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Domesticated Palms

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Johnson (1983) suggested that there are only four domesticated palms: date (*Phoenix dactylifera* L.), coconut (*Cocos nucifera* L.), areca (*Areca catechu* L.) and African oil palm (*Elaeis guineensis* Jacq.). Other authors take a similar position but without a clear definition of domestication in palms. As part of my research with pejibaye (*Bactris gasipaes* Kunth), I reviewed the question of domestication in palms and how many are domesticated or in the process of domestication. This paper discusses domestication in palms and reviews some of the palms identified as domesticated.

What Is Domestication?

This question has yielded different answers at different times, based upon accumulated knowledge of plant genetic-geographic variation, anthropological, archeological and ethnobiological studies of human/plant interactions, and the genetics of selection. In recent decades the discussion has been especially active (Harlan 1975, Hawkes 1983).

Harlan's (1975, p. 63–64) definition of domestication is clear:

> "To *domesticate* means to bring into the household. A domestic is one (servant) who lives in the same house. In the case of domesticated plants and animals, we mean that they have been altered genetically from their wild state and have come to be at home with man. Since domestication is an evolutionary process, there will be found all degrees of plant and animal association with man and a range of morphological differentiations from forms identical to wild races to fully domesticated races. A fully domesticated plant or animal is completely dependent upon man for survival. Therefore, domestication implies a change in ecological adaptation, and this is usually associated with morphological differentiation. There are inevitably many intermediate states."

The key phrase in this definition is "completely dependent upon man for survival" because this is the point of no return in the domestication process. In some annuals this means that the plant itself may not be able to survive without human preparation of a favorable agro-ecosystem and elimination of competition. In perennials and other annuals this means that the plant will not reproduce itself successfully and its genotype therefore fails to survive into the next generation. Botanical varieties and landraces (morphologically distinct races developed by humans in different geographical areas) of the same species may differ in the degree of modification due to selection, i.e., completely domesticated (dependent upon humans for survival) and semi-domesticated landraces, and wild types showing little or no modification. If a species has one or more fully domesticated landraces then it may be considered to be domesticated.

For palms it is also worth defining cultivation, since many palms are cultivated in some way, but are not domesticated. Again Harlan's (1975, pp. 63–64) definition is appropriate:

> "To *cultivate* means to conduct those activities involved in caring for a plant, such as tilling the soil, preparing a seedbed, weeding, pruning, protecting, watering, and manuring. Cultivation is concerned with human activities, while domestication deals with the genetic response of the plants or animals being tended or cultivated. It is therefore quite possible to cultivate wild plants, and cultivated plants are not necessarily domesticated."

Just as there are varying degrees of domestication, there are varying degrees of cultivation, from relatively primitive to highly sophisticated. While Harlan (1975) is correct in saying that cultivated plants are not necessarily domesticated, any plant that has been cultivated for a long period (many generations) will inevitably be modified by natural selection in cultivation and by the farmer's conscious or subconscious selection, i.e., it starts to become domesticated.

"Management" is a less sophisticated form of cultivation. The plant may be protected from human-caused environmental modification (opening of new fields, for example), it may occasionally be liberated from competition from other species and seeds and seedlings may even be planted, although without seedbed preparation *per se*. Anderson and Posey (1987) discuss a case of Amerindian perennial plant management, verging upon cultivation, practiced by the Kayapó indians on the Xingu River in southeastern Amazonia. This is an extremely sophisticated system of human/plant interaction and doubtlessly includes mass selection and thus genetic modification of the species managed. Balée (1988) points out that many Neotropical palms appear to have been managed in this or other ways and morphological modifications are frequently observed.

A continuum from wild and used, to managed, to cultivated, to domesticated (Fig. 1) becomes clear. This continuum refers not only to human interaction with the plant to obtain its economic product, but also to the plant's genetic response to this interaction (progressive changes in gene frequencies), leading finally to full domestication. Because each plant is different, it is not possible to put a numeric scale on either axis of this figure.

Therefore, for a palm to be considered fully domesticated it must have at least one landrace dependent upon human intervention for its continued genetic survival. Ideally it should present a variety of landraces, which can be considered as proof of its importance to early and modern humans. It is worth mentioning that 99+% of all domesticated plants were developed by pre-modern farmers (Harlan 1975, Hawkes 1983). The African oil palm is frequently cited as one of the few modern domesticates (Zeven 1972).

How then can domestication of a palm be proven, since few are abandoned in their native habitat and left to reproduce and even fewer of these are reported? During the domestication process a variety of morphological characters and ratios between diverse components of the reproductive and vegetative biomass or within the reproductive organ are modified, some of which are: increased proportion of usable product in the harvestable product (higher fruit to bunch ratio [Hartley 1977] or higher mesocarp to fruit ratio [Clement 1988]); increased proportion of harvestable product in the year's biological growth (increased Harvest Index, Corley 1983); reduction or elimination of spines; increased ease of propagation; more rapid germination; reduced natural dispersal ability (i.e., fruit do not abscise readily from the rachilla or are damaged by falling from the tree). Harlan (1975) and Hawkes (1983) summarize the modifications expected during domestication, although, obviously, not all modifications will be found in each species. In the following section each major palm is examined and an attempt made to quantify its degree of modification due to domestication.

The Major Palms

Areca. Bavappa et al. (1982) reviewed areca, although they did not specifically discuss its domestication. Areca has been cultivated for 2–3,000 years in India (Rao 1982), where it is a "recent" introduction. Therefore, the history of its interaction with humans is probably at least twice this, possibly as long as the date. Rao (1982) concludes that areca may have originated

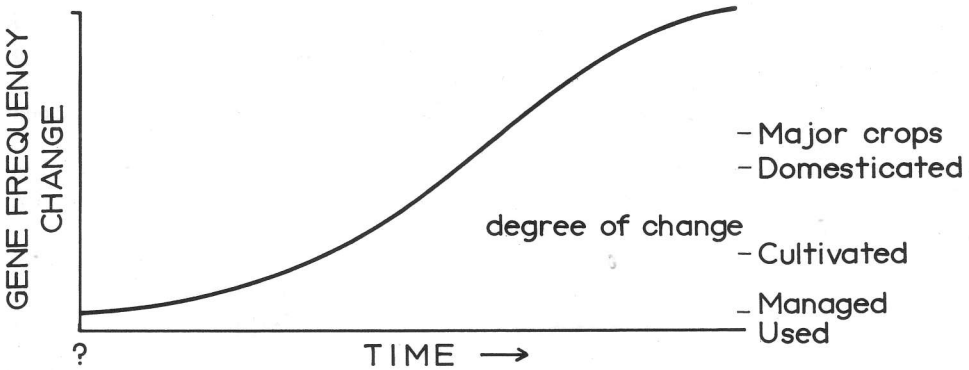

Fig. 1. A schematic representation of the plant genetic continuum from wild to domesticated. The area under the curve represents the degree of genetic modification due to human selection to make the plant conform to agricultural and social requirements.

in the East Indies (perhaps from the Philippines southward to Indonesia) and cites several botanical varieties described by Beccari (1919). The majority of closely related *Areca* occur in the East Indies and adjacent continent (i.e., Malaysia, etc.), which suggests a slightly expanded region as the center of origin. This wider origin is supported by Purseglove (1985).

From Bavappa and Nair's (1982) discussion of current breeding efforts, the characters most likely to have been modified by selection can be identified: larger nut size, better quality nut (meaning both in flavor and in active ingredient), higher fruit/bunch ratio and probably more bunches per tree. Unfortunately these authors do not provide enough information to quantify the modifications in areca over the millenia. They do, however, compare areca with *A. triandra* Roxb. ex Buch.-Ham., a related species occasionally used as a masticatory also. Although this species is not closely related (it has 3 stamens, rather than 6 [N. W. Uhl, pers. comm.]), it provides a rough comparison with areca to estimate modifications due to selection.

A. triandra has a 4 g fruit, while other areca fruit attain 43 g, a difference of about 1,000%; this relatively small difference is probably due to selection of the kernel rather than the mesocarp. *A. triandra* has about 500 fruit/bunch, while areca has about 200 (the negative correlation between fruit number and fruit size is common). If we assume a rachis weight of 300 g for *A. triandra* and 400 g for areca, these values give fruit to bunch ratios of about 87% and 95% respectively.

Bavappa and Nair (1982) analyzed several groups of areca populations with discriminant analysis and their results suggest the existence of landraces (although they do not use this term). A clear discrimination of landraces in areca may prove to be difficult, as landraces have undoubtedly been partially masked by continued and frequent migration of genotypes among areas of intensive selection in south and southeast Asia.

Given the time span of known interaction with humans in India (assuredly much longer in its center of origin), the magnitude of modification due to selection and the probable existence of landraces in south and southeast Asia, the areca is considered a domesticate. One important doubt remains: do the apparent landrace populations depend completely upon human intervention for their genetic survival?

Coconut. Harries' (1978) excellent summary of the coconut palm as a domesticate identifies trends in morpho-genetic modification due to selection and postulates

the most and least domesticated types. The coconut's center of origin is in the East Indies, although it is impossible to define exactly. Harries identifies the long, angular, thick husked coconut as most primitive (*Niu kafa*) and the round, thin husked coconut as most advanced (*Niu vai*). He mentions several criteria of interest in defining Niu vai as domesticated:

1. The proportion of useable product in harvestable product increases from Niu kafa to Niu vai—the Niu vai has up to 50% more solid endosperm (100+% more liquid endosperm when immature) than the Niu kafa, as well as a reduction of about 50% in the proportion of husk in Niu vai.

2. Propagation is facilitated by more rapid germination in the Niu vai, averaging 60–80 days, while the Niu kafa takes as much as 200 days.

3. The Niu vai is not as resistant to damage as the Niu kafa, both in terms of damage to the fruit due to mechanical factors (falling from the tree, being pounded by waves on the shore, etc.) and damage to the germinating seedling. This greater fragility probably reduces natural dispersal ability.

4. The Niu vai has greater resistance to windstorms (because of their smaller stature) and to diseases. Resistance to lethal yellowing is found in Niu vai areas, although the disease has not been reported there!

Harries (1978) cites Sauer (1971) as arguing that the coconut should be considered a semi-domesticate, some populations of which are independent of humans while others are completely dependent. If some are completely dependent, then the species is domesticated by our definition. It is clear that Harries (1978) agrees with this position.

Purseglove (1985), however, cites the reestablishment of coconuts on Krakatau as proof of its natural dispersal ability after floating in ocean currents. Gruezo and Harries (1984) and Buckley and Harries (1984) reported that Niu kafa types are found in wild, self-sown situations in the Philippines and Australia, where Niu vai types would also be expected but are not observed. This suggests that the Niu vai requires human intervention for continued survival.

Date. Chevalier (1952) suggested that the date palm has been cultivated since the Neolithic (at least 10,000 years) and may have been domesticated in any of several areas from India to the Atlantic ocean, although Munier (1981) and Zohary and Spiegel-Roy (1975) support the Fertile Crescent as its center of domestication. Its precise origin is clouded by the ease with which it hybridizes with other species of the genus, so much so that it is impossible to identify an ancestral date (Chevalier 1952). Zohary and Spiegel-Roy (1975) mention the occurrence of wild and weed populations of date in many areas of the Middle East, which may have been involved in the domestication of the species. This means that not only the date but all related sympatric species are subject to introgression that can change their original characteristics. For example, Chevalier (1952) and Munier (1981) mention that *P. atlantica* Chev. (whose taxonomic status is uncertain—it may be a weed date [J. B. Carpenter, pers. comm.]) is cultivated in Morocco and has edible fruit. This may be the result of introgression with the date, however, although these authors do not address this possibility.

Two characters that differentiate the date from other cultivated palms are its dioecious habit (making it extremely heterozygous) and its long history of vegetative propagation. The dioecious habit makes mass selection less efficient than in monoecious species. On the other hand, vegetative propagation can fix good qualities at once and allows the development of clones, some of which have existed continuously for 800 or more years (Goor 1967). Selection within widely planted, popular clones can result in rapid modification of any desired characteristic (Zohary and Spiegel-Roy 1975).

Although much has been written about the date, an estimate of modifications due to domestication is difficult. Oudejans (1976) even suggests that it is impossible to infer these, beyond increased succulence and ease of vegetative propagation. Zohary and Spiegel-Roy (1975) disagree, but do not give quantitative data. I think that fruit size is also a criterion, as in other palms.

From earliest human management and cultivation of date, it is probable that fruit size, succulence and sweetness were selected for. FAO (1982) reports that fruit vary from 2 to 60 g, while seeds vary from 0.5 to 4 g. Therefore, pulp (mesocarp + exocarp) to fruit ratios can be calculated; these vary from 75 to 93% within the species. It is safe to assume that smaller fruit, with lower pulp/fruit ratios are generally more primitive than larger fruit, with higher p/f ratios. J. B. Carpenter (pers. comm.) cautions that this may not always be true, however, as some highly prized clones have small, dry fruit. Nonetheless a 2 gram fruit is probably similar to a primitive date and the difference between it and a 60 g fruit is 3,000%, which is the same order of magnitude as in areca and pejibaye.

In general, vegetative propagation has become easier and fruit size and quality have been improved. Zohary and Spiegel-Roy (1975) point out, however, that vegetative propagation has drastically reduced the number of sexual generations under cultivation/domestication. They suggest that the few changes under domestication noted here probably do not make the date dependent upon humans, as a single generation of open pollination would produce abundant segregation, including wild and weed types of date. While this is doubtlessly true for seedling dates, I consider the date to be completely domesticated because a given clone is completely dependent upon vegetative propagation for its continued survival.

Oil palm. To Harlan (1975, p. 65–66) the oil palm is an "intermediate" species:

> "Wild stands occur near the edges of the forest, but the plant is not sufficiently tolerant of deep shade for it to grow in dense forest. However, as shifting cultivation has reduced the high forest to bush, the oil palm has invaded the forest zone. In the process of shifting cultivation, the farmers slash the bush during the dry season and burn it, reducing the vegetation sufficiently that one or two crops can be grown in the burned area. The oil palm, however, is spared. As a result, the palm is encouraged, and over a period of years, stands become thicker and thicker. In some areas, very extensive stands of oil palm developed without anyone ever purposely planting a seed.
>
> "Here we have a plant that is encouraged, disseminated, harvested, and selected without anyone deliberately planting a seed. Is the oil palm in indigenous agriculture a cultivated plant or not? In this century, it has become a very important plantation crop in the wet tropics, its hectarage is increasing, and the yields of new hybrids are very high. Under plantation conditions, the high-yielding hybrids are domesticated races, but under traditional systems, the status of the plant is very different.

By our definition the oil palm is a managed species in most of its natural distribution. Gene frequencies can be modified by selection during management, however, as shown by the high proportion of "tenera" palms where "dura" palms would be expected (Rajanaidu et al. 1979). Much of the increase in oil palm yields during this century is due to the use of "tenera" palms (Hardon 1976), although the Deli Dura variety's yield potential has been increased by 60% through breeding (Hardon et al. 1987).

Harlan's statement about the modern high-yielding hybrids being domesticated races is similar to the case of the date clones that depend completely on human intervention for their genetic integrity. Improved hybrids would certainly reproduce if returned to the oil palm's native habitat in Africa, although genetic advances would be slowly lost, mostly as a result of change in "tenera" frequency (R. H. V. Corley, pers. comm., estimates that tenera palm frequently would fall from 100% to 20% in 16 generations).

One datum that suggests the semi-

domesticated state of the oil palm is Rajanaidu et al.'s (1979) inability to distinguish landraces using discriminant analysis. Clement (1986) found that discriminant analysis was exceptionally useful in discriminating among landraces of pejibaye, as did Bavappa and Nair (1982) with areca, so that Rajanaidu et al.'s inability to distinguish them can only be due to the lack of landraces.

From the above considerations I conclude that the oil palm was a managed, incipiently domesticated species at the beginning of this century and that it may now be considered a domesticate because of the modern hybrid varieties and the trend towards clonal propagation (Hardon et al. 1987). Zeven (1972), with slightly different reasoning, arrived at the same conclusion.

Pejibaye. Sauer (1959) stated that pejibaye is domesticated, based upon the lack of an identifiable ancestor or wild population of the species and the fact that it only occurs where planted and does not survive long after being abandoned. The latter observation is in agreement with our definition of a domesticated species. My observations on some abandoned plants near Manaus suggest that as the forest canopy shades pejibaye crowns, fruit yield is progressively reduced to zero. Seedling growth in forest shade is extremely slow—only a few etiolated leaves/year. These observations suggest that genetic survival is improbable for pejibaye without human intervention.

The pejibaye is the only domesticated American palm (Clement 1988) and may have originated in southwestern Amazonia where *B. dahlgreniana* Glassman (syn. *Guilielma microcarpa* Huber) is native (Corner 1966, Clement 1988). Huber (1904) and Mora Urpi (1984) suggest that pejibaye is of hybrid origin, although their reasoning could also be explained by introgression with related species (Clement 1988).

Mora Urpi (1984), Clement (1986) and Mora Urpi and Clement (1988) have identified 10 landraces, organized into three racial groups based upon fruit size: "microcarpa" with 15–25 g fruit, two landraces; "mesocarpa" with 25–70 g fruit, 6 landraces; and "macrocarpa" with 70–200+ g fruit, two landraces. They consider the "microcarpa" to be domesticated but least modified by selection, while the "macrocarpa" are most modified.

Clement and Mora Urpi (1988) identified several trends from "microcarpa" to "macrocarpa" in vegetative and reproductive modifications that are those expected during domestication:

1. Trunk diameter and internode length become progressively smaller, which implies reduced vegetative biomass that could be repartitioned to increased reproductive biomass (i.e., higher Harvest Index).

2. Increased bunch weight (3+ kg to 8+ kg averages).

3. Increased fruit to bunch ratio (90% to 95%).

4. Increased fruit weight (15 g to 115 g averages [Clement (1988) mentions a 2,000% increase, but if calculated as done here with date and areca this would be closer to 5,000%: ancestral type fruit from *B. dahlgreniana* average 2 g, advanced fruit from the Vaupés landrace average 113 g]).

5. Increased pulp to fruit ratio (85% in "microcarpa" to 97% in "macrocarpa" landraces).

The least modified landraces have higher oil contents, while the more advanced are exceptionally rich in starch, which helps account for the very large increases in fruit size. Some landraces also have very high frequencies of plants without spines on the trunk and leaves, especially the Pampa Hermosa "mesocarpa" landrace.

Clement et al. (1989) showed that *B. dahlgreniana* fits nicely at the primitive end of this continuum for most of these characteristics, as well as germinating much more slowly (6 months vs. 2 months for

pejibaye). They hypothesize that high oil levels may have been the original attraction of pejibaye, because these are very high in *B. dahlgreniana* (to 60% dry mesocarp). This contrasts with Sauer's (1959) idea of starch being the original attraction.

As noted, I conclude that pejibaye is a completely domesticated palm. Because the modifications mentioned are so extensive and there are no indications of vegetative propagation (Patiño 1965), the time scale for this domestication must be at least as long as that for the date, perhaps longer. I think that it is safe to conclude that pejibaye started being managed, perhaps even cultivated, before the end of the last glacial event (12,000+ years ago).

Which Are "Most" Domesticated?

This question is extremely difficult to answer because there are different criteria for each palm, although I have tried to highlight similarities. One major criterion must be inability to survive without human intervention, as this is the most advanced stage in the domestication process. The whole pejibaye landrace complex clearly meets this criterion, as do the Niu vai coconuts and the date clones. The oil palm hybrids can probably survive but would slowly degenerate. I do not have data about areca.

Another important criterion is the existence of landraces within the species. Pejibaye and coconut surely meet this criterion and areca appears to, although this is an inference from the literature. The date clones can be thought of as extremely uniform landraces. The advanced oil palm hybrids are moving in this direction and the new tissue culture clones will meet this criterion.

Fruit size and quality modifications are also criteria. Pejibaye shows the greatest modifications in size, followed by date, areca and coconut. Coconut and areca are somewhat different, however, as it is the endosperm that is the useful product: this is energetically and physiologically difficult to increase in size beyond the limits that might compromise successful reproduction. Oil palm modifications are due principally to modern selection and the use of the "tenera" type and are still modest compared to the others.

Based upon this review, I am inclined to put these five species in the following order of most to least domesticated: pejibaye, coconut, date, areca, oil palm. Pejibaye first, because it shows the largest increase in fruit size; coconut second, because of smaller increase and the prevalence of Niu kafa types; date third, because only vegetative propagation maintains the fruit modifications noted; areca fourth, because of the doubts about dependence upon humans; oil palm last, because it is just becoming a domesticated species.

Are There Others?

Because of imprecise or varying definitions of domestication, other palms have been called domesticated at one time or another. Solid data about these species are scarce, inaccessible or non-existent, however. The four species mentioned are, or have been widely used or cultivated and perhaps domesticated in the past.

Sago (Metroxylon sagu *Rottboel*). There are two sago morphotypes, differentiated by the presence or absence of spines. Although the lack of spines might suggest domestication, Harlan (1975) considers sago to be an intermediate species, since the spineless populations are maintained by management rather than long term genetic modification. I agree with Harlan more because the spines are apparently the only character modified by management and because the species is not cultivated.

Palmyra (Borassus flabellifer *L.*). Davis and Johnson's (1987) excellent review of the palmyra does not even hint at a possible domestication. Due to its great usefulness,

it is a species that might have been genetically modified during the millenia of its interaction with humans. D. V. Johnson (pers. comm.), however, considers palmyra to be a managed species by our definition.

*Talipot (*Corypha umbraculifera *L.)*. Corner (1966) claims that the talipot is unknown in the wild. If this is true, the talipot may have been domesticated at one time and have fallen into disuse. This species needs further investigation.

*Doum (*Hyphaene thebaica *(L.) Mart.)*. Corner (1966) mentions that the doum palm was sacred in Egypt and appears to have been extremely important both in the ritual and the economy of the pharaohs. Again, I have found no information about its possible domestication.

With this short presentation, I hope to have stimulated some discussion of domestication in palms and hope that Principes might become a forum for continued discussion, with new and old data made available to us all. The history of domestication in the major palms can guide the domestication of new species, especially the many Neotropical palms that are currently being studied (i.e., *Acrocomia* spp., *Astrocaryum* sp., *Euterpe* spp. and *Jessenia bataua* (Mart.) Burret).

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