

# Prehistoric Development and Dispersal of the Desert Fan Palm

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The desert fan palm (*Washingtonia filifera* Wendl.) lives in a variety of arid and semi-arid natural environments throughout southern California and Baja California, and in two locations in western Arizona (Fig. 1). While it appears tolerant of these xeric climates, the tree survives only in the presence of a reliable source of groundwater (Read 1974). As a result of this phreatophytic quality, the species is found most typically in oases along hill-side seeps and in canyon washes, particularly on the western and northern slopes of the Coachella and Imperial valleys. Randall Henderson, who spent much of his life searching for groves of *W. filifera*, estimated in 1961 that a population of 11,000 of these trees grows wild in the southern California desert. Since then many new palm oases have been discovered, in both California (Jonsson 1985) and Arizona (Brown et al. 1976), as well as in Baja (Cornett 1987b). Despite these recent discoveries, Cornett (1984) estimates that the current wild population in the American Southwest covers less than 1,000 acres.

In the human environments of California, the fan palm's stocky trunk and distinct crown adorn many Central Valley farmsteads, and any visitor to the cities and suburbs of southern California knows well the aesthetic appeal of a street lined with these curious trees. It is fitting that *W. filifera* appears in so many California environments, for it is the only palm native to the state. Yet, as an ornamental novelty the species has travelled far beyond its native land, and is today one of the most widely grown members of the family Palmae

in the world (McClintock 1978). The great travel saga of this popular tree, however, began long ago, in the shroud of prehistory.

## Early Prehistoric Development

Where the earliest palms originated remains the subject of debate due to the paucity of Mesozoic pollen and fossil data. From what little paleobotanical information is available to as far back as the upper Cretaceous, three divergent hypotheses have been developed. Moore (1973), combining his knowledge of the fossil record (much of the paleobotanical work on palms was completed after his publication) and modern plant distributions suggested that the family Palmae originated during the Cretaceous in West Gondwanaland (modern South America), and subsequently migrated into East Gondwanaland and Laurasia. Contrary to Moore, Walker and Walker (1986, from Uhl and Dransfield 1987), by proposing a Laurasian origin for the monocotyledons, pointed to the Northern Hemisphere as a potential center of development and dispersal for the palms, a possibility Moore (1973) had earlier considered and rejected. More recently, Uhl and Dransfield (1987) taking into account palm morphology, as well as the paleobotanical record and log of current distributions, have suggested "the first palms may have originated at a time when the separation of Gondwanaland and Laurasia was incomplete and dispersal between the two supercontinents was still possible," allowing the family to become widespread on both landmasses.



1. The desert fan palm in its natural habitat; clarification of the palm's prehistoric development and dispersal will help determine our policies toward its conservation. Photo credit: Debbie Elliott-Fisk.

Regardless of where the palms first originated, it is clear that by the Paleocene they had begun to radiate from their origin, and to differentiate into identifiable groups. The coryphoid group, and in particular the Livistoninae subtribe to which *W. filifera* belongs, proliferated early and rapidly in response to a warming trend during the early Paleocene (Axelrod 1950). This warming trend continued into the Eocene, by which time the genus *Washingtonia* had fully established itself in the floral community of southern California. This floral province, called Mohavia, encompassed what are today the Mojave and Sonoran deserts; at that time much of the current range of the desert fan palm—the Imperial and Coachella valleys—lay submerged beneath the sea.

Over the ensuing course of the Oligocene and Miocene, this Tertiary warming trend developed into a trend toward aridity and cooler temperatures. This trend, climaxing in the middle Pliocene, was accentuated inland by the earlier uplift of the San Gabriel, San Bernardino, San Jacinto, and Santa Rosa mountain ranges (MacDougal 1914). The climatic changes accompanying these topographic modifications are considered responsible for the differentiation of the Sonoran and Mojave desert flora (Axelrod 1950). Lower winter temperatures and decreased annual rainfall signaled the disappearance of *W. filifera* from the Mojave plateau. Along the coast, prolonged humid conditions associated with increased orographic precipitation created an unfavorable habitat for the

species, resulting in both crown rot (Jaeger 1933) and a rapid decrease in seed germination (Moraes 1980). The distribution of the palm henceforth dwindled, leaving isolated stands surviving where groundwater seepage occurred along geologic faults on the leeward slopes of the Colorado Desert (Moran 1979, Vogl and McHargue 1966). As the water supply further decreased, so did the palm's habitat; unlike many other plant species which flourished during the Tertiary aridity by developing specialized xerophytic traits, *W. filifera* remained dependent upon groundwater sources for its survival. Consideration of the areal extent to which its population diminished raises important and unanswered questions about the origin and development of the palm's current distribution.

### Late Prehistoric Development

The traditional and most widely accepted view holds that *W. filifera* exists as a relic of a once widespread southern California population. The onset of a milder and moister climatic regime associated with the Pleistocene glaciation is credited with preserving the species, and along the shores of Lake Cahuilla, a fluctuating brine lake fed by the diverted Colorado River, the palm is said to have thrived (Parish 1907, MacDougal 1914, Jaeger 1933, Henderson 1965). There remains today a discontinuous belt of palms just above the ancient shoreline at the base of the Indio hills (Smith 1958). The lake level throughout the Pleistocene was notably unstable, however, and it has yet to be explained how a phreatophytic tree that cannot flower until it is at least 15 years old (Brown et al. 1976), and that reproduces once per century (Vogl and McHargue 1966) could maintain itself in such a dynamic environment.

Even more challenging to the relic hypothesis is a 1986 publication by McClenaghan and Beauchamp on the species' genetic variability. Through a series

of electrophoretic studies on 446 palms from 16 Colorado Desert sites, the authors discovered unexpectedly low genetic differentiation between oases, with only 2.3% of the total genetic variability attributable to between-population diversity; the remainder was due to within-population differences, which themselves were considered low. This finding runs counter to the tenet that small, isolated populations will genetically diverge.

As an explanation for this genetic similarity, one could offer van Valen's niche width-variation hypothesis, which states that an adaptive relationship exists between ecological amplitude and genetic variability. This would imply that the low diversity levels found among *W. filifera* populations are a function of the species' low ecological versatility. Likewise, one could anticipate uniform selection pressures evoking low genetic variability. Both of these possibilities, however, ignore important empirical characteristics of the desert fan palm and its distribution.

*Washingtonia filifera*, although a heliophyte, has a remarkable ability to endure frost and low temperatures; horticultural reports from Britain (Cooper 1983), Germany (Smith 1964), Ohio (Myers 1985), Alabama (Colvin 1983), and California (Cornett 1987a) have all reported *W. filifera* specimens surviving sub-freezing temperatures. The species also displays a high tolerance for alkaline soils (Jaeger 1933), as well as a notable resistance to fire damage, the result of a protective insulating sap which flows through its porous trunk (Henderson 1965). Most important, the fan palm survives in two distinct desert habitats—seeps and washes. A study by Vogl and McHargue (1966) of the vegetational composition of fan palm oases in the Colorado Desert helped reveal the tree's ecological adaptability: of the 78 species recorded by the authors, *W. filifera* proved to be the only one distributed among all 24 oases sampled. The low genetic differentiation among palm popu-

lations does not appear to be attributable to a narrow ecological amplitude.

McClenaghan and Beauchamp (1986) suggest the California populations of *W. filifera* are not relics at all, but rather represent the products of seed dispersal from a source population having low genetic variability. They reason that "climatic changes may have completely eliminated fan palms from the Colorado Desert and restricted the species to small refugia populations in Baja California." The dispersal of seeds from one of the refugia would have resulted in genetically similar colonizing populations.

Several migrating birds, including the western and mountain bluebirds (*Sialia mexicana* and *S. currucoides*), the cedar waxwing (*Bombycilla cedrorum*), and the house finch (*Carpodacus mexicanus*), could have acted as primary dispersal agents, but the possibility seems unlikely. Bullock (1980) has documented that birds have difficulty swallowing the seeds, and frequently regurgitate them. Furthermore, upon arriving at the oases, they tend to become sedentary in the shelter provided by the palms, thus limiting the potential dispersal range to only a few meters.

The coyote (*Canis latrans*) is considered to be the most likely disperser of *W. filifera* seeds. Henderson (1947) first proposed the coyote as a dispersal agent after noticing large amounts of undigested seeds in their scat on oases floors. Coyotes are known to consume large quantities of palm seeds, and to travel long distances (Bullock 1980). A report by Cornett (1985) that the ingestion of the seed by coyotes increases its germination success adds further support to the opinion that they have contributed to its dissemination. If it is assumed, however, that coyotes randomly consume the seeds, and that there existed more than one refugium population, it remains to be resolved how these animals could establish a widespread population of such striking genetic homogeneity. Undeniably, the coyote has contributed to the

observed genetic homogeneity of desert fan palm populations by facilitating gene flow, but our consideration of McClenaghan and Beauchamp's findings would be incomplete if we did not examine the potential influence of man—the anthropogenic factor.

### Anthropogenic Development

The distributional range of the Cahuilla Indians closely coincides with that of *W. filifera*. Larger groves of the palms were favorite habitation sites of the Cahuilla (Bean 1972), who are credited with having extended the tree's limits by carrying its edible seeds from one oasis to another (Chase 1919, Henderson 1947, McClinck 1978). Seed dissemination by random collection, however, cannot explain the low genetic variability observed among *W. filifera* populations. While archaeological evidence for prehistoric cultivation of *W. filifera* has not been uncovered (Wilke 1978), the Cahuilla are confirmed to have had contact with the Yuman Indians, known agriculturalists of the Colorado River Delta (Bean and Saubel 1972). The importance of the palm in the life of the Cahuilla invites consideration of the possibility that they long cultivated the tree.

Cultivated plants can be recognized by the following: 1) existence in an unnatural environment, 2) multiple use and integration into the social fabric of the tending society, 3) a body of myths and legends surrounding their origin and use, and 4) low genetic diversity throughout the population as a result of human selection. The majority of palms in the Colorado Desert survive along hillside seeps far above the valley bottom (Cornett 1984). While some consider this the natural habitat of the palm (Vogl and McHargue 1966), Henderson (1961, 1965), noting stands in canyons up to 1,000 meters, suggests these palms are descendants of the population that once grew along the fringe of Lake Cahuilla. Interestingly, the ancient lake shore is where Bean and Saubel (1972)

speculate the Yuman and Cahuilla tribes came into contact. Moran (1979) observes that "some plants used by the Indians are found near Indian campsites far from other known stands." He concludes that these were purposefully planted by the Cahuilla in prehistoric times.

If the utilitarian value of a plant is any indication of its desirability as a cultivar, then the Cahuilla had substantial reason for planting the palm. In addition to providing a sheltered habitat, the trees yielded a wide variety of useful products. The dried fronds were used as construction materials for houses, called "kish," and for granaries (Parish 1907). Sandals, baskets, utensils, and tools were fabricated from them as well (Moran 1977). As aesthetic additions, the leaf fibers were used for apparel (Bean 1972), and the seeds were considered excellent filling material for gourd rattles (Bean and Saubel 1972). The leaves were also used to make "nukily," images of the dead that were burned in Cahuilla memorial rites (Chase 1919), and served as symbols of victory (Stone 1959).

As a food source, the palm's spongy pith, when boiled, provided relief during times of famine (Bean and Saubel 1972). On a more regular basis, the fruit was consumed in several forms: both a beverage and a jam were made at times, but more commonly the small, sweet delicacies were eaten fresh, or were dried and ground into flour (Brumgardt and Bowles 1981). Cornett (1987c) has suggested that the fruit of *W. filifera*, by virtue of its high carbohydrate content, "... had the potential of being an important dietary mainstay."

The Cahuilla also utilized palm materials for making fire. The pithy wood of small floral branches was rotated against a larger piece of dry wood resting on a bed of leaves, creating heat by friction. The origin of this fire-making process is recounted in the creation myth of Ninmaiwaut (see Bean and Saubel 1972), indicating the important role of fire in Cahuilla society; indeed,

they are known to have burned the palm thatch regularly, but their purpose remains debated.

Henderson (1961) was of the opinion that the Indians burned the persistent dead shag to drive away evil spirits, while earlier Hubbard (1962) had speculated that the palms were burned as a smoke offering to the dead. From a functional point of view, Parish (1907) first suggested the Indians set fire to the thatch to increase the tree's yield by destroying insect pests harmful to the fruit (particularly the bostrychid beetle and the red spider mite), and recently Cornett and Stewart (1986) have documented an empirical increase in spadix production among burned trees. Brown et al. (1976) suggest, however, that yellowjackets were the pest the Indians desired to drive away. Vogl and McHargue (1966) add that "burning entire oases made them more accessible and facilitated hunting." Moreover, burning helped maintain the groves by increasing seed germination of the palm through the elimination of ground litter and undergrowth that would compete with the palm for water.

The trading of palm products among Indian groups (Bean and Saubel 1972), and the private ownership of groves and individual trees (Brumgardt and Bowles 1981) stand as further evidence of the extent to which *W. filifera* was integrated into Cahuilla society. Finally, Cahuilla oral legends, stemming from the prehistoric, leave little doubt that the palms were planted in aboriginal times. Patencio (1943) tells the story of the culture hero Sungrey and the creation of the first palm as follows:

One of the head men of the people of Sungrey felt his time was about gone. His years among his people were many, and he must be prepared to go. This man wanted to be a benefit to his people, so he said, "I am going to be a palm tree. There are no palm trees in the world. My name shall always be Moul (palm tree). From the top of the earth to the end of the earth my name shall be Moul."

So he stood up very straight and very strong and very powerful, and soon the bark of the tree began

to grow around him. And so he passed from the sight of his people.

Now the people were settled about the country in many places, but they all came to the Indian well to eat the fruit of the palm tree. The meat of the fruit was not so large, but it was sweet like honey and was enjoyed by everybody—animals and birds too. The people carried the seed to their homes and palm trees grew from this seed in many places. The palm trees in every place came from this first palm tree, but, like the people who change in customs and language, the palms often were somewhat different, but all, every one of them, came from this first palm tree, the man who wanted to be a benefit to his people.

Significant in this account is not only the carrying of seeds to home sites from whence all the palms grew, but the recognition of variation among the trees, a prerequisite for purposeful human selection. The low genetic diversity among California populations of *W. filifera* discovered by McClenaghan and Beauchamp may well reflect the results of such a selection process acting on the palms during their late prehistoric development.

### Conclusion

In the distant past, the survival of the desert fan palm relied upon the random gifts of nature, its distribution guided by unrelenting climatic and tectonic forces. Today, however, its continued existence depends upon the calculated decisions of humans. We have planted the tree on every inhabited continent, while simultaneously threatening its native habitat with the space and water demands of urban and agricultural development.

The status of the palm—whether it is an ancient relic, a product of recolonization, or a feral escape—will help determine our policies toward its conservation. Questions regarding its status, however, are not easily answered. To help resolve the question of recolonization, McClenaghan and Beauchamp recommend electrophoretic studies of *W. filifera* populations in Baja California as a means of searching for and identifying potential source refugia with genetic affinities to the Colorado Desert

oases. Using the same data, I believe we could shed new light on whether or not Indian selection and cultivation of the plant contributed to its relative genetic homogeneity: If similarly situated *W. filifera* oases in Baja display low genetic diversity, we can conclude that natural factors, be they environmental or botanical, have produced this condition. If the genetic differentiation in this region is high, however, we can regard the anthropogenic factor as dominant in California. In either case, the prehistoric development of the desert fan palm invites further investigation by the botanist, the geographer, the anthropologist, and the layman.

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