



The Biogeography of The Joshua Tree (*Yucca brevifolia*)¹

By Graeme Somerville,

We continued across in a southerly direction across the plain, to which as well as to all the country so far as we could see, the Yucca trees gave a strange and singular appearance.

John Charles Fremont 1844

Introduction

The Joshua tree is one of the most easily recognizable trees in the Southwest of North America. With its striking shapes, the Joshua tree is a very visible life form in what is often seen as a lifeless, barren landscape. Indeed, it is often the largest living thing around with perhaps the exception of Juniper (g. juniperus var.) and Pinyon Pine (Pinus monophylla) (Bakker 1971). When seen first hand they seem to possess a sublime presence and sense of human morphology² no more so than when visited on a summer evening or when the trees are cloaked in a winter snow. In fact, according to both Bakker (1971) and Royo (1997), the Joshua tree is said to have got its name from the Mormons who likened it to the prophet Joshua with arms aloft, waving.

Distribution

Yucca brevifolia is endemic³ to the Mojave Desert. The Mojave Desert ecosystem encompasses parts of California, Utah, Arizona and Nevada and is typically referred to as a 'high' desert. This ecosystem is the transition zone between the Great Basin to the North and the Sonoran desert to the South. On its western edge it is bordered by the San Bernardino Mountains and Tehachapi's and on its eastern flank it crosses the Colorado River into Arizona. This area encompasses the remarkable topography of Death Valley, Grand Canyon, Joshua Tree National Park and the Mojave National Preserve and is approximately 75,000 sq. miles with an elevation range from below sea level to around 11,000 ft.

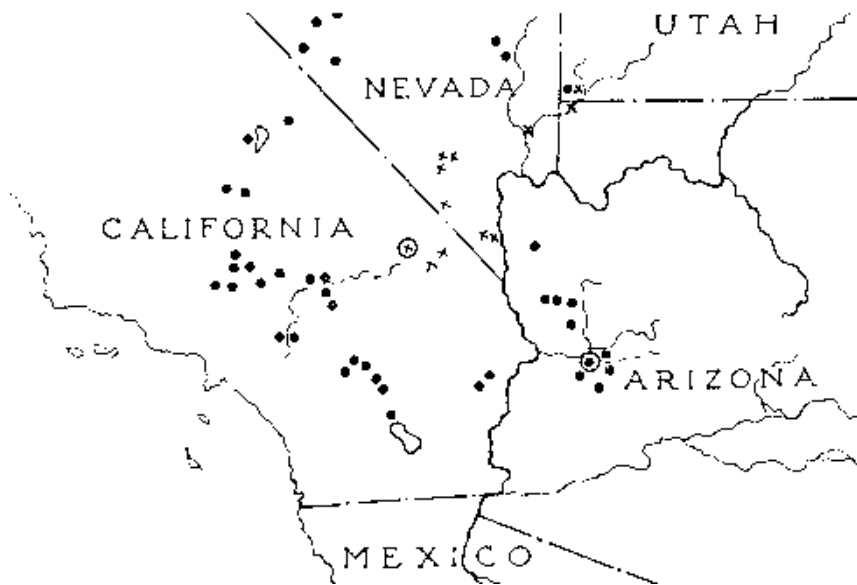
The distribution of the Joshua tree is confined solely to the 'higher' elevations. Most sources confine the distribution from 2000 ft to 6000 ft (Gossard 1992, Jepson 1922, McKelvey 1938) but others such as Sargent (1890) expand this range up to 7300 ft. George (1998), explains that within these elevation ranges populations are scattered throughout the Mojave in discrete and disjunct stands. This implies that perhaps the present population is only a remnant of what once was a larger population. The Fire Effects Information System (FEIS 1996) revealed that in the Southwestern edge of the Joshua tree ecosystem "It [the Joshua tree] reaches its greatest abundance in the vicinity of Joshua Tree National Park, California." The report continues to tell us that this western fringe is primarily made up of the variety Yucca brevifolia herbetti, with the eastern flank predominantly the species variety, Yucca brevifolia jaegeriana.

¹ Adapted from: <http://bss.sfsu.edu/geog/bholzman/courses/fall99projects/yucca.htm>

² The form or shape of, in this case, similar in shape to a human.

³ Used to describe a species of organism that is confined to a particular geographical region.

Distribution of Yucca brevifolia. (McKelvey 1938)



Ranges of Yucca brevifolia (•) and variety Jaegerianna (x)

Climate & Topography

The factors affecting the distribution of Joshua trees today are still largely unknown (George 1998). Recent paleontologic⁴ studies have shown that the distribution of this organism have changed and indicates that around 30,000 BP⁵ the Joshua tree existed 225 miles further south than present day, and at elevations 600-900 ft. below present ones (George 1998). One can speculate that the Mojave Desert was a wetter, cooler place 30,000 years ago, allowing this type of southerly and attitudinally descending migration. In fact Keith (1998) and Baker (1986) both speculate that climatic conditions have affected the distribution of Yucca brevifolia.

Climate data provided by the National Weather Service (NWS 1999) shows an ecosystem of incredible variation. During the winter months the temperature can fall to 0-10+ F° at night with winter highs usually in the 60's. In contrast, the summer highs can warm up over 115+/- F° without dropping much below 70° F at night (NWS 1999). Precipitation is elusive for most of the year. When it does arrive it can fall as either summer rain in convective thunderstorms or winter snow or rain depending on elevation. The rainfall averages anywhere from 2-10 inches depending on the location (NWS 1999).

Limiting Factors

In arid regions such as these one of the limiting factors effecting distribution of vegetation is the ability of the soil to hold moisture (Thornthwaite and Mather 1931). Thornthwaite and Mather go on to remark that soil moisture deficiency provides "indices of humidity and moisture that can be directly correlated to the distribution of vegetation." In Royo (1997), his explanation verifies this is the case with Y. brevifolia, but in a way that might not be expected. The Joshua tree prefers well draining soils such as those found on the "plains, slopes and mesa's" of the Mojave rather than in areas where water retention is greater. In these areas where the soil has poor drainage, Royo (1997) tells us "other desert plant communities often replace Yucca brevifolia."

⁴ paleontologic~ having to do with the study of life in prehistoric times by using fossil evidence.

⁵ BP ~ years **B**efore the **P**resent

Natural History

Dr. George A Engelmann first studied the Joshua tree in 1871 as part of the King Botanical Report (Sargent 1890). The natural history of the tree is one full of paradox, mistaken identity and intrigue. For instance, according to Gossard (1992) *Yucca brevifolia* has many of the attributes of a tree with branches and a trunk, flowers and fruit but it does not fit into either a coniferous or deciduous variety. Furthermore, Gossard (1992) explains that laypeople often mistake it for a cactus and even the botanists have had the family misclassified until only recently. The natural history of *Y. brevifolia* also involves some very intriguing relationships with desert fauna⁶, especially, with a small white moth. The tree has also been utilized periodically by humans.

Taxonomic Classification

The classification of the Joshua tree was originally thought to be part of the lily family Lilaceae (Riley 1892, Jepson 1922, Sargent 1890, Bakker 1971). It was classified thus because of the fact that it can only produce seeds after pollination and does not have tree rings but rather a "spongy growth" similar to a lily (Gossard 1992). The consensus now is that it is a member of the Agave family Agavaceae (Gossard 1992, Stricklin 1989, Rasmusson et al 1994, Petrides 1998). However I did notice that it is still occasionally cited as Lilaceae in some contemporary articles.

Kingdom ~ Plantae

Division ~ Magnoliophyta

Class ~ Liliopsida

Order ~ Liliales

Family ~ Agavaceae

Genus ~ *Yucca*

Species ~ *Y. brevifolia* var. *herbetti*

jaegeriana

brevifolia

Description

To try to describe an average Joshua tree is a little like trying to describe an average person. They all have the same functional components but on closer inspection of the species and its environment we find there are tremendous differences even between neighboring trees, sometimes only feet apart. It is probably the morphology (shape) of the Joshua tree that gives the tree the character that makes it one of the most unique organisms of the high desert. Some, as noted by Gossard (1992) have a thick and bushy growth resembling a typical tree in shape, with a definite trunk and tree like limbs reaching out and up. Others, Gossard explains, may grow straight up with only a few straggly branches appearing at irregular intervals and haphazard directions. The FEIS (1998) succinctly described the tree as a "large, erect, evergreen, arborescent⁷ monocot⁸."

McKelvey (1938) reasons that the size of Joshua trees depends on many factors most notably soil moisture. She initially refers to (Sargent 1890) when referring to tree size mentioning that initial estimations in the past have been "easily overestimated" when the trees were assessed to be around 30-40 feet in average height. McKelvey (1938) considers

⁶ The animal life in a particular region or period considered as a whole.

⁷ Resembling a tree especially in developing branches or similar parts.

⁸ A flowering plant that has a single leaf; the seed and floral parts form in multiples of three.

Jepson's (1922) account to be more accurate estimating the average size to be between 16 and 30 feet. According to FEIS (1998), the Joshua tree is the largest non-riparian plant of the Mojave.

When calculating the age of Y. brevifolia, it is more difficult than simply counting the annual rings because it consists primarily of a spongy pulp material and this makes age verification difficult (Gossard 1992). I could not find any information that indicated how estimations of age are determined, but according to McKelvey (1938) and Gossard (1992) some of the mature trees are estimated to be between 800 and 1000 years old.

Early estimations concerning the growth rate vary considerably depending on the literature you choose. McKelvey (1938) estimated the rate to be to be around one meter in the first 6 years and then slowing down towards maturity. Gossard (1992) indicates that later studies in Joshua Tree National Park argue that the growth rate is much slower, somewhere in the region of two feet every ten years, Gossard (1992). Although these growth rates are fairly high for a desert plant, Keith (1982) explains that the tree can remain in its 'juvenile' state (having not produced a flower) for many years. It is only when the tree is mature that shoots appear (McKelvey 1938). However there is still controversy as to exactly how new shoots develop. Some say insect infestation (such as that from the Yucca Boring Weevil) promotes the development of new shoots (Bakker 1971). Others believe shoots fork from the vicinity of the seedpod after dispersal, and depending on the location can give the tree its unusual branch direction (Gossard 1992).

The number of Yucca brevifolia varietals seems to warrant continued discussion. It is not clear whether there are two or three species. Early studies such as Riley (1892) and Sargent (1890) refer to the species as Yucca aborescens that was considered to be a synonym for all Yucca brevifolia species. Gossard (1992) explains that the species has two varieties Yucca brevifolia jaegeriana named after Dr Edmund Jaeger who did the first comprehensive study of the species in 1935 and Yucca brevifolia herbetti named after John Herbert Webber in 1942. According to the FEIS (1998) on quoting work by Philip Munz in 1974, Webber found this variety to be morphologically different enough to distinguish it as a different variety.

The species Yucca brevifolia jaegeriana according to Gossard (1992) differs with its smaller overall growth, numerous shorter branches and is located primarily in the drier eastern portion of the Mojave. Sawyer and Wolf (1995) and Munz (1974) propose that Yucca brevifolia has three varieties: Y. brevifolia jaegeriana, Y. brevifolia herbetti and Y. brevifolia brevifolia and they differ thus: Y brevifolia brevifolia has a single trunk; Y brevifolia jaegeriana has several trunks and Y. brevifolia herbetti is shrubby. I could not find any more information that corroborates this.

As I mentioned earlier there is still questions as to exactly how many varieties of the species exist. To report an opposing view and finish this discussion, Cronquist et al (1977) "found little evidence to delineate any species" (FEIS 1998).

Branch and the Leaf Structure

Gossard (1992) gives an excellent description with the important points summarized below: The Joshua tree is marked by growth straight up with initially "long pliable tender leaves" At this young stage it is very vulnerable especially to grazing animals and the surrounding mature trees providing protection. It is not until the plant has grown ten to twelve inches that it develops its customary "narrow, sword shaped pointed leaves." The leaf is evergreen and persists for several years clustered near the tips of the branches, widest nearest the base tapering to a point and covered with sharp teeth at the crown. This design helps prevent excessive water loss and creates a channel for rain to drip towards the base of

the trunk. The leaves of *Y. brevifolia* are shorter than those of most all other yuccas (hence the name *brevifolia* ~ “brief or shortened leaf”) and range from five to twelve inches long when fully grown. They also provide their own stomata located on the underside of the stem to help prevent unnecessary loss of water vapor.

Bakker (1971) explains that leaves more than a year old tend to shed their needles, turn brown and eventually droop “eventually becoming a bristling thatch that covers a good portion of the tree.” In time, “this shaggy matting drops off the trunk...exposing the bark beneath” and as a result only a small part of the tree remains green.

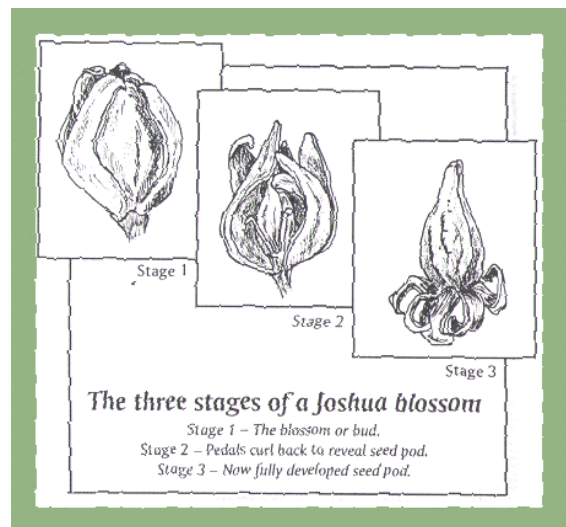
These characteristics explained by Bakker and Gossard show a complex system designed to withstand a harsh environment. It is no wonder that Gossard (1992) refers to the Joshua tree as “an excellent example of a drought resistant and water conservationist” and a “perfect symbol of the Mojave desert.”

The Flower and the Fruit

Young trees are considered to be juvenile when they still consist of one trunk and no branches. When they reach a height of around 8–10 ft they are usually at the stage to produce their first flowers (Bakker 1971). In early spring the stalk or branch is covered with a series of green pods that usually have 7-9 buds on each new branchlet in grouped clusters (McKelvey 1938). Gossard (1992) explains that pods do not appear on the same branches each year and ultimately need the perfect climatic conditions to produce an abundance of flowers essential to its pollination.

When the flowers do ripen however, the light cream or ivory colored waxy blossom emits a “musty odor similar to that of a toadstool” and reveals a seedpod that is “raspberry” or artichoke in shape. Gossard (1992) continues to explain that these blossoms open only at night and only partially, which is considered rather unusual.

The partial opening of the petals classifies the species as an indehiscent⁹ fruited species (Gossard 1992, McKelvey 1938) The Joshua usually produces inflorescences¹⁰ once or twice each year but rarely on the same branch. Many seasons may pass before years of copious blooming and hence a greater chance of successful pollination (Bakker 1971). The following diagram and table show the three stages of bloom along with variation in generalized flowering dates according to taxonomic variation and geographic location.



(Gossard 1992)

⁹ Not opening up to release seed when ripe.

¹⁰ Flowers and flowering parts.

Table 1 (FEIS 1998)

Location	Start of Flowering	End of Flowering	Variety	Fruiting
California	March	May	Brevifolia	-----
California	-----	-----	Jaegeriana	April
Nevada	April	May	-----	-----
Utah	March	March	-----	-----

*One night soon the yucca plant will bloom
and a yucca moth will find it.*

Katherine B. Hauth, *Life of the Yucca*

Reproduction

One of the most remarkable things about the Joshua tree is the unusual and essential relationship it has with the small white moth, the yucca moth, Pronuba tegeticula synthetica (Gossard 1992). In Charles Riley's 1892 book *The Yucca Moth* and *Yucca Pollination* he claimed that the Yuccas were particularly unusual because they were "the only species known at that time to be solely dependent on just one pollinator."

Y. brevifolia, like other members of the Lily family can only produce seeds after they have been pollinated (hence their original mistaken classification). Pollination was first noticed by Dr. George Engelmann in 1872, and since then there has been debate as to the complexities of yucca pollination (Baker 1986). To confuse the situation further, Riley (1892) drew attention to "bogus yucca moths" that visit the flowers but do not collect pollen and also validated reports of the species being capable of self-pollination.

Whether or not there are other influences that determine the reproductive traits of Y. brevifolia, there does exist a classic example of mutualism between Pronuba tegeticula synthetica and Yucca brevifolia. To paraphrase Gossard (1992) P. tegeticula, which are crepuscular (flying at night), are attracted to the white blossoms of Y. brevifolia. The tree can attract many moths at any time, each one pausing momentarily to collect the sticky pollen. This process continues until she has a ball of the "proper" size. The ball is forced into the pistil of a selected flower and into the pistil she injects her own eggs. Now the brilliant mutualistic¹¹ interaction takes place. The moth has deposited enough pollen into the tube to ensure growth of the Yucca brevifolia seeds and the fertilization of her eggs. The young moth larvae will eat some of the seeds but enough of the seeds will be spared to disperse.

Whenever interdependent relationships such as these exist, environmental factors are of paramount importance to both. Gossard draws attention to the possible population deterioration of tegeticula through pesticides and how human development may continue to adversely affect the population of the Joshua tree.

Habitat

In the Mojave ecosystem Joshua trees tend to be present where higher precipitation occurs and higher soil moisture penetration is permitted (Kornelge 1973). As a result most Joshua trees are found in the relatively flat areas of the high desert such as gently sloping

¹¹ A relationship between two organisms of different species that benefits both and harms neither.

alluvial fans where the soil is of well draining colluvial¹², alluvial¹³ derived. (Sawyer and Wolf 1995).

Within the Mojave ecosystem according to Sawyer and Wolf (1995), *Y. brevifolia* is the dominant species towering over a shrub canopy which includes but is not confined to: sagebrush (*Artemisia tridentata*), blackbrush (*Coleogyne ramosissima*), creosote bushes (*Larrea tridentata*), Mojave yucca (*Yucca schidigera*) cheesebrush (*Hymenoclea salsola*), and buckwheat (*Eriogonum fasciculatum*). Below this level, there is a ground layer consisting of various cacti species and perennial grasses. This kind of series is considered to be Joshua tree woodland in many texts. Sawyer and Wolf (1995) on citing Rowland (1978) explain that even with the large range of the *Y. brevifolia*, the existence of the Joshua tree as a plant community is questionable. Rowland (1978) postulates that perhaps it would be more accurate to consider the Joshua tree as a “component of other grassland and shrub communities regardless of density, because “[it] is common in some areas... and uncommon in others...and trees other than the Joshua are often present.” Sawyer and Wolf (1995) also refer to (Phillips et al 1980) who explain that there are stands of Joshua trees in Joshua Tree National Park that are considered to be a Joshua tree woodland series but they contain an abundance of other trees such as California juniper or in some cases Desert Scrub Oak or Pinyon pine. Sawyer and Wolf (1995) quote Phillips et al (1980) further, “these stands are better considered as belonging to the California juniper series.” According to the FEIS (1998) the Joshua tree is an “important member of the desert climax community but is generally not well represented in most seral or describe series of known succeeding plant communities.”

Many animals use *Yucca brevifolia* as a home or resource for food. Some of the more eloquent descriptions of fauna are found in McKelvey (1938) who quotes from letters compiled by H.J Webber of the Missouri Botanical Gardens on the subject of “animals that frequent the Joshua Tree environment” from prominent botanists of the day:

I have examined many trunks of the tree Yucca (Y. brevifolia) which have been ascended by a small desert mammal known as the wood rat (Neotoma Mexicana) The wood rats cut the leaves of the Yucca at the base and form a ladder around the trunk... The leaves are used to construct a nest made up of cactus, rocks and leaves.

Vernon Bailey 1894

Many species of wind broken branches afford the home of numerous ants, scorpions, spiders and several species of beetle. In a deep crack in one of these branches, a small lizard was discovered Xantusia vigilis (the desert night lizard) and in one instance as many as five, as many as were known in previous collections, were found under a single tree.

J. Van Denburgh 1922

Of certain insects utilizing this species of Yucca, the two chief causes of branching of the tree yucca appear to be the dying of the terminal buds after flowering and the injury caused by the yucca-boring weevil (Scyphophoroua yuccae)

E C Jaeger 1933

Gossard (1992) describes the beetle, noted by Jaeger, as preferring the tips of the branches. Here the weevil prefers to deposit its eggs and the larvae on hatching devour the

¹² Loose rock and soil at the base of a cliff or steep slope.

¹³ Used to describe the environment, action and sedimentary deposits of rivers or streams.

local plant tissue. This elicits a response from the tree into produce a silica deposit that petrifies the wood, presumably as protection.

Many other insects and termites use the dead and decaying branches that are scattered around which in turn attract other animals most notably the ladder-backed woodpecker, and Scott's Oriole (Bakker 1971).

Anthropogenic¹⁴ Uses

Native Americans in the region have used the tree for a variety of purposes. Although the leaves as suggested by (McKelvey 1938) were of no significant use, the cliff dwellers in the Southwest used the beams to create living structures (FEIS 1998). The seeds were considered very nutritional and were ground and eaten raw or cooked. Also the native Americans used the rootlets to make a red dye (Petrides 1998).

When Europeans settled in the area, McKelvey (1938) explains that the fibrous wood from the tree was used to manufacture paper pulp. McKelvey (1938) goes on to explain that an English company based in San Francisco in the late 1800's attempted unsuccessfully to make paper from Joshua trees into a profitable business endeavor. But even with their failure, it was still expected to "pay handsomely" in the future. McKelvey (1938) along with Sargent (1890) also inform us that an article in the U.S Dept of Agriculture Investigations report in 1897 revealed that several editions of the London Telegraph were printed upon Joshua tree paper but that endeavor also proved to be costly. If that is not enough another entrepreneurial Englishman attempted to extract the liquid found in the root system of the tree to create a drink similar to that of a pint of English Bitter. Nobody could tolerate it.

Evolution

When placing an organism in an evolutionary context a pathway must be determined and analysis conducted. Baker's (1986) study entitled *Yucca and Yucca Moths- A Historical Context* discusses how the yucca-yucca moth relationship has changed in terms of our historical knowledge and also offers an evolutionary history of the mutualistic relationship. I will summarize Baker's discussion referring to statements made by Gossard's (1992) comprehensive work.

Y. brevifolia Baker postulates did perhaps have a "conventional pollination mechanism" that is typical of "other American genera of the Agavaceae family. For some reason it developed a different strategy perhaps to attract pollination from tegeticula. Gossard echoes Baker's thoughts explaining that perhaps an ancestral *Yucca* developed "a sticky pollen instead of the usual powdery dust" which tegeticula was passionate about and hence found a niche for itself.

Gossard (1992) also speculates that Pronuba tegeticula may developed a unique way of collecting pollen, and the trees that had the easiest pollen to handle attracted the most moths and ensured reproductive success. Yucca brevifolia then lost its ability to be pollinated by anything else. Baker (1996) makes it very clear that the pollination mechanisms in Y. brevifolia and other *Yuccas* that we see today are still not entirely explained. For example "seed set" in Y. brevifolia has been noted in the absence of moth visits indicating as Riley did in 1892, that self-pollination or visits from other pollinators.

Keith (1982) explains that the "Joshua tree was far more abundant in humid prehistoric times [such as the Pleistocene¹⁵] and covered larger than today encompassing the lower desert elevations." I was able to find one such article (Laudermilk and Munz 1934) that

¹⁴ Relating to or resulting from the influence humans have on the natural world.

¹⁵ 14-30,000 years before the present.

corroborates Keith (1982) and is explained by McKelvey (1938) thus: Two paleontologists Laudermilk and Munz showed that in 1934 after examining prehistoric dietary remains of the now extinct ground sloth, evidence indicated that the animal fed almost entirely on Yucca with an special like for Y. brevifolia. The evidence of the sloth was found in a region called the Clark Mountains where no Yuccas are present today. In fact they are only found at elevations some 3,000 ft. or so higher. Understanding the sloth's' preferred habitat and range allows for speculation on paleoclimatic conditions, which in turn would allow speculation as to the prehistoric distribution of Yucca brevifolia. As Keith (1982) mentioned, the conditions would have to have been a lot wetter and humid for the species to be abundant in this area.

Conclusions

Fremont once said that the Joshua tree was “the most repulsive tree in the vegetable kingdom.” Having visited the high desert many times I do not share his views. After this project my views have only become more solidified. Yucca brevifolia is a unique biological organism of incredible complexity. It has adapted perfectly to the high desert environment and provides habitat for many other desert organisms. I am surprised at just how much is still not completely known about the species and especially its relationship to Pronuba tegeticula considering the notoriety and visibility of the tree. I agree with Gossard (1992) when she noted the tree and its environment to be one full of “intrigue and paradox”. I find some of that intrigue when walking through Joshua Tree National Park amongst the trees. In a way it resembles walking through a grove of redwoods where their majesty numbs your senses as they tower above all other organisms, it is only a matter of scale. It is from this intrigue springs the ultimate paradox despite its size, complex defense systems and its superbly adapted structure, it requires the services of a tiny little white moth in order to survive.

References

- ∨ **Baker, H. (1986)** Yucca and Yucca Moths- A historical Commentary Annals of the Missouri Botanical Gardens 73:pp. 556-564 (1986)
- ∨ **Bakker, Elna. (1971)** An Island called California. Univ. of CA Berkeley Press.
- ∨ **Christopherson, Robert W. (1997)** Geosystems, An Introduction to Physical Geography, Prentice Hall
- ∨ **Cronquist, P L, M. Olsen (1983)** The Plant Information System Network (PIN) database: Colorado, Montana, N. Dakota, Utah and Wyoming. FWS/OBS-83/86. Washington DC. US Dept of Interior. Fish & Wildlife. pp.786.
- ∨ **Fire Effects Information System (FEIS) (1996)** Prescribed Fire and Fire effects Research Work Unit, Rocky Mountain Research Station (producer). Website <http://www.fs.fed.us/database/feis/plants/tree/yucbre/> [1998, March 12]
- ∨ **George, Jane. (1998)** Recruitment Dynamics of Yucca brevifolia, the Joshua Tree, in the Mojave Desert. Univ. of CA Los Angeles. Abst. 1998 Annual Botanical Society Meeting, Baltimore MD.
- ∨ **Gossard, G. (1992)** The Joshua Tree, A Controversial, Contradictory Desert Centurion. Yellow Rose Publications.
- ∨ **Jepson, W L. (1922)** Flora of California. University of California Press. Los Angeles
- ∨ **Keith, S. (1982)** A Tree named Joshua. American Forests July 1982 pp. 40-42
- ∨ Other Sources:
- ∨ **Kornoelje, T.A. (1973)** Plant Communities of the Covington Area. CSU Long Beach MA Thesis.
- ∨ **McKelvey, S D. (1938)** Yuccas of the Southwestern United States, Part 1. Arnold Arboretum, Jamaica Plain, Massachusetts.
- ∨ **National Weather Service. (1999)** http://www.nws.mbay.net/clim_map.html 10/10/99
- ∨ **Phillips, E A. K K Page. S D Knapp (1980)** Vegetational characteristics of two stands of Joshua Tree Woodland Madrõno 27:43-47
- ∨ **Pretrides, G A. (1998)** A Field guide to Western Trees: Western United States and Canada. Houghton and Mifflin
- ∨ **Rasmusson, K E, J. Anderson, N. Huntly (1994)** Coordination of Branch Orientation and Photosynthetic in the Joshua Tree (Yucca Brevifolia) Great Basin Naturalist 54(3) pp.204-221
- ∨ **Riley, C. (1892)** Yucca Moth and Yucca Pollination. Annual Report of the Missouri Botanical Garden.
- ∨ **Rowland, P G. (1978)** The Vegetation dynamics of the Joshua Tree in the South West United States. Dissertation. Univ of California, Riverside.
- ∨ **Royo, A.R. (1997)** DesertUSA magazine Digital West Media Inc. Website http://www.desertusa.com/itree/josh_month.html
- ∨ **Sargent, C S. (1890)** Silva of North America P. Smith New York
- ∨ **Sawyer, J O, T K Wolf (1995)** A Manual of California Vegetation. California Native Plant Society.
- ∨ **Stricklin, N. (1989)** The effect of High Levels of Boron on Germination and Growth of the Joshua Tree Seedlings. CSU Long Beach MA Thesis
- ∨ **Thorntwaite, C W. JR Mather (1931)** The Water Balance, Publications in Climatology Vol VII No. 1 Drexel Institute of Technology.

Other resources:

- ∨ **Addicott, J F. (1998)** Regulation of Mutualism between Yucca and Yucca Moths: Population Level Processes. Oikos 81: 119-129 1998
- ∨ **Bogler, D.J, J L Neff, B.B Simpson (1995)** Multiple Origins of the Yucca-Yucca Moth Association. Proceedings of the National Academy of Sciences USA Vol. 92 pp. 6864- 6867 July 1995