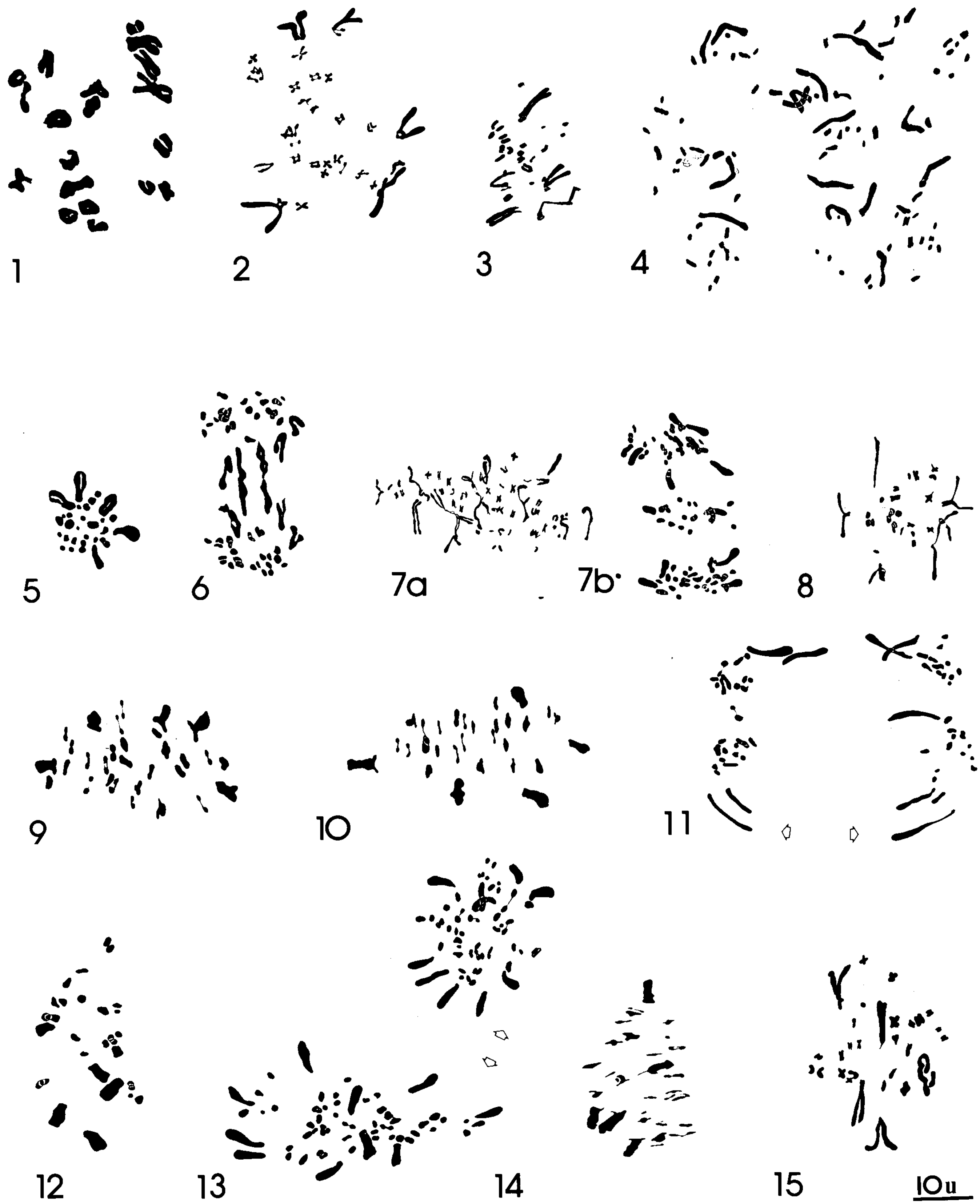
Taxon	Chromosome number	Collection data
NOLINEAE		
Nolina microcarpa Watson		
	**$2n = 19_{II}$	ARIZONA: Maricopa Co.: west side of Humboldt Mtn., 34°58′45″ N, 111°47′20″ W, *Baker 4698 & Mohlenbrock* (Fig. 1); Yavapai Co.: Rte I-17, Little Black Canyon opposite Sunset View Rest Area, *Pinkava 14064 & 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 Englemann 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 = 90_I. **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 = $30_{II} + 30_I$; *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
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. 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. 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. victoriae-reginae Moore. Marginatae; 2x (Cave, 1964), 4x (Granick, 1944)	*A. scabra* Salm-Dyck. Americanae; ca. 6x	Unnamed hybrid ?x; Gentry, 1982a
A. kerchovei Lemaire. Marginatae; 4x (Sharma & Bhattacharyya, 1962)	*A. marmorata* Roezl. Marmoratae; ?x 1982a	*A. peacockii* Croucher. ?x; Gentry, 1967, 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. toumeyana Trel. ssp. *toumeyana*. Parviflorae; px (Cave, 1964)	*A. chrysantha* Peebles. Dipetalae; 2x	Cline's agave 3x (this study)

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

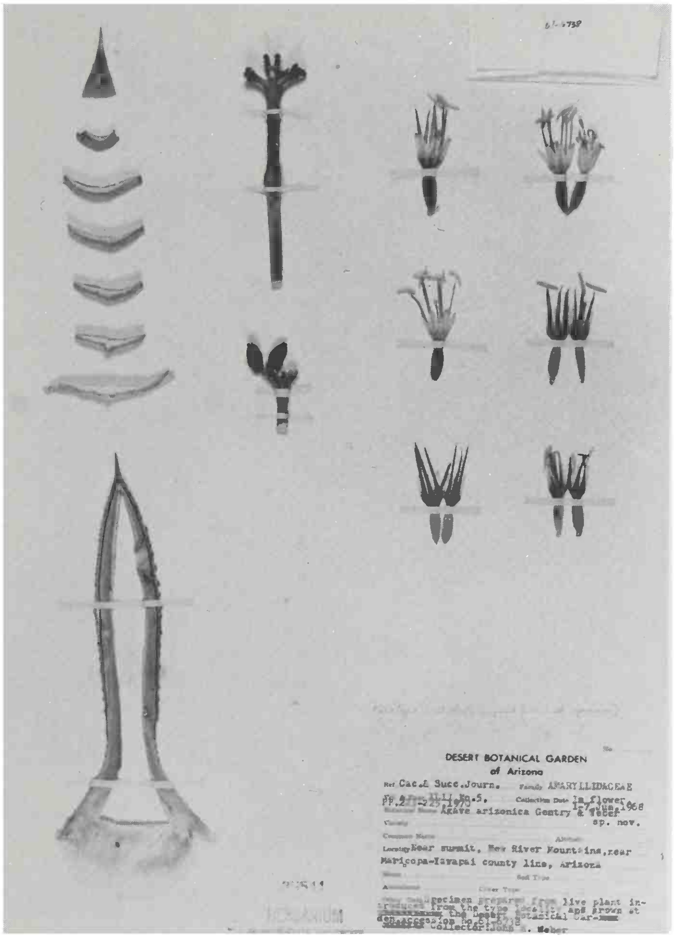


Figure 18. Photograph of herbarium specimen (ASU) of Agave arizonica *(Weber s.n., paratype). Scale: herbarium sheet measures 29 × 42 cm.*

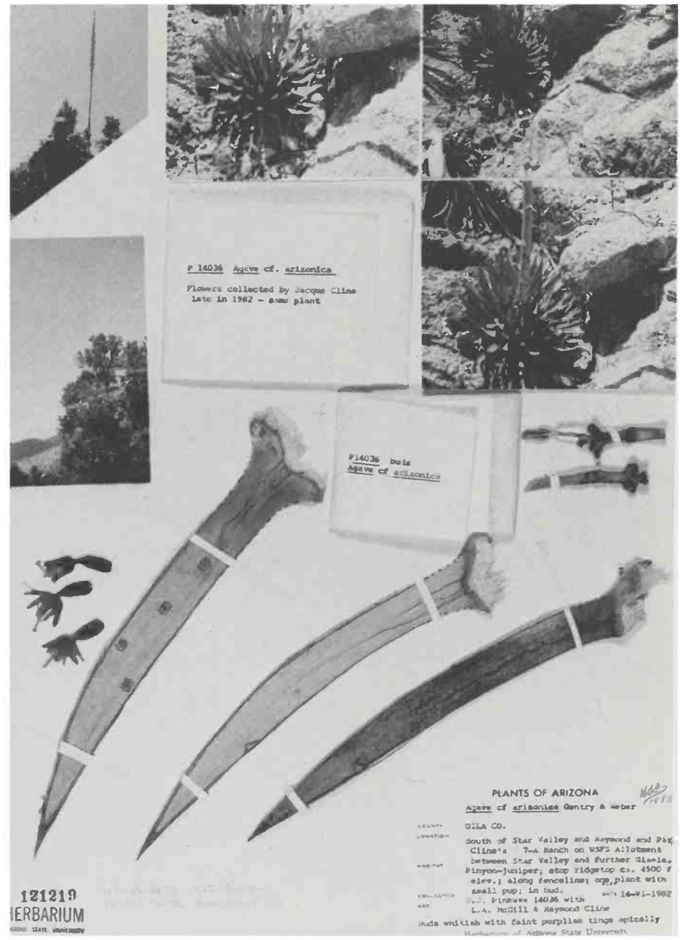


Figure 19. Photograph of herbarium specimen (ASU) of Agave *cf.* arizonica *(Pinkava et al. 14036). Scale: herbarium sheet measures 29 × 42 cm.*

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.

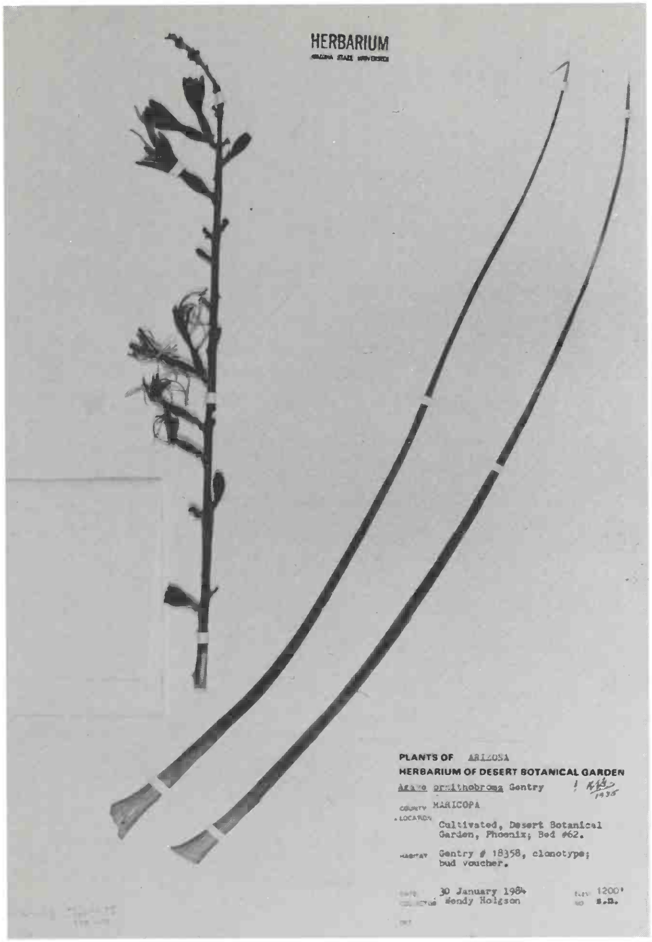


Figure 20. Photograph of herbarium specimen (ASU) of Agave ornithobroma *(Gentry 18358; from type collection). Scale: herbarium sheet measures 29 × 42 cm.*

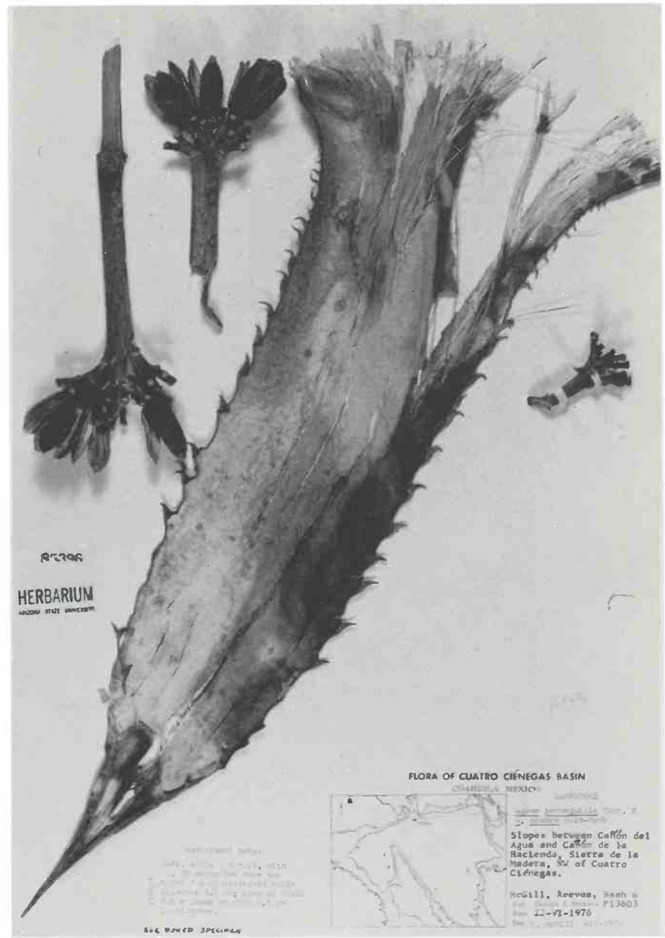


Figure 21. Photograph of herbarium specimen (ASU) of Agave *putataive hybrid between* A. lechuguilla *and* A. scabra *(Pinkava et al. 13603). Scale: herbarium sheet measures 29 × 42 cm.*

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.

Acknowledgments

We thank Jacque Cline, Ray Cline, James Drake, Margaret Gallagher, Wendy Hodgson, and the Desert Botanical Garden for providing collections and bud materials. Dr. Howard Scott Gentry kindly aided us in the identifications, but final determinations are our responsibility.

Literature Cited

Beeks, R.M. 1955. Improvements on the squash technique for plant chromosomes. *Aliso* 3:131-134.

Burgess, T.L. 1977. *Phenetic Structures of Selected* Agave *Populations in Guadalupe Mountains National Park, Texas.* M.S. thesis. Texas Tech Univ., Lubbock, Texas.

Cave, M.S. 1964. Cytological observations on some genera of the Agavaceae. *Madroño* 17(5):163-169.

Cronquist, A. 1968. *The Evolution and Classification of Flowering Plants.* Houghton Mifflin, Boston, Mass. 396 pp.

Doughty, L.R. 1936. Chromosome behaviour in relation to genetics in *Agave.* I. Seven species of fibre *Agave. Jour. Genet.* 33(2):197-205.

Ehrendorfer, F. 1980. Polyploidy and distribution. Pp. 45-60. *In:* W. H. Lewis (ed.), *Polyploidy, Biological Relevance.* Plenum Press, New York. 583 pp.

Gentry, H.S. 1967. Putative hybrids in *Agave. J. Hered.* 58(1):32-36.

Gentry, H.S. 1982a. *Agaves of Continental North America.* Univ. of Arizona Press, Tucson, Arizona. 670 pp.

Gentry, H.S. 1982b. On the evolution of agaves. *Saguaroland Bull.* 36(3):27-30.

Goldblatt, P. 1980. Polyploidy in angiosperms: monocotyledons. Pp. 219-239. *In:* W. H. Lewis (ed.), *Polyploidy, Biological Relevance.* Plenum Press, New York. 583 pp.

Gómez-Pompa, A., R. Villalobos-Pietrini, and A. Chimal. 1971. Studies in the Agavaceae. I. Chromosome morphology and number of seven species. *Madroño* 21(4):208-221.

Granick, E.B. 1944. A karyosystematic study of the genus *Agave. Amer. J. Bot.* 31(5):283-298.

Grant, V. 1963. *The Origin of Adaptations.* Columbia University Press, New York. 606 pp.

Inariyama, S. 1937. Karyotype studies in Amaryllidaceae. I. *Sci. Repts. Tokyo Univ.*, Sect. B 3(52):95-113.

Lenz, L.W. 1950. Chromosome numbers of some western American plants. I. *Aliso* 2(3):317-318.

Lewis, W.H. 1980. Polyploidy in species populations. Pp. 103-144. *In:* W.H. Lewis (ed.), *Polyploidy, Biological Relevance.* Plenum Press, New York.

Maneval, W.E. 1936. Lacto-phenol preparations. *Stain Tech.* 11:9-11.

McKelvey, S.D., and K. Sax. 1933. Taxonomic and cytological relationships of *Yucca* and *Agave.* Jour. Arn. Arboretum 14(1):76-81.

Müller, C. 1912. *Kernstudien an Pflanzen. I. u. II. Arch. Zellforsch.* 8(1):1-51.

Pinkava, D.J., R.K. Brown, J.H. Lindsay, and L.A. McGill. 1974. Reports. *In:* A. Löve (ed.), IOPB chromosome number reports XLIV. *Taxon* 23(2/3):373-380.

Satô, D. 1935. Analysis of karyotypes in *Yucca, Agave* and related genera with special reference to the phylogenetic significance. *Jap. Jour. Genet.* 11:272-278.

Satô, D. 1938. Karyotype alteration and phylogeny. IV. Karyotypes in Amaryllidaceae with special reference to the SAT-chromosome. *Cytologia* 9(2/3):203-242.

Satô, D. 1942. Karyotype alteration and phylogeny in Liliaceae and allied familes. *Jap. Jour. Bot.* 12(1/2):57-161.

Satô, D. 1953. Karyotype analysis and law of homologous series. *Sci. Papers, Coll. Genetl. Education Univ., Tokyo, Biol.* 12(2):173-210.

Sharma, A.K., and U.C. Bhattacharyya. 1962. A cytological study of the factors influencing evolution in *Agave. Cellule* 62(3):259-279.

Spellenberg, R. 1979. Chromosome numbers from some federally proposed threatened or endangered Southwestern angiosperms and other miscellaneous taxa. *Southwestern Nat.* 24(1):187-189.

Stebbins, G. L. 1980. Polyploidy in plants: unsolved problems and prospects. Pp. 495-520. *In:* W. H. Lewis (ed.), *Polyploidy, Biological Relevance.* Plenum Press, New York. 583 pp.

Vignoli, L. 1937. Cariologie del genere *Agave* Nota II. *Lavori Res. Ist. Bot. Palermo* 8:1-4.

deWet, J.M.J. 1980. Origins of polyploids. Pp. 3-15. *In:* M.H. Lewis (ed.), *Polyploidy, Biological Relevance.* Plenum Press, New York. 583 pp.

Prehistoric Agave Cultivation in Southern Arizona

Continued from page 112

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.

References Cited

Castetter, E. F., W. H. Bell, and A. R. Grove. 1938. The early utilization and distribution of *Agave* in the American Southwest. *University of New Mexico Bulletin* 6.

Crosswhite, Frank S. 1981. Desert plants, habitat and agriculture in relation to the major patterns of cultural differentiation in the O'odham people of the Sonoran Desert. *Desert Plants* 3:47-76.

Evenari, Michael, Leslie Shanan, and Naphtali Tadmor. 1971. *The Negev: The Challenge of a Desert.* Harvard University Press, Cambridge.

FAO/WHO. 1973. Energy and protein requirement: report of a joint FAO/WHO ad hoc expert committee. *World Health Organization Technical Report Series* 522.

Felger, Richard. 1985. *Ethnobotany of the Seri: People of the Land and Sea.* University of Arizona Press, Tucson.

Ford, Richard I. 1981. Gardening and farming before A.D. 1000: patterns of prehistoric cultivation north of Mexico. *Journal of Ethnobiology* 1:6-27.

Gasser, Robert, and Charles Miksicek. The specialists: a reappraisal of Hohokam exchange and the archaeobotanical record. *The Arizona Archaeologist.* In press.

Gentry, Howard S. 1972. The agave family in Sonora. *United States Department of Agriculture Agricultural Handbook* 399.

Gentry, Howard S. 1982. *Agaves of Continental North America.* University of Arizona Press, Tucson.

Johnson, Kirsten. 1977. Disintegration of a traditional resource-use complex: the Otomi of the Mezquital Valley, Hidalgo, Mexico. *Economic Geography* 53:364-367.

Messer, Ellen. 1978. Zapotec plant knowledge: classification, uses, and communication about plants in Mitla, Oaxaca, Mexico. *Memoirs of the Museum of Anthropology, University of Michigan* 10.

Minnis, Paul E., and Stephen E. Plog. 1976. A study of the site specific distribution of *Agave parryi* in east central Arizona. *The Kiva* 41:299-308.

Ross, Winifred. 1944. The present day dietary habits of the Papago Indians. M.S. thesis. University of Arizona, Tucson.

Sanders, W. T., J. R. Parsons, and R. S. Santley. 1979. *The Basin of Mexico: Ecology Processes in the Evolution of a Civilization.* Academic Press, New York.

Wilken, G. C. 1976. Traditional slope management: an analytical report. *In:* J. Luchok, J. D. Cauthon, and M. J. Preslin (eds.), *Hill Lands.* University of West Virginia, Morgantown.