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YUCCAS (AGAVACEAE) OF THE INTERNATIONAL FOUR CORNERS:  
SOUTHWESTERN USA AND NORTHWESTERN MEXICO

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ABSTRACT

*Yuccas* (*Yucca*, Agavaceae) are an easily recognizable constituent of the vegetation of the International Four Corners; an area made up of portions of Arizona, New Mexico, Sonora and Chihuahua. We recognize three species as native to the region, *Yucca baccata*, *Y. elata* and *Y. madrensis*, together with interspecific hybrids, and document for the first time naturally occurring intersectional hybridization between baccate-fruited (sect. *Yucca*) and capsular-fruited (sect. *Chaenocarpa*) species. We examine the reproductive barriers to hybridization operating within the genus, i.e., spatial, temporal and ethological, and we consider circumstances that may have been responsible for the production and widespread distribution of hybrids in the IFC. These include establishment of sympatry, pollinator biology, founding hybrids and human activities. We also reflect on the present situation regarding sexual reproduction in species of *Yucca* in the Southwest.

Key words: Agavaceae, biogeography, climate, hybridization, pollination, sympatry, taxonomy, *Yucca*.

INTRODUCTION AND PHYSICAL SETTING

The International Four Corners (IFC) includes southeastern Arizona, southwestern New Mexico, northwestern Chihuahua and northeastern Sonora (Fig. 1). It is part of what the early Jesuits called *Pimeria alta* (Bolton 1919). It is also a part of a larger region known as the Madrean Archipelago, a group of isolated fault-block ranges located between the Sierra Madre Occidental of western Mexico and the Rocky Mountains. The yuccas of the IFC have created problems for taxonomists in the past and earlier workers (McKelvey 1938; Kearney and Peebles 1960; Webber 1953; Gentry 1972; Benson and Darrow 1981; Hess and Robbins, [submitted]), have dealt with them in a variety of ways. Our account is based upon field, herbarium, and experimental garden studies conducted over a period of five years.

TAXONOMY

*Foreword*

Within the IFC we accept three species of *Yucca*: *Y. baccata* Torr. and *Y. madrensis* Gentry (*Y. schottii*.

auct., non Engelm.), both members of section *Yucca* (sect. *Sarocarpa* Engelm.), and *Y. elata* Engelm., a member of section *Chaenocarpa* Engelm. (Fig. 1). The first two possess baccate fruits, the last, dehiscent capsules. The three species are not closely related (McKelvey 1938, 1947; Matuda and Piña Lujan 1980; Clary 1997). We also recognize interspecific hybrids, and present the first account of naturally occurring intersectional hybrids within the genus. Due to phenotypic plasticity intrinsic to the genus, together with interspecific hybridization, it is difficult to precisely circumscribe taxa morphologically. Earlier students have recognized this problem (Sargent 1890; Trelease 1902; McKelvey 1938; 1947; Webber 1953; Clary 1997). Members of the genus may have independently evolved identical morphological features making it difficult to differentiate synapomorphic from homoplastic characters (Clary 1997). Floral characters are relatively uniform throughout the genus and are of limited taxonomic value. Two exceptions are *Y. baccata* and *Y. endlichiana* Trel. The flowers of *Yucca baccata* are unique within the genus and Robbins (1983) found that flower data for the fleshy-fruited yuccas of the

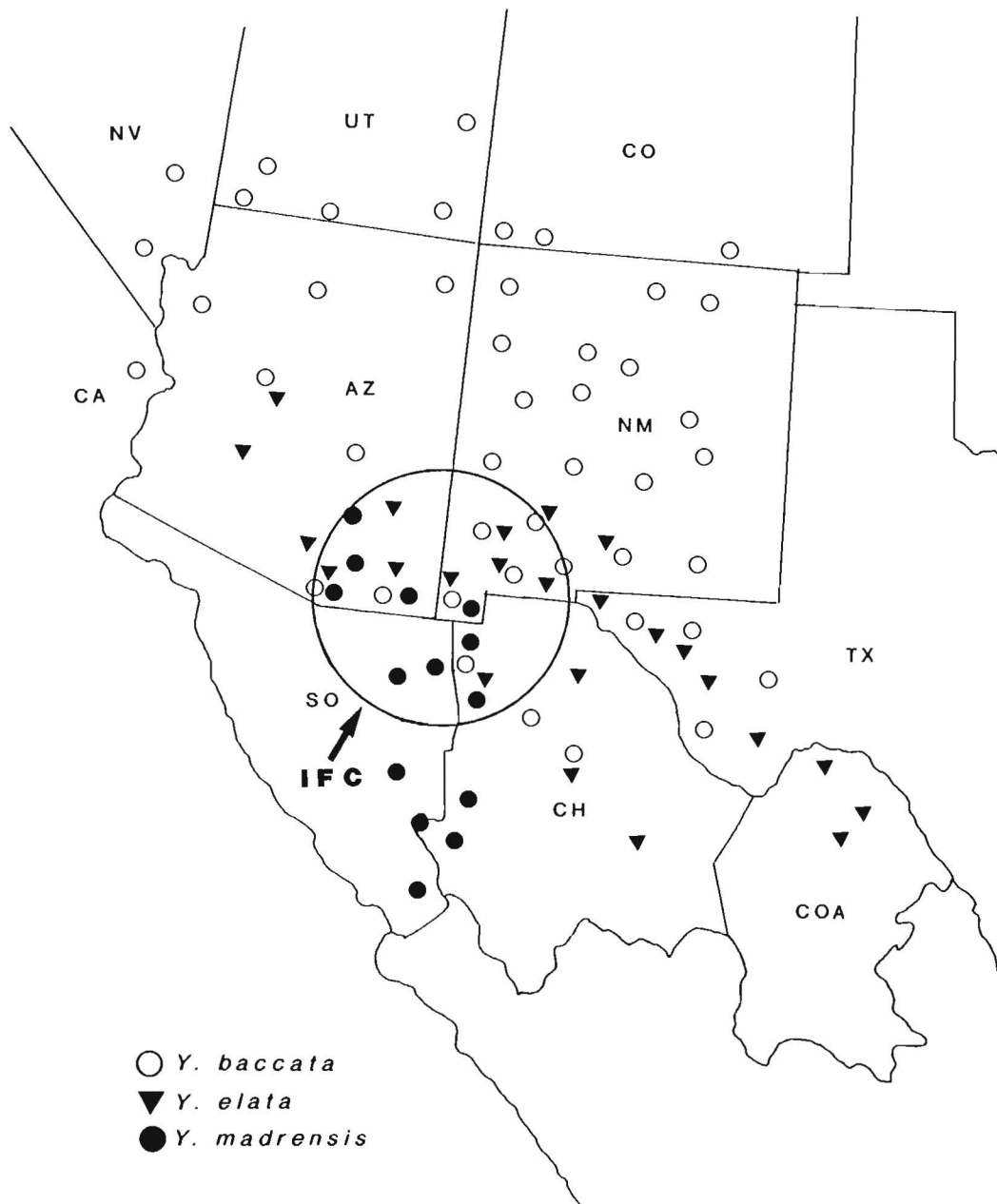


Fig. 1. Geographical distribution of three species of *Yucca*. Area of sympatry indicated by circle. Distribution shown by counties in the United States and by municipalities in Mexico.

Chihuahuan Desert correctly identified *Y. baccata* 100% of the time. In the yuccas of the IFC, the nature of fruit is highly significant; each has a distinctive and characteristic form (Fig. 2). In baccate-fruited yuccas, the occurrence of irregularly shaped fruits is of no taxonomic significance. It is the result of damage to the ovary caused by the *Yucca* moth's ovipositor (Powell 1984). The fruits of *Y. madrensis* often have a median constriction. This is the result of the moth probing the ovary as many as seven times as she moves around selecting a site to deposit an egg. This leaves a ring of damaged tissue that later appears on the fruit as a 'waist' (Fig. 3).

Infrequently gathered, *Yuccas* are not suitable for standard herbarium studies; many collections consist of a few dried flowers and a portion of a leaf and are of little or no taxonomic value. *Yuccas* are better understood through herbarium studies supported by fieldwork, photographic documentation, experimental garden plantings, and molecular analysis. In the three IFC species the overall impression of the plant is significant, that is, size, form, branching, and leaf presentation. The presence or absence of pubescence on branches of the inflorescence, although widely used in taxonomic treatments, has no value, as both conditions may be present within a single population. In this

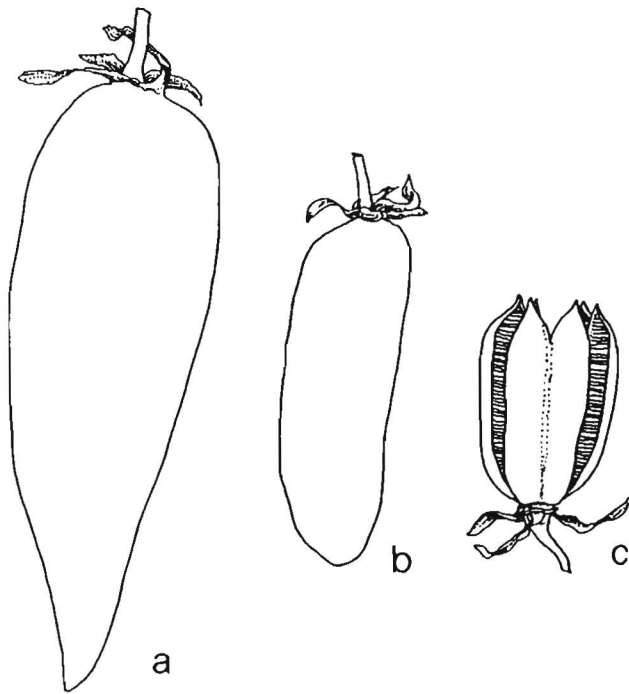


Fig. 2. Typical fruits. a, *Yucca baccata*; b, *Y. madrensis*; c, *Y. elata*.  $\times$  ca.  $\frac{1}{2}$ .

study, numbers Y-500+ refer to 35-mm photographic slides deposited in Special Collections in the herbarium at the Rancho Santa Ana Botanic Garden (RSA).

Due to our inadequate knowledge of the genus as a whole, we are not recognizing infraspecific taxa at this time. We apply the specific names, *baccata*, *elata* and *madrensis* to plants that would be taxonomically identified as such. We do not address the issue of their genetic constitution. It has been shown by molecular methods that individuals that taxonomically would be identified as *Y. baccata* may contain genetic material from a second species (*Y. schidigera* Roez. ex Ortgies), the presence of which was not detectable morphologically (Hanson 1993; Hanson and Riesberg, unpub.).

#### Accepted Species

*YUCCA BACCATA* Torr. In Emory, W. H. *Rep. U. S. Mex. Bound.* 2: 221. 1859.—TYPE: U.S.A. New Mexico. Guadalupe Co., Camp 52, Cedar Woods, 24 Sep 1859, *Bigelow s.n.*, LECTOTYPE: (chosen by J. L. Reveal. In A. Cronquist, et al., *Intermountain Fl.* 6: 528. 1977) NY. Non McKelvey 1938.

*Y. baccata* var. *vespertina* McKelvey, *Yuccas of the Southwest United States* 1: 45. 1938.—TYPE: U.S.A. Arizona. Mojave Co., just east of Peach Springs, about 1600 m, 12 May 1931, McKelvey 2167, (HOLOTYPE: A).

*Y. confinis* McKelvey, *Yuccas of Southwestern United States* 1: 49. 1938. TYPE.—USA. Arizona [Cochise Co.], on the road from Rodeo [New Mexico] to Douglas [Arizona], about 14 or 15 miles northwest of the latter, ca. 4500 ft, among mesquite. 3 May 1931,

McKelvey 2099 (photo. 105-1), (HOLOTYPE: A). Examination of photographs XVI and XVII show that she erred in identifying the associated shrubs as mesquite. They are clearly creosote bush (*Larrea tridentata* (DC) Cov.) present in the area today together with scattered ocotillo (*Fouquieria splendens* Engelm.).

**Vernacular names.**—Banana yucca (general); Mexico, palma (Matuda and Piña Lujan 1980); Acoma and Laguna—*hatyani* or *hatami mushi* (Castetter 1935); Apache—soapweed, *datil*, *etlude* (Castetter and Opler 1936); Navajo—yucca, *latil*, *tsá ászí*; Papago—*h'wich* (Hrdlicka 1908), *datil*, *hoi*, (fruits) *howitc* (Castetter and Underhill 1935; (fruit) *howij*; Papago-Pima—(plant) *howij-je'e nteelt* (Saxton, Saxton and Enos 1983); Walpai—*m'nat* (Hrdlicka 1908); Mojave cattlemen—oose dagger (Knutte and Faber, ca. 1991).

**Description.**—Plants acaulescent, or rarely short caulescent with short assurgent or procumbent stems, spreading by short rhizomes to form clumps as much as 5 m across. Leaf head often asymmetrical, and disorganized in appearance. Leaves coarse, stiff, mostly ~30–75 cm long, ~3–5 cm wide, broadened toward the middle, concavo-convex, often twisted, green, yellow-green, bluish or purplish green, margins with coarse, broad, flattened, recurved fibers, terminal spine stout. Inflorescence usually borne entirely within the foliage or with a short scape thus slightly topping the leaves, branches of panicle subtended by large chartaceous bracts. Flowers large, ~6–9 cm long, pendent, campanulate, expanding at the tip, cream-colored or tinged with purple (Y-516); pistil 40–70 mm long. Fruits relatively few per inflorescence, pendent, large, to ~25 cm long and ~6 cm wide, smooth, succulent, usually beaked, green, or tinged with orange or tan, soft on maturity and detaching readily from the stalk (Y-517). Seeds flat, black, wingless with ruminant endosperm. Mainly spring flowering.

**Distribution, habitat and ecology.**—*Yucca baccata* is one of the most widely distributed members of section *Yucca*, extending over an area ~12 degrees longitude and ~10 degrees latitude. It occurs in eastern California, southern Nevada, southern Utah, south-central and southwestern Colorado, Arizona (rare in the Sonoran Desert), western New Mexico, and southwestern Texas (McKelvey 1938). In Mexico it is found in Chihuahua (Matuda and Piña Lujan 1980), Coahuila and Sonora (Espejo-Serna and Lopez-Ferrari 1992) (Fig. 1). This is essentially the distribution of the pinyon-juniper woodland during the late Wisconsin glaciation (Van Devender and Spaulding 1979). In addition to its occurrence in pinyon-juniper woodland, it is now established in many other communities, even occasionally in creosote bush scrub in the Sonoran Desert (Turner et al. 1995). The species is found in a wide range of soil types. It is also common on limestone. Although *Y. baccata* is shallow rooted (Yeaton et al. 1983) it



Fig. 3. Three fruits of *Yucca madrensis* showing constrictions resulting from damage to the ovary caused by multiple probing by the moth's ovipositor as she moved around the ovary.

rarely is found on thin soils (Wallen and Ludwig 1978) and it favors open, sunny sites and is not deep-shade tolerant (Bennett et al. 1996). Depending on precipitation, three years may be required to build up stored energy to the level required for the costly reproductive effort (Wallen and Ludwig 1978). Flowering may take place as early as March or as late as October. Mature fruits are produced in approximately ten weeks (Turner et al. 1995). Although inflorescences may be multi-flowered, the number of fruits reaching maturity is often small; in one study the number was 3.2–5.6 per inflorescence (Wallen and Ludwig 1978). In one survey of 1358 rosettes only 7.7% produced inflorescences, with 6% bearing fruits (Wallen and Ludwig 1978). Following favorable weather conditions in 1998, plants in the eastern Mojave fruited heavily with a number of inflorescences bearing 10–12 fruits (LWL, pers. observation.).

*YUCCA MADRENSIS* Gentry. *The Agave Family in Sonora*, U. S. Dept. Agric. Handbook 399: 159. 1972.—TYPE: Mexico, Chihuahua-Sonora boundary, 4500–5000 ft., in pine-oak forest, 9 Sep 1965, Gentry 21209, (HOLOTYPE: US!, ISOTYPE: MEXU).

*Y. schottii* auct., non Engelm.

*Vernacular names*.—Mountain yucca, hoary yucca, *soco* (Gentry 1972; Matuda and Piña Lujan 1980; Van Devender, pers. com.); Mountain Pimas—*jamole*, *sahualiqui* (Laferrière 1990); Papago/Pima—*utoka-jehj* (Saxon, Saxon and Enos 1983; Tarahumara—*soko* or *so* (Thord-Gray 1955).

*Description*.—*Plants* caulescent, to ~3.5 m tall, simple or few-branched from the base with branches of varying length and covered with old, reflexed leaves. *Leaves* numerous in terminal heads but not congested, spreading, to ascending, rarely recurving, to ~1 m long and ~3.5–6.5 cm wide, flexible, blue-green or rarely yellow-green, without marginal fibers, terminal spine soft. *Inflorescences* ~0.3–0.75 m long, borne on a short scape or included within the leaf head. *Flowers*

globose, ~35 mm long, numerous, cream-colored or tinged with purple. *Fruit* fleshy, to ~12 cm long, oblong, symmetrical or irregularly shaped (Y-526), early deciduous. *Seeds* thick, dull black, wingless, with ruminant endosperm. *Summer flowering*.

*Distribution, habitat and ecology*.—*Yucca madrensis* is found in four counties in Arizona, Cochise, Pima, Pinal and Santa Cruz, and in Hidalgo Co., New Mexico (McKelvey 1938). In Mexico it occurs in Sonora, and in Chihuahua as far south as Cascada de Basaseáchic (Matuda and Piña Lujan 1980; Spellenberg et al. 1996; Martin et al. 1998) (as *Y. schottii*) (Fig. 1). The densest populations in Chihuahua are in Mpio. Guerrero (Matuda and Piña Lujan 1980). In Mexico it is a member of the pine-oak forest (Gentry 1972) or oak woodland (as *Y. schottii*) (Spellenberg et al. 1996). In the Chiricahuas it is common in the riparian woodland (Y-522), in oak woodland, and communities up to and including the second growth mixed conifer forest where it occurs in considerable shade (Y-518). There it may be a recent arrival following earlier logging. *Yucca madrensis* occurs in the Madrean and Apachian floristic provinces and is found on soils of volcanic or granitic origin, occasionally on limestone in Mexico (Gentry 1972) but not in Arizona (Wentworth 1982, 1985). The species is variable in height and in leaf width and to some extent in color, and introgression cannot be ruled out Gentry (1972). One character that appears to be consistent in *Y. madrensis* is the soft leaf tip. The type specimen consists of a single leaf and a portion of an old inflorescence and the original description is based on two collections, (Gentry 21209) for leaf and old inflorescence and (Gentry 2304) for flower; further field study is obviously desirable.

There is preliminary evidence from experimental garden plantings that in areas of Chihuahua *Y. madrensis* may have hybridized with *Y. treculeana* Carr. As circumscribed by Hess and Robbins (submitted) *Y. treculeana* includes *Y. torreyi* Shafer, a species known to occur in Chihuahua (Matuda and Piña Lujan 1980).

*YUCCA ELATA* Engelm. *Bot. Gaz. (Crawfordsville)* 7: 17. 1882.—TYPE: U.S.A. Arizona. Graham Co., Camp Grant, July 1874, J. T. Rothrock 382. LECTOTYPE (chosen by McKelvey) NY.

*Y. angustifolia* Carr. var. *radiosa* Engelm. In C. King, *Rep. Geol. Explor. 40<sup>th</sup> Parallel*, appendix, 496. 1871.

*Y. angustifolia* Carr. var. *elata* Engelm. *Trans. Acad. Sci. St. Louis* 3: 50, 51, 1873, a superfluous substitute.

*Y. radiosa* Trel. *Annual Rep. Missouri Bot Gard.* 13: 56. 1902. "Central Arizona, and northward to borders of Utah," *Palmer 201*, "Arizona," near Navajo Springs, Apache Co., Arizona, 24 June 1869. (Locations determined by J. L. Reveal). (LECTOTYPE: (chosen by J. L. Reveal. In A. Cronquist et al., *Intermountain Flora* 6: 533). MO).

- Y. constricta* sensu Baker 1880. *J. Linn. Soc., Bot.* 18: 229. Sensu Sargent. *Silva N. Am* 10, 27. 1896. Sensu Trel. *Annual Rep. Missouri Bot. Gard* 9: 146, t. 43, 1898. Non Buckley 1863.
- Y. utahensis* McKelvey, *Yuccas of Southwestern U.S.* 2: 94. 1947. TYPE: U.S.A. Utah, Washington Co., McKelvey 4167, 7–9 miles northwest of St. George, 8 May 1934, Photos, 149-9, 10, 11, 12: pls. XXXII, XXXIII, (HOLOTYPE: A). *Y. elata* var. *utahensis* (McKelvey) J. L. Reveal. In A. Cronquist, et al. *Intermountain Fl.* 6: 533, 1977.
- Y. verdiensis* McKelvey. *Yuccas of Southwestern U.S.* 2: 98. 1947. TYPE:—U.S.A. Arizona, Yavapai Co., McKelvey 752. Between Clarkdale and Cottonwood [AZ], 7 May 1933, (HOLOTYPE: A.). *Y. elata* var. *verdiensis* (McKelvey) J. L. Reveal. In A. Cronquist et al. *Intermountain Fl.* 6: 533, 1977.

**Vernacular names**—Soaptree, soapweed, *palmella* (Webber 1953), *cortadillo*, *palmilla*, *palmito*, *soyate* (Martínez 1987), *palma* (Matuda and Piña Lujan 1980). State flower of New Mexico.

**Description.**—Plants caulescent to arborescent, to ~9 m tall. Stems often with a few branches toward the top, densely clothed with old reflexed leaves, frequently closely branched from the base. Leaf heads conspicuously large, up to ~1 m across, symmetrical. Leaves abundant, crowded, gracefully recurved, narrowly linear, plano-convex, to 90 cm long, and ~0.8–.5 cm wide, pale green, flexible, with white margins and with fine marginal fibers. Inflorescence large, borne on a scape 1.5–4 m long, greatly exceeding the foliage, panicle ellipsoidal. Flowers numerous, ~35–50 mm long, campanulate to globose, cream-colored, sometimes tinged with green or pink; pistil 22–30 mm long. Fruit a smooth, dry, and upright, thin-walled, dehiscent capsule, persistent. Seeds waferlike, with a broad marginal wing, endosperm nonruminant. Spring flowering.

**Distribution, habitat and ecology.**—*Yucca elata* is a common, conspicuous, and generally easily recognized species distributed from Pecos County, Texas, through southern and south-central New Mexico to Yuma and Maricopa cos. Arizona (Webber 1953), and in Mexico in Sonora, Chihuahua and Coahuila (Matuda and Piña Lujan 1980) (Fig. 1). The species is found at elevations of ~450–1800 m on dry plains and mesas, commonly in desert grasslands, savanna, or in desert scrub, and it may occupy disturbed land (Campbell and Keller 1932; Bennett et al. 1996). Flowering normally takes place in April and May. Although encountered on all types of soil, including gypsum, the species favors deep, sandy soils. It possesses a vertical rhizome (Simpson 1975) that develops slowly throughout the plant's life. The rhizome permits plants to reach deep water and to adjust to changing soil levels (Campbell and Keller 1932). *Yucca elata* is primarily a member of the Chihuahuan and Apachian floristic provinces, but occasionally occurs in the Sonoran province.

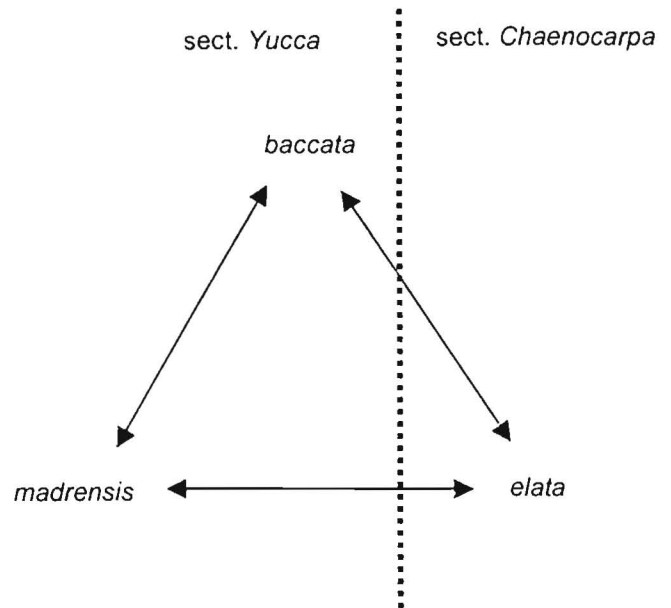


Fig. 4. Crossing diagram of three species of *Yucca* indigenous to the International Four Corners.

#### Naturally Occurring Hybrids

Plants combining species-specific morphological characters of *Yucca baccata*, *Y. elata*, and *Y. madrensis* are widespread in the IFC. Here we accept *Y. ×schottii* Engelm. pro. sp. as a collective epithet that includes all recognizable hybrids and backcrosses among the three species (Lenz and Hanson 2000) (Fig. 4). A collective name is sanctioned by the International Code of Botanical Nomenclature (Article H. 3.1) “hybrids between representatives of two or more taxa may receive a name” (Greuter et al. 1994). McKelvey (1938) was aware of the presence of hybrids in Arizona when she wrote, “for, in a small area—comparatively—grow four species [of Series *Baccatae*] each of which . . . is extremely variable (in large part because of the facility which crossing occurs within its own membership).” Later Webber (1953) discussed what he termed apparent hybrids between *Yucca baccata* and *Y. arizonica*, *Y. baccata* and *Y. torreyi* Shafer, and between *Y. baccata* var. *vespertina* and *Y. schidigera*. Neither Vines (1960) nor Benson and Darrow (1981) recognized hybrids.

In the discussion of hybrids that follows it is impossible to identify the species that functioned as female (♀) or as male (♂) parent. We follow the recommendation of the *International Code of Botanical Nomenclature* (H.2A.1) (Greuter et al. 1994) and list the presumed parental species in alphabetical order. The term *hybrid* has been used in various ways (see Arnold 1997 for a review). We use it in a limited sense, “in taxonomy, often restricted to the offspring of interspecific crosses” (Lincoln et al. 1998), but broaden it to include members of later generations that

are morphologically distinct from the parental species. Further, we are concerned only with *natural* hybrids, that is, matings that occur in a natural setting. Inasmuch as the plants are not the result of controlled pollinations, or their hybrid nature established through the use of molecular markers, or by other means, they should correctly be referred to as *presumed* or *putative* hybrids. However, for practical reasons, the term presumed (or putative) will be understood but not repeated.

*Y. ×SCHOTTII* Engelm. pro. sp. TYPE.—U.S.A. Arizona, [Santa Cruz Co.] Sierra del Pajarito, near the monument, 28 July 1855. Schott. s.n., LECTOTYPE: (chosen by L. W. Lenz, *Aliso* 19: 97) (NY!).

*Y. puberula* Torr. In Emory, W. H. *Rep. U. S. Mex. Bound.* 2, 221. 1859. Non Haworth. 1819.

*Y. brevifolia* A. Schott MSS. Mexico, Sonora. Valley of the Santa Cruz River, and Sierra del Pajarito, near the monument, June [1855]. In Emory, W. H. *Rep. U. S. Mex. Bound.* 2: 221. 1859. Nomen nudum.

*Y. brevifolia* Schott ex Trel., *Annual Rep Missouri. Bot. Gard.* 13: 100. 1902.

*Y. treleasei* J. F. Mcbr. *Contr. Gray Herb.* 56: 15. 1918, nomen. nov. based on *Y. brevifolia* Schott ex Engelm., non *Y. ×treleasei* Springer, 1901, fide G. Molon, *Le Yucche*, p. 192.

*Y. thornberi* McKelvey, *J. Arnold Arbor.* 16: 268, t. 138. 1935. TYPE.—U.S.A. Arizona, Pima Co., foothills of Rincon, Mts., slightly north of Rincon Creek, tributary of Pantano Wash, alt. 2000 m, 19 March 1932, *McKelvey 1627* (photos 80–3, 4), HOLOTYPE: A.

*Y. arizonica* McKelvey, *J. Arnold Arbor.* 16: 270. 1935. TYPE.—U.S.A. Arizona, Santa Cruz County. "Valle de Tuback VI, VII, 1855." A. Schott s.n. LECTOTYPE: (chosen by McKelvey, in *Yuccas in the Southwest U. S.* 1: 54, 1938:.) A!. See, Lenz and Hanson, (*Aliso* 19: 93–98, 2000) for a discussion of McKelvey's typification of this taxon.

*Y. baccata* Torr. var. *brevifolia* (Schott) L. D. Benson and R. A. Darrow, *Trees and shrubs of the Southwestern deserts.* 55. 1943.

*Y. grandiflora* Gentry, *Madroño* 14: 51. 1957. TYPE.—Mexico, Sonora, above Tierra Negra, Cedrus Range, east of Río Cedrus, 14 Feb 1952, *Gentry 11601*. HOLOTYPE: US 2089433. ISOTYPE: 2089434 here designated.

In the following discussion of interspecific hybrids all are considered a part of *Yucca ×schottii*, sensu lato.

#### *Yucca elata* × *Y. madrensis*

A plant growing on private property in dense desert scrub on an alluvial fan in San Simon Valley (Arizona: Cochise Co.) (Fig. 5) immediately draws attention. This in view of the fact that it combines morphological features of the two species growing in the area, *Y. elata* and *Y. madrensis*. Hereafter it will be referred to as *Lenz 9613* (Fig. 5), Y-502, 524, 527, 528). Originally thought to be a single plant surrounded by numerous younger plants, it was discovered, after an intense windstorm, that it was what others have described as a 'yucca ring' (Simpson 1975; Vasek 1995). In this instance a circle, about seven meters in diam-

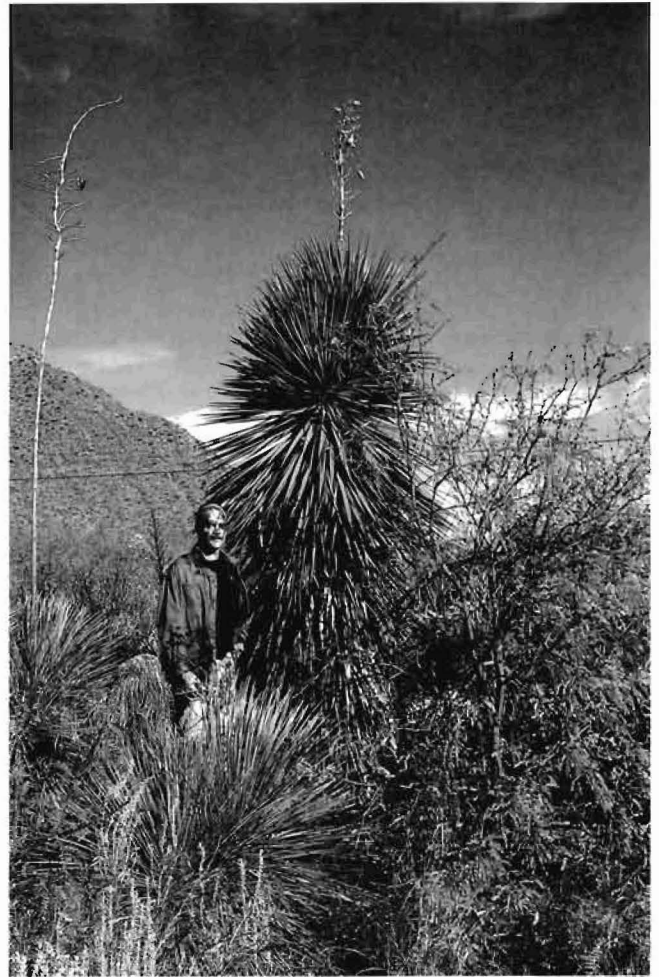


Fig. 5. *Yucca* hybrid 9613. Cochise County, Arizona. Mike Hanson shown. Photo taken 1998.

eter composed of an undetermined number of ramets derived from the original plant. In the center of the ring are two decaying stumps each ~30 cm in diameter and ~1.5 m tall (Y-525). All evidence indicates that the clone is old. At present the tallest living upright stem is ~4 m in height, densely clothed with leaves similar to those of *Y. madrensis* in width, length, and texture, but green instead of bluish-green as in *Y. madrensis*. The leaves possess a few fine fibers near the base as in *Y. elata*. The inflorescence produced in 1996 was borne on a stalk ~2 m long, somewhat shorter than those commonly associated with *Y. elata*, but conspicuously elevated above the leaf-head (Y-502) (the plant did not flower between 1996 and 2000). A stalk produced in 2000 was somewhat shorter than the one produced in 1996. The small flowers, ~35 mm long, were mostly globular and cream-colored. In 1996 the plant produced nine relatively small (~8 cm long), pendent, fleshy, nondehiscent fruits, that on aging became black and exceptionally hard, and were still on the plant in late December at which time they were harvested (Lenz prop. nos. 9613 1–9). The waferlike

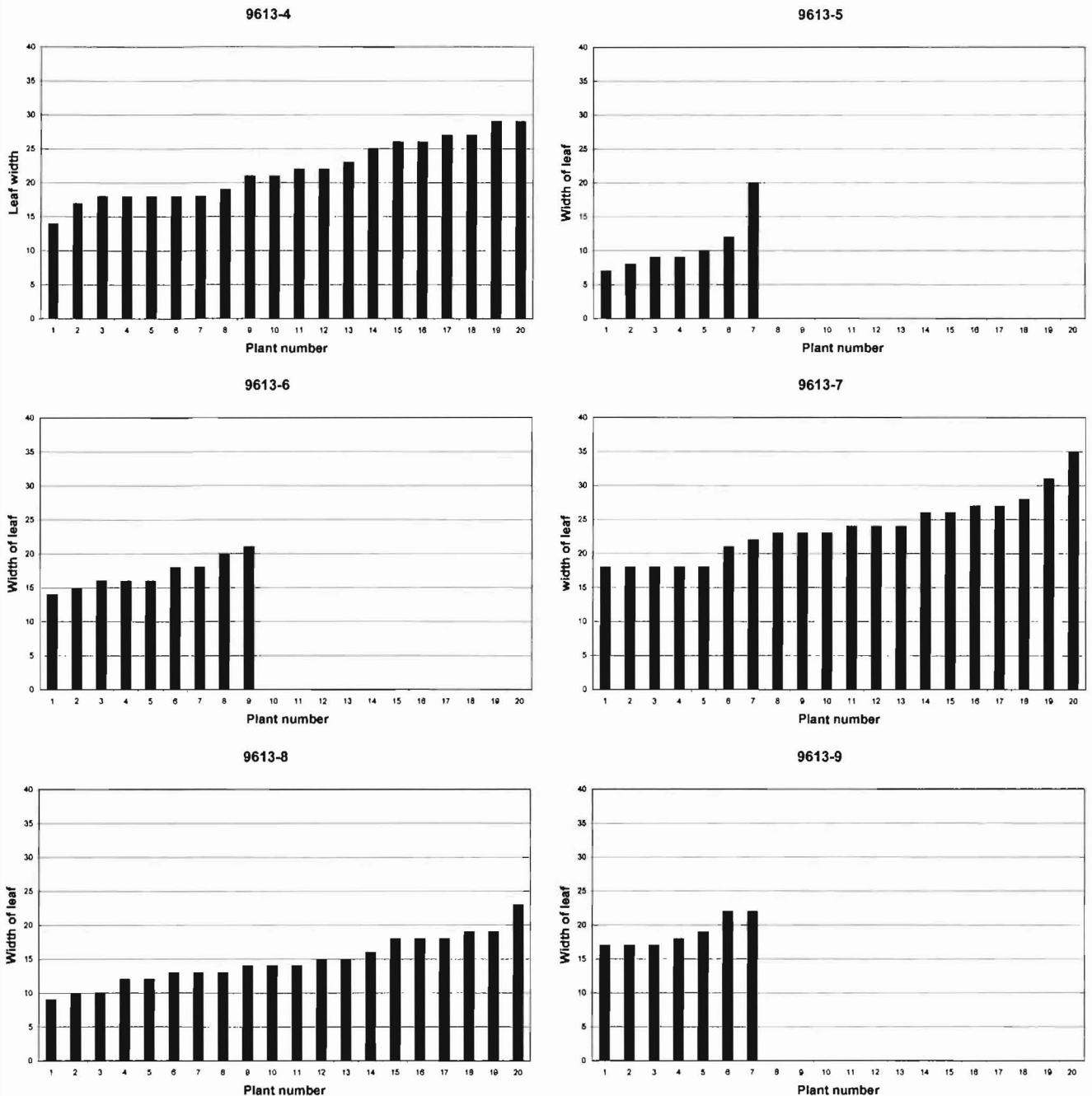


Fig. 6. Leaf width measurement for each plant in eight populations grown from individual fruits harvested in 1996 from hybrid 9613. See text for explanation.

seeds, more resembling those typical of *Y. elata* than *Y. madrensis*, were germinated and 114 seedlings are growing in the experimental garden at RSABG, Claremont, California. At the age of three years, leaf widths were determined for each plant in six populations in the RSABG experimental garden, (9613 4-9) each grown from the separate fruits harvested from 9613. Seeds from fruits 9613 1-3 were combined and are not included (Fig. 6). No similar-age plants of *Y. elata* and *Y. madrensis* were available for comparison, however mature leaves of *elata* range from ~8–15 mm in width

and those of *madrensis* ~35–65 mm in width. Particular plants in populations 9613-5 and 9613-8 are remarkable in that they possess morphological characters not observed in the other populations. Plants in 9613-8, numbers 3, 4, 5, 6, 12 and 17 have leaves thicker and more rigid than those of the other plants. The leaves of number 5 are undulating and those of number 6 are cup-shaped in cross section and twisting. Those morphological characters are associated with *baccata* and are unknown in either *Y. elata* or *Y. madrensis*. Except for one plant (#7), population 9613-5 is com-



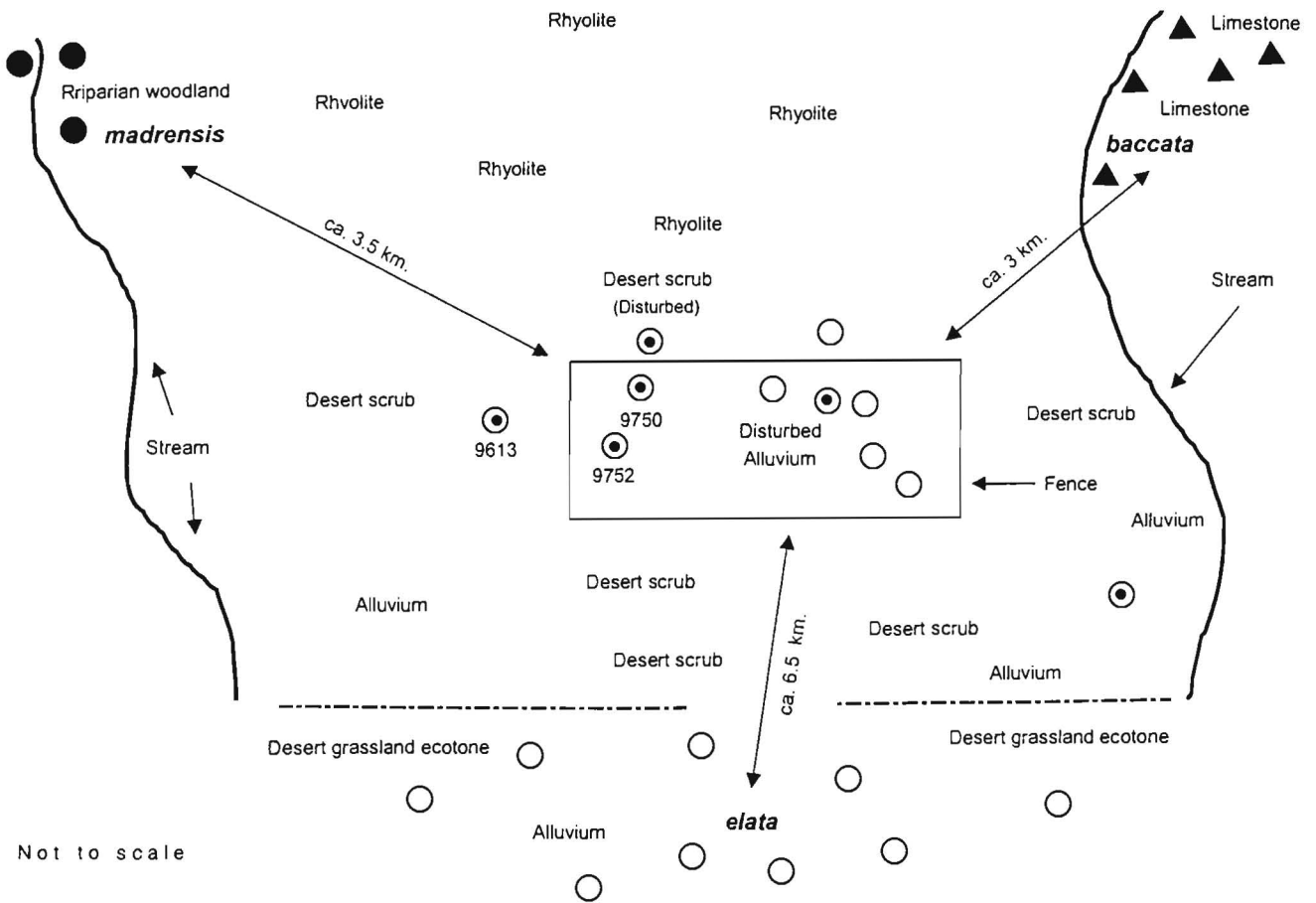


Fig. 7. Chiricahua study area. See text for explanation.

parable to population 9726 that was grown from a large *Y. baccata*-like fruit collected in a vacant lot at Nogales. The exceptional plants in populations 9613-5 and 9613-8 strongly indicate the influence of *Y. baccata*. The pollen parent, or parents, of the 1996 fruits are unknown. At the time 9613 was in flower *Y. elata* was in early fruit and no *Y. madrensis*-like plants were observed nearby. No *Y. baccata*-like plants have been detected within the immediate vicinity of 9613, and the nearest population of the species is approximately 3 km distant.

Located some distance from the above site, also on private land, is a classic example of Edgar Anderson's (1948) "hybridization of the habitat" (Fig. 7). Originally grassland, and later desert scrub the area was later cleared of all shrubs most likely by backhoeing (David Jasper, pers. comm.). In doing so the soil was disturbed leaving small mounds and depressions still visible today, thereby creating a variety of new open habitats available for colonization. It is unknown if the area was fenced before or after clearing. Today the vegetation within the fenced area differs markedly from that of the surrounding region. There are a few creosote bushes (*Larrea divaricata*) rare in the area, a few mesquite bushes (*Prosopis* sp.), a single juniper

(*Juniperus deppeana* Steud.) also rare in the area, together with *Opuntia* sp. and annual herbs not generally found in desert scrub. There is also what appears to be mature, same-age plants, that are presumed to be F<sub>2</sub> hybrids derived from 9613. Two plants in the fenced area are notable. The first (9750) is ~2 m tall, branched from the base with broad green leaves that in 1997 produced a large inflorescence on a short stalk with numerous, large, oblong, pendent fruits, as in *Y. madrensis*, but persistent, dry and dehiscent as in *Y. elata* (Fig. 8, Y-505). A second plant (9752) similar to that of 9750, bore exceptionally large, oblong, dehiscent fruits that were randomly oriented on the branches of the tall *Y. elata*-like inflorescence. No other plants combining so uniquely the features of the two species have been observed anywhere else in the IFC. Within a few hundred meters of 9613 are other plants that from their appearance, size and apparent age give the impression of also being second generation hybrids (Y-530, 531) but morphologically more similar to *Y. madrensis* than to *Y. elata*. Also in the area are plants that on the basis of the density of the leaf head and somewhat in leaf width, as well as length of flower stalk, are more like *Y. elata* than *Y. madrensis*. These plants have long decumbent branches unlike either *Y. mad-*

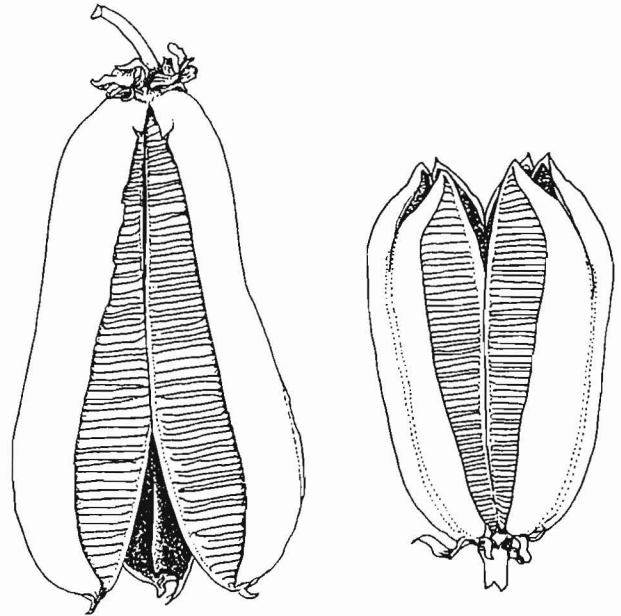


Fig. 8. Inflorescence of hybrid 9750 showing large, dry, pendent, dehiscent fruits [left]. Fruit of 9750 (left); fruit of *Y. elata* (right) [right].  $\times \sim 1$ .

*rensis* or *Y. elata*. A number of *Yucca elata*, or *elata*-like, plants in the immediate area show no obvious indication of being hybrids (Y-529). In view of the fact that seed of *Y. elata* is presumably wind distributed, it is possible that those plants originated from plants of *Y. elata* growing in the desert grassland ecotone approximately 6.5 km. distant. In grassland in Sulphur Springs Valley, Cochise Co., what appear to be isolated clumps of low-growing *elata* are, on examination, found to be single plants with long, decumbent stems radiating from the original central stem, each with a large upturned *Y. elata*-like head of leaves. These plants have not been observed in either flower or fruit.

#### *Yucca baccata* $\times$ *Y. madrensis*

Populations that on casual inspection appear to be *Y. madrensis* are common along the northwestern slopes of the Chiricahua Mountains, along the lower portion of Pinery Canyon, and in the adjacent Chiricahua National Monument. One plant 9728 (Y-507) had the wide, flexible, blue-green leaves of that species, and the inflorescence was stemless and nested in

the terminal cluster of leaves. The fruits were similar to those of *Y. madrensis*, though larger than typical of that species, and were partially colored, comparable to those often encountered in *Y. baccata*, but to our knowledge never found in *Y. madrensis*. One fruit was harvested, and a population of 22 plants is growing at RSABG (9728). Leaf characters of some of the plants strongly suggest the influence of *Y. baccata*.

#### *Yucca baccata* $\times$ *Y. elata*

In southern Santa Cruz Co., Arizona, populations that combine in a variety of ways and degrees, morphological characters of both *Y. baccata* and *Y. elata* are common (Y-508, 509). Fruits vary in shape and size. Many of the plants bear large pendent fruits suggestive of *Y. baccata* (Y-510, 513, 514, 515, 521) but are borne on stalks well above the leaves (Y-519, 521). Leaves vary in width from narrow, typical of *Y. elata* to broad typical of *Y. madrensis*. Many of the plants branch from the base and sometimes form large clumps typical of *baccata*. Such plants have been recognized as *Y. arizonica* McKelvey (McKelvey 1935,

1938; Kearney and Peebles 1960; Webber 1953; Gentry 1972). Plates XIX–XXIV in McKelvey (1938) are illustrative. Plants with decumbent, conspicuously long (3–5 m), branched, serpentlike, often blackened stems, turned up only at the tips are frequent on dry rocky slopes in the Sierra del Pajarito (Arizona: Santa Cruz Co.) often with ocotillo (*Fouquieria splendens*), a species characteristic of the Chihuahuan and Sonoran deserts. Each branch bears a terminal cluster of short, narrow, rigid, yellowish-green leaves (Y-512, 513, 520). The inflorescences usually have short scapes with the panicle borne above the leaves. We theorize that those plants represent extreme recombination of characters of *Y. baccata* and *Y. elata*. The former is found in the Sierra del Pajarito at higher elevations (Humphrey 1987) and the latter is frequent at lower elevations in grassland and savanna. In a review of misconceptions concerning hybrids, Riesberg (1995) pointed out that in an analysis of 46 studies involving interspecific hybrids, it was disclosed that over 10% of the morphological characters present in the primary hybrids were 'extreme' or 'novel' and not present in the parental species. In later generations the percentage increased to over 30%. We believe that it was from this area, and from among such hybrids, that Arthur Schott or an assistant, made the collection that was later designated *Yucca schottii* by Engelmann (Lenz and Hanson 2000).

Specimens identified as *Yucca baccata* × *Y. aff. elata* hybrids have been reported from Coconino Co. Arizona, (Brian et al. 1999).

#### DISCUSSION

In the preceding sections, we have shown that interspecific hybridization has taken place among the species of *Yucca* of the IFC. A morphological study of individual populations grown from seeds from nine fruits collected from a single plant argues for the existence in the IFC of hybrids that incorporate genetic material of two, or all three, of the species of *Yucca* native in the area. It has yet to be determined whether introgression (as defined by Riesberg and Wendel 1993) has taken place. Here we consider conditions that may have favored the establishment of hybrid populations. They are the establishment of sympatry, pollination biology, founding hybrids and human activities.

##### *Establishment of Sympatry*

We maintain that the three species of *Yucca* native to the IFC were originally allopatric and reproductively isolated: *Y. baccata* in the pinyon-juniper woodland, *Y. madrensis* in the Madrean evergreen woodland, and *Y. elata* in desert grassland. Over time, southwestern plant communities have expanded or contracted in re-

sponse to climatic changes (Van Devender, and Spaulding 1979; Van Devender et al. 1987; Betancourt 1990; Cole 1990). Plant species respond individually to climate change (Gleason 1939; Cole 1985; Van Devender et al. 1987; Schoonmaker and Foster 1991). One way species may respond to climatic change is through persistence, for the most part by asexual reproduction (cloning) (Thompson 1988). *Yuccas* are inherently long-lived (Hollick 1932; Webber 1953; Lapré 1979; Vasek 1995), persistent and capable of tolerating unfavorable climatic conditions, and many (all?) are capable of regenerating from underground parts (Webber 1953). In discussing the age of *Y. schidigera* in the Santa Rosa Mountains (Riverside Co., California), Lapré (1979) estimated that about one-half of the clones in a one hectare plot were not less than 500 years old. In the Mojave Desert one *Y. schidigera* ring (clone) ~10 m in diameter was estimated by Vasek (1995) to be ~2500 years old. Simpson (1975) reported that a single Joshua tree (*Y. brevifolia*) [clone] growing near Gorman (Los Angeles Co.), California, covered a circular area of about one acre (4051 sq. m). In accord with Webber's (1953) estimate, Gentry (1972) placed the possible age of yuccas in the thousand-year-old range.

It has generally been accepted that changes in climate, and vegetation, take place gradually over a timespan of centuries or millennia. Evidence is mounting that the past few million years have been punctuated by many significant climatic shifts (see Adams et al. 1999 for a review). Present evidence indicates that these changes have taken place in sudden jumps rather than incrementally. The rapid warming at the end of the Pleistocene is thought to have come about within a matter of decades (Taylor et al. 1993; Dansgaard et al. 1993; Steig et al. 1998; Adams et al. 1999). By means of cloning, and with major climatic shifts occurring over short intervals, an exceptional yucca plant (or clone) might linger long after the climate and vegetation had changed, a straggler from an earlier time in an altered environment and in a another plant community. This would be especially likely in a region of great topographic and substrate diversity. It is conceivable that in this way sympatry of the three species of *Yucca* in the IFC was achieved.

##### *Pollination Biology*

Each of the three species of yucca native to the IFC has its own specific pollinating moth, members of the genus *Tegeticula* (Lepidoptera: Prodoxidae). *Yucca baccata* is pollinated by *Tegeticula baccatella* Pellmyr, *Y. elata* by *T. elatella* Pellmyr and *Y. madrensis* by *T. maderae* Pellmyr (Pellmyr 1999). In addition, *Y. madrensis* has a second pollinator, *Parategeticula pollenifera* Davis (Davis 1967; Powell 1984). Barriers to

gene flow due to pollinator preference have been termed *ethological isolation* (Grant 1949). By examining the condition of the mature fruit and determining the number of seeds produced, it is possible to identify the pollinator: *Tegeticula* moths destroy numerous developing seeds whereas *Parategeticula* larvae destroy only two or three seeds (Powell 1984). Evidence from seed production on 9613 reveals that both *Tegeticula* and *Parategeticula* effectively pollinate hybrids between *Y. elata* and *Y. madrensis*. Theoretically, to maximize a plant's potential for sexual reproduction it would be to the plant's benefit for its flowers to be pollinated by *Parategeticula* rather than *Tegeticula*.

In a region where *Y. baccata* and *Y. schidigera* are sympatric, Leebens-Mack et al. (1998) found that in a collection of 281 moths all but one had been found on the 'correct' host; that is *T. baccatella* on *Y. baccata*, and *T. mojavelle* Pellmyr on *Y. schidigera*. These authors concluded that this was evidence of a high degree of maintained specificity by the moths. Nevertheless, they acknowledged that morphological intermediates [hybrids] between the two species of *Yucca* were evidence of occasional host substitution; however, they considered it a rare event. Miles (1983) reported hybrids between *Y. baccata* and *Y. torreyi* Shafer, and she concluded that the pollinating moths usually maintained host specificity; however, they did exploit alternate hosts if the preferred host was unavailable. She also reported that in New Mexico where *Yucca baccata*, *Y. torreyi* and *Y. elata* were sympatric, that flowering dates of *Y. baccata* and *Y. elata* were a month apart, and she concluded that temporal isolation constituted the principal barrier for reproductive separation of the two species. Leebens-Mack et al. (1998) predicted that the ability of moths to include multiple hosts in their 'diet' might be determined less by spatial than by temporal barriers. Personal observations (LWL unpub.) as well as herbarium records clearly reveal that time of flowering of yuccas is highly variable and off-season blooms are not uncommon. In southeastern Arizona following the dry winter of 1998–1999, few *Y. elata* plants flowered during the spring of 1999; however following the summer monsoon rains there was sporadic flowering between July and October, (David Jasper and LWL, pers. obs.). In the Chiricahuas in July, 2000, plants of *Y. madrensis* were observed with both flowers and full-sized fruits on the same plant (Lenz, pers. obs.) (Y-523). Unfortunately, as vital as it is to the yucca/yucca moth story, the distance that moths may fly between plants is unknown (Leebens-Mack et al. 1998; Marr et al. 2000; Pellmyr, pers. comm.).

#### Founding Hybrids

During five years of investigation, we have encountered a single plant that we can confidently, on a mor-

phological basis, regard as a first generation ( $F_1$ ) hybrid (9613). Based on analyses of natural and experimental populations of both plants and animals, Arnold (1997: 149–150) concluded that, although under controlled conditions  $F_1$  hybrids might easily be produced, under natural conditions they are relatively difficult to form. According to Arnold, numerous reproductive processes may be responsible for the scarcity of  $F_1$  hybrids. In three interbreeding species of Louisiana irises studied, he concluded that differences in phenology, interspecific pollen competition and extrinsic selection represented a genetic bottleneck. However, once rare  $F_1$  individuals are formed and established, natural hybridization is accelerated. This was based on the prediction that the frequency of formation of  $F_2$  and  $B_1$  individuals should be significantly greater than the formation of  $F_1$  hybrid individuals in a mixed population of two taxa. According to Arnold extreme, genetic bottlenecks, that is barriers to the formation of  $F_1$ s, and the subsequent relaxation of the barriers to hybridization in later generations might, for many plant and animal species, be a general rule rather than an exception. Within the genus *Yucca*, no internal barriers to hybridization have been documented although their presence can not be ruled out (Webber 1953; 1960; Lenz 1998). In the three species in the IFC, we believe that spatial, temporal and ethological barriers limit the formation of  $F_1$  individuals. On exceptional occasions when the three reproductive barriers are simultaneously surmounted, hybridization becomes a possibility. The resulting infrequent  $F_1$  hybrids might be termed Founding Hybrids.

#### Human Activities

*Prehistoric.*—In a region not noted for its wealth of food plants, the large sugar-rich fruits of *Y. baccata* were without a doubt utilized by the earliest humans to enter the Southwest. Archeological evidence verifies the fact that *Y. baccata* was one of the three most important nondomesticated food items found at the Basketmaker II site in the Turkey Pen rockshelter [Utah] (Lepofsky 1986) and dated 150 B.C. to A.D. 50 (Matson 1991). In our investigations the most abundant, as well as the most conspicuous hybrids (*Y. arizonica* of authors) were encountered in the general vicinity of Nogales, Arizona, where they are common to abundant even on undeveloped land within the city. Until McKelvey's investigations there had been no mention of an extension of the range of *Y. arizonica* beyond the Nogales region and the Sierra Pajarito (McKelvey 1938: 57).

El Macayo, a prehistoric site located in the Santa Cruz River Valley near present-day Nogales, Arizona, was occupied for six centuries between A.D. 550–1150 by people considered to have been both foragers

and agriculturists (Deaver and Van West, in press). As foragers, they undoubtedly collected yucca fruits and, as agriculturists, they would have recognized the connection between seeds and a valuable item for consumption. What role the people of El Macayo may have played, intentionally or unintentionally, in the early history of the yuccas of the Santa Cruz Valley is unknown. It is reasonable to assume that over a period of 600 years there may have been a link between the people and an important native food item.

*Historic.*—Extensive changes have taken place in the vegetation of the Southwest within historic times, in part due to human activities (see Bahre 1991 for a comprehensive review). The major impact during the Spanish-Mexican occupation (A. D. 1536–1854) was the introduction of large-scale cattle ranching in what are now southern Arizona and adjacent Chihuahua and Sonora (Wagoner 1952). At one time Rancho Bernardo is reported to have had 100,000 cattle, 10,000 horses and 5000 mules (Haskett 1935). With the Apache uprising between 1822 and 1872 many of the ranches were abandoned and livestock scattered, multiplied and roamed over the region even into the highest mountains “as wild and more fierce than buffalo” (Bartlett 1854). The greatest environmental change in the Southwest however came after 1870 with major Anglo-American settlement and economic development. In 1891, there were estimated to be 400,000 head of cattle in southeastern Arizona (Hendrickson and Minckley 1984). Between 1893 and 1934 when the Taylor Grazing Act was enacted, almost the entire region was continuously overstocked and overgrazed (Bahre 1991).

Many animals, including coyotes, gray fox, black bear, raccoons, coati, ringtail, peccary and deer are known to consume *Yucca* fruits (Hoffmeister 1986). There is no confirmed evidence that livestock distribute the seeds of the fleshy-fruited yuccas. It is reasonable to assume, however, that at times livestock would have consumed the fleshy fruits of both *Y. baccata* and *Y. madrensis*, and at least a few seeds would have passed intact through the animal’s digestive system. During historic times livestock may also have played a role in changing the geographical ranges of the yuccas, a supposition also reached by Clary (1997). Livestock grazing changes soil surfaces physically and chemically and in doing so creates new niches suitable for occupation—Edgar Anderson’s ‘Hybridization of the Habitat.’ Seedling establishment is more often than not the most critical phase in the life cycle of a plant and trampling and grazing by livestock would have had an adverse affect on the establishment of young plants. On the other hand, plants unpalatable to livestock may have served as nurse plants for the young seedlings. It may be significant that the hybrid 9613 is

surrounded by dense desert scrub. *Yuccas* normally produce large quantities of highly viable seed. With a lessening in pressure from livestock grazing following the passage of the Taylor Grazing Act, seedlings, including those of hybrids, would have had a greater chance of reaching sexual maturity. Arthur Schott’s collections of *Yucca* made in southern Arizona in 1853 are believed to be of hybrid origin (Lenz and Hanson 2000). If cattle (and other livestock) were responsible for conditions that permitted hybridization to have taken place prior to 1853, it would have been as the result of cattle ranching of the Spanish and Mexican periods. On the other hand, it may have been due to naturally occurring events: sympatry through changing environment and the breakdown of the three external barriers to hybridization previously considered.

#### CONCLUSIONS

We believe that the present *Yucca* situation in the IFC is the result of three fortuitous events. Through natural environmental changes, or through anthropogenic intervention, or both, three formerly allopatric species of *Yucca* became sympatric. Because of occasional overlapping of flowering periods, together with rare or infrequent heterospecific pollinations by yucca moths, interspecific hybrids have been produced. It has been theorized that under natural conditions the production of F<sub>1</sub> hybrids may be rare occurrences. However, a few hybrids produced over decades or centuries, by back crossing to parental species could in time lead to the establishment of widespread hybrid populations, and possibly, introgression (as defined by Riesberg and Wendel 1993). The probability of plants with novel genotypes becoming established in the IFC has been enhanced as a result of human activities in the Southwest, possibly over the past 12,000 years, certainly during the past 450 years. We further extend our conclusions and argue that the major reproductive barriers to gene flow among species of *Yucca* are spatial, temporal, and ethological isolation. With a collapse of these barriers, hybridization has taken place among the members of the genus, not only in recent times, but also in all probability in the past as well. The chance for the successful establishment of resulting hybrids has been enhanced as a result of new or unique environments having been created through changing climatic conditions and due to human activities.

#### ADDENDUM

*Sexual reproduction.*—During our investigation of the yuccas of the IFC we have been impressed by the apparent absence or scarcity of seedlings or juvenile plants over much of the area. Other observers have commented on the rarity or absence of seedlings in

other regions. Webber (1953) reported that in the more arid regions of the Southwest reproduction of yuccas by seed was limited. He found only 9 seedlings of *Y. baccata*, 8 of *Y. torreyi* Shafer, 7 of *Y. arizonica*, 5 of *Y. constricta*, 1 of *Y. schidigera* and no seedlings of *Y. schottii*, *Y. faxoniana* (Trel.) Sarg., *Y. carnerosana* (Trel.) McKelvey, *Y. rostrata* (Engelm.) ex Torr. and *Y. thompsoniana* Trel. [Names are those used by Webber]. In an investigation of *Y. schidigera* in the Santa Rosa Mountains (California, Riverside Co.) Lapré (1979) reported that a careful search revealed no seedlings anywhere, and he concluded that there had been no seedlings for the past 40 to 50 years. In a study of *Y. brevifolia* in the Mojave Desert, Comanor and Clark (2000) reported that over a period of 20 years they had found only two germinated seedlings neither of which survived. In an investigation of *Y. elata* in New Mexico, Campbell and Keller (1932) reported that reproduction by seed was limited. In their study plots over a 17-year period, they observed only 10 seedlings. Field studies in central Baja California have revealed no seedlings or young plants of *Y. valida* Engelm. (pers. obs. LWL). An explanation for the absence or rarity of sexual reproduction in the Southwest may be at least in part due to the fact that at lower elevations, environmental conditions necessary for successful germination and establishment of *Yucca* seedlings have not existed, or been marginal, for an extended period. Webber (1953) reported that at lower elevations in the Mojave Desert where precipitation was meager there were few seedlings of *Y. brevifolia*, whereas in the higher mountain areas where rainfall was greater seedlings of *Y. brevifolia* were prevalent. Though we have found very few seedlings or juvenile plants of *Yucca madrensis* at lower elevations in the Chiricahuas, at elevations of ~1700–2400 m where precipitation is from 508 to 635 mm the species is reproducing sexually as evidenced by vigorous mixed-age populations. However, other factors may limit sexual reproduction. These include predation of young seedlings by rodents and rabbits. According to Webber (1953) at higher elevations with greater rainfall and consequently better forage conditions, there is rarely evidence of rodent damage to young seedlings. In many parts of the Southwest grazing by sheep, cattle and goats has been particularly detrimental to yucca seedlings (Webber 1953).

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