



Floating, Boating and Introgression: Molecular Techniques and the Ancestry of Coconut Palm Populations on Pacific Islands

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Abstract

It has previously been suggested that the coconut populations of Pacific islands arose by introgression between wild types that disseminated by floating from an ancestral center of origin and domestic types that were brought in small boats from a center of domestication. This simplistic model is complicated by the subsequent movement of the introgressed germ plasm in large boats, particularly following the industrialization of coconut growing for copra in the late 19th century. Although copra is no longer an attractive article of trade, the coconut palm continues to be an attractive eco-amenity for the tourist industry. The occurrence of epidemic lethal diseases in previously important copra producing areas, and the increasing opportunity for pathogens and vectors to be transmitted by innocent tourists and uninformed landscape developers is a potential threat to coconuts and other palm species. It has also been suggested that disease resistance arose during domestication. If that is so, then the ability to use molecular techniques to characterize coconut varieties will help accelerate selection, which presently can only be based on survival in long-term field exposure trials.

Flotación, Navegación e Introducción: las Técnicas Moleculares y el Antepasados del Coco en las Islas del Pacífico. Se ha sugerido previamente que las poblaciones de coco en las islas del Pacífico surgieron por introducción entre tipos silvestres que se diseminaron por flotación desde un centro de origen ancestral, y tipos domesticados que se trajeron en barcos pequeños desde un centro de domesticación. Este modelo simplista se complica por la diseminación en embarcaciones grandes del germoplasma derivado de tal introducción, particularmente a raíz de la industrialización de la copra a finales del siglo XIX. Aunque la copra ya ha perdido su atractivo comercial, la palma del coco se ha mantenido como un elemento importante del entorno ecológico y el paisaje de zonas turísticas. La aparición de enfermedades letales

epidémicas en zonas cultivadas con coco, y la oportunidad creciente para que los patógenos y vectores involucrados sean dispersados accidentalmente por turistas y paisajistas, representan una amenaza potencial para esta y otras especies de palmas. Se ha sugerido también que la resistencia a enfermedades en el coco surgió durante su domesticación. Si este es el caso, entonces la aplicación de técnicas de genética molecular en la caracterización de variedades de coco ayudar a acelerar los procesos de selección convencionales en este cultivo, los cuales actualmente dependen de la realización de pruebas de exposición a largo plazo en el campo.

Introduction

Throughout the humid tropical Pacific, the coconut palm, *Cocos nucifera* L., is found in the wild and in cultivation, on atolls, high islands and the continental rim coastlines, from sea level to hilltops (but fruiting poorly above 1000m). In fact it has world-wide distribution at tropical and sub-tropical latitudes, where altitude (affecting temperature), soil, rainfall or groundwater allow. It grows in more than 86

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Ethnobotany Research & Applications 2:37-53 (2004)

countries which can be grouped into eight distinct coastal/oceanic regions on four continents (Harries 2001). This treatment concerns itself mainly with about twenty Pacific territories from Indonesia eastwards, and only slightly with the nine Latin American countries whose Pacific coast coconut palms probably derive from introductions made just 500 years ago (Zizumbo et al. 1993).

The coconut palm generally produces a new leaf every three or four weeks and, a few years after seed germination, each leaf axil of the young palm has the potential to produce an inflorescence. Regular monthly flowering continues until the palm becomes senile, after 80 years or more. Inflorescences bear both male and female flowers and self- or cross-pollination ensures year-round production of anything from a few to more than one hundred seeds per palm. At any time during the year, the adult palm carries bunches of nuts at every stage of develop-

ment. Branching or suckering is rare (perhaps following damage) and the coconut palm can only be propagated naturally from seed or from zygotic embryos in vitro (but laboratory techniques for clonal propagation through tissue culture are not yet perfected).

The well-known fruit is protected by a thick fibrous husk and the entire fruit can fall from the tallest palm without damage. Germination may then occur sometime in the next three to seven months, during which period the fruit can be carried by people or by sea currents over long distances to new locations. The coconut palm owes its world wide distribution to natural dissemination by floating and to the nautical, mercantile and agricultural activities (Harries 2001) engendered by the multiplicity of uses of all parts of the plant (Table 1). For these reasons the coconut palm has met basic human needs in the Pacific and Indian Oceans for food, drink, fuel and shelter long be-

Table 1. Traditional, agro-industrial and ecological uses of various parts of the coconut palm.

Parts of palm	Edible uses	Traditional	Agro-Industrial	Ecological
Germinating fruit	Haustorium (or apple)	+	-	-
Sap obtained by tapping inflorescence	Toddy (unfermented)	+	-	+
	Sugar (by boiling)	+	-	+
	Alcohol (by fermentation & distillation)	+	-	+
	Vinegar (by fermentation)	+	-	+
Immature female flowers	Pickled (in vinegar qv)	+	-	-
Immature husk & shell (endocarp)	Chewed like sugar cane (not bitter)	+	-	+
Water from immature (tender or jelly) fruit	Sweet, refreshing, uncontaminated, some with aromatic flavour	+	(+)	+
Mature endosperm	Jelly-like, filling nut cavity (makapuno type)	+	(+)	+
	Ball copra (dried unopened nuts)	+	+	+
	Coconut flour	+	+	+
	Milk & cream (oil emulsions)	+	+	+
	Edible oil (solid at low temperature or hydrogenated to ghee and margarine)	+	+	+
Unopened vegetative bud (destroys palm)	Heart of palm, palmito, Millionaire's Salad	-	-	+
Copra cake	Animal feed	-	+	-

Table 1. Traditional, agro-industrial and ecological uses of various parts of the coconut palm. (continued)

Parts of palm	Edible uses	Traditional	Agro-Industrial	Ecological
Medicinal Uses				
Water from immature fruit	Naturally sterile, isotonic substitute for blood plasma in emergency surgery; athletic rehydration drink; diuretic; diluent in artificial insemination	+	(-)	+
Oil, glycerine & monolaurin	Medicines, cosmetics, nutriceuticals, HIV/AIDS treatments	-	+	+
Industrial Uses				
Coconut oil	Lubricant (and anti-rust)	+	+	+
	Illuminant (stearine candles)	+	+	-
	Fuel (direct substitute for diesel with or without esterification)	-	+	+
	Ingredient for soap, shampoo, cosmetic	+	+	+
	Glycerine for high explosives	-	+	-
Shell (endocarp)	Flour (plastics filler and metal polish)	-	+	(-)
	Charcoal (excellent for activation in gold recovery & gas production)	-	+	+
	Directly burnt as fuel	+	+	-
	Half shell as a container (collecting latex when rubber tapping, etc.)	+	+	+
Husk	Fibre (coir) for ropes, mats & geotextiles (stabilise road foundations & embankments)	+	-	+
	Cocopeat for horticultural soil mixtures	(-)	(+)	+
Stem	Timber (lumber, roof shingles, furnature, flooring, etc.)	+	+	+
Root	Minor uses as toothbrush allopathic remedies	+	-	-
Inflorescence	Minor use as brushes and fuel	+	-	-

fore recorded history began (Alzina 1668, Moore 1948; Child 1974; Ohler 1999) but in the Western Hemisphere for the last 500 years only (Zizumbo et al. 1993). The coconut was a major export crop for Pacific ocean islands for more than 100 years, when used to produce copra, and other industrial raw materials. Its ascendancy at the beginning of the 20th century, driven by commercial and colonial interests, resulted in large plantations and also in cash cropping by small farmers, has declined within the last 40 years. The coconut is called the "Tree of Life", with "as many uses as there are stars in the sky". But, whilst this might remain true on an atoll where very little else can grow, almost every use of the coconut can be substituted from another crop, or from petroleum based plastics. Such competition has virtually eliminated the large plantations and 90% of commercial coconut production now comes from small-holders, especially as for inter-cropping where the palm provides excellent shade for crops such as cocoa (*Theobroma cacao* L.). In many of the less favored locations (for example most Pacific islands are at a distance from the major markets) the coconut is reverting to a subsistence crop (Massal & Barrau 1956). But optimists hope that coconut oil will have a secure future as a source of nutriceuticals and, such is the flexibility of the prince of palms that, although it may never again be the mainstay of migrating Polynesian populations or of multi-national (neo-colonial) agro-industrial corporations it remains a desirable amenity plant, and a symbol of the tropics for the both the tourist and the ecotourist.

The most common use is as a source of vegetable oil rich in lauric acid (equaled but not excelled by palm kernel oil from the African oil palm (*Elaeis guineensis* Jacq.) but under future threat from genetically modified rapeseed (canola) oil (*Brassica napus* L.). The kernel of the coconut is dried to produce copra, from which oil is extracted, but this is a sunset industry and is being replaced by direct oil extraction methods. Soybean (*Glycine max* (L.) Merr. producers advertisements against "tropical oils" is recognized as biased (Enig & Fallon 1998-9) and the health benefits of the coconut's medium chain fatty acids and derivatives such as monolaurin are being applied in HIV/AIDS treatment (Enig 1998). Coir fibre extracted from the husk has traditional importance where coconuts grow but although coir mooring lines have been widely displaced by nylon ropes, geotextiles and cocopeat are valuable eco-friendly uses. Shell (particularly for charcoal) and stem (for timber) also have economic value. But the one product, for which coconut is supreme above any other plant is the portable, palatable and potable water from the immature nut. It was as a source of water that Pacific coconut populations were first important and this could yet see a commercial revival.

Pacific Coconut Populations

To all the uses in Table 1 can be added an even more extensive list of names for coconuts (Appendix 1). The list, of about 340 names gleaned from a variety of sources and covering about 30 Pacific locations (over 100 from Indonesia alone), is far from complete. The data are not claimed to be exhaustive but merely serve to show that everywhere coconuts grow, distinctive individual palms are given names and groups of palms are named as if they were recognizable varieties. Botanically, all that can be said is that *C. nucifera* is a monotypic species and that sub-specific forma and terms like variety, cultivar, ecotype, clade, etc., are needed when trying to resolve the variability into manageable concepts for botanists and agriculturalists. The only method of classification based on morphology to produce consistent results, irrespective of environment, has been fruit component analysis (FCA) in which the proportion of husk in the whole fruit and the proportions of water, shell and endosperm in the de-husked nut are compared (Foale 1964, 1987, Whitehead 1966, 1968, Harries 1978, 1981a, Krishnamoorthy & Jacob 1984, Raveendra et al. 1987, Gruezo 1990, Zizumbo et al. 1993, Ashburner et al. 1997a, Vargas & Blanco 2000).

It is to this situation that the application of DNA techniques such as RFLP, SSR, RAPD, AFLP, ISTR, and STS have to be applied. It is the purpose of this paper to show how traditional sources of geographical, historical and ethnographical information can also be taken into account when interpreting laboratory gel/plate data generated by these molecular techniques.

The ancestry of Pacific coconut palm populations will be dealt with under the following sub-headings:

- Floating - the evolution by natural selection of a wild type and arrival in the Pacific by floating from a non-Pacific center of origin.
- Boating - human selection of domestic type in a specific western Pacific location followed by dissemination by ancestral Polynesians to the eastern Pacific (and elsewhere).
- Introgression - interbreeding between wild and domestic types followed by nautical, mercantile and agricultural dissemination of introgressed populations.

Floating - natural selection

As Last (2001) has pointed out, ". . . interest in coconut palm owes much to the ability of its fruits to tolerate immersion in salt water - a feature rare among tree crops". There is no question that the coconut can float in sea water and germinate on the beach when washed above the high water line. Any question must be directed at the effectiveness, or otherwise, of such a method of dissemination. Clearly floating depends on buoyancy and, in the coconut, this is not only the result of a thick husk but, because the kernel (endosperm) is limited to a 12mm layer lining the shell (endocarp), there is a large cavity. The liquid which partially fills this is absorbed as the fruit matures

and it floats high in the water unless the husk becomes saturated (Edmondson 1941; Rock 1916).

The success of natural dissemination must depend on a balance between fruit number and fruit size. Further selection for one would be antagonistic to the other and it was proposed by Harries (1978) that a continuous cycle of natural selection could produce a coconut palm with the following characteristics: perennial growth (50-100 years), few fruit (50-100 per year), large fruit size (1-2kg), thick husk (up to 70% fresh weight), much endosperm (200-300g), slow germination (more than 200 days). None of these parameters exceed the natural range found in the Palmae (Arecaceae), yet taken together they represent a formidable dispersal mechanism. They also represent, very closely, the characteristics of varieties found as far apart as Palmyra Atoll in the Pacific and the Seychelles Islands in the Indian Ocean (Sauer 1971). It had been suggested that the speed of germination was a characteristic of taxonomic significance (Whitehead 1965) and germination rate was subsequently related to the maintenance of genetic uniformity of coconut populations on remote oceanic islands, despite founder effects, after long distance dissemination by floating (Harries 1981b).

There was no doubt in the minds of 16th century Europeans who sailed across the Pacific that "... the germs of these trees were brought by the waves from unknown regions" (Martyr d'Anghiera 1552) but it was not until an experiment was made in Pearl Harbor (shortly before the outbreak of the Pacific theater of the Second World War) that Edmondson (1941) showed that coconuts were capable of developing after having floated in the sea for periods of up to 110 days and gave an estimate of the distance that might be traversed in that time, if carried by a favorable current (of 1 knot or 0.5 m/s), as about 3,000 miles (or about 4,800 km).

These results have been accepted uncritically by other authors whether supporting or refuting natural dissemination by floating (Sauer 1971, Dennis & Gunn 1971). Brumman (1944), seeking the origins of coconuts found on the Pacific coast of America in the 16th century, suggested, on the basis of Edmondson's experiment, that coconuts would take about 7 months to float on the Pacific Equatorial Countercurrent from Palmyra Atoll. The question of whether coconuts floated to the west coast of America remains open (Ward & Brookfield 1992), but natural dissemination over shorter distances elsewhere in the Pacific Ocean is a reasonable assumption.

At one time it was thought that the ancestors of modern *C. nucifera* had arrived in the Western Pacific area by long distance dispersal along a southern route from America, with a fossil (*Cocos zeylandica*) in New Zealand as a remnant of such a pathway (Purseglove 1972). The concept of a southern route is an unnecessary complication. An

origin for the whole Cocoeae tribe in western Gondwanaland seems most compatible with the present day distribution (Uhl & Dransfield 1987). The tribe probably differentiated shortly before the break up of that super-continent. Members radiated and became very diverse in the Americas; some rafted on the African and Madagascar Plates, where they survive to the present day (Dransfield 1989); others rafted on the Indian plate, where they are now extinct (fossil stem (Sahni 1946) and fossil fruit (Kaul 1951) have been identified as *Cocos* whilst coral and algae are recognizable in Himalayan rocks). With its ability to float the coconut became independent of plate tectonics for its dispersal. The wild type evolved by floating between the volcanic islands and atolls where these fringed the continental plates and not on the land masses at all. The coasts and islands of the Tethys Sea could have been the ancestral home of the coconut, from where it dispersed by floating to other islands in the Indian Ocean and from there into Pacific (but not into the Atlantic) Ocean (Harries 1990). The robber crab, *Birgus latro* L., probably used this coconut for its own dispersal over the same area (Harries 1983) taking advantage of the thick husk (rather than causing the thick husk as suggested by Chiovenda (1922 & 23)).

Boating - domestication in the Western Pacific

The distinction between a wild type coconut and a domestic type (Harries 1978) was developed in subsequent publications and the continental coast and larger islands of Malesia were proposed as the site for domestication (Harries 1990). It was argued that the coastal fishing communities that would be expected to be the first to come into contact with a naturally disseminated coconut would value it for one purpose in particular - as a source of liquid refreshment. The water in the immature coconut is not merely potable, it is very palatable and conveniently portable.

Natural selection and domestic selection also account for other differences between wild and domestic types, from fruit shape, plant habit and rate of germination to wind-storm tolerance and disease resistance (Harries 1978, 1981b, 1990, 1998, 1999). But although the theory may have received casual acceptance, there are some unanswered questions:

- How and where could non-agricultural, coastal fishing communities grow large coconut populations that would be isolated from recurrent retrogression from wild types continually arriving by floating?
- Why should selection pressure be applied just for drinking when other qualities, particularly husk fibres for coir rope production, call for diametrically opposing demands on selection?

The following explanation of these points depends on interpretations of geological events that may themselves be controversial. It has been suggested that catastroph-

ic sea-level rises were the result of a massive release of water following ice sheet collapse in the North American glacier lakes 8, 11 and 14 thousand years before present (Blanchon & Shaw 1995) and that these resulted in the submergence of a land mass equivalent in size to the Indian sub-continent which had been the center for the development of paddy rice by agriculturally-based civilizations (Oppenheimer 1998).

The area in question, which extended from the Thai-Malay peninsula in the west, Sumatra and Java in the south, east to Borneo and north to Vietnam and Cambodia, is shown in the map (Figure 1) by the 50m and 100m contour depths beneath today's mean sea level. The area of land that could have been above sea level prior to flooding is impressive but, more important is the fact that it would have been gently sloping to almost level and well watered by rivers coming from rain fed higher ground. These represent ideal conditions for agriculture. It would also have been located in that part of the Pacific where seasonal droughts can be expected and where tropical windstorms (cyclones) are ferocious. Large agricultural communities occur there today despite those conditions.

If an agricultural civilization did populate this extensive area then coconuts would have been grown as a fruit crop (not for copra or oil which were 19th century developments). And, once the coconuts had been taken hundreds of kilometers inland (probably by boat along the major rivers) they would be beyond the introgressive effects of the wild type coastal coconuts. To this day, wild type coconuts can be found around the periphery of this area, on the Indian Ocean coast of Thailand (Harries et al. 1982) and Indonesia (Koorders 1911, quoted by Harries 1990) or the Pacific Ocean coast of the Philippines (Alzina 1662, Gruezo & Harries 1984, Gruezo 1990) as indicated in Figure 1. Yet, except during seasonal droughts, the coconut palms would have been a minor source of drinking water in a land so well served by rivers and rainfall. Nor would it have been required for coir fibre where rattans and various forms of hemp were readily available where rope and twine were needed. Coconuts would have been used in food preparation, including fattening pigs and feeding chickens. The coconut palm was a fruit tree - the haustorium inside of the germinating nut is a sweetmeat for children, varieties with edible husk (even with edible shell

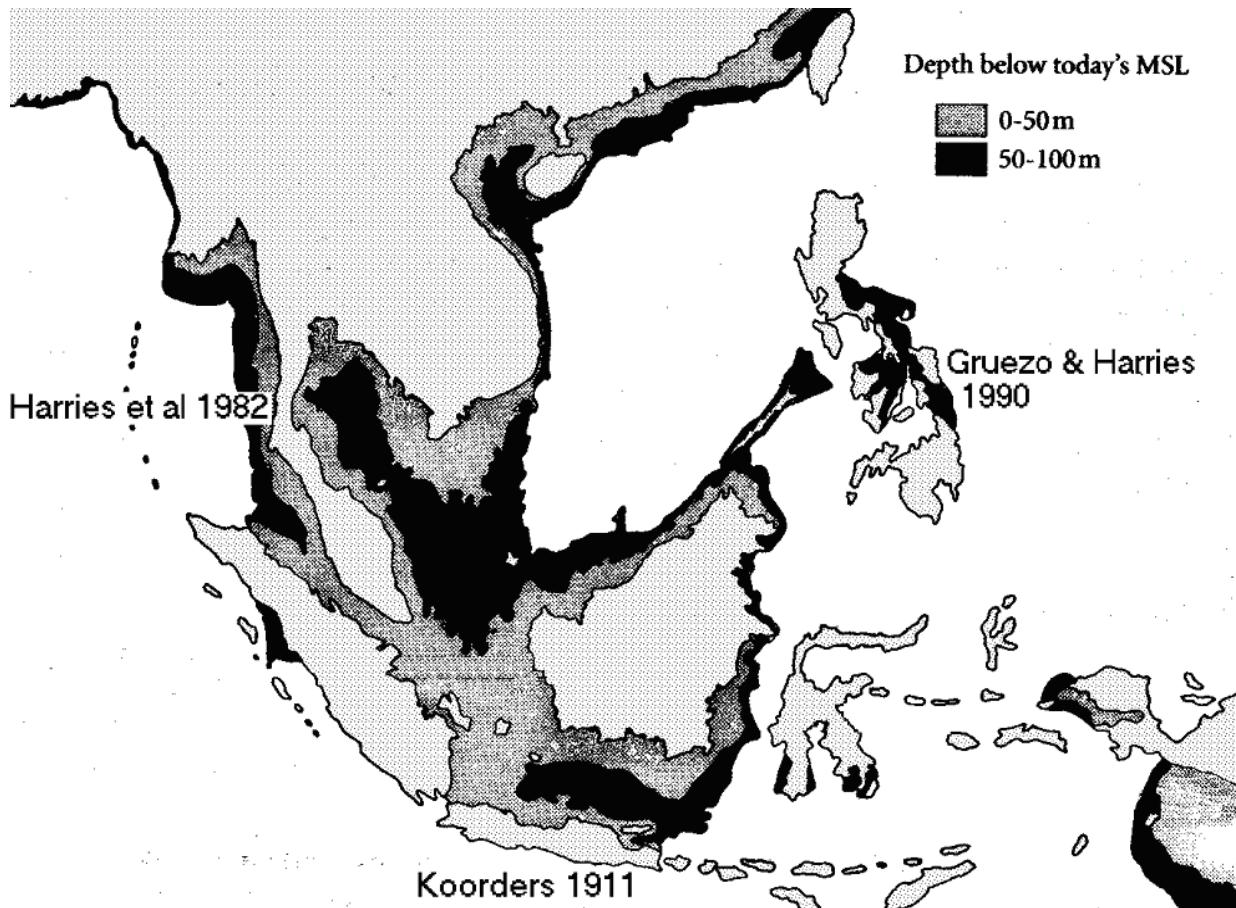


Figure 1. Area proposed for domestication of coconut in Indo-Malaysia.

when immature (Will McClatchey, pers. comm.) and with jelly-like endosperm (makapuno) would be popular.

After the initial catastrophic rise in sea level the area of land flooded by sea water it would have fluctuated as geological settling occurred but the process would have been progressive, extending over decades or even centuries (not the Biblical forty days and nights). In that period the coconut palms, which tolerate semi-saline groundwater conditions better than other plants, would have become immensely important to human population deprived of drinking water (Harries 1979). Early germination, while the fruit was still on the palm, would also be a desirable characteristic in area where fallen fruit might be washed away by flooding (Harries 1978, 1990). Palms surviving windstorms and epidemic diseases would account for the tolerance and resistance exhibited by the domestic type (Harries 1978, 1998, 1999).

Whether the ancestral Polynesians chose to migrate because of the flooding, or for whatever other reason, they would certainly carry selected, domestic types with them. This would account for these types being away from the coastline on Pacific high islands (like Rennell, Rotuma, Wallis, etc.) where wild type coconuts could only reach beaches or fringing reefs. People who chose to venture into the Indian Ocean would also have taken these selected types to India, Sri Lanka and Mozambique (Harries 1978).

Introgression - nautical, mercantile and agricultural dissemination

If the domestic type was carried to Pacific islands where the wild type was not already present then it would predominate but if the wild type was already present then introgression would occur. This was the explanation for the two forms being identified in Western Samoa (Harries 1978) a remote and relatively small island location, where coconut predates human occupation (Whistler 1992) where it would have been impossible to select simultaneously for both coir fibers (Niu kafa) and drinking water (Niu vai) types. Introgression accounts for the presence of the two contrasting type as individual palms in a single population. On the basis of fruit component analysis (FCA) data collected by many individuals from many coconut varieties in many locations it was possible to distinguish between predominantly wild and predominantly domestic introgressed types (Harries 1978, 1981a).

The dissemination of introgressed types for nautical, mercantile and agricultural purposes is recently described (Harries 2001) and need not be repeated here. What needs to emphasized is that within any introgressed progenies, three types may be found - the bulk of the population would be intermediate between the two extreme forms and these would be represented by a few individual resegregants, their actual numbers depending on the degree of initial introgression and subsequent founder

events and single generation selection for domestic purposes (fibre or water). The use of names like "Pacific Tall", "Polynesian Tall" or a "Fiji Dwarf" is no better (or worse) or more informative than using traditional names like "Niu vai", "Niu kafa", "Niu leka" (see Appendix 1).

Molecular Techniques

Attempts to classify coconut varieties and resolve the origin and evolution of coconut have not benefited from the pan-tropical distribution of this monospecific genus (Martius 1823-50, de Candolle 1884-5, Beccari 1916a, Chiovenda 1921, 1923, Werth 1933, Mayuranathan 1938, Fosberg 1960, Eden 1963, Mahabale 1976). Earlier classification systems described local populations in India and Sri Lanka in terms of their growth habit and physical appearance, fruit size and colour etc (Narayana & John 1949, Liyanage 1958). These systems, which called palms from Papua New Guinea *Cocos nucifera* var *typica* forma *novaguineensis*, fail to recognize that the introduced exotic form is the "typica" in the country it comes from. Thus "typica" is best regarded as an "introgressed" population with a general appearance that depends on whether the wild or domestic characteristics predominates. The "nana" and "javanica" are dwarf forms and therefore have predominantly domestic characteristics. That is so because they can only have arisen during domestication and been maintained because of their higher degree of self-pollination and their yellow, red, brown or green coloured leaf stalks and fruits. The predominantly cross-pollinated character of tall palms contrasted to the predominantly self-pollinated character of the dwarf was used to classify varieties as allogamous or autogamous but although this is important to commercial seed production it has shed no light on the ancestry of coconut palm populations. Finally, there is classification by geographical distance, that is based on the assumption that local populations are more likely to be closely related and exotic populations less likely to be so. With coconut this can give anomalous results, as when a palm that is called "Fijian Dwarf" in Australia is recognized in the Caribbean as "Malayan Dwarf" while the "Fijian Dwarf" in Florida is not the same as the "Fiji-Malayan" in Jamaica. Likewise the "Australian Tall" is reported from Indonesia but some Australian conservationists consider the coconut palm is non-indigenous and a weed (even though it was a strand plant before European settlement) (Bentham 1863-1878, Buckley & Harries 1984)

DNA profiling of coconut palms is relatively recent. The advantages and disadvantages of the various available methods have been reviewed for this species by Ashburner (1995, 1999) and Hamon (1999). In comparison with the robust but cumbersome RFLP (restriction fragment length polymorphism) analysis, methods for identification of markers from DNA sequencing of individual regions have become preferred tools in the characterization of coconut germplasm. Their ease of analysis has brought a recent

boom to their specific application in coconut. One of these marker types, the simple sequence repeats or microsatellites (SSRs), represent a novel and promising tool in this context. Because of the ability to be expressed as codominant markers, SSRs share the robustness of RFLPs for measuring heterozygosity. Additionally, these markers are very reproducible, enabling their parallel analysis in different laboratories, and the exchange of the resulting data. Its use in coconut is increasingly favored, and an initiative to develop and release a STMS kit for this species has recently been undertaken (Baudouin, in prep.).

Different authors have applied DNA profiling with coconut palms. Reference to these works and their corresponding methods can be found in Table 2. The objectives approached by those publications range from the implementation of particular techniques, to their application in the analysis of different materials. In a particular case, different DNA marker data were used to construct a first linkage map of the coconut palm (Herran et al. 2000).

Considered as a whole, the research so far performed on molecular characterization of coconut diversity supports previous conclusions from FCA analysis, regarding the major distinctions between coconut genotypes and their geographical origin. Also, the expected implications on the heterozygosity level of those genotypes, from what is known about their reproductive behavior, have found to be confirmed. More particularly, DNA profiling studies have already provided some insights. For example, Teulat et al. (2000) found that the populations from Tonga and Fiji generally had distinct alleles from those of the rest of the South Pacific. They considered that the high levels of polymorphism revealed by the SSRs indicate that popula-

tions could be identified and information on allelic diversity obtained with relatively few loci. Together with multiplexing of the SSRs chosen, the number of gels required for screening could, thus, be significantly reduced. The SSRs would be easily exchangeable between different groups and the data are more amenable for use in databases. For gene-banking purposes, given the amount of additional information obtained and the exchangeability of the data, they considered that SSRs would provide the most informative means for evaluating genetic diversity in coconut populations.

Discussion

Some of the molecular marker studies have supported parts of the floating-boating-introgression theory; none have disproved it, either in general or in specific aspects. The theory bearing on domestication can account for differences in plant habit and fruit form, in germination and growth rates, leaf lengths and flowering patterns, phytoplasma disease resistance, windstorm tolerance, etc. But a theory has to do more than account for previously unexplained differences. A theory is only as good as the predictions it makes. By considering and describing what the likely appearance and properties of a wild type coconut might be it was possible not only to show these might be found as far apart as Palmyra Island in mid Pacific and the Seychelles in the Indian Ocean (Sauer 1971, Harries 1978) but also to locate previously unsuspected specimens in Australia (Buckley & Harries 1984) and in the Philippines (Gruezo & Harries 1984) and on the Malay peninsula in Thailand (Harries et al. 1982). This helps to confirm reports in the literature of coconuts found growing wild in Australia (Bentham 1863-1878) and Indone-

Table 2. References on use of different DNA profiling methods for analysis of coconuts.

Codominant markers detected	RFLP (Restriction fragment length polymorphism)	Lebrun et al. 1998, 1999; Rohde et al. 1992
	SSR (Simple sequence repeat or microsatellite DNA)	Duran et al. 1997; Karp 1999; Perera et al. 1999, 2000; Rivera et al. 1999; Teulat et al. 2000
Mainly dominant markers detected	RAPD (Random amplified polymorphic DNA)	Anzizar et al. 1998; Ashburner & Harries 1999; Ashburner & Rohde 1994; Ashburner et al. 1997; Banks 1994; Cardeña et al. 1999; Duran et al. 1997; Rohde et al. 1999; Upadhyay et al. 2002; Wadt et al. 1999
	AFLP (Amplified fragment length polymorphism)	Perera et al. 1998; Rohde et al. 1999; Teulat et al. 2000
	ISTR (Internal sequence tagged repeat)	Anzizar et al. 1998; Duran et al. 1997; Rohde et al. 1995, 1999
	STS (Sequence tagged site amplification)	Rohde et al. 1999

sia (Koorders 1911) and elucidate previously reported, but unexplained, different forms attributed to different growing conditions or fertilizer response in Papua New Guinea (Dwyer 1938) or to a theory that coconut crabs caused hypertrophy of the pericarp resulting in thicker husk (Chiovenda 1921 & 3). Archaeological evidence in support of the domestication theory was subsequently located in Borneo (Harries 1981c) and Society Islands (Lepofsky et al 1992) but efforts to identify shell fragments in Papua New Guinea (Hossfeld 1948, Kirch, personal communication 1987) and Solomon Islands (Spriggs 1984) have been less successful. Currently shell fragments from Northern Marshall Islands are under consideration (Marshall Weissler personal communication).

Bridge Building

It now only remains to be seen whether the genetic fingerprinting techniques resolve the differences recognized by FCA but in finer detail. So far dwarf can be distinguished from tall but that is not very difficult to do by eye. Markers for domestic characters have been indicated (Ashburner & Harries 1999). Unfortunately there is a tendency to try to identify Indo Pacific and Asian types or differences between named types such as the Rennell Tall or Fiji Dwarf. This ignores the fact that the palms in such groups have a mixture of wild and domestic characters. If the introgression theory stands up to DNA techniques we should expect to find that within any of the named population both wild type and domestic markers will be found. A "pure" wild or domestic palm population, or even individual palm, will be very unlikely following the intense activity in planting and disseminating coconuts for nautical, mercantile or agricultural uses.

Despite the small number of publications on coconut molecular genetics it appears to be difficult for research workers to keep up to date. For example Teulat et al. (2000) writing as recently as October 1998 say "... there are conflicting theories regarding the origin and domestication of coconut" but refer to only two publications which had appeared twenty years previously. One of these (not cited here because it contains the preposterous statement that the most likely route for coconut to have reached West Africa was overland) was in a text book that had already been amended in an updated second edition (Smartt & Simmonds 1995). In contrast, the other theory mentioned by Teulat's group has been used to make predictions and has generally stood up to testing. It is, in fact the theory that has been put forward here in the expectation that DNA techniques, which cannot of themselves produce a theory of coconut evolution, will be used to test predictions such as:

- Palmyra coconuts are closely allied to those 3,000 km away on the Seychelles in the Indian Ocean.

- Rennell and Rotuma coconuts share DNA markers with Niu vai in Samoa and with coconuts from Bali in Indonesia or the Ka Loke in Thailand.
- Dwarf forms in India and Sri Lanka of common ancestry with those in Malaysia, Indonesia or the Philippines.
- The Niu leka is a compact habit tall rather than a dwarf

The future looks interesting for unraveling the coconut story but only if ethnobotany is involved.

Acknowledgments

Dedicated to the memory of Jack Doyle (1944-1999), who added the coconut palm to his other interests when he met and married Gabrielle Persley. The coconut, once so important in the social economy of the Pacific region, for the survival of the pioneer settlers and later as the primary cash income of their descendants, is now marginalised by the present dominance of the oil palm and threatened by the future imperative of genetically modified rapeseed. Nevertheless, as long as there are people like Jack, to encourage those who try to relate molecular biology and traditional knowledge, the coconut will continue to be the prince of palms in the Pacific.

The authors publish with permission of their respective organizations but the opinions expressed do not imply any opinion whatsoever by those organizations. Thanks go to Roger Ashburner (ISIA), for reviewing the drafts and to members of the Internet Coconut Cultivar Reference Archive (ICCRA) email discussion group <http://www.yahoogroups.com/iccra> and in particular Lalith Perera (CRI, Sri Lanka), Alan Meerow (USDA-ARS-SHRS) & Mike Foale (CSIRO retd) for free and frank exchange of information, views and opinions. The senior author would particularly like to thank John Dransfield (RBG) for his continuing interest in the subject and to Barbara Pickersgill and Will McClatchey for the invitation to make this presentation.

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Appendix 1. Vernacular names of coconuts.

Location	Vernacular	Location	Vernacular
Caroline Islands	Thifow Tall	Indonesia	Cidapap
Cook Islands	Nu Araketa		Cistiformis
	Nu Kura		Dilie
	Nu Mangaro		Fragilis
	Nu papua red dwarf		Grokgak
	Nu tea		Holland Giant
	Nu uri		Holland King
Fiji	Fiji Dwarf		Igo Duku
	Fiji Medium Round		Ilo-ilo Tall
	Fiji Ringed		Inobonto IV/A
	Fiji Tall		Java Tall
	Long Tongwan		Jepara Tall
	Niu Damu		Jombang Dwarf
	Niu Dina		Kalapa Babi
	Niu Kitu		Kalapa Bali
	Niu Ni Magimagi		Kalapa Besar
	Niu Vula		Kalapa Beureum
	Rotuman Tall		Kalapa Bokoe
French Polynesia	Cook Is Green Dwarf		Kalapa Gading
	Fiji Yellow Dwarf		Kalapa Gading Hedjo
	Haari erere		K Gading Koneng
	Haari oviri		Kalapa Gendjah
	Haari teitei ordinaires		Kalapa Idjo
	Haari ute-ute		Kalapa Kasoemba
Guam	Bibola		Kalapa Kenja
	Cannon (Canuon)		Kalapa Kepating
	Chaca		Kalapa Lansa
	Dagua		Kalapa Manis
	Lapugua		Kalapa Merah
	Manila		Kalapa Parang
Indonesia	Aertembaga Tall		Kalapa Pinang
	Alba		Kalapa Poejoe(h)
	Angustifolia		Kalapa Poetih
	B. Genteng		Kalapa Radja
	Bali Tall		Kalapa Sikat
	Bali Yellow Dwarf		Kalapa Tawar
	Banyumas		Kalapa Teboe
	Banyuwangi Tall		Kalapa Tjoktjok
	Batu Kapal		Kalasey Tall
	Bawang		Kalbar I/1
	Beji Tall		Kebumen I
	Boa II/4		Kelapa Gading
	Boyolali Tall		Kelapa Kopyor
	Bulan		Kelapa Linin
	Calappa Capuliformis		Kelapa Pujuh
	Calappa Cythiformis		Kelapa Radja
	Calappa Lansiformis		Khina-1
	C Machaeroides		Kinabubatan Tall
	Calappa Pultaria		KT II
	Calappa Pumila		Kubu Tambakan
	Calappa Regia		Lansiformis
	Calappa Rutilla		Lolak V/B
	Calappa Saccharina		Lubuk Pakam Tall
	Calappa Vulgaris		Luwu I
	Callappa Canarina		Macrocarpa
	Capuliformis		Machaeroides

Appendix 1. Vernacular names of coconuts. (Continued)

Location	Vernacular	Location	Vernacular
Indonesia	Magelang Mapanget Tall Marinsow Tall Microcarpa Nias Green Dwarf Nias Yellow Dwarf Nior Gading Palu Tall Pandu Tall Pangandaran Tall Paslaten Tall Poigar Budiday Polmas Preciosa [pretiosa] Pungkol Tall Raja Dwarf Rubescens Rutila Saccharina Salak Dwarf Sawarna Tall Sea Tall Silian III/A Stupposa Tacome Takome Tall Talise Tall Tebingi Tinggi Dwarf Tenga Tall Ternate Brown Tontalete Tall Viridis Wusa Tall	New Caledonia	Lifou Tall New Caledonia Tall Nu Oua Wen Nufella Nugili Nuhimi Kupin Nuwallis Nuwe Hung Niu Fisi Niu Gau Niu Hiata Niu Kini Niu Leku Niu Malua Niu Pulu Niue
Kiribati	Christmas I. Tall Marshall Is Dwarf Te ni	Palau	Bertachel Emadech Eriiech Minado Oilol Ongchutel To Tobi Emadech Dwarf Turang
Line Islands	Ninigaun	Papua New Guinea	Bougainville Tall Bronze Dwarf Gazelle Tall Karkar Tall Kokosnas Madang Brown Dwarf Markham Valley Tall New Guinea Brown Dwarf
Loyalty Is	Nu fell Nu gilli Nu himikupen Nu qeawen Nu wenug	Philippines	New Guinea Tall Spicata Dwarf Agta Tall Aguinaldo Tall Bago-oshiro Tall Baguer Dwarf Banga Dwarf Banigan Tall Baybay Tall Benigan Bilaka Bunawan Coconino Culaman Tall Cuyamis
Marshall Islands	Ni Jok Ni Maro Ni Mej Ni Mur Ni Rik Ni Yalu		Dahili Dailig Dalig Galas Dwarf Galimba Gatusan Tall Hijo Tall
Northern Mariana Islands	Niyug Agaga Niyug Dagua Niyug Kunon Niyug Laipuga Niyug Mogmog Niyug Samoa		

Appendix 1. Vernacular names of coconuts. (Continued)

Location	Vernacular	Location	Vernacular
Philippines	Kapatagan Dwarf Kinabalon Dwarf Klambahim La Victoria Dwarf Laguna Tall Limbajon Lono Loong Tall Lupisan Macapuno Magtuod Dwarf Makapuno Makilala Dwarf Malapon Mamareng Mangipod Marure New Buswang Dwarf Orange Dwarf Palavan Pascual Pilipog Green Pugai Pula Puringkitan Rabara Romano Giant Salambuyan Tall San Ramon Tall Silver Queen Sto. Nino Dwarf Tacunan Green Dwarf Tagnanan Tall Tagnanum Talisay Dwarf Tambolilid Tampakan Tupi Dwarf Venus Tall Yellow Dwarf Zamboanga Tall	Sabah Sarawak Solomon Islands	Standard Kudat Sarawak Tall Bellona Tall Fiami Dwarf Gilbertese Tall Kira Kira Red Dwarf Kukum Dwarf Ngohara Rennell Tall Solomons Red Dwarf Solomons Tall Vanikoro Tall Vinikoro Tall
Pohnpei	Nih Atohl Nih Karat Nih Lap Nih Mwotomwot Nih Rir Nih Tik Nih Tol Nih Weita Short Yellow Dwarf Rangiroa Dwarf Rangiroa Tall	Tahiti Tonga	Tahiti Tall Tahitian Green Dwarf Haari Papua Niu Ati Niu Kafa Niu Leka Niu Loholoho Niu Matakula Niu Mea Niu Mealava Niu Ta'ukave Niu yalewa Niu tauve Niu tea Niu 'uli Niu 'utongau Niu vai Tongan Tall Liap/Nifik Nu Bo/Atton Nu Mun Nu Nupin Nu Pwiniech Nu Sessen Nu Umum Yap Tall Fuanui Niu Gealava Niu Kula Te ui Te uto Tuvalu Tall
Rangiroa	Niu Uta Kong Thein Yong Pinggang-pinggan	TTPI Tuvalu	New Hebrides Tall Vanuatu Red Dwarf Vanuatu Tall
Rotuma		Vanuatu	Fiji Red Dwarf Haari Papua La'ita Niu Afa
Sabah		Western Samoa	Niu fetepulu Niu le'a Niu vel Niuui

Appendix 1. Vernacular names of coconuts. (Continued)

Location	Vernacular
Western Samoa	Niualava
	Niutetea
	Samatau
	Samoan Green Dwarf
	Samoan Tall
	Samoan Yellow Dwarf
	Nu Gel
	Partagel
	Welol
	Yalaaz
Yap	Yuginuw

The word "redondo" is generally applied on the Pacific coast of Latin American countries (Colombia, Costa Rica, Ecuador, El Salvador, Honduras, Mexico, Panama, and Peru). **Choco** in Panama and **Chocuanos** in Costa Rica may be preferred selections.

The names in the above table are an indication only. Some may be synonyms. Many names are not included. Corrections and additions can be sent to ICCRA@yahooroups.com