

Congratulations! Your Agave is the granddaughter of

Ode to an Odd Agave This one! ↓

How Does Our Agave Grow? Reproductive Biology of a Suspected Ancient Arizona Cultivar, *Agave murpheyi* Gibson

Karen R. Adams

Archaeobotanical Consultant
2837 E. Beverly Dr.
Tucson, Arizona 85716
kadams@crowcanyon.org

Rex K. Adams

Laboratory of Tree Ring Research
University of Arizona
Tucson, Arizona 85721
radams@ltr.arizona.edu

Abstract

More than one species of *Agave* may have been cultivated by ancient farmers in Arizona. The arguments for this include apparent range extensions, burned *Agave* parts in archaeological roasting features, archaeological sites with *in situ* agaves thought to be relics of past human management, and limited molecular evidence. The reproductive biology of a single *Agave murpheyi* Gibson, one of the suspected cultivated species, is documented here in detail. After nine years of growth in a residential backyard in Tucson, Arizona, a flowering stalk rapidly elongated to 4.73 m (15.5 ft) during both daytime and nighttime hours from January through May. Daily records kept for much of that time revealed the stalk averaged 4.69 cm (1.85 in) of growth per day. Maximum growth spurts correlated with both high daily temperature and mean daily temperature. Lateral branches, eventually totaling twenty-two, began developing during March in the upper portion of the flowering stalk. Over a period of five weeks from late May to late June, these lateral branches flowered with normal-looking flowers, attracted a variety of potential pollinators, but produced no mature fruit. Instead, by the summer monsoon season of July and August, the mother plant had produced 359 miniature agaves or bulbils in these upper side branches. The bulbils appeared to arise from enlargements of tissue in the vicinity of the former flowers. Without releasing on their own, these bulbils became water-stressed and had to be forcibly removed a year later. By this time they were quite variable in fresh weight and size. Once planted, they rehydrated and immediately began to grow. This single plant shares aspects of bulbil production with three *Agave murpheyi* plants observed by others.

An *Agave* weighing less than a pound
And measuring very few inches around,
Grew up fast, and then,
Before it turned ten,
Sent a stalk soaring way above ground.

This *Agave* then flowered, and said,
"Why waste time making seeds for a bed?
It seems faster to me,
(As I'm sure you'll agree),
I'll make little *Agaves* instead!"

So "pups" were formed high in the air,
Attached firmly to branches up there.
Then an inca dove family,
Set up housekeeping, grandly,
And raised two young doves oh so fair.

At 20 months after the start,
A storm split the stalk from the heart.
Those pups, it was deemed,
Were *past* time to be weaned,
So we broke each one carefully apart.

The pups, totaling 359,
Were quite varied, after all of this time.
If this pattern keeps up,
We'll be *drowning* in pups,
A fate both bizarre and divine!

Introduction

If Ogden Nash were with us today, he might pen such an ode to *Agave*, a genus composed of over 200 species of succulent aloe-like plants native to dry regions of the New World (Gentry 1982). Agaves are commonly but incorrectly known as "century plants", because it was once thought they flowered only after attaining the age of 100 years. Historic groups in the American Southwest and Mexico have utilized them for a wide variety of purposes, perhaps the most important of which are food and fiber (Castetter et al. 1938).

An agave's succulent leaves are arranged in a basal rosette, and the plant grows relatively slowly. At some point, an individual amasses enough reserves to send up a main stalk which flowers and (usually) bears fruit. The stalk is composed of a tall stout stem (scape) supporting an elevated flowering portion (the inflorescence) high above ground. In some species of *Agave*, flowers are in an open flowering arrangement (a panicle), having numerous side or lateral branches (secondary peduncles). In other species, the flowers are clustered against the upper portion of the main stalk in a compacted arrangement (a raceme), with each individual flower having a very short stem or pedicel.

Vegetative reproduction is common in some *Agave* species, achieved via formation in one or more of the following ways. Basal shoots (hijuelos) can form in the axils of the leaves of an adult plant, rhizomatous suckers (ramets or chupones) may extend out from the base, and aerial rosettes (often called “pups” or “bulbils”) can be produced in the flowering stalks (Gentry 1982; Szarek et al. 1996). Researchers suggest that if, for some reason, seed production fails due to cold weather, lack of potential pollinators, etc., the production of bulbils acts as an insurance mechanism to utilize the already-mobilized metabolic resources to perpetuate the species (Arizaga and Ezcurra 1995). Bulbils are also produced if the stalk is damaged, for example by herbivores or by humans.

Agaves in Southwestern Prehistory

Ancient dwellers of the Sonoran Desert of Arizona planted and tended agaves at elevations lower than their normal mountain and foothills habitats (Gentry 1972, 1982; Ford 1981; Crosswhite 1981; Fish et al. 1985; Fish et al. 1992; Fish and Nabhan 1991; Hodgson and Slauson 1995). Ancient Hohokam groups living in the Phoenix, Tucson, Tonto and New River Basins put effort into raising plants that required up to a decade of patient waiting before the desired products, including carbohydrates concentrated just prior to flowering and useful fibers from the leaves, could be harvested. This scenario is in sharp contrast to the better-known prehistoric Southwestern domesticated plants. For example, crops from Mesoamerica such as corn (*Zea mays*), beans (*Phaseolus*, *Canavalia*), squash (*Cucurbita*), gourds (*Lagenaria*), and cotton (*Gossypium*), and lesser-known indigenous cultivated/managed plants such as little barley (*Hordeum*), are all able to yield resources within a single growing season. *Agaves* join a very short list of perennials, including cholla cactus (*Opuntia*) and Mexican crucillo (*Condalia*), that ancient farmers were either moving across landscapes or managing in other ways (Bohrer 1991). The ability of agave plants to survive in marginally arable land, needing little if any care, would have appealed to agriculturalists.

Evidence for prehistoric *Agave* cultivation is not in the form of distinctive morphological attributes of the plants, which are usually identified at the genus level in the archaeological record. Rather, the accumulating evidence is primarily circumstantial. Noted long ago were the anomalous distributions of agave parts in Hohokam roasting pits located some distance from and somewhat lower than natural agave populations (Fewkes 1912; Hayden 1957:103; Haury 1945:39; Fish, et al. 1985; Fish et al. 1992). More recently, associations of some out-of-range agave roasting pits with adjacent agricultural features and agave lithic-processing assemblages (turtleback scrapers, knives) all point to actual production in these lower basin locations (Miksicek 1984; Gasser and Miksicek 1985; Fish et al. 1985), rather than long-distance gathering or trade of the extremely heavy plants. Both the overall quantity and variety of agave parts recovered support an interpretation of cultivation near the sites themselves.

An astounding fact is that some living *Agave* plants currently in association with archaeological sites in Arizona are most likely the *direct descendants* of agaves planted and tended by ancient groups. These plants provide a *living* link to the past, with a genotype probably identical to those of prehistory.

The Hohokam prepared extensive rockpile fields to host agaves, and perhaps other crops at the same time (Fish et al. 1985:108; Fish et al. 1992). They also planted agaves in terraces and check dams, which helped to stabilize water-control systems. One can imagine huge fields of agaves in different stages of growth, with harvest efforts centered on those plants ready to send up a flowering stalk. Rhizomatous suckers and an occasional stalk left to flower and then produce miniature agaves, as described below, would provide plenty of starter plants, for future fields.

It is likely that more than one species of agave was of ancient interest. Epidermal patterns on leaf bases suggest at least two or three different species (Fish et al. 1985). Some terminal leaf spines and marginal teeth compare favorably both to *Agave murpheyi* and *A. parryi*. In east-central Arizona, the modern distribution of *A. parryi* has been linked to archaeological sites (Minnis and Plog 1976), and more research should be done on this species. Modern range data suggest that *A. murpheyi*, *A. delamateri* and a third, unnamed agave from the Grand Canyon (Hodgson 1996), were transported and managed by ancient groups.

Agave murpheyi advantages

Since this report focuses on *Agave murpheyi* reproductive biology, the reasons why it may have been of particular interest to prehistoric farmers are enumerated (Hodgson et al. 1989; Hodgson 1994; Nabhan et al. n.d.; Szarek et al. 1996).

- a. The amount of time an *Agave murpheyi* plant requires to grow to a mature plant with abundant carbohydrate reserves can be as little as nine years, under favorable circumstances (this report). Other agaves, such as *Agave delamateri*, are also known to become quite large and flower in a similar amount of time (W. Hodgson, personal communication).
- b. When the leaves are harvested for fibers, the acidic liquid in *Agave murpheyi* leaf tissue is less caustic to human skin than that of other agaves. Also, the leaves are somewhat easier to cut off with stone tools, and the rather small marginal teeth are not particularly bothersome to harvesters.
- c. *Agave murpheyi* has value because timing of caudex (often called the heart) readiness is during a potentially food-stressed time of the year. *A. murpheyi* plants prepare to send up their flowering stalks in mid-winter, up to two to three months before any other wild or potentially managed agave species are ready to do the same. Humans can recognize the signs of flower stalk initiation, when the caudex is carbohydrate-rich, and available for harvest as food or beverage.

d. *Agave murpheyi* plants produce flowers, but instead of developing mature fruit, they are more likely to develop numerous miniature agave plants, referred to interchangeably in this report as “bulbils” or “pups”, in the branches of their flowering stalks. Only rarely does an *A. murpheyi* produce capsules with viable seeds (Gentry 1982; Szarek et al. 1996). Bulbil formation occurs even when a stalk is not damaged. This strategy produces asexual clones, all identical genetically to the mother plant. Although this method lacks the gene-mixing benefits of sexual reproduction, the success rate for establishing a new plant from a bulbil may be higher than starting a plant from a seed. The young pups, produced just at the start of the summer monsoon season (July-August), could be planted with some assurance of receiving moisture.

e. Compared to other *Agave* species, the bulbils or pups of *Agave murpheyi* have a fairly high survival rate, persisting for up to two to three years on the main stalk. While attached they begin to photosynthesize and become larger, produce root primordia (embryonic tissue composed of cells capable of further differentiation), and develop an extensive cuticle or protective outer layer of lipid material (Szarek et al. 1996). These traits would all contribute to increased success in transporting and/or trading the pups over long distances. Once detached, *Agave murpheyi* bulbils have the ability to quickly become established, providing they receive some maintenance, especially moisture, when planted (Szarek et al. 1996).

f. A study of nine stands of *Agave murpheyi*, spread from northern Sonora, Mexico to central Arizona showed no allelic variation at seven scorable loci for three enzyme systems, consistent with the hypothesis that this species was culturally dispersed from its origin with little or no subsequent genetic change (Nabhan et al. n.d.). This supports the idea that these geographically dispersed *Agave murpheyi* stands were probably derived from a single or very limited number of plants.

g. When tended in the same field, plants that are clonal or closely related might all be expected to send up flowering stalks within a few years of each other, a feature that is helpful in planning harvesting and roasting events.

h. Repeated efforts to locate *Agave murpheyi* “in the wild” in northern Sonora have failed, even though local people say that the plant can be found in nearby hills. It has been suggested that *A. murpheyi* originated through clonal mutation in Sonora, and that prehistoric harvesters selectively transplanted and managed these mutants, thus fixing the preferred characteristics cited above. Other examples of such mutants, when they naturally occur, might not easily persist in the wild, and hence be difficult to locate by botanists occasionally visiting an area.

***Agave murpheyi* growth**

In early 1984 we planted in our Tucson (Arizona) backyard a small *Agave murpheyi* bulbil from a mother plant at the

Desert Botanical Garden in Phoenix. As it grew over the years, the plant received no direct care, but quietly garnered benefits from extra water and fertilizer applied to adjacent garden areas. Each year the plant would produce up to three to four rhizomatous suckers at the base; however, nearly all these died within a few years of forming. By the time the *Agave* mother plant prepared to send up its flowering stalk early in 1993, only a single small plant was attached at the base. This circumstance differs from *A. murpheyi* plants growing in the desert, which have been observed to have numerous vigorous suckers around their base.

Flowering stalk growth and development

Evidence that the stalk was ready to flower became apparent to us in January 1993, as the apex of the developing flower stalk increased in size, lightened in color, produced a number of new leaves, and started to elongate. The plant at this time measured 120 cm (47 in) in width and was 85 cm (33.5 in) tall. In Mexico, *Agave* farmers and indigenous groups can predict when a plant is going to flower as early as the previous growing season (Arizaga and Ezcurra 1995; del Barco 1980).

Methods

Records were not kept during the initial period of stalk growth in late January and early February. Twice daily (9:00 a.m. and 9:00 p.m.), measurements made between February 7 and April 29, documented the height of the elongating main stalk, starting from where it joined the caudex [35 cm (13.75 in) above ground surface] to its apex. After April, when the growth rate had slowed considerably, occasional measurements were made only to determine when the stalk reached its maximum height. This project quickly required the use of a very long measuring stick and increasingly taller ladders. Developmental events such as lateral branch emergence and growth, flowering, visiting potential pollinators, flower abscission (release), bulbil development, etc. were kept track of in a daily log. Weather data were recorded from the newspaper.

Results

One of the most impressive observations that can be made about *Agave murpheyi* flowering stalk development is its growth rate (Table 1, page 18). When daily record-keeping started February 7th, the flowering stalk was already 60 cm (24 in) tall. By then, it seemed to grow skyward as we watched (Plate 1A, page 19). There were ten days when stalk growth was over 8 cm (3.2 in) within a 24-hour period. Between February 7 and April 29, stalk growth averaged 4.69 cm (1.9 in) a day, ranging from 1-12 cm (0.4-4.8 in). During May the stalk gained an additional 33 cm (13 in), reaching a maximum height of 4.73 m (15.5ft) (Plate 1B, Page 19), which is nearly three times taller than an average person. Others report the length of three *Agave murpheyi* scapes (the flower-bearing stems) in central Arizona to average 4.1 meters (± 0.1 m) (13.5 ft) (Szarek et al. 1996).

Stalk measurements made at dawn and dusk revealed that although growth occurred primarily during the daylight hours, some elongation also occurred between 9:00 p.m. and 9:00 a.m. For example, during February the stalk grew an average of 3.22 cm (1.3 in) [range = 1-6 cm (0.4-2.4 in)] during the day, and added an additional average of 0.72 cm [range = 0-3 cm (0-1.2 in)] at night. During March, the stalk growth rate was even higher, averaging 3.45 cm (1.4 in) [range = 0-9 cm (0-3.5 in)] during the daytime, and 1.86 cm (90.8 in) [range = 0-5 cm (0-2 in)] at night.

Weather

For a substantial portion of the month of January 1993, an unusual amount of rain fell in southern Arizona, saturating the ground, and fully hydrating the *Agave* plant. Weather data reported in the *Arizona Daily Star* allow an examination of stalk growth and weather variables. To statistically assess if any stalk growth variables (24 hour growth, daytime growth, nighttime growth) correlated with any recorded weather variables (high daily temperature, low daily temperature, mean daily temperature, humidity at 5:00 a.m., humidity at 5:00 p.m.), a series of Pearson correlations (SPSS 7.5 Base 1997) were performed. Two of the weather variables, high daily temperature and mean daily temperature, were positively correlated with all three growth variables at

significance levels of 0.01 or 0.05 (Table 2, Page 18). The correlation between mean daily temperature and 24 hour growth is depicted in Figure 1, which also reveals that by early to mid-April this positive relationship had ceased, after the *Agave* stalk had begun lateral branch development. Other weather variables perhaps played a minor role in stalk growth during the observation period. The only notable amounts (from 0.23-0.36 inches) of precipitation fell on four occasions in February and March. Other species of *Agave* are sensitive to low temperatures (Nobel and McDaniel 1988), but at no time during this study did the thermometer drop below 36° F. In previous years, we had observed frost damage on the leaves during nights when the temperature dropped below freezing.

Others have documented a number of environmental flowering triggers for Sonoran Desert plants, including photoperiod, minimum rainfall, and mean degree-day requirements (Bowers and Dimmitt 1994). During an eight year period of observation, flowering of *Agave deserti* was best predicted by the number of wet days occurring two years previously (Nobel 1987). Our limited study suggests that daily temperatures influenced flowering stalk growth; our data are too limited to evaluate possible environmental triggers for flowering stalk initiation.

Correlation of Growth with Temperature

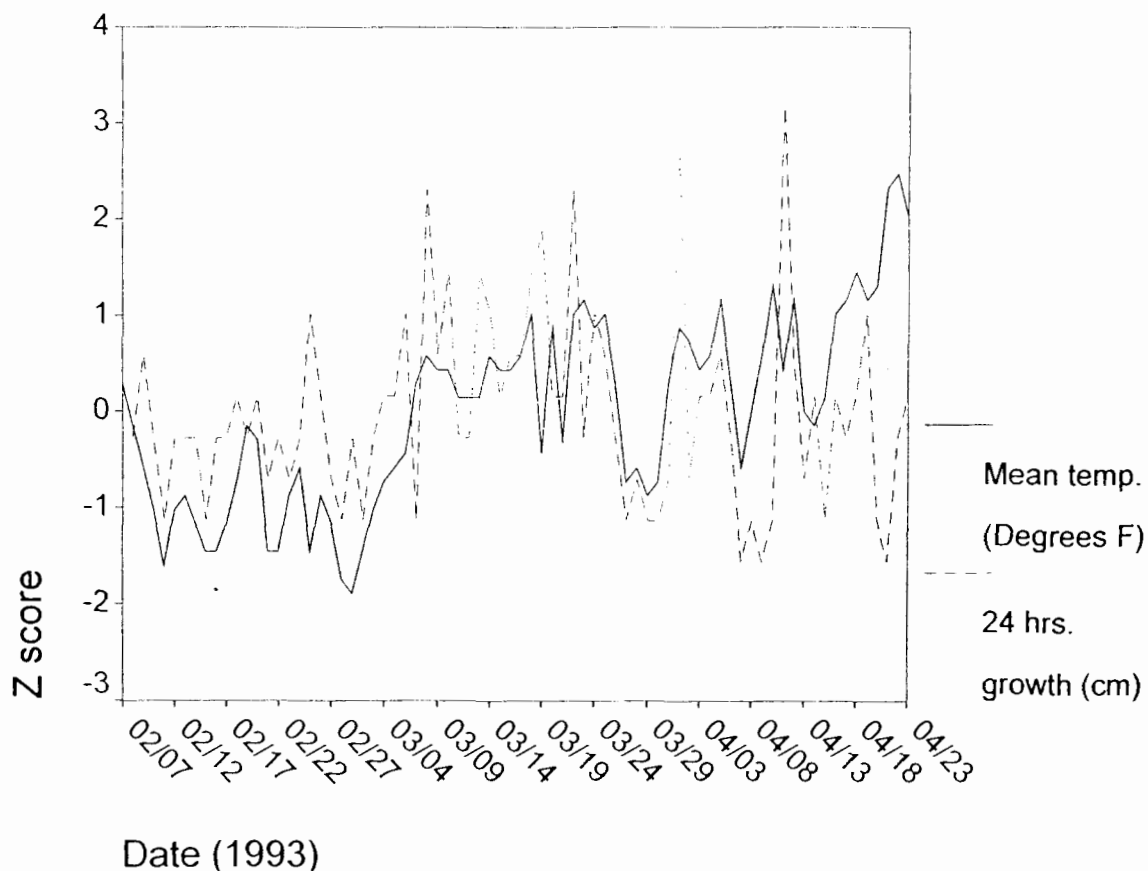


Figure 1. Correlation of daily growth and same day temperature. Variables converted to |Z| scores for comparability. Data displayed in five day increments (1993).

*Metric measurements are correct throughout document.

Main flowering

An impressive event in *Agave* flowering development is the appearance of lateral branches within the upper flowering portion of the stalk. *Agave murpheyi* exhibits the panicle type growth form, with a number of lateral branches (secondary peduncles) extending away from the main stalk. Bulges along the main stalk were first noticed March 10. By March 21, a minimum of nine emerging branches were arranged in a clockwise spiral along the main stalk. A total of 22 lateral branches eventually developed. Others have reported an average of 18 (± 1.5) panicles (equivalent to the lateral flowering branches discussed here) on three *Agave murpheyi* plants in central Arizona (Szarek et al. 1996).

Lateral branch development was quite regular. The first and lowermost branch to emerge (#1) did so 253 cm (100 in) above the main stalk base. Each subsequent lateral branch developed approximately 10 cm (4 in) above, and at approximately 135° of clockwise rotation, from its predecessor, resulting in an arrangement in which branch #9 was aligned over #1, as were numbers 10 and 2, 11 and 3, etc. Each branch diverged approximately 60 degrees from the vertical main stalk. The last lateral branch to emerge (#22) did so at the stalk apex. Some of the lower and upper lateral branches were shorter than those in the middle, giving the flowering portion of the stalk an elliptical appearance in silhouette.

The flowers

The first and lowest lateral branch to emerge (#1) was also the first to flower, beginning in mid-May. On a nearly daily basis, a new branch flowered in succession from bottom to top. Pale waxy green perianths sitting atop unfertilized ovules displayed fully developed pistils and exerted stamens (Plate 1C, Page 19). The flowers on a lateral branch opened, attracted potential pollinators, dried, and abscised all within a two week period. When branch #1 was losing its dried flowers, branch #12 was just starting to bloom. The last and highest lateral branch to emerge (#22) flowered June 14. The entire stalk flowered within the five week period May 20-June 26.

Potential pollinators

Birds and insects visited the agave during the day, many at the same time. Separate pairs of Gila and ladderback woodpeckers stopped by regularly, along with hummingbirds and finches. At least three kinds of bees, including honey bees, bumble bees, and carpenter bees were drawn to the flowers, as were spadefoot bugs that normally live on nearby pomegranate trees, and a variety of small fly-like insects. At night various types of moths and other unidentified insects were seen.

Despite the variety of potential pollinators, each ovary and its perianth flower parts shriveled and fell off. *Agave* plants are considered obligate outcrossers (Szarek et al. 1996), and the absence of nearby flowering *Agave murpheyi* plants to facilitate cross-pollination may explain why the flowers weren't fertilized. On rare occasions *Agave murpheyi* does

produce seeds (Gentry 1982), with up to 50 percent of them able to germinate successfully (Szarek et al. 1996).

Aerial bulbil emergence

Immediately following flower loss, aerial bulbil development began May 29 on branch #1, recognized as cream-colored enlargements of tissue appearing near the point of flower attachment. Others report that bulbils arise from axillary buds on the sides of pedicels after flowers abscise (Szarek et al. 1996). Five weeks later, these tissues had turned a light green color and looked more like leaves. By August 5, they were clearly recognizable from a distance as miniature *Agave* plants. As these bulbils grew, they appeared to vary in size within each lateral branch (Plate 1D, Page 19).

Limited additional flowering

In early July, on lateral branch #3 and successively later on some others, a second limited set of nearly normal flowers developed and dehisced as before. Shortly thereafter, all lateral branches with growing bulbils developed yet a third, limited set of incomplete and distorted flowers, in the same progressive order (bottom to top) as all previous developmental events. These aberrant flowers, tucked down in among the bulbils, never abscised from the branches, but dried and remained attached to the branches for months afterwards.

Finally in mid-September, a final set of flowers appeared on branch #3. This time the structure supporting the flowers looked like a miniature flowering stalk, possibly produced by a precocious bulbil, and complete with five tiny lateral flowering branches (Plate 2A, Page 20). Each lateral branch of this miniature stalk contained one or two very small flowers, whose sequential development from lowest to highest branch mirrored that of the larger *Agave* flowering stalk.

The mother plant

As the main stalk grew skyward, flowered and produced bulbils, the mother *Agave* lost color and diminished in size. Having started out a healthy dark green plant, by August its leaves were yellow, shrunken and limp. The caudex or heart, however, was still about the same size.

Bulbil history

The bulbils or pups of the mother *Agave murpheyi* plant all remained firmly attached to the lateral branches through the remainder of 1993 and well into 1994. It was impossible to tell whether any bulbils emerged from beneath the flowers of the 2nd and 3rd flowerings, because these flowers were too closely integrated into lateral branches developing pups from the original flowering. No pups were produced on the separate miniature stalk that developed and flowered in mid-September on branch #3. In the spring of 1994, a pair of Inca doves built a nest in a lateral branch midway up the stalk, and fledged two young in April.

Through the hot 1994 summer months of May and June, the little pups began to show moisture stress as their leaves

shriveled and wrinkled. By then the mother plant had completely exhausted all reserves in service to the flowering stalk, and had little to offer her abundant, miniature progeny. In total she had produced over 120 fiber-filled leaves, and a plethora of pups.

The fact that all the pups were still attached and clearly undergoing moisture stress a full year *after* they first appeared is intriguing. This agrees with other reports on *Agave murpheyi*, where current-year bulbils were difficult to remove by hand-picking (Szarek et al. 1996), and where bulbils are said to remain attached to the stalk into the second or third year (Gibson 1935:85). It also agrees with observations of other *Agave* species, where it has been reported that only a small percentage (1.8 percent) of *Agave* bulbils establish themselves successfully (Arizaga and Ezcurra 1995). However, *Agave murpheyi* bulbils have long survival rates, with more than 25 percent of them still alive after three years of growth chamber storage (Szarek et al. 1996).

We had expected the bulbils to start abscising, but this was not the case. Under human management, plants may lose certain characters adapted in the wild. In this situation perhaps *Agave murpheyi* had lost its ability to naturally disperse its pups and humans filled the role of dispersal agent. For ancient farmers, it might be better for an agave to keep all its pups together and safe above ground, until needed. We envision an ancient farmer with an agave stalk over his shoulder passing from rockpile to rockpile, detaching pups as he goes. This is admittedly speculative.

Finally, a summer storm with high winds in August 1994 caused the flowering stalk to tilt severely. We considered it time to remove, weigh, and measure all the water-stressed bulbils. They were still so tightly attached that pruning shears were required to release them. Although we did not observe this, others have reported that *Agave murpheyi* bulbils that remain attached to the main stalk into the second year can continue to grow and produce root primordia, and that natural abscission of bulbils does begin during the second season of growth (Szarek et al. 1996).

Bulbil characters

A total of 359 bulbils were recovered from the 22 lateral branches. This total is quite similar to an average of 369 bulbils (± 87) for three *Agave murpheyi* plants reported from central Arizona (Szarek et al. 1996). Total bulbil production in *Agave murpheyi* is actually low, when compared to three other species of agave (*Agave angustifolia*, *A. fourcroydes*, *A. vilmoriniana*) which produce an average of 516-3255 bulbils per plant (Szarek et al. 1996).

The number and fresh weight of the bulbils on each branch were quite variable, as was length and width (Table 3, Page 18; Plate 2B, Page 20). Water loss had reduced their fresh weight to some unknown, but possibly considerable, extent. The total fresh weight for all bulbils was 3141.5 g, with an

average fresh weight of 8.75 g. In another study, after four days of oven drying at 80° C, total dry mass of *Agave murpheyi* bulbils for three plants in central Arizona averaged 1410 g (± 268 g), with a mean individual dry weight of 3.4 g (± 0.6 g) (Szarek et al. 1996).

The branches differed to a notable extent in their bulbil production. Although branch #8 produced the greatest number of bulbils (39), branch #6 had the greatest average bulbil fresh weight (17.2 g), the greatest total bulbil fresh weight (395.5 g), and the greatest standard deviation in bulbil weight (21.6 g). By the time branch #14 began developing its bulbils, the mother plant had less to offer, as the number of bulbils per lateral branch dropped noticeably. Once planted, each bulbil quickly developed roots, plumped up by taking on water, and began rapid growth.

Summary

The reproductive biology of a single *Agave murpheyi* Gibson living in a residential backyard in southern Arizona is documented here in detail. Certain aspects of bulbil production of this single plant are similar to those of three other plants reported from the region. After nine years of growth, and following a particularly wet January, a flowering stalk rapidly elongated during both daytime and nighttime hours. Between February 7th and April 29th, growth averaged 4.69 cm (2 in) per 24 hour period, ranging between 1-12 cm (0.4-4.5 in). By May 29, the stalk had reached its maximum growth of 4.73 m (15.5 ft). Stalk growth spurts generally correlated with relatively warm days. A total of twenty-two lateral branches developed, and within a five week period flowered in succession from the bottom to the top. Although visited by a wide variety of potential pollinators, all flowers shriveled and dehisced without producing any mature fruit. Instead, the mother plant produced 359 miniature agave bulbils or pups from enlargements of tissue in the vicinity of the former flowers. By the summer monsoon season of July and August, these swollen tissues were recognizable as miniature agaves. The stalk remained upright with pups firmly attached for over a year, at which time the miniature agaves were notably moisture stressed. When the pups were intentionally detached from the mother plant nearly 14 months after they formed, they displayed notable variability in weight and size. Once planted, however, they immediately began to thrive.

This detailed set of observations on an *Agave murpheyi* plant provides perspective on a relationship between agaves and humans. The short, less than a decade, period from planting to caudex availability, coupled with mid-winter readiness, would be two traits that humans would value. For those plants left to develop a flowering stalk, over 300 miniature agaves or bulbils could be produced in the flowering stalk branches. Because the bulbils don't dehisce naturally, humans might have a certain level of control over these clonal progeny, perhaps letting them stay safely attached to the plant until planting, and possibly using the stalk as a means of easy transport. Bulbils produced by a single mother plant

would presumably develop somewhat in unison, allowing a certain level of advance harvest planning. Ogden Nash would indeed have found this interesting agave worth a limerick or two.

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References Cited

- Arizaga, S. and E. Ezcurra. 1995. Insurance against reproductive failure in a semelparous plant: bulbil formation in *Agave macrocartha* flowering stalks. *Oecologia* 101:329-334.
- Bohrer, V. L. 1991. Recently Recognized Cultivated and Encouraged Plants Among the Hohokam. *Kiva* 56(3):227-235.
- Bowers, J. E. and M. A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121(3):215-229.
- Castetter, E. F., W. H. Bell and A. R. Grove. 1938. VI. The Early Utilization and the Distribution of Agave in the American Southwest. *Ethnobiological Studies in the American Southwest*, University of New Mexico.
- Crosswhite, F. 1981. Habitat and agriculture in relation to the major pattern of cultural differentiation in the O'odham People of southern Arizona. *Desert Plants* 3:47-76.
- del Barco, Miguel, S. J. 1980. The Natural History of Baja, CA. Translated by Froylan Tiscareno. Introduction by Miguel Leon-Portilla. Dawson's Book Shop, Los Angeles, CA.
- Fewkes, J. W. 1912. Casa Grande, Arizona. 28th Annual Report of the Bureau of Ethnology, 1906-1907. Washington, D.C.
- Fish, S. K., P. R. Fish and J. H. Madsen. 1992. Evidence for large-scale *Agave* cultivation in the Marana community. In: *The Marana Community in the Hohokam World. Anthropological Papers of the University of Arizona*, No. 56. University of Arizona Press, Tucson, AZ.
- Fish, S. K. P. R. Fish, C. Miksicek, and J. Madsen. 1985. Prehistoric *Agave* cultivation in southern Arizona. *Desert Plants* 7:107-112.
- Fish, S. K., and G. P. Nabhan. 1991. Desert at context: the Hohokam environment. In: *Exploring the Hohokam, Prehistoric Desert Peoples of the American Southwest*, George J. Gumerman, editor. University of New Mexico Press, Albuquerque.
- Ford, R. I. 1981. Gardening and farming before A.D. 1000: Patterns of prehistoric cultivation north of Mexico. *Journal of Ethnobiology* 1:6-27.
- Gasser, R. and C. Miksicek. 1985. The Specialists: A reappraisal of Hohokam exchange and the archaeobotanical record. In: *Proceedings on the 1983 Hohokam Symposium*, edited by A. E. Dittert and D. E. Dove, pp. 483-498. Arizona Archaeological Society Occasional Paper 2.
- Gentry, H. S. 1972. The Agave Family in Sonora. *U.S. Dept. Agriculture Handbook* 399.
- Gentry, H. S. 1982. *Agaves of Continental North America*. University of Arizona Press, Tucson.
- Gibson, F. 1935. *Agave murpheyi*, a new species. *Contributions from the Boyce Thompson Institute* 7:83-85.
- Haury, E. 1945. The excavation of Los Muertos and neighboring ruins in the Salt River Valley, southern Arizona. *Papers of the Peabody Museum of American Archaeology and Ethnology* 24.
- Hayden, J. 1957. Excavations, 1940, at University Indian Ruin. *Southwestern Monuments Association Technical Series* 5.
- Hodgson, W. 1994. *Agave murpheyi* Gibson. Status Report. Submitted to U.S. Fish and Wildlife Service, Ecological Services State Office, Phoenix.
- Hodgson, W. 1996. Fieldwork and legwork finding a new species. *The Sonoran Quarterly* 50(4):10-11.
- Hodgson, W., G. Nabhan and L. Ecker. 1989. Prehistoric fields in central Arizona: Conserving Rediscovered *Agave* Cultivars. *Agave*:9-11.
- Hodgson, W. and L. Slauson. 1995. *Agave delamateri* (Agavaceae) and its role in the subsistence patterns of pre-Columbian Cultures in Arizona. *Haseltonia* 3:130-140.
- Miksicek, C. 1984. Historic desertification, prehistoric vegetation change, and Hohokam subsistence in the Salt-Gila Basin. In: *Hohokam Archaeology along the Salt Gila Aqueduct, Central Arizona Project, Vol. 7: Environment and Subsistence*, edited by L. Teague and P. Crown, pp. 53-80. *Arizona State Museum Archaeological Series* 150.
- Minnis, P. and S. Plog. 1976. Study of the site specific distribution of *Agave Parryi* in east-central Arizona. *The Kiva* 41:299-308.
- Nabhan, G. P., W. Hodgson and J. Hickey. n.d. Domestication, cultural diffusion and *in situ* conservation of *Agave murpheyi* Gibson: An Ethnobiological Perspective. Manuscript on file, Arizona-Sonora Desert Museum, Tucson and Desert Botanical Garden, Phoenix.
- Nobel, P. S. 1987. Water relations and plant size aspects of flowering for *Agave deserti*. *Botanical Gazette* 148(1):79-84.
- Nobel, P. S. and R. G. McDaniel. 1988. Low temperature tolerances, nocturnal acid accumulation, and biomass increases for seven species of *Agave*. *Journal of Arid Environments* 15:147-155.
- Szarek, S. R., B. Driscoll, C. Shohet, and S. Priebe. 1996. Bulbil production in *Agave* (Agavaceae) and related genera. *The Southwestern Naturalist* 41(4): 465-469.
- SPSS 7.5 Base (1997). SPSS, Inc. Chicago, IL.

Table 1. *Agave murpheyi* flowering stalk growth during the February 7–April 29 period when daily records were kept. By February 7th, the stalk was already 60 cm (24 in) tall. During May, it gained an additional 33 cm (13 in), for a total gain of 4.73m (15.5 ft).

Month	Total Days	Total cm (in)	Min cm (in) per day	Max cm (in) per day	Avg cm (in) per day
February	21	91 (36)	2(0.8)	8(3.1)	4.33 (1.7)
March	31	163 (64)	2(0.8)	9(3.5)	5.26 (2.1)
April	29	126 (50)	1(0.4)	12 (4.7)	4.34 (1.7)
Totals	81	380(150)			4.69 (1.9)

Table 2. Correlations of *Agave murpheyi* growth variables with weather variables recorded in the daily newspaper. HTEMP = high daily temperature (degrees F); LTEMP = low daily temperature; HI-LOW = the difference between the high and the low temperature; MTEMP = mean daily temperature; HUM5AM = humidity at 5:00 a.m. (expressed as a percent); HUM5PM = humidity at 5:00 p.m.

Growth variables	Statistics	Weather variables					
		HTEMP	LTEMP	HI-LOW	MTEMP	HUM5AM	HUM5PM
CM24HRS	Pearson Correlation	.280*	.264*	-.070	.258*	-.115	-.212
	Sig. (2-tailed)	.015	.022	.552	.025	.325	.067
	N	75	75	75	75	75	75
CMDAY	Pearson Correlation	.369**	.224	.120	.347**	-.364**	-.305*
	Sig. (2-tailed)	.004	.088	.366	.007	.005	.019
	N	59	59	59	59	59	59
CMNITE	Pearson Correlation	.386**	.208	-.155	.378**	-.233	-.275*
	Sig. (2-tailed)	.003	.120	.251	.004	.081	.038
	N	57	57	57	57	57	57

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 3. Bulbil (pup) number and fresh weight (g) per lateral branch. Data gathered September 1994, a full year after bulbils had formed.

Branch Number	Number of pups	Average Weight (g)	Total Weight (g)	Range (g)	s.d. (g)
1	13	13.2	172.0	2.5-33.5	10.4
2	28	5.8	162.5	1.0-29.5	5.8
3	15	13.0	195.0	2.0-37.5	11.3
4	15	10.8	162.0	2.0-53.0	13.4
5	21	8.9	187.5	1.0-48.0	12.8
6	23	17.2	395.5	1.0-71.0	21.6
7	30	6.4	192.5	1.0-29.5	6.2
8	39	8.3	324.0	0.5-57.5	11.6
9	19	9.2	175.0	0.5-45.0	11.6
10	29	8.1	235.0	1.0-30.0	8.4
11	27	7.3	196.5	0.5-23.0	9.7
12	24	9.2	221.5	0.5-39.0	9.9
13	23	7.6	174.0	1.0-49.0	10.7
14	13	9.7	125.5	0.5-36.5	9.5
15	8	7.6	60.5	2.0-36.5	11.7
16	9	7.6	68.0	3.5-10.0	2.1
17	6	5.6	33.5	2.0-17.0	5.7
18	5	4.3	21.5	1.5- 8.5	3.1
19	1	—	7.5	—	—
20	4	8.0	32.0	1.0-21.5	9.4
21	0	—	—	—	—
22	7	4.2	29.5	0.5- 8.0	2.6
Total	359	8.75	3141.5		

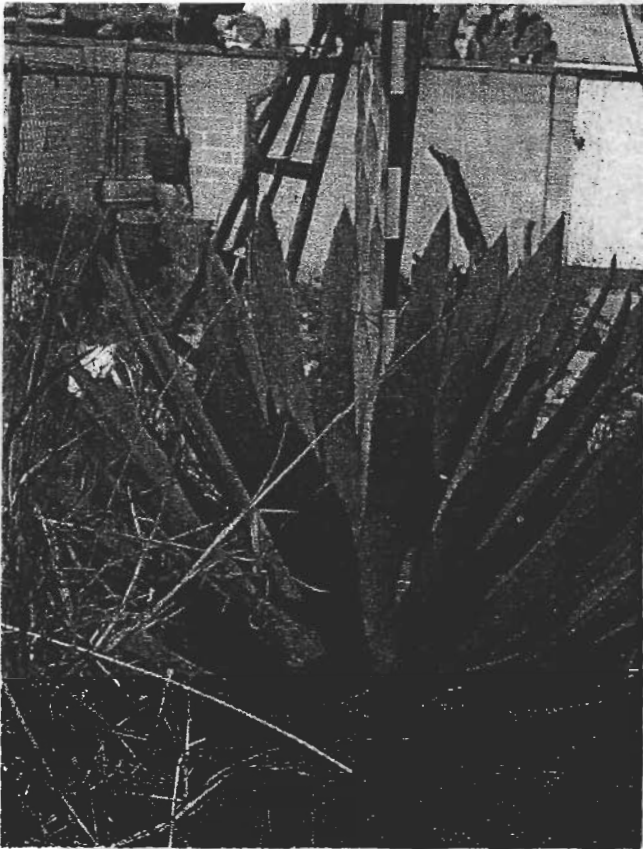
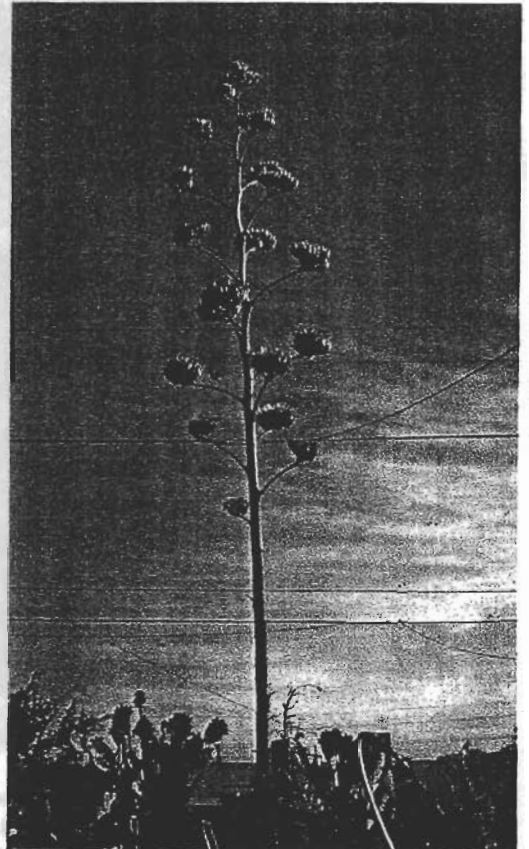
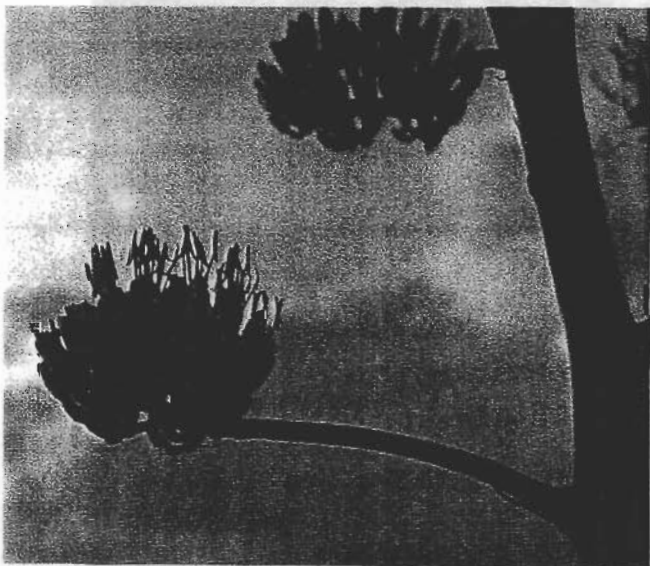


Plate 1A. In late January, the main stalk had begun to emerge and had reached a height of 78 cm (31 in) by February 10th.



1B. The main stalk reached a maximum height of 4.73 m (15.5 ft) by May 29th. Lateral branches had begun to emerge as early as March 10th.



1C. By May, flowers had fully developed pistils and exerted stamens.



1D. After normal flowers had dehisced, tissue enlargements initiated development of miniature Agave bulbils which eventually displayed diversity in size.

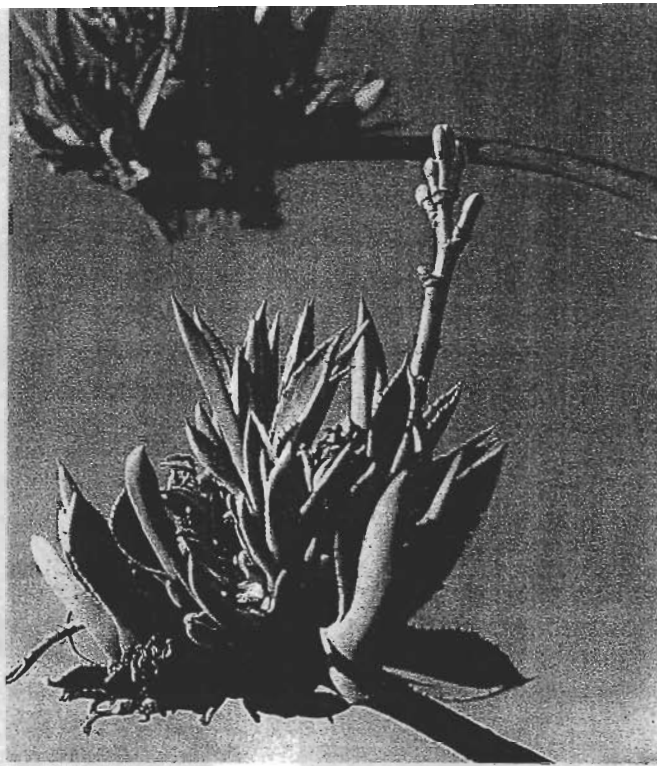
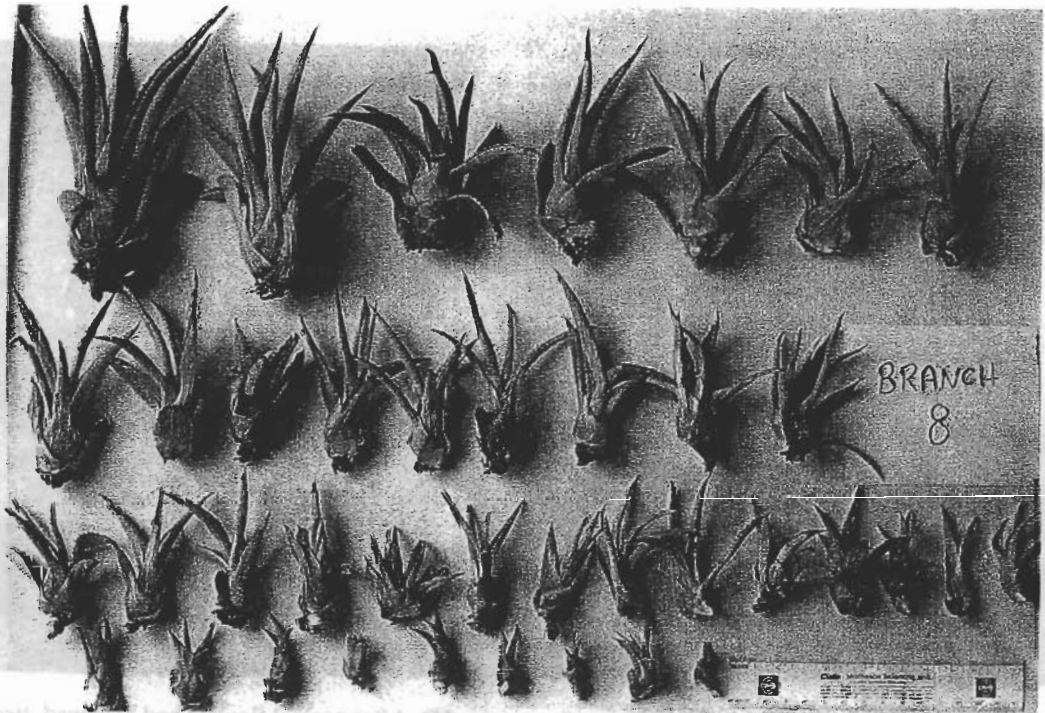


Plate 2A. In July, a second set of normal appearing flowers developed in many lateral branches.

In September, an unusual miniature flowering stalk in branch #3 had both a main stalk and four lateral branches.



2B. A full year after developing, and suffering from moisture stress, the bulbils displayed variability in size and shape, represented by those on branch #8.