

Fruit component analysis of south Pacific coconut palm populations

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Abstract

The south Pacific region contains a large genetic resource for the genetic improvement of coconut palms (*Cocos nucifera* L.). A study of the diversity in the species was made during 1992/3 using fruit component analysis on a representative sample from 29 distinct south Pacific populations in order to characterise the germplasm present in the region. A large diversity in fruit morphology was found that ranged from populations exhibiting wild-type characters in central Pacific to populations displaying domesticated characteristics in Rennell Island, the Sikaiana Islands, the Marquesas Islands, and in Papua New Guinea. Many populations exhibited fruit characteristics intermediate between the two, which were thought to have arisen due to introgressive hybridisation between the wild and domesticated populations. Continuous variation in fruit morphology was found in these populations, and cluster analysis arbitrarily divided the continuum into discrete groups which were consistent with geographic affinities. Groups were defined in Melanesia, Western Polynesia and Eastern Polynesia. The continuum displayed clinal variation from populations with small fruit and low husk content in the west to large fruit and more husk in the east of the region. The wild and domesticated populations were found in disjunct pockets throughout the area, and did not form part of the clines. Most populations consisted of a wide range of fruit morphology, from individuals expressing wild-type characters to those with domestic-type characters. The occurrence of both wild and domesticated populations within the clinal variation indicates that further exploration should be made to determine the presence of other potentially useful populations. While this activity is proceeding, collection and conservation can proceed using the classification already defined.

Abbreviations: BP – before present

Introduction

The coconut palm (*Cocos nucifera* L.) is an important plant in the humid tropical regions of the world where it is grown both as a cash and subsistence crop. The coconut is thought to have evolved in the ancient Tethys Sea, which includes the present-day Pacific region (Harries, 1990). There is a persuasive argument that much of the diversity in fruit morphology in coconut results from domestication by human populations in the Asia/Pacific region (Harries, 1978). Pre-

vious surveys indicated that the south Pacific region contains considerable coconut diversity (Whitehead, 1966; Parham, 1966; Harries, 1978; Foale, 1987; Ashburner et al., 1997) and current thinking dictates that this diversity should be conserved (UNCED, 1992). The first step in such conservation is to conduct an extensive survey of the genetic diversity present.

The conservation of coconut germplasm is costly and logistically difficult. Collections must be maintained as perennial field plantings since the coconut is exclusively seed-propagated and its seeds are bulky and

recalcitrant. Furthermore, since coconut generally has a mixed mating system, with dominant outcrossing, a high degree of genetic variation is expected (Ashburner, 1995). As such, in situ surveys must be carried out to direct future collecting activities.

Fruit morphology measurements have been the most extensively used set of criteria to characterise coconut diversity because they are simple to measure, are environmentally stable, and have been subjected to strong selection pressures from both natural and human influences (Whitehead, 1966; Harries, 1978, 1981). Fruit morphology characters were first used by Whitehead (1966) to survey coconut diversity in the south Pacific region. His method, subsequently termed 'fruit component analysis', was further refined by Harries (1978) to characterise coconut variation world-wide. Other morphological characters have been recommended for characterising diversity in coconut germplasm, such as vegetative and floral characters (IBPGR, 1992), but are strongly influenced by environmental conditions, and their usefulness has yet to be demonstrated outside germplasm repositories. DNA markers have recently been applied to the description of coconut diversity (Ashburner et al., 1997) and corresponding morphological data are required to complete the description.

Fruit characteristics are generally indicative of the amount of artificial selection that has occurred in a coconut population, and are correlated with other artificially-selected and agriculturally important traits, such as early germination, precocity of flowering and resistance to strong wind, insects and diseases (Harries, 1978). The wild-type coconut is postulated to possess long angular fruit with a high husk-to-nut ratio resulting from strong natural selection for enhanced floating ability. Domesticated fruit, on the other hand, tend to have been selected by humans for less husk and larger size, and are consequently more rounded (Harries, 1981). As well, the nut of a wild-type coconut is found to have a lower liquid-to-solid endosperm ratio than those of a domesticated-type, as a consequence of being smaller. Intermediate characteristics can arise due to introgressive hybridisation between the two different forms of coconut. Harries (1978) considers that introgressive hybridisation occurred in the Pacific region after the introduction of the domesticated coconut type into the wild-type gene-pool by colonising humans.

This paper reports a survey of coconut diversity in the south Pacific region as measured by fruit component analysis, and it further evaluates the similarities

between the various coconut populations in order to develop collection, conservation and utilisation policies.

Materials and methods

Sampling

One mature fruit was sampled from 5 to 45 randomly selected coconut palms corresponding to 29 accessions from the south Pacific region (Table 1). Sampled palms were at least 200 m apart and in the case of sporadically occurring genotypes, such as NAT, NAD, NLD, NST, NVT and VRD or those from germ-plasm collections, palms were selected at random without a distance criterion.

Measurements

Fruit components were measured fresh, using the method described by Harries (1981) including fruit weight, proportion of: husk to total fruit weight (% husk) endosperm to nut weight (% endosperm); shell to nut weight (% shell); and water to nut weight (% water). To avoid variation due to differences in maturity of the fruit, all fruit were selected at the stage where the colour was changing from its immature colour to brown. At this stage, the liquid endosperm made a splashing sound when shaken.

Analyses

Differences in measured characters between populations were tested by analysis of variance. The presence of clinal variation was determined by linear regression using the geographic longitude of the sampled population, and two variables, fruit weight and husk proportion.

The data were also subjected to canonical variate analysis (multiple discriminant variate analysis) (Sokal & Rohlf, 1981) and presented as an ordination. A pair-wise similarity matrix was also calculated between individuals using the Manhattan metric (Sokal & Rohlf, 1981), and this was reduced to a two-way population similarity matrix by averages. This matrix was then used in hierarchical cluster analysis using an average fusion strategy (UPGMA) (Sneath & Sokal, 1973). Sporadically occurring named genotypes were omitted from the multivariate analyses, as only the predominant local populations were studied. The multivariate

Table 1. Coconut population location and number of palms sampled per population for fruit component analysis.

Code	Name of population	Origin				No.
		District	Country	Latitude	Longitude	
CIT*	Kiritimati Tall	Kiritimati	Kiribati	2° 00' N	157° 30' W	10
CKT1	Rarotonga Tall	Rarotonga	Cook Islands	21° 15' S	159° 45' W	30
CKT2	Aitutaki Tall	Aitutaki	Cook Islands	19° 00' S	159° 45' W	10
FIT	Fiji Tall	Taveuni	Fiji	17° 10' S	180°	23
GET	Gazelle Peninsula Tall	New Britain	Papua New Guinea	4° 20' S	152° 10' E	30
KIT	Kiribati Tall	Tarawa	Kiribati	1° 30' N	173° 00' E	25
NAD	Niu Ati	Upolu	West. Samoa	14° 00' S	172° 00' W	10
NAT	Niu 'Afa	Upolu	West. Samoa	14° 00' S	172° 00' W	9
NLD	Niu Leka	Taveuni	Fiji	17° 10' S	180°	21
NST	Niu Samatao	Upolu	West. Samoa	14° 00' S	172° 00' W	10
NUT	Nauru Tall	Nauru	Nauru	0° 30' S	166° 55' E	10
NVT	Niu Vai	Upolu	West. Samoa	14° 00' S	172° 00' W	10
MAT	Mo'orea Tall	Mo'orea	French P'Nesia	17° 30' S	149° 50' W	27
MST	Marquesas Tall	Nuku Hiva	French P'Nesia	10° 30' S	140° 00' W	29
PXT	Phoenix Tall	Phoenix Is.	Kiribati	3° 00' S	171° 30' W	18
RAT	Rangiroa Tall	Rangiroa	French P'Nesia	16° 00' S	146° 50' W	28
RLT	Rennell Tall	Rennell	Solomon Is.	11° 30' S	160° 00' E	30
ROT*	Rotuma Tall	Rotuma	Fiji	13° 20' S	176° 40' E	5
SAT	Samoa Tall	Upolu	W. Samoa	14° 00' S	172° 00' W	10
SKT	Sikaiana Tall	Sikaiana Is.	Solomon Is.	8° 30' S	162° 30' E	10
SNT	Russell Tall	Russell Is.	Solomon Is.	9° 10' S	159° 00' E	5
TAT1	Tongatapu Tall	Tongatapu	Tonga	21° 20' S	175° 20' W	24
TAT2	Ha'apai Tall	Ha'apai	Tonga	20° 00' S	173° 35' W	30
TAT3	Vava'u Tall	Vava'u	Tonga	18° 55' S	173° 35' W	29
TUT1	Funafuti Tall	Funafuti	Tuvalu	9° 05' S	179° 30' E	45
TUT2	Nanumanga	Nanumanga	Tuvalu	5° 35' S	176° 10' E	43
VRD	Vanuatu Red Dwarf	Espiritu Santo	Vanuatu	15° 30' S	165° 30' E	10
VOT*	Vanikoro Tall	Vanikoro	Solomon Is.	11° 30' S	167° 00' E	10
VUT	Vanuatu Tall	Espiritu Santo	Vanuatu	15° 30' S	165° 30' E	39

* Sampled from the collection at Russell Islands Plantation Estates Ltd., Yandina, Solomon Islands.

analysis of fruit components used the following data: fruit weight; % husk; log(% endosperm/% shell) and log(% water /% shell). Multivariate logistic transformations were required because % endosperm, % shell, and % water sum to 100% and therefore do not have multivariate normal distributions (Aitchison, 1982). All characters used in the analysis were range standardised by dividing by their highest value.

Within-population variation of fruit characters was estimated by the variance of the Euclidean distances of individual palms from their population centroids, in the two-dimensional space created by the first two discriminant functions of the canonical variate analysis (Jordan et al., 1993).

Results

The south Pacific region contains coconut palms with a large range of fruit weight and components (Table 2), ranging from the KIT population of 807 g to NVT with a mean weight of 3522 g. Individual fruit in the region ranged from 260 g up to 4750 g, with endosperm ranging from 50 to 1210 g, and water from 0 g in some dry atoll conditions to 1779 g in other locations.

Fruit size and husk proportion of the predominant coconut populations generally increased eastwards (Figures 1 and 2). This clinal variation was broken by the occurrence of populations with small fruit in the Micronesia area (KIT, TUT1) and populations with large fruit with a low husk proportion, such as GET, SKT, RLT and MST.

Table 2. Population mean of measured and derived fruit component characters of south Pacific coconut populations, and their multivariate variance (weight in grams).

Pop.	Fruit weight	Husk (%)	Endosperm weight	Shell weight	Water weight	Multivariate variance
Phoenix Islands Group						
PXT	834	39.4	44.5	21.5	34	0.69
Wild Group						
KIT	807	57.3	52.6	30.2	17.2	0.56
TUT1	1,155	59	53.9	27.3	18.9	0.4
mean	981	58.2	53.3	28.8	18.1	0.48
Melanesian Group						
VUT	1,260	40.4	45.4	24.2	30.2	0.4
VOF	1,238	43.5	45.6	23.4	31	0.31
SNT	1,323	47.4	45.7	24.9	29.5	0.16
TUT2	1,311	42.8	51.6	23.3	25.1	0.34
NUT	1,358	49	48.7	26.7	24.4	0.61
FIT	1,247	50.1	53.5	26.2	20.3	0.4
CIT	1,448	52.9	50.9	22.6	26.4	0.46
mean	1,312	46.6	48.6	24.5	26.7	0.38
West Polynesian Group						
TAT1	1,714	48.8	48.3	26.4	25.3	0.6
ROT	1,736	43.1	46.2	28.9	24.9	0.19
SAT	1,606	46.5	47.9	25.9	26.2	0.15
CKT2	1,748	50.8	45.5	28.4	26.2	0.34
TAT2	1,913	49.2	47.7	27	25.3	0.89
TAT3	1,765	49.6	46.3	28.7	25.1	0.37
CKT1	1,878	48.4	42.1	29.4	28.5	0.65
mean	1,766	48.1	46.3	27.8	25.9	0.45
East Polynesian Group						
RAT	1,879	56.7	46.2	25.7	28	0.79
MAT	1,947	55	48	25	27	0.71
mean	1,913	55.9	47.1	25.4	27.5	0.75
Domesticated Group						
MST	2,299	44.6	43.2	25.1	31.6	0.52
RLT	2,180	40.6	42.8	22.2	35.1	1.05
GET	1,627	40.6	42	24.5	33.5	1.14
SKT	1,596	35.5	46.5	20.5	33	0.33
mean	1,923	40.3	43.7	23.1	33.3	1.01
Named types						
VRD	837	37	42.3	25.8	31.9	–
NAD	1,003	39.1	47.4	20.3	32.3	–
NLD	1,767	55.2	50.9	26.5	22.7	–
NST	2,214	40.7	37.3	21.4	34.2	–
NAT	2,911	55.2	45.2	23.3	31.3	–
NVT	3,522	34.5	38.9	17.8	43.3	–

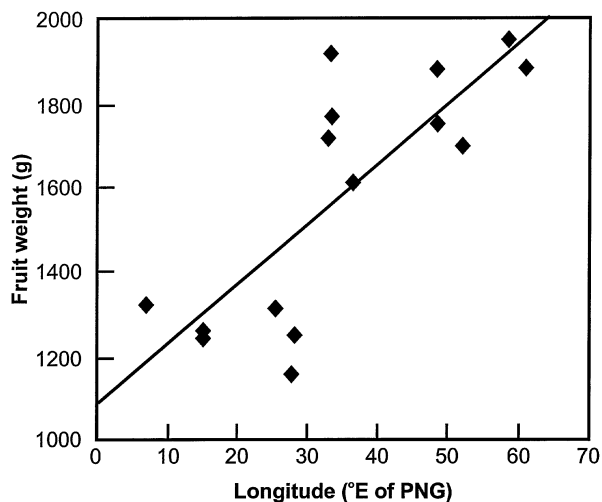


Figure 1. The relationship of fruit size of south Pacific coconut landraces with degrees of longitude east from Papua New Guinea, in the south Pacific. Actual values appear as diamonds. The response function was fitted by the model: $y = 1041 + 15.8x$, $r^2 = 0.71$ where y = fruit weight and x = longitude from Papua New Guinea. Note that this analysis excludes the disjunct domestic- and wild-type populations identified in the paper.

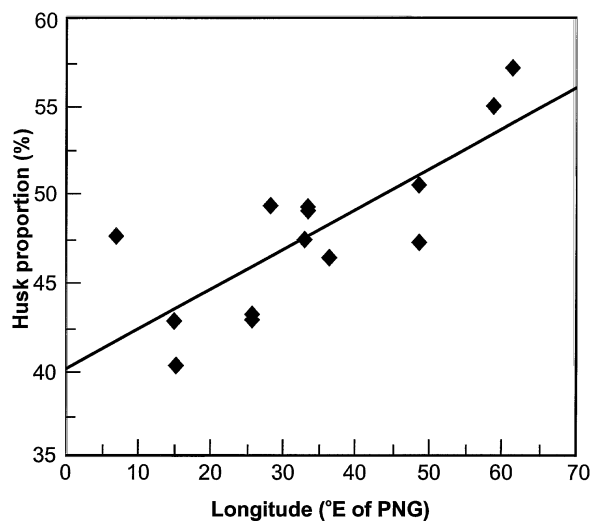


Figure 2. The relationship of husk proportion of south Pacific coconut landraces with degrees of longitude east from Papua New Guinea in the south Pacific. Actual values appear as diamonds. The response function was fitted by the model: $y = 40.1 + 0.23x$, $r^2 = 0.61$ where y = husk proportion and x = longitude from Papua New Guinea. Note that this analysis excludes the disjunct domestic- and wild-type populations identified in this paper.

To classify the coconut palm populations in the region and to find any discontinuities in the variation, multivariate analyses were performed. Cluster analysis

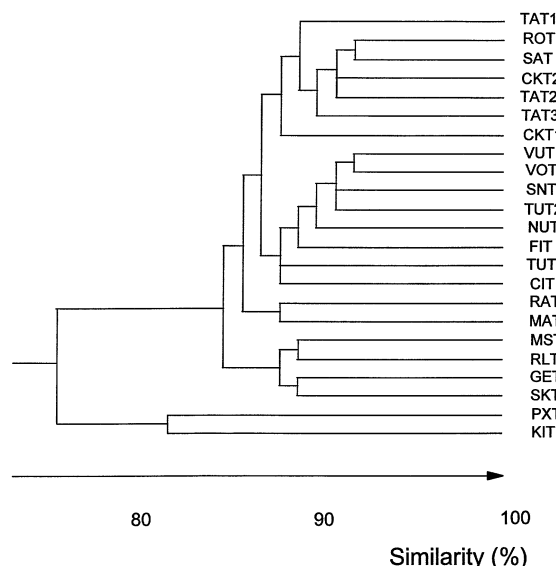


Figure 3. Average-link dendrogram of south Pacific coconut populations derived from hierarchical cluster analysis of a Manhattan similarity matrix of fruit component data.

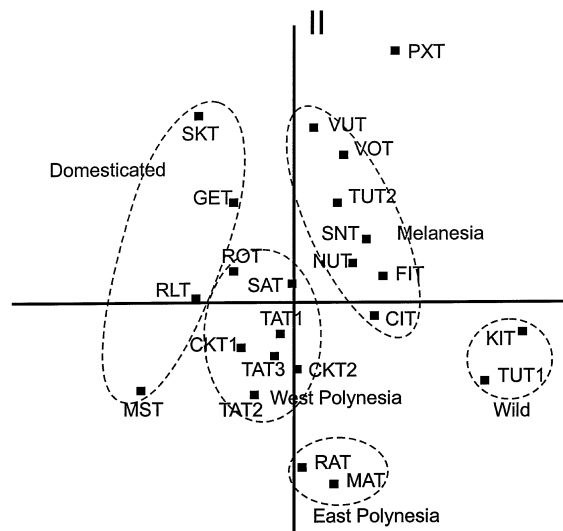


Figure 4. Ordination by canonical variate analysis of south Pacific coconut populations on the basis of fruit components.

was used to classify the populations and the resulting dendrogram is presented in Figure 3. Although most populations fell within a large group of 80% similarity indicating continuous variation, it was possible arbitrarily to divide the populations according to common geographic and cultural origins at 85%.

Discontinuities in the variation were determined using ordination (Figure 4). The presence of generally

continuous variation was confirmed as discrete clusters were not evident in most populations. The KIT and NUT1 populations formed a discontinuity as did those of SKT, RLT, GET and MST.

On the basis of the evidence presented by the classification and ordination studies, six groups of populations were defined (Table 2). The PXT population was clearly disjunct from the other populations and formed its own group, the Phoenix group, which is characterised by having small fruit, low husk proportion, a low solid-to-liquid endosperm ratio and moderate within-population variation. The KIT and TUT1 populations from central Pacific formed another discontinuous group which was characterised by having small fruit, a high husk proportion, a high solid-to-liquid endosperm ratio and moderate within-population variation. As the characteristics of these populations are consistent with those defined for wild-type populations, the group was named Wild group.

The MST, RLT, GET and SKT populations formed a disjunct group that was characterised as having large fruit, low husk content, a low solid-to-liquid endosperm ratio and high within-population variation. As the characteristics of these populations are consistent with those defined for domesticated populations, the group was named Domestic group.

Three groups of populations with fruit characteristics intermediate to the Domestic and Wild groups were also defined. The Melanesian group was characterised as having small fruit, intermediate husk content, intermediate solid-to-liquid endosperm ratio and low within-population variance. The Western Polynesian group was characterised as having intermediate fruit size, intermediate husk content, low to moderate solid-to-liquid endosperm ratio and moderate within-population variation. The Eastern Polynesian group was characterised as having large fruit, high husk content, high solid-to-liquid ratio and high within-population variation.

Discussion

The coconut populations of the south Pacific region displayed large variation in fruit morphology, and cluster analysis arbitrarily divided the populations into groups that generally reflected their morphological and geographic similarity. The morphological variation ranged from a group of populations displaying fruit morphology consistent with domesticated types (Domesticated group), through to a group with fruit morphol-

ogy consistent with wild-type coconut palms (Wild group) (Harries, 1978). Between those extreme groups, there were populations of intermediate fruit characteristics. These populations were divided into groups that reflected both their geographic and morphological similarities, with groups being defined from Melanesia, Western Polynesia and Eastern Polynesia. These populations displayed continuous variation, and were distinct from the wild and domesticated populations. The population from the Phoenix Islands formed a group of its own.

Populations exhibiting wild-type characteristics were described in the central Pacific (Figure 5), specifically in the Gilbert (Kiribati) (KIT) and Ellice (Tuvalu) Islands (TUT1). Tuvalu generally has populations of intermediate fruit characteristics (e.g. TUT2) (Anon. 1982), although the occurrence of wild-type population in an area of more domesticated coconut palms is not unusual since the wild-type coconut maintains the ability to migrate on the ocean currents (Harries, 1978). Other isolated wild-type populations have been found elsewhere in the Pacific region (Buckley & Harries, 1984; Gruezo & Harries, 1984). Furthermore, most intermediate populations contain individuals that display wild-type characters, and entire wild type populations probably only exist in uncultivated areas.

Domesticated populations were described from the region's westernmost edge in Melanesia, through to its easternmost edge in the Marquesas Islands (Figure 5). In general, these populations were found in areas inhabited by Polynesians, with the exception of the coconut population in the Gazelle Peninsula, which is thought to have originated from a selection from the Witu Islands (Dwyer, 1938). The Witu Islands population probably experienced considerable Polynesian influence in the past. Domestic populations probably resulted from either introduction, or introgression with the local population and re-selection, as was probably the case in Sikaiana and the Gazelle Peninsula populations and the NVT and NST genotypes from Samoa (Table 2). Such populations could also result from introduction into an area of very few, or no natural coconut palms, as was probably the case with the Rennell and Marquesas populations. In general, the domestic populations were more variable than other populations.

The population of the Phoenix Islands displayed domestic characters but with small fruit, similar to fruit of dwarf ecotypes. This occurrence may be a result of introgression with a small-fruited locally-occurring

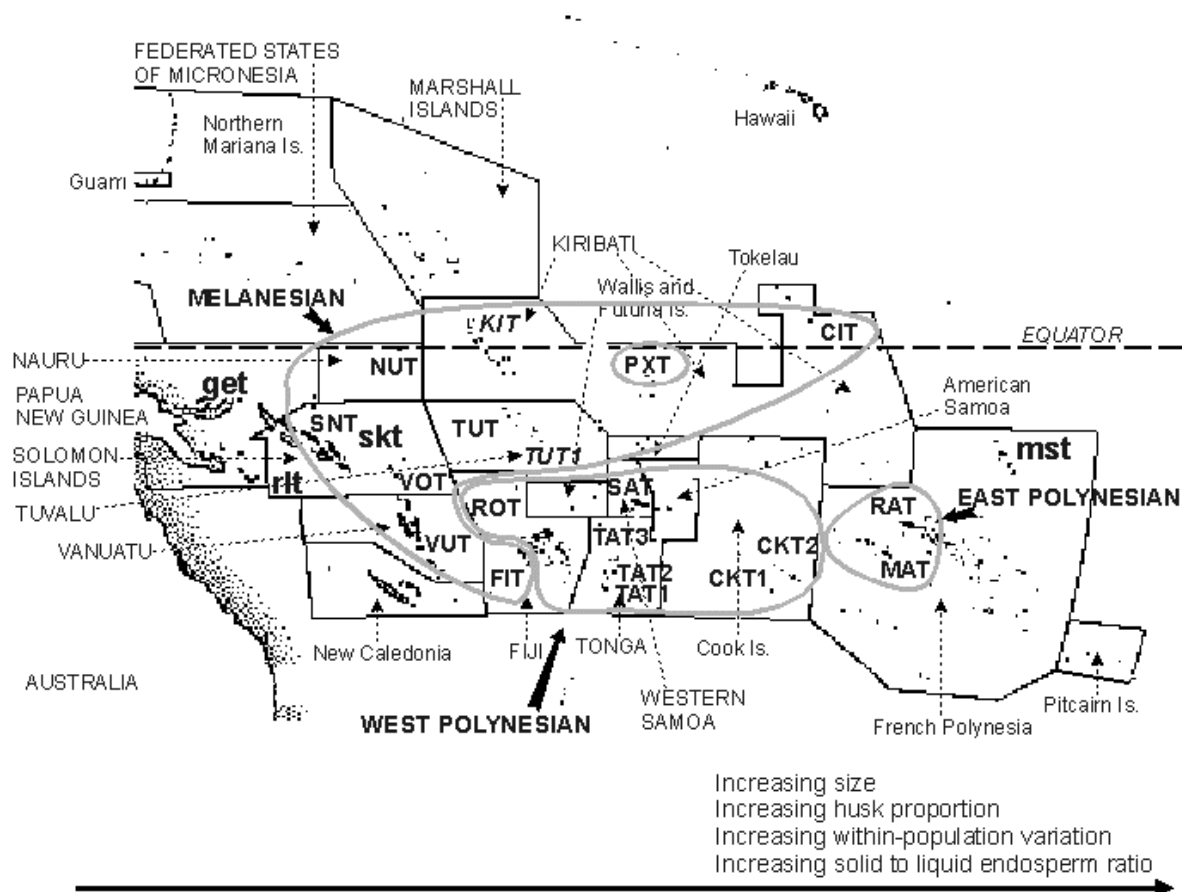


Figure 5. Location of coconut populations sampled for fruit component analysis and their morphological alliances. The following named varieties are not shown on the map but are located with the populations shown in the parentheses: NAT, NAD, NST, NVT (**SAT**), NLD (**FIT**), and VRD (**VUT**). Groupings as determined by multivariate analysis are shown. The populations represented by lower case codes (**get**, **rlt**, **skt** and **mst**) have been determined to be domestic-type and those represented by italic codes (**TUT** and **KIT**) have been determined to be wild-type.

population or as a result of an introduction of small-fruited palms.

Populations that displayed intermediate fruit characteristics, probably resulted from introgression between the introduced domesticated population and the original wild-type populations (Harries, 1978). They were found throughout the south Pacific region (Figure 5), and comprised individuals which varied greatly in their degree of domestication. A number of discrete groups could be distinguished in the continuum of fruit morphology, such as those from the south-western Pacific (Melanesian group), the south-central Pacific (West Polynesian group) and from the south-eastern Pacific (East Polynesian group). Further geographic patterns were difficult to deduce because of the impact of founder effects (Ashburner et al., in press)

and human activities. Some of the human influences include the introduction of domesticated individuals, re-selection of the diverging population and the rapid expansion of the coconut growing area during the last century for the production of copra.

The clines in fruit characters indicated that fruit size and husk size increased eastwards in the south Pacific (Figures 1 and 2). As well, the solid-to-liquid endosperm ratio and within-population variation tended to increase likewise. This would indicate that domestication status of populations decreased eastwards as well. Superimposed on the clinal variation were wild and domesticated populations that were probably maintained by natural and artificial selection, respectively.

Fruit size is also believed to increase in relation to the distance from the centre of origin, or from the next largest coconut population (Harries, 1978). As well, large fruit size was characteristic of the Polynesian groups and could be explained by the predilection of the Polynesian sea-farers for large coconuts as a source of liquid during voyages; a large coconut was a more convenient water container than a smaller one. This is also reflected in the solid-to-liquid endosperm ratio.

Increases in husk proportion to the east, in the south Pacific, may be due to the length of time that introgression and artificial selection has occurred. The period of human inhabitation generally decreases east from Melanesia. For example, the earliest evidence for human inhabitation in the Solomon Islands is 28 000 BP (Loy et al., 1992), in Samoa it is 3100 BP (Kirch, 1986), in the Marquesas Islands it is 1900 BP (Kirch, 1986), in the Society Islands it is 1400 BP (Lepofsky et al., 1992) and in the Cook Islands it is 1300 BP (A. Parkes pers. comm.). It is possible that the period of time under selection also affected within-population variation, as that measure tended to increase eastwards in the clinal groups.

Studies of south Pacific coconut palm diversity using DNA markers also showed the presence of continuous variation, but with less accordance with geographic distribution (Ashburner et al., 1997). From this we can conclude that fruit morphology is under more direct selection than DNA sequences, and is a useful adjunct in the characterisation of germplasm for conservation purposes. The results of the present study further classify the results of Nuce de Lamothe and Wuidart (1981) who determined that coconut populations in the south Pacific could be divided into two groups: the Melanesian group that is characterised as having a large number of small oblong fruit with round nuts and precocious phenology, and the Polynesian group that is characterised as having medium to large fruit and an excellent copra yield.

A number of named forms of coconut also exist in the south Pacific region, which consist of genotypes that have been recognised and cultivated by the indigenous people, but which are distinct from the local populations. Two ubiquitous dwarf types were characterised, the first a red dwarf (e.g., VRD) that has been reported from: French Polynesia, where it is known as Haari Papua (Whitehead, 1966); the Cook Islands, where it is known as Niu Papua (Foale, 1987); Samoa and Niue, where it is known as Niu Niukini (Leach, 1977; Yunker, 1943); the Solomon Islands, where it is called Niu Etiati (Leach, 1977); and Papua New

Guinea, where it is called New Ireland Red Dwarf (Whitehead, 1966). The second dwarf, found in Fiji, is known as Niu Leka (NLD) (Short Coconut) and is also found in: Tonga and Western Samoa where it is known as Niu Le'a (Whitehead, 1966); the Cook Islands (Foale, 1987); and French Polynesia where it is called Haari Haeha (Whitehead, 1966). Another dwarf type, Niu Ati, was found only in Samoa (NAD). The red dwarf and NAD fit the model of dwarfism as outlined by Harries (1978), but the Niu Leka is different from other dwarfs in that it is of short stature but exhibits characteristics consistent with tall coconut populations, such as wild-type fruit characters and allogamy. This dwarf type probably originated in the Pacific region since it has retained wild-type fruit and is not present in south-east Asia which is considered the centre of coconut domestication (Harries, 1990).

The named forms of tall coconut palms found in Samoa were quite extreme compared with other south Pacific populations and are probably selections from the Samoan population which segregated due to wild-domestic introgression (Harries, 1978). Niu Samatao (NST) is consistent with domesticated populations and represents an 'improved' local type. Niu Vai (NVT) (Water Coconut) containing an average of 998 g of liquid endosperm per fruit, is a selection for high liquid endosperm. Niu 'Afa (NAT) (Sennit Coconut) which contains an average of 1608g of fibre per fruit, is a selection for long fibres. The fact that Niu 'Afa appears to be a conscious selection and has fruit characteristics very different from wild-type, leads us to propose that the Harries (1978) system of naming wild-type forms as 'Niu Kafa types' should not be used in future. These selections from the general population are probably maintained by self-pollination (Leach, 1977) and selection on the basis of a petiole colour marker (Foale, 1987).

The south Pacific region is a unique genetic resource for coconut improvement which should be further conserved, collected and evaluated in breeding programs. Thought should be given to designing conservation strategies for the region's coconut germplasm because of the current down-turn in the market for copra. This, coupled with the movement away from traditional foods, the introduction of exotic coconut germplasm in the Pacific region, and the danger posed by an expected rise of sea level, means that some of this germplasm is in danger of being lost. The loss could be the result of neglect by the human population, or due to flooded habitat.

The present study, in using multivariate clustering techniques to define discrete groups in continuously varying populations, provides a guide to those populations which should be given priority in the execution of conservation and utilisation strategies. Priority should be given to collecting populations from each of the groups defined in this study in a manner similar to that described for the creation of core collections (Brown, 1989). Selection within these groups could be made giving priority to the most variable populations.

The presence of disjunct domesticated and wild populations in the clinal variation of coconut palms in the south Pacific suggests that further germplasm exploration should aim to discover other such disjunct populations. The wild-type populations could theoretically be found anywhere in the region, but uninhabited and remote islands would be likely areas of occurrence. Domesticated populations tended to be found in Polynesian outlying areas, and further exploration should be concentrated there.

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References

- Aitchison, J., 1982. The statistical analysis of compositional data (with discussion). *Journal of the Royal Statistical Society B* 44: 139–177.
- Anon, 1982. Annual Report, Department of Agriculture 1982, Ministry of Commerce and Natural Resources, Tuvalu.
- Ashburner, G.R., 1995. Reproductive biology of coconut palms. In: C. Oropeza, F.W. Howard & G.R. Ashburner (Eds.). *Lethal yellowing: Research and practical aspects*, pp. 173–186. Kluwer, Dordrecht.
- Ashburner, G.R., W.K. Thompson & G.M. Halloran, 1997. RAPD analysis of South Pacific coconut palm populations. *Crop Science* 37: (in press).
- Brown, A.H.D., 1989. Core collections: a practical approach to genetic resources management. *Genome* 31: 818–824.
- Buckley, R. & H.C. Harries, 1984. Self-sown wild-type coconuts from Australia. *Biotropica* 16: 148–151.
- Dwyer, R.E.P., 1938. Coco-nut improvement by seed selection and plant breeding. *New Guinea Agricultural Gazette* 4: 24–102.
- Foale, M.A., 1987. Coconut germplasm in the south Pacific islands. ACIAR Technical Reports No. 4., Australian Centre for International Agricultural Research, Canberra.
- Gruezo, W.S. & H.C. Harries, 1984. Self-sown, wild-type coconuts in the Philippines. *Biotropica* 16: 140–147.
- Harries, H.C., 1978. The evolution, dissemination and classification of *Cocos nucifera* L. *The Botanical Review* 44: 265–319.
- Harries, H.C., 1981. Practical identification of coconut varieties. *Oleagineux* 36: 63–72.
- Harries, H.C., 1990. Malesian origin for a domestic *Cocos nucifera*. In: P. Baas et al. (Eds.). *The Plant Diversity of Malesia*, pp. 351–357. Kluwer, Dordrecht.
- IBPGR, 1992. Descriptors for coconut. International Board for Plant Genetic Resources, Rome.
- Jordan, G.J., B.M. Potts, J.B. Kirkpatrick & C. Gardiner, 1993. Variation in the *Eucalyptus globulus* complex revisited. *Australian Journal of Botany* 41: 763–785.
- Kirsch, P.V., 1986. Rethinking Polynesian prehistory. *Journal of the Polynesian Society* 95: 9–40.
- Leach, B.J., 1977. Observations on flowering and morphology of coconuts in Western Samoa. Internal report, Food and Agriculture Organisation, Rome.
- Lepofsky, D., H.C. Harries & M. Kellum, 1992. Early coconuts from Mo'orea Island, French Polynesia. *Journal of the Polynesian Society* 101: 299–308.
- Loy, T.H., M. Spriggs & S. Wickler, 1992. Direct evidence for human use of plants 28,000 years ago: starch residues on stone artifacts from the northern Solomon Islands. *Antiquity* 66: 898–912.
- Nuce de Lamothe, M. de & W. Wuidart, 1981. Les cocotiers grands de Port-Bouet (Cote-d'Ivoire). 2-Grand Rennell, Grand Salomon, Grand Thaïlande, Grand Nouvelles-Hebrides. *Oleagineux* 36: 353–365.
- Parham, R.W., 1966. Coconut and breadfruit surveys of the south Pacific region. Technical Information Bulletin No. 1, South Pacific Commission, Noumea.
- Sneath, P.H.A. & R.R. Sokal, 1973. *Numerical Taxonomy*. Freeman, San Francisco.
- Sokal, R.R. & F.J. Rohlf, 1981. *Biometry*. Freeman, San Francisco.
- UNCED, 1992. The global partnership for environment and development, a guide to Agenda 21. United Nations Conference on Environment and Development, Geneva.
- Whitehead, R.A., 1966. Sample survey and collection of coconut germplasm in the Pacific islands (30 May–5 September 1964). Ministry of Overseas Development and HMSO, London.
- Yunker, T.G., 1943. The flora of Niue Island. *Bulletin* 178, Bernice P. Bishop Museum, Honolulu.