Five Features Correlate with Seed Weight in Yuccas to Support a Seed-Dispersal Hypothesis

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Abstract

Morphological observations were made on fruits, seeds, stems, leaves, and flowers of 13 species of Yucca at various locations in California, Arizona, and eastward. The dates of flowering, fruit production, and fruit fall (or fruit persistence) were recorded. Seed samples for 12 of the 13 species were weighed, and fell into two different weight classes: light and heavy. It was observed that the species producing light seeds had a suite of five other correlated morphological characteristics. Conversely, most of the heavy-seeded yucca species had five different or contrasting features. Neither the seed weight classes nor their systematic correlation with the other five traits were covered in the *Yucca* literature consulted. Seeds of 14 additional *Yucca* species and one *Yucca* subspecies, taxa that were unavailable during the field studies, were commercially available from seed suppliers. It was possible to determine from the literature which of these 14 species possessed dehiscent pods, one of the attributes correlating with light seeds; and which ones produced indehiscent pods—the contrasting feature regularly associating with heavy seeds. The weights of the purchased seeds were consistent with the predictions that: (1) seeds from plants known to possess dehiscent pods would be light, and (2) the seeds from plants having indehiscent fruits would be relatively heavy. The few exceptions to other correlated features are listed and analyzed. It is proposed that the five features correlating with light seeds aid in transport of the seeds by wind. It is further hypothesized that the five contrasting attributes, which are usually present in heavy-seeded yuccas, foster seed dispersal by animals. These two hypotheses find support in the present data. Several additional morphological traits were analyzed and appear to be unrelated to seed dispersal or to phylogeny, posing a problem for neo-Darwinian macroevolution. The yucca correlations support a non-evolutionary origins model for *Yucca* species. Based on these data, further predictions are made, including the prediction that the correlations of seed weight with other features will also exist in the species and subspecies of Yucca not yet analyzed. Other possible avenues for future yucca research are enumerated.

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Introduction

The genus *Yucca* is comprised of several dozen species. In my original yucca paper (Howe, 1986), I used numerical taxonomy to show patterns of similarity among nine western yucca species. Based on that analysis, some morphological correlations became obvious. The deciduous pod was tied to three other features—pod indehiscence, non-erect fruit, and relatively short inflorescences (see Appendix 1). Persistent pods, to the contrary, were found to relate to fruits that dehisce, pods that stand erect, and inflorescences that are long. Thus there are six morphological correlations reported here—the original four plus two others: seed weight and ovary wall thickness.

The Creation-minded reader will find that a divine plan for seed dispersal in the genus *Yucca* becomes apparent. The details of *Yucca* seed weight, and other correlated characteristics, are fully consistent with the Creator's intelligent activity. Furthermore, these data cannot be readily explained by a coherent naturalistic scheme of origins.

Methods

The original field research, done in the western United States (Howe 1986), has been expanded here to cover two other western species, *Y. schotti* and *Y. arizonica*, for a total of nine western yuccas, as well as four other *Yucca* species eastward. Measurements were made in the field on these nine western and four other species, 13 total (see Tables 1-4). Records were kept on the locations of *Yucca* plants being studied and the nearby vegetation—Tables 6 and 7.

During the 2003 flowering period, certain individual *Yucca* plants in California and Arizona were chosen for repeated visitation from 2003 to 2007 in order to collect detailed information on plant morphology and on the phenology of such events as flowering, fruit development, fruit ripening, seed dispersal, and the abcission or persistence of the ripe pods. The other yucca localities outside of California and Arizona were visited only once or, in some cases, twice.

Small quantities of seed from 11 *Yucca* species studied in the field (nine from the west and two from the east) were secured. The average weight per seed was determined for them by weighing all the seeds and dividing by the seed number (Table 1). Also, packets of seeds were ordered from several suppliers for the species not studied in the field, for some species that were not producing seeds at the time(s) of my visitation and as a check on some of the field species that did yield seeds (Tables 4 and 5). In Tables 4 and 5, each seed was weighed individually, allowing computation of the mean weight per seed and the standard deviation. The differences between the mean seed weights of what can be called the "lightest of the heavy-seeded species" (*Y. entlichiana)* and the "heaviest of the light-seeded species" (*Y. peninsularis)* could then be evaluated by computing and comparing the standard errors of the means.

Results

Seed Weight

Weights of seeds I collected for 11 of the 13 *Yucca* species studied in the field are reported in Table 1, along with the weight of commercially available seeds of *Y. torreyi* (because no seeds for *Y. torreyi* were present in the field). The tables include no seed weight data for *Y. gloriosa* (one of those species studied in the field), because pods were not present and seeds were unavailable from nursery catalogues. Weights for purchased seeds of some of these same 11 *Yucca* species of Table 1 are also found in Table 4.

Seeds of 14 other *Yucca* species and one *Yucca* subspecies, none of which were part of the field research, were later purchased and weighed (See Table 5). Thus, this paper contains weights for 26 of the 49 total species of *Yucca* and one of the 24 subspecies, as recognized by Hochstätter (2004). I could find no other published records of seed weights for yucca species in the literature. Seeds of 23 more yucca species and 23 subspecies need yet to be weighed.

Whether from the field or from seed suppliers, all of the *Yucca* seeds consistently fell into two general weight classes with no overlap: 14 taxa (13 species and one subspecies) possessed light seeds, whereas 13 species possessed distinctly heavier seeds (Tables 1, 4, and 5). The mean for all the averages of heavy-seeded yucca species (n=14 species) was 89 mg (S.D. = ± 38; S.E. = ± 10.30). The mean of average weights for all light-seeded yuccas (n=13 species) was 12 mg (S.D. = ± 5.9; S.E. = ± 1.64). These sample means for the heavy-seeded and the light-seeded species are significantly different from each other.

To illustrate the extreme weight differences involved between the heavy and the light seeds, *Y. schottii* contained the heaviest seeds in the "heavy-seeded" group at 175 mg average (Table l), while the lightest of all the light seeds were those of *Y. pallida*, weighing 4 mg per seed average (Table 5); almost 44 times lighter than seeds of *Y. schottii*. The "gulf" separating the average seed weights of light-seeded yucca species from the heavy-seeded ones was typically quite large, as in the case of *Y. harrimanae* (a light-seeded species) having seeds weighing only 13 mg compared to the heavy-seeded *Y. perisculosa*, having an average seed weight of 103 mg, about eight times heavier (Table 5).

The closest that the average seed weight of any heavy-seed species came to the weight of a light-seeded yucca was *Y. entlichiana* (the "lightest of the heavy-seeded yuccas") at 39 mg average (S.D. = ± 12.7; S.E. = ± 1.13). *Y. peninsularis* was the "heaviest of the light-seeded group," at 23 mg average seed weight (S.D. = ± 6.24; S.E. = ± 1.30; see Table 5 and Figure 1). Even in the

Table 1. Correlated Seed-Dispersal Features in 13 Species of *Yucca*.

Yucca species	Average Seed Weight Milligrams (mg)	(+) = Ripe Pods Adherent (-) = Ripe Pods Deciduous	(+) = Ripe Pods Dehiscent (-) = Pods Indehiscent	(+) = Ripe Pod Walls Thin (-) = Pod Walls Thick, Fleshy or Dry	(+) = Pods Usually Erect (-) = Pods Not All Erect
Light-Seeded					
1. *angustissima*	22 n=10	+	+	+	+
2. *elata*	19 n=31	+	+	+	+
3. *filamentosa*	9 n=10	+	+	+	+
4. *glauca*	19 n=10	+	+	+	+
5. *whippleii*	13 n=20	+	+	+	+
Heavy-Seeded					
6. *aloifolia*	51 n=20	-	-	-	-
7. *arizonica*	159 n=30	-	-	-	-
8. *baccata*	171 n=40	-	-	-	-
9. *brevifolia*	78 n=37	-	-	-	-
10. *schottii*	175 n=10	-	-	-	-
11. *shidigera*	83 n=10	-	-	-	-
12. *torreyi*	94 n=26	-	- [a]	- [a]	- [a]
Possibly Heavy-Seeded					
13. *gloriosa*	? [b]	? [b]	- [a]	- [a]	- [a]

[a] This information is from the literature.
[b] Information unavailable in my field or literature work.

case of this extreme example, the heavy seeds were still about 1.3 times heavier than the light seeds, and their sample means differed significantly from each other. In all other comparisons between light-seeded and heavy-seeded species, the weight separations were even much greater than this distinct separation between Y. *entlichiana* and Y. *peninsularis*.

Five Traits Found Correlated with Light Seed Weight

The five light-seeded *Yucca* species of the field research (*Yuccas angustissima*, *elata*, *filamentosa*, *glauca*, and *whippleii*)

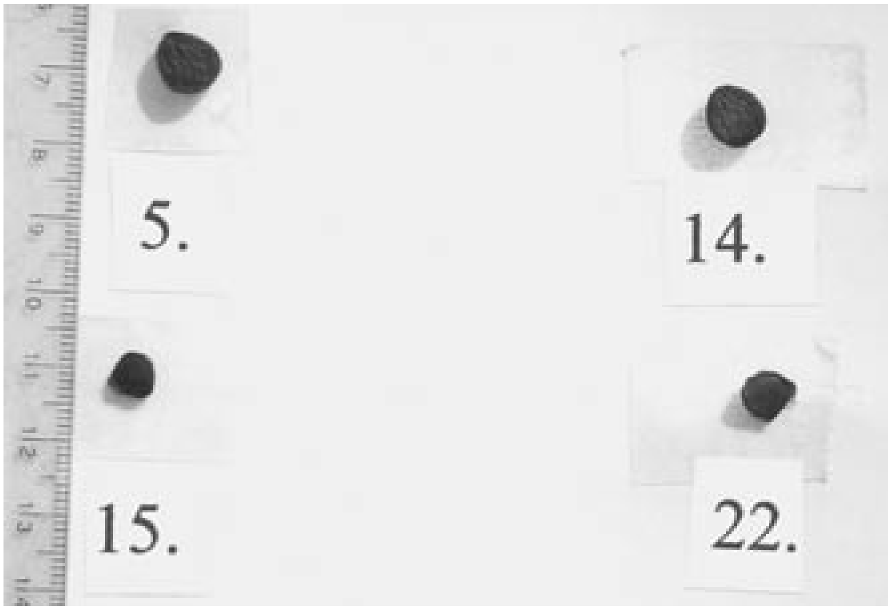

Figure 1. Seeds of four *Yucca* species. Number five is a seed of *Y. arizonica*, a species having heavy seeds (159 mg average) and indehiscent fruit. Seed number 14 is from *Y. australis*, which also produces heavy seeds (125 mg average) and pods that are indehiscent. Number 15 is a seed of *Y. entlichiana*, another heavy-seed indehiscent yucca. *Y. entlichiana* has the lightest seeds among all the heavy-seeded yuccas I weighed—39 mg average. Seed 22 is from *Y. peninsularis*, which has light seeds. These light seeds of *Y. peninsularis*, however, are the heaviest seeds among the light-seeded, dehiscent yuccas—22 mg average. It was one of the yucca seedlots that I purchased and then weighed after making weight predictions. A clear centimeter-millimeter ruler can be seen far left.

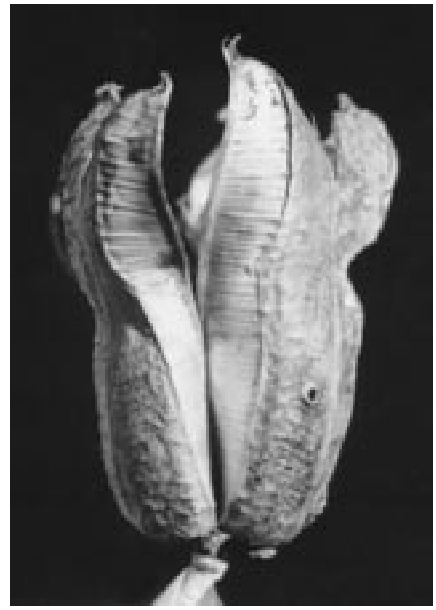

Figure 2. A capsular (dehiscent) fruit of *Y. angustissima*, showing erect pod stature and dehiscence, both of which are characteristics of light-seeded species. A hole in the fruit wall made by an emerging yucca moth is visible, lower right. The long split at center is septicidal, and the shorter suture line at the right demonstrates loculicidal dehiscence—both of which can occur on the same pod in various yucca species.

each possessed these five characteristics in addition to light seeds:

1. Pods of the light-seeded *Yuccas* are dehiscent (Figures 2 and 3). All of the other 10 light-seeded taxa (Table 5) among the purchased seeds are also reported to have dehiscent pods (Hochstätter, 2000, 2002, and 2004).
2. The fruits of all five light-seeded species remain attached to the flower stalk (Figure 4 and Table 1), thus being "persistent." (This does not mean that all the pods remain permanently attached. Various fruit do fall over a period of weeks, but numerous pods persist, continuing to shed seeds.)
3. Ovary walls are thin and dry upon ripening, in all the light-seeded species (Figure 5 and Table 1).
4. Pods have an erect, upright stance in the light-seeded species (Figures 2, 4, and Table 1).
5. *Yuccas* having light seeds all possessed inflorescences that held the fruit well above the leaf crown (Figure 4 and Table 2). This clearance is accomplished by an inflorescence possessing an elongated scape (Figure 4) or by a fruit-bearing portion of the inflorescence that is long enough to hold most of the fruit above the crown.

The five light-seeded *Yuccas* (species 1–5, Table 2) have the inflorescence extending above the crown to an average height of 111 cm. In contrast, the eight heavy-seeded species (species 6–13, Table 2) have an average inflorescence height above crown of 41 cm, despite the exceptionally tall inflorescence of *Y. gloriosa*. Discussion of *Y. gloriosa* and other exceptions is presented below.

The scape in the light-seeded species (1–5 of Table 2) made up 50% of the total inflorescence length, while in the heavy-seeded *Yuccas* the scape composed only 25% of the inflorescence length (6–13 of Table 2). The longer scape positions pods containing light seeds well above the fruit crown.

Figure 3. Pods of three different *Yucca* species—two that favor seed distribution by wind *(Y. angustissima and Y. whipplei)*, and one that favors seed distribution by animals *(Y. brevifolia)*. From left to right they are Y. *angustissima* (a species with dehiscent pods), two pods of Y. *brevifolia* (note their indehiscence), and one pod at the right of Y. *whipplei*, which is another dehiscent species, like Y. *angustissima*. This *angustissima* fruit (left) demonstrates both loculicidal and septicidal dehiscence occurring in the same fruit—sutures occurring in the carpels and between the carpels. The Y. *brevifolia* pods (center) have thick, although dry, fruit walls. The *whipplei* fruit at far right has loculocidal dehiscence and light seeds.

Five Reverse Traits Often Found in Heavy-seeded *Yuccas*

Most of the *Yucca* species that had the heavier seeds also manifested a suite of five "reverse" anatomical traits when compared to the light-seeded yuccas.

1. Pods of the seven heavy-seeded species studied (species 6–12 of Table 1) were indehiscent (Figure 3).
2. Fruits of most of the heavy-seeded *Yucca* species fall off upon ripening. (While most of the fruit does fall, a few pods may persist for weeks.) Six of the seven heavy-seeded *Yuccas* had deciduous fruits (Figures 6 and 7). The fruits of *Yucca aloifolia* are an exception to be discussed separately.
3. Ovary walls of the heavy-seeded *Yuccas* are thick and in most cases rather fleshy when ripe (Figure 3 and Table 1).
4. Pods of the heavy-seeded *Yuccas* (Table 1) were positioned in various directions, not always upright (Figure 6).

Table 2. Correlated Inflorescence Characteristics in 13 Species of Yucca.

Yucca Species	Inflorescence Length (cm)	Scape Length (cm)	Distance Inflorescence Extends above Leaf Crown (cm)
Light-Seeded			
1. *angustissima*	117 n=10	51 n=18	90 n=8
2. *elata*	195 n=20	106 n=20	143 n=20
3. *filamentosa*	129 n=10	65 n=10	101 n=10
4. *glauca*	81 n=20	39 n=10	40 n=10
5. *whippleii*	231 n=14	118 n=16	181 n=16
Heavy-Seeded			
6. *aloifolia*	93 n=13	29 n=13	56 n=13
7. *arizonica*	106 n=21	23 n=30	67 n=20
8. *baccata*	46 n=12	11 n=10	6 n=13
9. *brevifolia*	37 n=12	0	14 n=21
10 *schottii*	87 n=13	10 n=11	10 n=11
11. *schidigera*	51 n=49	0	17 n=24
12. *torreyi*	113 n=10	57 n=10	52 n=8
Possibly Heavy-Seeded			
13. *gloriosa*	145 n=11	60 n=12	103 n=12

Table 3. Some Noncorrelated Features in the 13 Yucca Species Studied.

Yucca species	Leaf Margin	Leaf Length (cm)	Leaf Width (cm)	Typical Crown Height (cm)	Inflo-rescence r = raceme p = panicle
Light-Seeded					
1. *angustissima*	Fibrous	31 n=33	0.51 n=31	0[a]	r
2. *elata*	Fibrous	45 n=21	0.75 n=20	110 n=20	p
3. *filamentosa*	Fibrous	52 n=13	2.6 n=13	0	p
4. *glauca*	Fibrous	52 n=13	0.75 n=12	0	p or r
5. *whippleii*	Serrated	70 n=10	2 n=10	0	p
Heavy-Seeded					
6. *aloifolia*	Serrated	49 n=15	4.4 n=15	102 n=5	p
7. *arizonica*	Fibrous	52 n=20	2.3 n=21	198 n=13	p
8. *baccata*	Fibrous	61 n=22	3.3 n=4	—	p[b]
9. *brevifolia*	Serrated	25 n=62	1.5 n=52	505 n=21	p
10. *schottii*	Smooth	62 n=21	3.2 n=19	144 n=19	p
11. *shidigera*	Fibrous	56 n=28	4.0 n=21	147 n=20	p
12. *torreyi*	Fibrous	131 n=2	4.0 n=8	285 n=9	p[d]
Possibly Heavy-Seeded					
13. *gloriosa*	Smooth[c]	60 n=23	3.9 n=11	45 n=10	p

[a] Y. *angustifolia* usually has no trunk, but in some populations there is a short trunk. This is also true for Y. *glauca*.
[b] Stalk of Y. *baccata* usually procumbent or absent, but in certain locations there is a short upright stalk.
[d] Taken from the literature.
[c] Sometimes very young leaves of Y. *gloriosa* are slightly serrated on a temporary basis.

5. The height of inflorescences and the distance that ripe pods were held above the leaf crown in heavy-seeded yuccas was on average smaller than in the light-seeded *Yucca* species (Figure 10). The average length of the entire inflorescence usually is shorter for the four species that have heavy seeds (77 cm) than for the light-seeded species (151 cm)—see Table 2. The distance that the inflorescence stands above the leaf crown and the average scape length are both shorter for heavy-seeded species, as pointed out earlier.

Purchased Seeds and Collected Seeds

Seed packets of eight *Yucca* species, seeds of which had likewise been secured in the field, were purchased and weighed in order to compare weights of field and purchased samples (Table 4). No major weight differences were found between the field seeds and purchased seeds (compare values of Table 1 with those of Table 4). These data demonstrate the consistency of average seed weights between various populations of a given *Yucca* species.

Verification of all Predicted Seed Weights for Purchased Yucca Seeds

Seeds of 15 *Yucca* taxa (14 species and one subspecies) not covered in the field studies were ordered from seed suppliers. Predictions were then made, and the purchased seeds were subsequently weighed. All the predictions were verified such that species known from the literature to produce dehiscent pods always had light seeds; and yuccas known to bear indehiscent pods all had heavy seeds (Table 5).

Several Other Morphological Traits—Largely Uncorrelated

Other morphological traits show few, if any, consistent correlations to the light-seeded species, the heavy-seeded category, or amongst themselves (Table 3). Fibrous, serrated, and smooth leaf margins (Figure 3) are found in various species with no consistent relation

Figure 4. Y. *elata* plants growing east of Sonoita, AZ in late winter, 2002. Two stems are bearing inflorescences with ripe pods attached—one along the fence and one nearly in the center. The stalk along the fence line manifests how these putatively wind-distributed seeds are held high above the level of the leaf crown (143 cm average for Y. *elata*). Note on those inflorescences how the long, slender scape (lower portion of the inflorescence) bears no fruit. Some of the fruit of 2001 have already fallen, but many remain on these inflorescences. The upright pod stance seen here and the persistence of fruit prepare light-seeded species using wind to distribute seed.

to seed weight or to the other traits so closely associated with seed weight. Likewise, long or short leaves; wide or narrow leaves; and short or long crown heights appear in both the light and heavy-seeded groups with no regular relationship to the correlated features. (Note that crown height is a different characteristic than the height of the inflorescence, a trait already discussed.) Other traits showing no consistent tie with seed weight are blue-green versus green leaf color, and mountain versus desert habitat preference (Tables 6 and 7).

Field Data for the *Yuccas* Studied

Tables 6 and 7 contain geographic, altitudinal, and vegetational details for most of the sites where a particular species of *Yucca* was observed. Annual observations are reported on both Tables 6 and 7 for events having a phenological periodicity, such as dates of flowering, fruit ripening, pod depletion (for most of the heavy-seeded species), and pod adherence (for the light-seeded *Yuccas*).

The light-seeded, non-deciduous fruits remained attached to the inflorescence for months after having undergone dehiscence (Table 6). Table 7 shows that pods of heavy-seeded species generally underwent abcission soon after ripening, with the exception of Y. *aloifolia*.

For each study site some remarks have been made concerning nearby vegetation. These comments are not intended to serve as an ecological report for those localities, but as an illustration of the general differences in the plants associated with the various *Yucca* species. Note that common names are usually used and generic names occasionally.

Discussion

Two Hypotheses about the Function of Seed Weight and Correlated Features

Based on these data, I hypothesize, first, that the presence of light seeds together with the traits occurring in conjunction with light seeds favor the distribution of seeds by wind. Light seeds are more buoyant, which is a definite advantage in wind transport. Lightness of seeds also conserves plant resources. I observed that wind does indeed carry the seeds of Y. whipplei, a light-seeded species, and I theorize that seeds of all

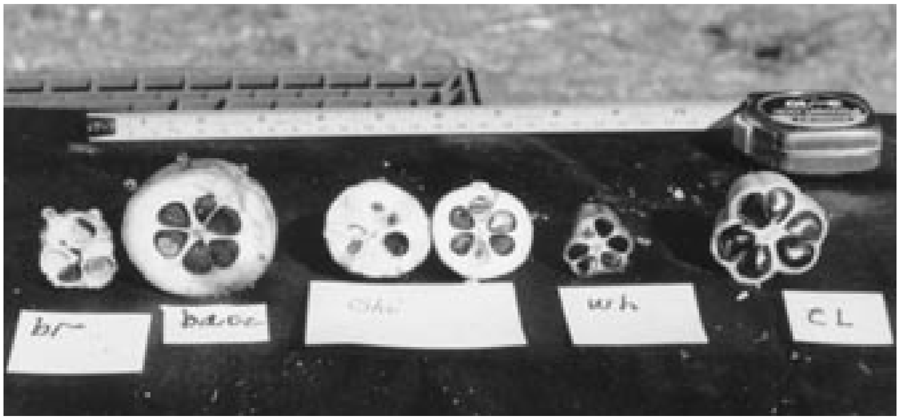

Figure 5. Fruit of five different *Yucca* pods cut in cross section. Beginning on the left, Y. *brevifolia* (br) is a heavy-seeded indehiscent yucca, which, nonetheless, has dry fruit walls. Next, Y. *baccata* (bacc) is a typical deciduous-fruited, indehiscent yucca, producing a thick ("baccate") fruit wall, and heavy seeds. Next, the two fruit sections seen in the center are Y. *shidigera* (shi), another heavy-seeded plant having deciduous pods that are also indehiscent. Y. *shidigera* has a thick fleshy fruit wall that is a characteristic of many heavy-seeded yuccas—possibly designed as a reward to attract animals. Y. *whipplei* (wh, second from right) is a light-seeded yucca with thin fruit walls, as is also Y. *elata* (el) on the far right. The seeds of *elata* are large in terms of length and width, even though they are quite light in weight. These pods show the fact that most yuccas having wind-distributed seeds possess thin walled pods while most of those that presumably use animals for food transport have thick fruit walls.

the light-seeded *Yuccas* are distributed mostly by wind.

1. In addition to light seeds, it is important that the mature fruit split open to allow release and lateral dispersal of seeds. Indehiscence of pods would inhibit aerial transport of seeds.
2. In releasing these light seeds for air transport over time, it is likewise a distinct advantage that the fruit be non-deciduous, remaining attached to the inflorescence.
3. Seed transport by wind is favored for the fruit pods that have relatively thin ovary walls. This enables pods to split open readily while at the same time conserving plant resources.
4. Wind distribution of seeds is enhanced by the pods standing upright on the fruit stalk. If the pods were not positioned upright, most seeds would fall downward. With an erect fruit, however, ripe seeds remain stationed in the ovary that has undergone dehiscence until the wind carries most of them away from the parent plant.
5. The fact that most of the fruit in light-seeded species is perched significantly higher than the surrounding leaves enhances lateral seed transport by wind.

Second, I also propose the hypothesis that the heavy weight of certain yucca seeds is a planned inducement for animals such as pack rats to harvest and carry pieces of the yucca fruit with the seeds. While the fruits are being carried, and perhaps hidden, by animals, many seeds will be lost and not eaten, providing for efficient seed dispersal.

1. It is advantageous to animal transport of seeds if fruits of heavy-seeded *Yuccas* do not split open. Indehiscence of pods enables animals to locate, grasp, and transport the fruit and seeds together. Dehiscence would cause a scattering of seeds prematurely, making them more difficult for animals to locate and damaging the fruit wall, which is itself an attractive animal food.
2. It is likely advantageous for animal-transport of seeds if the fruits abcise, dropping into the leaf crown or onto the ground near the parent plant. In either case, the deciduous trait makes fruit available in or near the plant. Collection of the seeds by animals would be less efficient if the pods were to remain attached, high up on the inflorescence. Gnawed fragments of fruit with seeds inside are found near *Yucca* plants (Figure 8), and many animal burrows surround the heavy-seeded species of *Yucca* (Figure 9).
3. Thick fruit wall structure in heavy-seeded yuccas is likely an inducement for foraging animals to harvest and transport the fruit and seeds. Some of the thick-walled pods, especially those of Y. *baccata*, have been roasted and eaten by humans.
4. Erect pod posture would be of no obvious advantage in the transport of heavy seeds by animals and accordingly, pods are not all positioned erectly but point in various directions.
5. The shorter length of inflorescence and the shorter scape found in most heavy-seeded yuccas causes fruit to be held closer to the leaf crown (Figure 10). This may make it more

Figure 6. Three flowering stalks of a Y. *brevifolia* plant (commonly called the Joshua tree.) This specimen showing ripe indehiscent fruit was photographed 25 April 2003 near Palmdale, CA. Like most of the indehiscent and heavy-seeded yuccas, its fruit point in various directions. Y. *brevifolia* also illustrates the fact that yuccas depending on animal seed transport usually have their inflorescence extending only a short distance beyond the leaf crown—14 cm on average for Y. *brevifolia*. On the stalk at the right, some dried remnants of the inflorescences from previous years can be seen.

Figure 7. The same three Y. *brevifolia* flowering stalks shown in Figure 6 are seen here 81 days later (14 July 2003). Numerous pods have fallen during this time period. This deciduous character of pods in heavy-seeded yuccas is likely of help in enabling animals to harvest the fruit and thereby distribute the seeds.

likely that most fruits fall into the crown, allowing easier collection.

Seed Weights and Correlated Traits in the Literature

There was no information on yucca seed weight in any of the literature sources I consulted, even though the dimensions, colors, surface features, marginal rims (also called "wings"), and other traits of yucca seeds have been widely discussed (for examples, see Hochstätter, 2000, 2002, 2004; Small, 1933; Trelease, 1902; and Webber, 1953). Sargent (1921) measured the seed length and width for each *Yucca* species he covered, listing the presence or absence of a wing, but did not mention seed weight classes or the five other features coordinated with seed weight.

Characteristics of fruits, inflorescences, leaves, and stems have likewise been described and employed in the construction of taxonomic keys for the *Yucca* species (Bailey, 1939; Fernald, 1950; Hochstätter, 2000, 2002, 2004; Jepson, 1960; McDonald, 1973; Munz and Keck, 1968; Preston, 1961; Small, 1933; and Webber, 1953– to list a few). In these keys, however, no mention was made of the tie by which contrasting attributes are rather regularly correlated to either light or heavy seeds. And, I found no published hypotheses concerning possible functions of the features examined in this paper and the seed weights.

Some Correlations Already Reported

1. The Dehiscence or Indehiscence of Fruit as Discussed in Yucca Taxonomic "Keys"

Webber (1953) and Preston (1961) each utilized the dehiscence or indehiscence of pods as the factor in their keys intended for separating Yucca into two groups above the taxonomic level of "section." Other workers also have made that same

Table 4. Average Seed Weights and Correlations Evident for Purchased Seeds of Certain *Yucca* Species Reported in Table 1.

Species of *Yucca*	Avg. Weight per Seed (mg) ± standard deviation	d = Pods Dehiscent i = Pods Indehiscent	+ = Correlation evident (dehiscent pod with low seed weight: or indehiscent pod with high seed weight.) - = Above Correlation not evident.
Light-Seeded			
elata	22 ± 4.25 n=87	d	+
filamentosa	10 ± 2.52 n=16	d	+
glauca	21 ± 7.02 n=53	d	+
whippleii	16 ± 4.64 n=14	d	+
Heavy-Seeded			
aloifolia	51 ± 9.55 n=9	i	+
arizonica	117 ± 34 n=19	i	+
baccata	135 ± 27.8 n=9	i	+
brevifolia	52 ± 11.7 n=14	i	+

separation based on dehiscence (e.g., Cronquist et al., 1977; McKelvey, 1938; and Gentry, 1972).

Sargent (1921, p. 111) did not use dehiscence versus indehiscence or deciduous versus persistent as salient fruit criteria for keying yuccas to the proper species. Recognizing a link between dehiscence and erect fruit, however, he did mention that Y. *elata*, being "capsular," has erect fruit. But he did not state the reverse correlation of indehiscence with non-erect fruit. Patraw (1936, p. 38) reported that the pods of Y. *schottii* do not split open and that they fall off before winter, thus denoting a correlation in that one species between the indehiscent and deciduous pod traits.

2. Dehiscent Pods, Dry Capsules, Erect Pods, or Other Features Correlated

Webber (1953, pp. 16–17) noted that those species that have dehiscent pods also produce a "dry capsule, soon becoming erect." Small (1933) penned similar comments about Y. *filamentosa*. Thus dehiscence, dry fruit walls, and erect pods had been observed to coexist in yuccas many years before my 1986 paper was published. But concerning the converse choices involving indehiscence, Webber simply wrote the word "indehiscent," adding nothing about the features often associated with indehiscence (Webber, 1953, p. 16). McDougall (1973) correctly contrasted Y. *angustissima* with Y. *baccata* by stating that *angustissima* fruits are dry walled and dehiscent while those of *baccata* are "fleshy and indehiscent" (p. 103).

Benson and Darrow (1981) mentioned persistence of the capsule as being linked to the dehiscent fruit trait: "fruit drying and splitting open at maturity, the opened capsules persist on the old inflorescence through the winter" (p. 48). These authors did not indicate, however, that this pod persistence might play a functional role in wind transport of seeds.

In their corresponding key choice for indehiscent pods, Benson and Darrow (1981) correctly noted that where pods were indehiscent, the fruit was "fleshy or spongy, not splitting open, not persisting on the inflorescence through the winter" (p. 48). They did not state, however, that deciduous fruit might be part of a functional program to assist animals in the harvest and dispersal of seeds.

Irish and Irish (2000) described the relationship between the inflorescence and the leaf crown in 19 species of *Yucca*. They scored most of the dehiscent species as having the inflorescence extending above (or at least slightly above) the leaf crown. They classified most of the inflorescences of the indehiscent (heavy-seeded) species, on the other hand, as being half or more in the leaf crown, while listing some notable exceptions.

3. A Relationship of Dehiscent or Indehiscent Pods with Seed Shape

Webber (1953, p. 67) recognized the tie between the dehiscence or indehiscence of pods and the corresponding differences in the morphology of seeds (wings versus no wings, etc.) but did not report the correlation of dehiscence with the other traits enumerated here.

McDougall (1973) referred to the seeds of Y. *whippleii as* "very thin."

Table 5. Predictions and Weights of Seeds Purchased for Yucca Species Not Included in the Field Study.

Species of *Yucca*	d = Pod Dehiscent i = Pod Indehiscent[a.]	Predicted Seed Weight: l = low if pod dehiscent, h = high if pod indehiscent[b.]	Seed Weight (mg) ± standard deviation	v = prediction verified (No predictions were falsified.)
Dehiscent				
harrimaniae	d	l	13 ± 2.87 n=24	v
harrimaniae subspecies *neomexicana*	d	l	10 ± 3.85 n=24	v
pallida	d	l	4 ± 3.24 n=25	v
peninsularis	d	l	22 ± 6.24 n=23	v
rigida	d	l	9 ± 3.64 n=10	v
rostrata	d	l	10 ± 3.3 n=41	v
rupicola	d	l	7 ± 1.73 n=25	v
thomposiana	d	l	6 ± 3.17 n=25	v
Indehiscent				
australis[c.]	i	h	125 ± 18.9 n=22	v
entlichiana	i	h	39 ± 12.7 n=127	v[d.]
faxoniana	i	h	53 ± 8.53 n=16	v
filifera	i	h	57 ± 11.7 n=14	v
mixtecana	i	h	98 ± 16.9 n=10	v
perisculosa	i	h	103 ± 23.3 n=10	v
valida	i	h	57 ± 14.6 n=24	v

a. It was determined from the literature whether the pod is dehiscent or indehiscent.

b. The "prediction" as to *light* or *heavy* seed weight was made before purchasing and weighing the seeds. No information about seed weight was available in the literature.

c. Hochstätter (2004, p. 33) had Y. *australis* as synonymous with Y. *filifera*. Based on the sizeable difference between the average seed weight for these two taxa here, however, I question that conclusion.

d. Y. *entlichiana* seeds are rather light for an indehiscent species (39 mg), but they are still 17 mg heaver than Y. *peninsularis*, which is the heaviest of those with dehiscent pods.

Table 6. Field Data for the Five Dehiscent-Fruited Yucca Species Studied.

Species of *Yucca*	Altitude in Feet, if known	General Location	Associated Vegetation	Dates Observed Flowering	Dates Pods Ripe	Dates Old Pods Still Seen Present
angustissima	4500	At 680l N. Hwy. 89, Chino Valley, AZ, Yavapai Co.	Cylindropuntia spp., Platyo-puntia spp., Also grasses including ring muhley, buffalo grass, and others.	17 May 2002 26 May 2003	15 July 2003	3 Feb. 2003 18 Apr. 2005
	5300	Along I-40 about 14 mi. W of Seligman, AZ, Yavapai Co.[a.]	Grasses: various species including ring muhley. Also apache plume, pinyon pine, juniper.		15 July 2003 pods not open yet but almost.	1 Oct. 2007
	5300	Along I-40 about four mi. W of Seligman, AZ, Yavapai Co. [b.]	Utah juniper, grasses (including ring muhley), prickley poppy, apache plume, and *Playtopuntia*.			26 Aug. 2004 1 Oct. 2007
elata	2900	On east side of AZ Hwy. 71, 1.7 mi. S of interchange with Hwy. 93, 24 mi. NW of Wickenberg, AZ., Yavapai Co.	*Cylindropuntia*, mesquite, creosote bush, ironwood, and other desert shrubs.	26 May 2003	15 July 2003 4 Aug. 2003	4 Feb. 2003 25 Mar. 2002 19 Apr. 2005 26 Aug. 2004 1 Oct. 2007
	4850	Along AZ Hwy. 82 eastbound, 0.75 mi. E of interchange with Hwy. 83, Sonoita, AZ., Santa Cruz Co.	Grassland with sotol, catclaw acacia, agave, mesquite, and sunflower.	17 June 2002	15 July 2003	25 Mar. 2002 26 Aug. 2004 2 Oct. 2007
	4500	In a yard at Sierra Vista, AZ., Cochise Co.	In gravel surface along with saguaro and other cultivated desert plants.	15 May–7 June 2002		4 Aug. 2003 9 Aug. 2002
filamentosa		A business, Harrison Pike, Cincinnati, OH, Hamilton Co.	Planted at entrance of a business establishment.	25 June 2003		
		At a business, Brice Rd., Columbus, OH, Franklin Co.	Planted specimen in business parking lot.	10 June 2003		
		Near Newkirk, OK, Kay Co.	In yard of a farm.	11 June 2004		26 Sept. 2004
		South Shore Dr., Surf City, NC, New Janover Co.	In vacant lot, one block west of the ocean.			15 Feb. 2003

Table 6 (continued)

glauca		Frontage lane N of westbound I-20, mi 170, W of Big Spring, TX, Howard Co. [c]	Farms and grassland.			18 Sept. 2002
		I-40, westbound, mi 126, roadside, NM, Valencia Co.	High desert.	13 June 2004	13 June 2004	
whipplei	2900	Escondido Canyon Rd. from CA Hwy. 14, Acton, CA, Los Angeles Co.[d]	Mixture of chaparral and Mohave Desert plants: California juniper, bladderpod, false buckwheat, Platyopuntia, Mormon tea,	18 Apr. 2005 18 May 2002		
	1380	Chaparral woodland across from 23544 Maple St., Santa Clarita, CA, Los Angeles Co.	Chaparral: greasewood, purple sage, white sage, California sagebrush, California coast live oak, horehound.		29 July 2004	15 Aug. 2004 1 Nov. 2007

a. Right shoulder of eastbound I-40, miles 105.8–107.
b. Right shoulder of eastbound I-40, miles 114.5–116.
c. Other locations where *Y. glauca* was studied include I-10, mile 73 off-ramp, near Fort Hancock, TX., Hudspeth Co.; N of Woodland Park, CO, Teller Co.; and along US Hwy 24 near Manitou Springs, CO, El Paso Co.
d. Go 0.2 miles SE on Escondido Canyon Road, then hike N of road into mixed desert-chaparral woodland.[c]

McKelvey (1947) also recognized that seeds in the dehiscent [capsular] species of *Yucca* are relatively thin: "seed in the capsular species is thinner than in the baccate" (p. 12). But McKelvey did not speculate on possible seed-dispersal roles that this relationship between dehiscent pods and thin seeds might play.

Modes of Pod Dehiscence and the Differentiation between Yucca Sections

Sargent (1921, p. 111) noted that the dehiscence of *Y. elata* fruit involves its splitting open on a line between the carpels (also called "locules"), in a manner known as "septicidal dehiscence." In a capsule having "loculicidal" dehiscence, however, the splitting occurs *within* each carpel, so that the locule is itself cleaved open in the middle (Figures 2 and 3). Using this contrast, Webber (1953) placed *Y. whipplei* into its own taxonomic section (Hesperoyucca) because its pods ordinarily undergo loculicidal dehiscence. Pods of all the other dehiscent-fruited species (section Chaenocarpa) generally split in a septicidal manner—"capsule commonly septicidally…dehiscent" (Webber, 1953, p. 16)—and were accordingly all placed into a different section: Chaenocarpa. But Webber (1953) also qualified this statement about members of the Chaenocarpa by noting that some of them dehisce both ways, being "occasionally septicidally and loculicidally dehiscent" (p. 16).

In the key of his first yucca book, Hochstätter (2000, p. 13) used this dehiscence distinction to separate *whipplei* from the other dehiscent-fruited yuccas. By the time he wrote his third volume in 2004, however, he no longer proposed it as a criterion. In that third book (Hochstätter, 2004), he separated Hesperoyucca from Chaenocarpa by means of inflorescence length and other inflorescence traits, without any reference in the key to the mode of pod dehiscence.

Figure 8. Pods and seeds on ground under a Y. *shidigera* plant, Kelbaker Road, Mohave National Preserve, CA, 15 July 2003. The Y. *shidigera* pod (lower center) is deciduous, does not split open (indehiscent), and has heavy seeds. These and other characteristics putatively prepare the plant for animal seed transport. Marks caused by the gnawing of animals can be seen on this fruit.

The Very Short Scape of *Y. shidigera*

McKelvey (1938) reported that the scape of Y. *shidigera* can be as long as the rest of the inflorescence: "scape 15 cm. in length or at times as long as inflorescence proper" (p. 92). Table 1 shows that the Y. *shidigera* inflorescence protrudes above the leaves only 17 cm on average. Figure 10 shows a Y. *shidigera* with its entire inflorescence surrounded by leaves of the crown. Furthermore, the length of the scape on the *shidigera* plants that I measured (near Barstow, CA and at the Mohave National Preserve) was usually zero—no scape at all (Table 2). This suggests that Y. *shidigera* fits the pattern for a heavy-seeded species quite well. My observations conflict, however, with those of McKelvey (1938) and this warrants additional analysis.

A Taxonomic Suggestion

Pod dehiscence or indehiscence is presently considered to be a salient taxonomic trait that has long been used to divide the genus into two great but unnamed groups (Hochstätter, 2000). It would be reasonable and useful therefore to establish names for these two taxa. Perhaps they should have the category designation of subgenera, beneath the level of genus but above the level of section.

One proposed subgenus has dehiscent fruit and thus includes all the species in the sections Hesperoyucca and Chaenocarpa, which putatively bear light seeds. If it is found that the rest of the species in Chaenocarpa not weighed here do in fact have light seeds, this subgenus could be called Oligosperma (Greek: light seeds). The other subgenus would then contain the heavy-seeded (indehiscent) yuccas and might be called Barysperma (Greek: heavy seeds)—if the rest of its species are found to have relatively heavy seeds. The subgenus Barysperma would contain the sections Yucca and Clistocarpa.

Obvious Exceptions to the Correlated Features

1. Not All Heavy-Seeded Species Have Short Inflorescences

Recognized exceptions to the correlated traits can be seen in the tables. *Y. torreyi*, *aloifolia*, and *Y. arizonica* are heavy-seeded species, but they have unusually long inflorescences. I found nothing in the literature about the seed weight of *Y. gloriosa*, but it probably has heavy seeds too. Along with *Y. torreyi* and *Y. aloifolia*, *Y. gloriosa* has a long inflorescence, while most yucca species (having heavy seeds) produce short inflorescences in which the fruit is borne either in the leaf crown or not very high above it (see Figure 10). The associations in the heavy-seeded species are "often" (but not always) present and trait 5' (short inflorescence) is not characteristic of a few of the heavy-seeded species.

2. The Short Inflorescence of *Y. glauca*, a Light-Seeded Species

Fernald (1950) wrote concerning *Y. glauca* that leaf tips are almost as high as the peduncle (flower stalk), with "peduncle little overtopping the leaves" (p. 438). This means that the flower stalk is almost entirely surrounded by the leaf crown. The data in Table 2 of this paper shows that *Y. glauca* inflorescences protrude only 40 cm above the leaf tips, whereas the average distance of such protrusion for the inflorescence of dehiscent species was 111 cm. But even though *Y. glauca* inflorescences are relatively short, they are taller than what Fernald described, an apparent discrepancy that deserves further investigation.

3. The Unusually Dry Fruit Walls of Two Indehiscent Species

Since *Y. brevifolia* has heavy seeds, it ought to likewise have a thick, fleshy fruit wall, not a dry one. The wall of *Y. brevifolia*, however, is dry and thus resembles the fruit wall of the dehiscent yucca species (McKelvey, 1938, p. 92). Nonetheless, the *Y. brevifolia* fruit wall is thick and spongy on maturity, not thin, so it is unlike the thin fruit wall of the dehiscent yuccas. Based on this dryness of its ovary wall and on other traits, *Y. brevifolia* has been separated into its own taxonomic section (Clistocarpa), while all the other indehiscent yuccas are put into a different section, now called "Yucca."

Y. gloriosa also has indehiscent fruit and accordingly should have a fleshy fruit as well. But Preston (1948, p. 369) wrote that the fruit of *gloriosa* has "thin dry flesh." Bailey (1939, p. 353) also classified the fruit wall of *gloriosa* as being "dry." But all the other indehiscent yucca species (except *brevifolia*) have fleshy fruit. Thus, both *Y. gloriosa* and *Y. brevifolia* have fruit walls that are exceptionally dry for indehiscent *Yucca* species.

(continues, p. 172)

Figure 9. A possible animal burrow near a Y. *brevifolia* plant, Pearblossom, CA. Fallen pods can be transported readily by animals such as pack rats.

Table 7. Field Data for the Eight Indehiscent Yucca Species Studied.

Species of *Yucca*	Altitude (Feet) if known	General Location	Associated Vegetation	Dates Observed Flowering	Dates Pods Ripe	Dates Pods Falling	Dates Pods All Gone
aloifolia	unknown	In a yard on MS Hwy 588, several mi. W of Ellisville, MS, Jones Co	These were possibly native or else planted, among pine trees	2 May 2002	13 Feb. 2002 (pods from 2001 season)		
	unknown	Lawn along NC Hwy. 17 near Jacksonville, NC, Onslow Co.	Probably planted	14 June 2002			
	unknown	Near 38th and Ocean Blvds., Myrtle Beach, SC, Horry Co	In yards and pine woodlots close to Atlantic Ocean with *Y. gloriosa*		15 Feb. 2002 (from 2001 season)		
	unknown	In a front yard facing beach, S. Shore Dr., Surf City, NC, Janover Co	Close to Atlantic Ocean with *Y. gloriosa* and *filamentosa*		15 Feb. 2002 (from 2001 season)		
arizonica	3950	E side of AZ Hwy 82, 150 yds S of N Royal Rd & 0.1 mi S of "3 mi" sign, Nogales, AZ, Santa Cruz Co	prickley poppy, coachwhip, catclaw acacia, sotol, oak-mesquite-grassland	19 April 2005 21 April 2002 27 April 2002	3 August 2003	20 Oct 2007	
	3900	E side of AZ Hwy 82, 0.4 mi N of "9 mi" sign, E of guard rail. From 10.8 to 11.2 mi on E shoulder, Nogales AZ, Santa Cruz Co	*Y. schottii*, mesquite, grasses, *Agave sp.*, oak,prickley poppy, sotol	late April 2002	3 August 2003 late pod stage		
baccata	4200	99 mi E of Barstow (44 mi west of Needles, CA). Go N and W on Essex Rd from I-40 to Black Canyon Rd, then N 10 mi to Hole-in-the-Wall Campground, Mohave National Preserve, San Bernardino Co	holly grape, cholla, cat claw acacia, snakeweed, *Y. shidigera*, ironwood, mormon tea, pencil cactus	9 April 2003 25 April 2003 1 May 2002	25 May 2003	1 Oct 2007	

Table 7 (continued)

baccata (continued)	4040	6 mi E of Kingman AZ, DW Ranch Rd 0.2 mi S of I-40 parking area W side of rd. Grove is 360' S on dirt rd., Mohave Co	desert grasses, shrubs, *Cylindropuntia spp.*, palo verde, cat claw acacia, snakeweed, holly grape	9 April 2003 18 April 2005 25 April 2003	26 May 2003	14 July 2003	4 Aug 2003 26 Aug 2004 1 Oct 2007 1 Dec 2001 12 Jan 2002
	unknown	S of Congress AZ on AZ Hwy 89, 2 mi N of "271 mi" sign	creosote bush, ironwood, *Platyopuntia spp.*, *Cylindropuntia spp.*	19 April 2005	19 April 2005		
brevifolia	2940	Intersection of Pearblossom Hwy and Sierra Hwy, grove 150' NEE of traffic light and extending E for 300', Palmdale, CA, Los Angeles Co	Mohave desert flora: California juniper, *Platyopuntia spp.*, *Y. whippleii*, fiddleneck, gold fields, filaree, California goldenbush and California poppy	9 April 2003 18 April 2005	9 April 2003 18 April 2005 25 April 2003 25 May 2003	25 May 2003 14 July 2003 24 Aug 2004	14 July 2003 30 Sept 2007
	3040	along N side CA Hwy 138 (Pearblossom Hwy), 180' W of 123rd St E, Pearblossom, CA, Los Angeles Co	a single *Y. brevifolia* several feet N of roadway with others nearby, creosote bush	9 April 2003	9 April 2003 25 April 2003 25 May 2003	25 May 2003	14 July 2003 5 Aug 2003 30 Sept 2007
	3380	Both sides CA Hwy 138, E of intersection of Hwy 138 with CA Hwy 18, both Los Angeles Co and San Bernardino Co, CA[a.]	creosote bush, four-winged salt bush, gold fields, filaree, CA juniper, CA goldenbush, fiddleneck	7 March 2005 (early onset of flowering			30 Sept 2007 (a few pods) 1 Dec 2001 (just a few pods left) 28 Jan 2003 1 Feb 2003 (a few pods left)
gloriosa	1195	24773 Valley St., Newhall, CA, Los Angeles Co	Two planted specimens on a lot now used for business. Other planted specimens in Los Angeles bloom either in May or September.	1 May 2004, 14 May 2007, and Sept 2007 (first two weeks)	No fruit has ever been seen to "set" here, even with artificial pollination		

(continues on next page)

Table 7 (continued)

Species of *Yucca*	Altitude (Feet) if known	General Location	Associated Vegetation	Dates Observed Flowering	Dates Pods Ripe	Dates Pods Falling	Dates Pods All Gone
gloriosa (continued)	sea level	Myrtle Beach, SC, Horry Co; Clermont Shores MS, Hancock Co; Surf City NC, New Janover Co	In NC and SC growing in beach sand of yards adjacent to houses. In MS near sea level, small woodlot of pines and oaks, 0.5 mi from Gulf of Mexico	These locations were visited in Feb, 2003; no plants seen flowering	No lingering fruit observed on *gloriosa* at any of these locations, Feb, 2003		
schottii	3900	E side AZ Hwy 82, 0.4 mi N of "9 mi" sign, E of a guard rail; 10.8-11.2 mi many on E shoulder AZ Hwy 82, Santa Cruz Co	with Y. *arizonica*, mesquite, century plant, oak, prickley poppy, cat claw acacia	18 July 2002 4 Aug 2003	4 Aug 2003		2 Oct 2007
	4050	Patagonia AZ, Santa Cruz Co	in Patagonia city park with elderberry, ash, and several large mesquite	4 Aug 2003	4 Aug 2003		2 Oct 2007
	5280	Coronado National Memorial. AZ Hwy 92 to CNM entrance rd. CNM entrance rd about 5 mi [b]	sycamore, oak, sotol, century plant, mesquite, pine	15 July 2003 18 July 2002 25 July 2003 29 July 2003 19 Aug 2003	18 July 2002 9 Aug 2002 12 Aug 2002 19 Aug 2003 23 Aug 2002	9 Aug 2002 23 Aug 2002	14 Sept 2002 11 Oct 2002 (just a few pods left) 20 Oct 2007
shidigera	2950	15 miles N of Victorville, CA, San Bernardino Co, I-15. Take Wild Wash Rd east to an unmarked rd. on which go S. At end of pavement, hike or drive 1 mi S and then hike W onto ridge separating unmarked rd from I-15, 900' E of I-15	Clocks, creosote bush, fiddleneck	9 April 2003 18 April 2005	18 April 2005 25 May 2003	14 July 2003 (many pods on ground, gnawed) 8 Aug 2003 (some still attached, most fallen)	30 Sept 2007

Table 7 (continued)

shidigera (continued)	3100	I-40 about 65 mi W of Needles, CA, San Bernardino Co. Go 0.7 mi NE on Kelbaker Rd. Hike 380' N into Mohave National Preserve	Grove of over 100 Y. *shidigera* with *Eriogonum inflatum*, creosote bush, Mormon tea, and other desert shrubs	9 April 2003 18 April 2005	18 April 2005		
torreyi	4700	Eastbound I-10, east of El Paso, TX, Hudspeth Co					
	4220	Van Horn, TX, near Pilot Travel Center, Culbertson Co					
	unknown	Rest stop along I-10 westbound, at about mi 138, west of Van Horn, TX, Culbertson Co					19 Sept 2002
	4440	I-10 west of Kent TX, mi 175, Culbertson Co					
	unknown	I-20 mi 3, TX, Reeves Co		11 Feb 2002			

a. One very large Y. *brevifolia* near NW corner at intersection of Verbena St and Hwy 138, Victorville, CA, San Bernardino Co, was also studied. It is 18 mi E of the 138 intersection with Hwy 18. 3150' altitude.

b. Other Y. *schottii* study locations: 6000' summit on AZ Hwy 90, N of Bisbee AZ, Cochise Co; 5200' on AZ Hwy 186 in Chiricahua National Forest, where Y. *schottii* grows with pine trees and alligator juniper; various locations along a road going into the Chiracahua Mountains from Portal AZ, west of the ranger station—growing at 5660' with ponderosa pine, oak, sycamore, mountain mahogany, and alligator juniper, as well as up to 7400' at Onion Saddle where *schottii*grows with white fir, Douglas fir, and ponderosa pine. All pods were gone at these locations 25 March 2002.

Figure 10. Y. *shidigera* (commonly called the Mohave yucca) growing near the Wild Wash Road exit of I-15 near Barstow, CA, 25 May 2003. Like many other species of heavy-seeded yuccas, the inflorescence of Y. *shidigera* can be completely surrounded by the crown of large leaves as seen here. This attribute may be part of a "package" aimed at assisting animals in the harvest and distribution of seeds.

4. The Peculiar Splitting of an Indehiscent Fruit in *Y. aloifolia*

Elias (1980, p. 908) remarked that the fleshy purple fruit of Y. *aloifolia* possesses these two attributes: (1) the ripe pod does not drop off the inflorescence and, yet it (2) sheds its seeds while the pod is still attached to the plant. Elias (1980) supplied no further details regarding these events, which are different from the usual dehiscence of pods of the heavy-seeded yuccas. I examined the Y. *aloifolias* in Mississippi twice and found that their fruit was indeed indehiscent. I was unable to examine these plants later, however, to determine whether or not the pods split open, distributing the seeds while the pods are still attached to the inflorescence.

Current Reproduction by Seeds in Western Yuccas

Yucca plants carry out vegetative reproduction horizontally, but they also produce generous quantities of seeds. Reproduction by seeds in the southwestern United States, however, is probably not as prevalent now as it was hundreds of years ago. It is generally believed that in the past there was greater humidity in western yucca habitats. Hochstätter (2000) indicated that yucca reproduction by seed in the wild is presently quite restrained, "suggesting that current climatic conditions are less than favorable" (p. 13).

Webber (1953) wrote about reproduction by seedlings, "although the southwestern yuccas produce an abundance of viable seed, reproduction by seed is very limited" (p. 71). Webber tabulated all the seedlings he could find for 21 yucca species over a period of four years and noted that the numbers were very small, even zero for some of

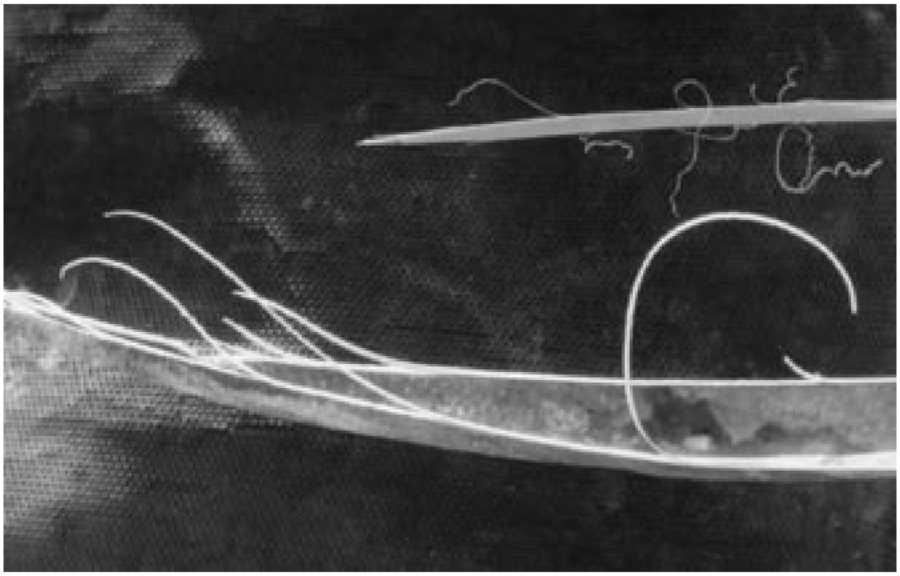

Figure 11. Leaves of Y. *shidigera* (below) and Y. *angustissima* (wisely called the narrow-leaved yucca) above. These fibers threading away from a leaf margin may be wide as in Y. *shidigera* (below) or narrow—Y. *angustissima* (right). Leaf margin characteristics appear in parallel fashion among various indehiscent and dehiscent (heavy-seeded or light-seeded) yuccas with little or no clue concerning phylogeny. Vegetative attributes such as these are not correlated to the two seed-distribution "packages" of traits. This lack of correlation for some traits coupled with correlation for seed-dispersal traits creates a problem for evolution theory.

the species. He attributed this decline in reproduction by seeds and seedlings to three factors: meager and irregular rainfall, slow growth, and rodent damage. Campbell and Keller (1932) found that reproduction by seeds in Y. *elata* is quite limited because "few seedlings become established, and their growth is extremely slow" (p. 371), which was caused, in their opinion, by the limited growth of seedling root systems. The growth rate they reported for Y. *elata* seedlings was one inch per year (Campbell and Keller, 1932, p. 373.)

The origins model that includes a global flood indicates that the drying of the western yucca habitats is one of the continual changes in climate that have been occurring for centuries following the Flood of Noah. The numerous scientific papers discussing this possible post-Flood climatic shift include Williams et al. (1992). In any case, the seed-distributing mechanisms of the yuccas were likely of greater importance back when the southwestern U.S. was more mesic and favorable to seed germination and the establishment of yucca seedlings.

Wind Distribution of Yucca Seeds in the Literature

The only reference I found to yucca seeds being carried by wind was in Campbell and Keller (1932), concerning Y. *elata*: "The seeds are light and well disseminated by wind when the pods open during the late summer and autumn" (p. 371). Having written this, however, they did not mention any of the other factors that may work together with light seeds to make wind distribution feasible for members of what I am calling the subgenus Oligosperma.

Literature Citations on the Possible Distribution of Yucca Seeds by Animals

I found only three comments regarding animals interacting with yucca plants. Concerning Y. *shidigera*, Jaeger (1940) reported that "pack rats often gnaw off the bitter outer covering of the fruit, which is rich in sugar" (p. 19). Baerg (1973) asserted that Y. *brevifolia* is "food for various desert animals, chief of which is probably the pack rat" (p. 61). Regarding the soft, fleshy fruit of Y. *aloifolia*, Elias (1980) commented that it is bitter and is "not favored by wildlife" (p. 907). On several occasions, during daylight hours and from secluded locations near Y. *baccata* plants bearing ripe pods, I monitored the plants but did not observe any animals harvesting the pods. Figure 8 shows marks of chewing on fruit of Y. *shidigera*, possibly made by pack rats. The holes and burrows of animals are frequently found near individual Y. *brevifolia* plants (see Figure 9).

A Major Scientific Problem Facing the Origin of *Yucca* Species by Evolution

As shown in the "Results" section, traits involved with seed dispersal are well correlated with each other (Tables 1, 2, 4, and 5), whereas vegetative characteristics (Table 3) are neither correlated with the dispersal features nor correlated among themselves in the *Yucca* species. This intermingling of six well-correlated seed-dispersal features with more than six vegetative traits that are uncorrelated is antithetical to patterns expected to arise from neo-Darwinian evolution. If one phylogeny were proposed on the basis of the vegetational and ecological traits (Table 3, 6, and 7) while another were based on the seed dispersal features (Tables 1, 2, 4, and 5), two very different and highly speculative schemes of "relatedness" or "descent" would emerge.

This contrasting coexistence of features correlated to seed dispersal and other uncorrelated characteristics suggests that the distribution of traits in the *Yucca* species has had little to do with the natural selection of gene mutations and much to do with conscious control. I discussed this evolutionary puzzle previously:

> The present three yucca groups (or the four groups of Benson and Darrow) do not submit easily to an evolutionary scheme of development. There is not . . . a coherent and phylogenetic distribution of traits in these three groups but instead, a series of embarrassing parallelisms between members of different groups (Howe, 1986, p. 13).

Correlation of traits related to seed dispersal and the simultaneous lack of correlation for other traits fits well with the idea that a plan for efficient seed distribution was executed during the origin of the yucca species.

Research Possibilities

A careful analysis of fruit and seed characteristics should be made for Y. *gloriosa*. Further study should be undertaken concerning a possible bi-seasonal (spring and fall) flowering for Y. *gloriosa*, as I observed in California (Table 7). Studies also should be made to determine what factors cause fruit production to be scarce in Y. *gloriosa* (Sargent, 1921).

Knowledge of the feeding habits of various animals on yucca fruits could be obtained by using surveillance cameras at night when the pods are ripe. A study might be made on what effect (if any) the presence of the so-called "wings" or "marginal rims" has on wind-transport of yucca seeds. Yet another area of research would be to test the aerodynamic properties of both light and heavy yucca seeds.

Additional Predictions

Based on the existing associations of characteristics, more predictions are possible and can be evaluated in later yucca analyses. The hypotheses allow the following prediction for the yuccas not yet studied:

1. Those species bearing dehiscent pods will be found to have relatively light seeds.
2. Species with light seeds and dehiscent fruit will likewise manifest the four other accompanying features.
3. Species bearing indehiscent pods will possess heavy seeds.
4. They will usually possess the other four features correlated with indehiscent fruit and heavy seeds.

As the remainder of the 49 species and 24 subspecies of *Yucca* are studied, it will become clear how strongly these four predications will be supported.

Conclusion

There is a consistent correlation of certain morphological traits with seed weight in yuccas. It is proposed that these coordinated features foster seed transport by two distinct means—wind and animals. I am unaware of such a correlation being previously reported. This pair of dispersal systems illustrates a skillful origin carried out by the Creator, showing distinct features of design even at the inter-species taxonomic level.

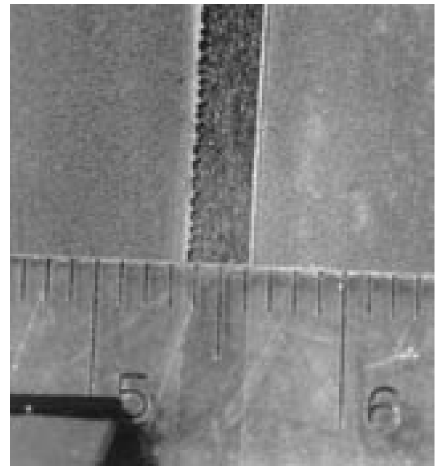

Figure 12. Close-up photograph of yucca leaf margins—serrated margin of *Yucca aloifolia* on the left and smooth leaf margin of Y. *gloriosa* on the right. A millimeter ruler is below both leaves. Smooth, serrated, and fibrous margins; wide or narrow leaves; curved or flat leaves; green versus blue-green overall leaf color, mountainous or desert habitat, and many other vegetative attributes are found distributed here and there, throughout the four yucca sections in rather parallel fashion. This provides very few phylogenetic evidences for building a "tree" of evolutionary descent among yucca species. On the other hand, the seed-dispersal traits are in consistent "packages" that suggest purposeful programming in origins.

Appendix I. Comparisons between nine southwestern species of yucca according to 11 contrasting traits (from Howe, 1986).

Species Characteristics	*angustissima*	*arizonica*	*baccata*	*brevifolia*	*elata*	*glauca*	*shidigera*	*schottii*	*whipplei*
1. Leaf margin	fibers	a few fibers	fibers	serrations	fibers	fibers	fibers	no fibers no serrations	serrations
2. Leaf width* in mm± S.D.	narrow 4.2 ± 1.80 n=10	narrow	Broad 22.3 ± 3.25 n=22	narrow 9.7 ± 1.17 n=20	narrow	narrow	broad 29.2 ± 3.74 n=10	broad	narrow
3. Leaf color	blue-green	——— **	blue-green	blue-green	yellow-green	———	yellow-green	yellow-green	blue-green
4. Leaf cross section plano or concavo convex	plano	concavo	concavo	plano	plano	plano	concavo	concavo	plano
5. Trunk	absent	erect but obscurely so	procumbent	erect	erect	absent	erect	erect	absent (under-ground)
6. Inflorescence character	raceme	panicle	panicle	panicle	panicle	raceme	panicle	panicle	panicle
7. Inflorescence length	long	long	short	short	long	long	indeterminate	indeterminate	long
8. Fruit stance	erect	not erect	not erect	not erect	erect	erect	not erect	not erect	erect
9. Fruit splitting?	dehiscent	indehiscent	indehiscent	indehiscent	dehiscent	dehiscent	indehiscent	indehiscent	dehiscent
10. Fruit fall?	persistent***	deciduous****	deciduous	deciduous	persistent	persistent	deciduous	deciduous	persistent
11. Altitude and ecological associations	high with pinyon pine and juniper	low 2000–4000 feet	high with pinyon pine and juniper	low with creosote bushes	low with creosote bushes	high with pinyon pine and juniper	low with creosote bushes	high with oak woodland	low with chaparral

* A mean followed by the standard deviation (in millimeters) is given for each of two typically "narrow leaved" species and two "broad leaved" species. n is the number of leaf width measurements taken.

** A blank line indicates that field and/or library data were not available.

*** In the 1986 paper this said "deciduous"—an error. Needs to read "persistent."

**** Left blank in the 1986 paper—now known to be "deciduous."

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Glossary

abcission (n): the falling off of a piece or organ of a plant, such as a seed pod.

abcise (v): to fall off of a plant, e.g., a seed pod.

baccate (adj): fleshy, indehiscent, deciduous, like the pods of Y. *baccata.*

carpel (n): one of the sections of a compound fruit or ovary.

capsule (n): a dry yucca fruit like that of Y. *whippleii.*

capsular (adj): like a capsule—dry.

category (n): any of the levels in the hierarchy of classification—e.g., family, genus, etc.

Chaenocarpa (n): one of the taxonomic "sections" in the genus *Yucca.*

Clistocarpa (n): one of the taxonomic "sections" in the genus *Yucca.*

crown (n): the circle of leaves at the top of a yucca stem.

crown height (n): the distance from ground level up to the crown of a yucca plant.

deciduous (adj): a plant organ (e.g., leaf or pod) that is prone to falling off the plant.

dehisce (v): to split open, as some pods are able to dehisce.

dehiscence (n): a splitting open of an organ—e.g., a pod.

dehiscent (adj): prone to splitting open—e.g., a pod of Y. *filamentosa.*

evolution (n): the descent of all taxa from a common ancestry by mutation, natural selection, and other natural processes.

fibrous (adj): having slender fibers attached as in a fibrous leaf margin.

Hesperoyucca (n): one of the four taxonomic "sections" in the *Yucca* genus.

indehiscent (adj): not prone to splitting open as a pod of Y. *schottii.*

indehiscence (n): the quality of not splitting open.

inflorescence (n): a stalk bearing flowers and ultimately fruit.

key (n): a series of paired choices useful in identifying a living organism.

leaf crown (n): a circle of leaves atop a yucca stem.

locule (n): a carpel or cavity of a compound ovary.

loculicidal (adj): given to splitting open in a carpel in the middle.

loculicidally (adv): refers to the splitting open of a carpel in its center.

morphology (n): the form of an organ—here, of a plant organ such as a leaf or fruit.

non-deciduous (adj): not prone to falling off the plant—e.g., pods of Y. *elata.*

numerical taxonomy (n): a mathematical classification evaluating the many similarities and differences existing between the various groups involved.

peduncle (n): an inflorescence, or flower stalk.

persistence (n): the quality of remaining on the flower stalk, not falling off.

persistent (adj): not falling off the flower stalk, remaining attached.

phenological (adj): pertaining to events occurring on an annual, seasonal basis.

phylogenetic (adj): related to a supposed long-term descent from common ancestry.

pod (n): a fruit; ripened ovary.

scape (n): a lower section of an inflorescence bearing no flowers.

section (n): a category level in plant taxonomy below a subgenus and above a series.

septicidal (adj): at the edge of a carpel, along the line where two carpels of a compound ovary meet, as in septicidal dehiscence of a pod.

septicidally (adv): in such a way that it occurs at the juncture between two carpels.

serrated (adj): having a saw-toothed character, as in serrated leaf margin

standard deviation: (abbreviation = S.D.)

$$s = \sqrt{\frac{\sum (x-\bar{x})^2}{n}}$$

standard error of the sample mean: (abbreviation = S.E.)

$$se = \frac{s}{\sqrt{n}}$$

subgenus (pl. *subgenera*) (n): a taxonomic category level above a section and below a genus.

subspecies (n): a taxonomic category level below that of a species.

suture (n): a line along which a dehiscent pod may split.

taxon (pl. *taxa*) (n): any particular group in the taxonomic system, such as Chaenocarpa (a particular section in the genus yucca) or *filamentosa* (a particular species in genus *Yucca)*.

taxonomic (adj): having to do with the science of taxonomy.

taxonomy (n): the science of classifying and naming living organisms.

Yucca (n): one of the four sections in the genus *Yucca*.

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