

- Takahashi, R. 1964. Further studies on the phylogenetic differentiation of cultivated barley. *Barley Genetics* 1: 19–26.
- Takahashi, R. 1972. Non-brittle rachis 1 and non-brittle rachis 2. *Barley Genetics Newsletter* 2: 181–182.
- van Zeist, W., K. Wasylikowa, and K. E. Behre. 1991. *Progress in Old World Palaeoethnobotany: A Retrospective View on the Occasion of the International Work Group for Palaeoethnobotany*. Balkema, Rotterdam, The Netherlands.
- Wolfe, K., P. M. Sharp, and W.-H. Li. 1989. Rates of synonymous substitution in plant nuclear genes. *Journal of Molecular Evolution* 29: 208–211.
- Zohary, D. 1996. The mode of domestication of the founder crops of Southwest Asian agriculture. In D. R. Harris (ed.), *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, 142–158. UCL Press, London, UK.
- Zohary, D. and M. Hopf. 2000. *Domestication of Plants in the Old World*, 3rd ed. Clarendon Press, Oxford, UK.
- Zvelebil, M. 2000. The social context of the agricultural transition in Europe. In C. Renfrew and K. Boyle (eds.), *Archaeogenetics*, 57–79. McDonald Institute Monographs, Cambridge, UK.
- Zvelebil, M. and M. Lillie. 2000. Transition to agriculture in eastern Europe. In T. D. Price (ed.), *Europe's First Farmers*, 57–92. Cambridge University Press, Cambridge, UK.
- Zvelebil, M. and P. Rowley-Conwy. 1986. Foragers and farmers in Atlantic Europe. In M. Zvelebil (ed.), *Hunters in Transition*, 67–93. Cambridge University Press, Cambridge, UK.

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CHAPTER 10

## Breadfruit Origins, Diversity, and Human-Facilitated Distribution

I received the seeds of the bread tree. . . . One service of this kind rendered to a nation, is worth more to them than all the victories of the most splendid pages of their history, and becomes a source of exalted pleasure to those who have been instrumental in it.

—Letter from Thomas Jefferson to M. Giraud (1797)

### Background

Breadfruit (*Artocarpus altilis* (Parkinson) Fosberg, Moraceae) is a staple crop in Oceania, where it was originally domesticated. It is a versatile tree crop with many uses including construction, medicine, animal feed, and insect repellent. However, it is principally grown as a source of carbohydrates and is an important component of agroforestry systems. Unlike many herbaceous starch crops harvested for their vegetative storage tissues, breadfruit is a large tree grown for its fruit (technically an infructescence, as the breadfruit is a syncarp made up of many small fruitlets fused together) (figure 10.1). Many cultivars have no seeds, just tiny aborted ovules (these will be called seedless cultivars), whereas others may have few to many seeds. Breadfruit typically is harvested when it is slightly immature and still firm, and seedless cultivars are prepared in much the same way as potatoes: baked, boiled, steamed, roasted, or fried. Ripe fruits are sweet and used in desserts. In seeded cultivars, seeds are chestnut-like in both size and taste and are boiled or roasted.

Although breadfruit yields vary between individual trees and cultivars, productivity typically is quite high. A commonly cited figure for seedless

breadfruit is 700 fruits per tree per year, with each fruit averaging 1–4 kg (Purseglove, 1968). In a specific case study of an agroforestry system in Pohnpei of the Federated States of Micronesia, average yields for five cultivars ranged from 93 to 219 fruits per tree per season. In-depth yield studies for more than 100 cultivars growing in a common location are being conducted by Diane Ragone. Breadfruit is a seasonal crop, and because trees produce large quantities of highly perishable fruit, various methods of preservation have been developed for long-term storage. Some traditional preservation methods include fermentation in underground pits (Atchley and Cox, 1985; Aalbersberg et al., 1988) and the production of a starchy, sun-dried paste (Coenen and Barrau, 1961). A limited number of studies have examined breadfruit's nutritional value. Compared with other starch crops it provides comparable levels of carbohydrates and is a better source of protein than cassava and equivalent to banana and sweet potato (Graham and Negron de Bravo, 1981).

#### Breadfruit Biology

Breadfruit plants are monoecious with separate pistillate and staminate inflorescences borne in the leaf axils of a single tree. The pistillate inflorescence is typically globose to subglobose, whereas the staminate inflorescence is cylindrical. Both inflorescences consist of hundreds of tiny flowers, which are tightly packed together and sit on a fleshy receptacle. The staminate flowers of fertile cultivars produce copious amounts of viable pollen, whereas few-seeded and seedless cultivars produce little or no viable pollen (Sunarto, 1981; Ragone, 2001). It has been demonstrated that fruit development in seedless breadfruit is parthenocarpic and does not require pollen to be initiated (Hasan and Razak, 1992). As the pistillate inflorescence develops, the fleshy perianths of the individual flowers expand and provide the edible starchy portion of the syncarpous fruit (figure 10.1). Little is known about pollination in seeded cultivars or wild relatives of breadfruit, although both wind (Jarrett, 1959a) and insect pollination (Brantjes, 1981; Momose et al., 1998; Sakai et al., 2000) have been suggested for various *Artocarpus* species.

Thousands of years of breadfruit cultivation and human selection in Oceania have given rise to a tremendous amount of morphological diversity, including variation in the number of seeds per fruit. Cultivars in Melanesia typically produce viable, edible seeds and are propagated by

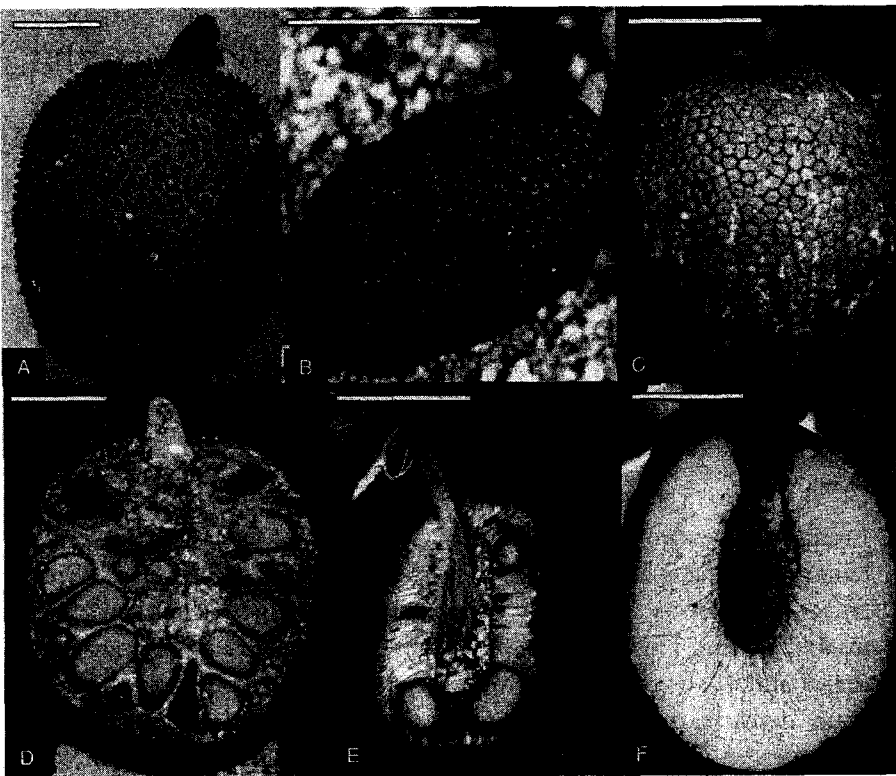


FIGURE 10.1 Breadfruit and wild relatives. (A–C) Syncarp surfaces of (A) *Artocarpus camansi*, Zerega 88; (B) *A. mariannensis*, Zerega 107; and (C) *A. altilis* cultivar Mei uhp from Pohnpei, Zerega 172. (D–F) Cross-sections of (D) *A. camansi*, Zerega 88; (E) *A. mariannensis*, Zerega 146; and (F) seedless *A. altilis* cultivar Lemae from Rota, Mariana Islands, Zerega 142. Scale bar = 5 cm. (Full-color version of this figure follows page 230.)

seed. Other cultivars, especially in Polynesia and Micronesia commonly produce few to no seeds and must be propagated vegetatively. This is usually accomplished by planting of root suckers, through air layering, or by grafting. The loss of fertility is caused by triploidy ( $2n = 3x = \sim 84$ ) or is the result of hybridization in the case of sterile diploids ( $2n = 2x = 56$ ) (Ragone, 2001; Zerega et al., 2004).

### Breadfruit Distribution

At the end of the sixteenth century, European explorers and naturalists traveling to Oceania quickly recognized the potential of breadfruit as a highly productive, cheap source of nutrition and introduced a limited number of cultivars to their tropical colonies (Ragone, 1997). The most famous of these attempts was led by William Bligh and culminated in the mutiny aboard the *H.M.S. Bounty* (Bligh, 1792). Today breadfruit is grown throughout the tropics but is especially important in Oceania and the Caribbean. Breadfruit historically has had little commercial value outside the Pacific islands, where it has served primarily as a subsistence crop. However, in the last few decades, the Caribbean Islands have become the primary exporter of fresh breadfruit to Europe and North America (Marte, 1986; Andrews, 1990), and the Fijian Ministry of Agriculture reported breadfruit as one of Fiji's top four agricultural exports to New Zealand in the *Pacific Business News* in December 2001. Additionally, promising methods of preservation that could increase the export market for breadfruit include fried breadfruit chips, freeze drying, flour, canning, and extracting starch for use in the textile industry (Roberts-Nkrumah, 1993; Ragone, 1997).

### Breadfruit Diversity and Conservation in Oceania

Over millennia, Pacific Islanders have selected and named hundreds of traditional cultivars based on fruiting season, fruit shape, color and texture of the flesh and skin, absence or presence of seeds, flavor, cooking and storage qualities, leaf shape, and horticultural needs (Wilder, 1928; Ragone, 1997). These cultivars have adapted to local climates and soils, including the harsh saline soils of coral atolls, and many of them are endemic to a single island group. However, the use of breadfruit has been declining since World War II with the introduction and convenience of a western-style diet, causing some cultivars to be neglected and knowledge about fruit storage and preparation to be lost. Climate change and cyclones also

contribute to the loss of cultivars. To help conserve and study breadfruit, many germplasm collections have been assembled throughout the tropics, especially in the Pacific islands, over the last several decades. Because most cultivars are seedless, and even when seeds are present they are recalcitrant and cannot be dried or stored, collections must be maintained as living trees in field gene banks. This is a time-consuming and expensive task. For this reason, many collections are no longer being maintained (Ragone, 1997). A noteworthy exception is the Breadfruit Institute at the National Tropical Botanical Garden in Hawaii. This collection, with 120 cultivars and 192 accessions from 18 Pacific island groups, Indonesia, the Philippines, Papua New Guinea, and the Seychelles, represents a broad range of diploid, triploid, and hybrid cultivars and accessions of breadfruit's wild progenitors and has become an important genetic repository for conservation and research. Several other important collections representing primarily local cultivars are being maintained in various Pacific and Caribbean islands.

### Breadfruit's Closest Relatives

Breadfruit belongs to the genus *Artocarpus* in the Moraceae family. This family also includes other important members such as figs, mulberries, and jackfruit. The wild species of *Artocarpus* are restricted to Southeast Asia and the Indo-Pacific and comprise nearly 60 species divided into two subgenera, four sections, and eight series based on leaf and inflorescence morphology and anatomy (Jarrett, 1959a). Recent phylogenetic analyses of morphological and DNA sequence data from the nuclear ribosomal internal transcribed spacers (ITS) and the chloroplast *trnL-F* region for 38 *Artocarpus* species representing each of the 8 series and 13 Moraceae outgroup taxa indicated that *A. camansi* Blanco and *A. mariannensis* Trécul form a very highly supported monophyletic lineage with *A. altilis*, and they are breadfruit's closest relatives (figure 10.2; Zerega, 2003). *Artocarpus camansi* (figure 10.1), commonly called breadnut, is native to New Guinea and possibly the Moluccas (Jarrett, 1959b). It has been introduced for its edible seeds to other tropical locations outside Oceania and is especially common in the Caribbean and South America. *Artocarpus mariannensis* (figure 10.1) is native to the Mariana Islands and Palau and has been introduced to a limited number of Micronesian and Polynesian islands for its edible fruits and seeds (Ragone, 1997, 2001). Both species are diploid ( $2n = 2x = 56$ ) (Ragone, 2001) and produce viable seeds.

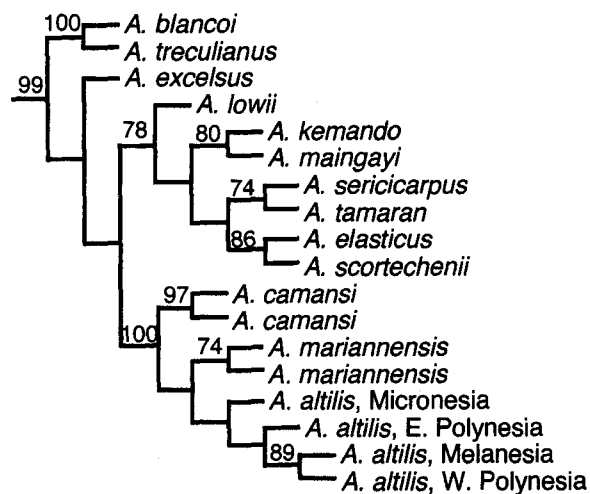


FIGURE 10.2 Strict consensus tree of 20 most parsimonious trees derived from *trnL-F* DNA sequence and morphological data. Jackknife support values are indicated above the branches. Breadfruit and its putative progenitors form a strongly supported clade. (Modified from Zerega, 2003.)

Zerega et al. (2004) explored the origins of breadfruit using amplified fragment length polymorphism (AFLP) (Vos et al., 1995) and found that both *A. camansi* and *A. mariannensis* played roles in the origins of breadfruit to varying degrees in different regions of the Pacific. These data will be summarized and elaborated on here in combination with additional isozyme data (Ragone, 1991) in order to identify the role of wild progenitors in breadfruit origins, assess genetic diversity and relationships between wild relatives and breadfruit cultivars throughout Oceania, and trace historical human-mediated breadfruit movement through Oceania.

### Origins of Breadfruit

In order to discuss the regions of Oceania, the geographic classification originally proposed by French voyager Dumont d'Urville (1832) is followed. Although the regions do not necessarily reflect cultural or historical unity, they are a commonly used, practical way in which to describe the islands of the Pacific Basin. The regions are Melanesia (included in this study: Papua New Guinea, Solomon Islands, Vanuatu, Fiji, and Rotuma), western Polynesia (included in this study: Samoa), eastern Polynesia

(included in this study: Cook Islands, Society Islands, Hawaii, and the Marquesas), and Micronesia (included in this study: Mariana Islands, Chuuk, Yap, Palau, Kiribati, Kosrae, and Pohnpei).

The roles that *A. camansi* and *A. mariannensis* may have played in breadfruit origins throughout Oceania were explored using AFLP data. Using three different primer pair combinations, AFLP data were collected from a total of 254 individuals. These samples came from accessions in the Breadfruit Institute or from field collections deposited at the New York Botanical Garden (NY). Samples comprised 24 *A. mariannensis*, 30 *A. camansi*, and 200 Pacific breadfruit cultivars from the island groups of Fiji (9), the Solomon Islands (7), Vanuatu (7), Rotuma (8), Papua New Guinea (3), Chuuk (9), Palau (6), the Mariana Islands (21), Pohnpei (47), Yap (2), Kiribati (2), the Society Islands (45), the Cook Islands (11), the Marquesas (9), Hawaii (1), and Samoa (13) (accession information is listed in Zerega et al., 2004). The AFLP data were collected and scored as a binary matrix to indicate the presence or absence of each AFLP fragment. Three AFLP primer pair combinations yielded 149 polymorphic markers across all 254 individuals (52 markers from *EcoRI-ACA/MseI-CTC*, 44 markers from *EcoRI-ACA/MseI-CAT*, and 53 markers from *EcoRI-AAG/MseI-CTG*).

To better understand the relationships between breadfruit and wild relatives, the AFLP data were analyzed using several methods. First, unweighted pair group method with arithmetic mean (UPGMA) dendrograms were drawn using Nei's (1978) unbiased genetic identity and distance based on AFLP data in PopGene version 1.31 (Yeh et al., 1999). Cultivars from the same island group were treated as a population, and *A. camansi* and *A. mariannensis* samples were treated as separate populations. The cultivar from Hawaii was not included in this analysis because only one individual was available. To further investigate relationships, the AFLP data were also analyzed using principal component analysis (PCA) on a square symmetric matrix of covariances in the software package JMP (SAS Institute, Cary, NC, USA). Finally, in examining the AFLP data from breadfruit's progenitors, four markers were found that were diagnostic and constant, one in *A. camansi* and three in *A. mariannensis*. That is, one marker was present in all *A. camansi* individuals and never in *A. mariannensis*, and three markers were present in all *A. mariannensis* individuals and never in *A. camansi*. These diagnostic markers are distributed variously throughout breadfruit cultivars and play a role in the discussions of breadfruit origins and human-mediated dispersal (figure 10.3).

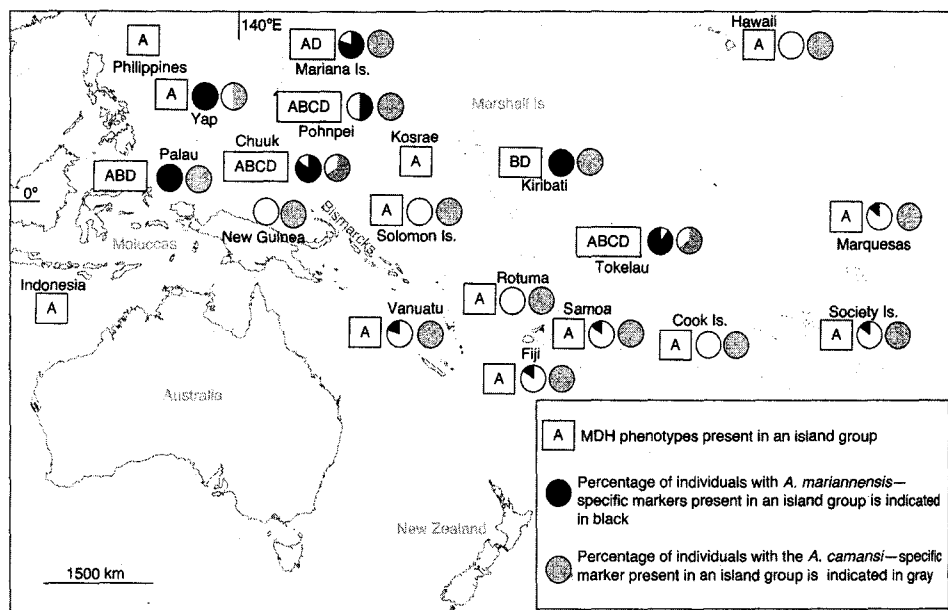


FIGURE 10.3 Map of Oceania indicating the distributions among breadfruit cultivars of malic dehydrogenase (MDH) isozyme phenotypes and *A. camansi*- and *A. mariannensis*-specific AFLP markers. Letters in the boxes refer to the four different MDH isozyme phenotypes present in an island group. The percentage of individuals within an island group with *A. mariannensis*-specific AFLP markers is indicated by the black portion of the pie chart on the left for each island group. White portions of the pie chart indicate the percentage of individuals with no *A. mariannensis* markers present. The percentage of individuals in an island group with an *A. camansi*-specific marker is indicated by the gray portion of the pie chart on the right for each island group. The percentage of individuals with no *A. camansi*-specific marker is indicated by the white portion of the pie chart.

In the UPGMA dendrogram, all of the island groups in Polynesia cluster together, as do most of the Melanesian islands (Fiji, Rotuma, Solomon Islands, and Vanuatu), and the cultivars from both Polynesia and Melanesia share a higher genetic similarity with *A. camansi* than with *A. mariannensis* (figure 10.4). Interestingly, the cultivars collected in Papua New Guinea are sister to Polynesian rather than to other Melanesian cultivars. This is not surprising because they are seedless cultivars that are believed to have been introduced from elsewhere. The AFLP data suggest they were brought

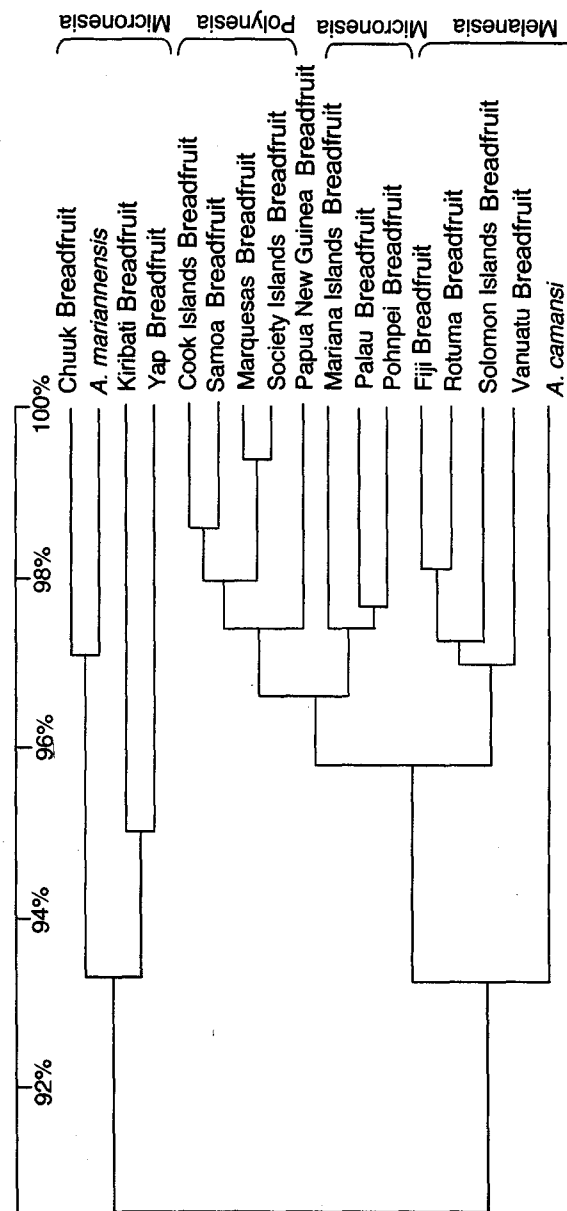


FIGURE 10.4 UPGMA dendrogram based on AFLP data of breadfruit cultivars from various island groups in Oceania and progenitor species, *A. camansi* and *A. mariannensis*.

from Polynesia. Among cultivars in Micronesia, some (Mariana Islands, Palau, and Pohnpei) share a higher genetic similarity with *A. camansi*, whereas others (Chuuk, Kiribati, and Yap) are more similar to *A. mariannensis*. The results from the PCA analysis demonstrate a similar pattern (figure 10.5a). Cultivars from Melanesia and Polynesia cluster with one another and with *A. camansi*, and Micronesian cultivars cluster between *A. mariannensis* and the Polynesian and Melanesian breadfruit. These results

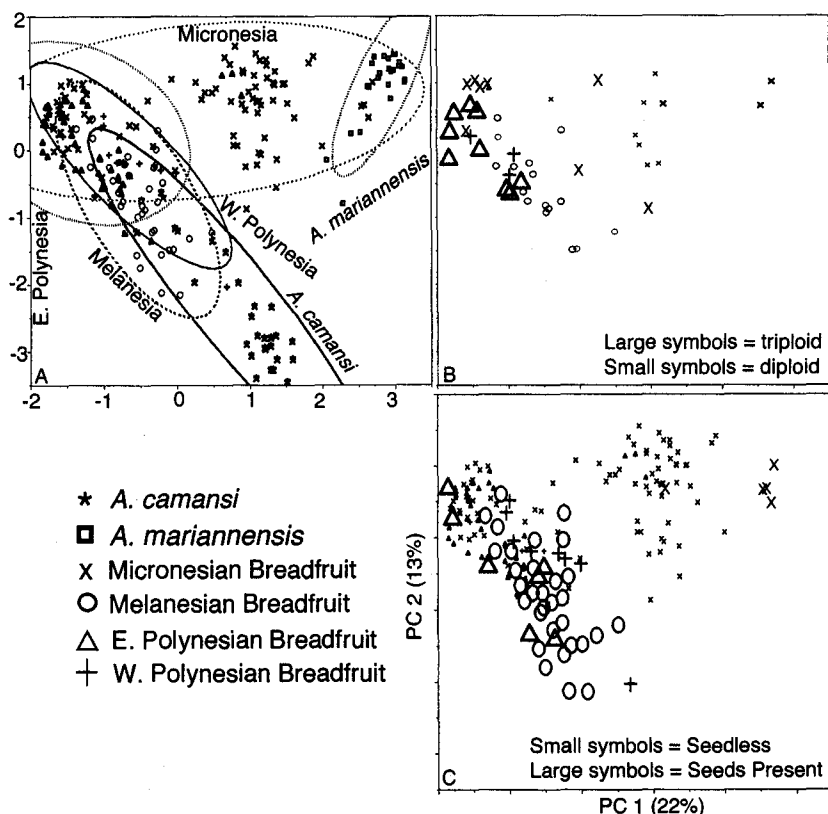


FIGURE 10.5 Principal component analysis (PCA) of 200 breadfruit cultivars and wild relatives (24 *A. camansi* and 30 *A. mariannensis*) based on 149 AFLP markers. (A) Bivariate normal ellipses with  $p = .95$  are drawn around *A. camansi*, *A. mariannensis*, Melanesian breadfruit, western Polynesian breadfruit, eastern Polynesian breadfruit, and Micronesian breadfruit. (B) The same PCA, showing only breadfruit cultivars whose ploidy level has been tested (Ragone, 2001). (C) The same PCA analysis with seedless cultivars and seeded cultivars indicated by small and large symbols, respectively.

suggest that Melanesian and Polynesian breadfruit cultivars may share similar origins, whereas many of the Micronesian cultivars have a different evolutionary history.

Melanesian and Polynesian breadfruit cultivars are more closely related to *A. camansi* than *A. mariannensis* and may have been derived from the former species. The distribution of both *A. camansi* and *A. mariannensis* diagnostic markers further illustrates this point (figure 10.3). All Melanesian and Polynesian cultivars have the *A. camansi* marker present, whereas very few have *A. mariannensis* markers. The rare presence of *A. mariannensis* markers in these regions is discussed in more detail in the section about human-mediated dispersal of breadfruit later in this chapter.

Micronesian cultivars are closely related to Polynesian and Melanesian *A. camansi*-derived breadfruit and to *A. mariannensis*, as revealed by UPGMA (figure 10.4) and PCA (figure 10.5a) analyses. This suggests that many Micronesian cultivars may be the product of hybridization between *A. camansi*-derived breadfruit and *A. mariannensis* and subsequent introgression. This is illustrated by the prevalence of both *A. camansi* and *A. mariannensis* diagnostic AFLP markers throughout individual Micronesian breadfruit cultivars and by additional evidence from isozyme data (figure 10.3).

### Diversity in Breadfruit and Its Closest Relatives

Despite the fact that many breadfruit cultivars are vegetatively propagated, a great deal of morphological diversity has been selected for by humans. This is evident in gross fruit and leaf morphology, the number of cultivar names that exist, and the various environments in which breadfruit can thrive (Wilder, 1928; Ragone, 1988, 1997). However, little is known about the underlying genetic diversity of breadfruit. Here we examine diversity in breadfruit and its wild relatives using protein and DNA techniques.

### Isozyme Data

Data from six different enzyme systems (aconitase [ACO], alcohol dehydrogenase [ADH], isocitrate dehydrogenase [IDH], leucine aminopeptidase [LAP], malic dehydrogenase [MDH], and phosphoglucosmutase [PGM]) were collected for 204 individuals (accession information listed in Ragone, 1991) (table 10.1). The samples came largely from the Breadfruit Institute collection and comprised 6 *A. camansi*, 3 *A. mariannensis*, and 195 breadfruit

Table 10.1 Genetic Diversity Estimates of Breadfruit and Wild Relatives Based on Isozyme and AFLP Data

Species	Locality	Iso/AFLP (n)	Isozyme Data		AFLP Data		Shannon Index	G <sub>st</sub>
			% PES	% UZ	% PL			
Breadfruit	Fiji	9/9	83.3	89	30	.1322		
Breadfruit	Solomons	7/7	66.7	100	22	.1040		
Breadfruit	Vanuatu	6/7	66.7	83	23	.1073		
Breadfruit	Rotuma	6/8	50	83	20	.0932		
Breadfruit	PNG	0/3	NA	NA	9	.0518		
Breadfruit	Chuuk	26/9	83.3	96	24	.1195		
Breadfruit	Palau	6/6	83.3	67	21	.1104		
Breadfruit	Marianas	2/21	0	NA	32	.1617		
Breadfruit	Pohnpei	36/47	66.7	58	66	.2716		
Breadfruit	Yap	3/2	66.7	100	5	.0311		
Breadfruit	Kiribati	1/2	NA	NA	9	.1748		
Breadfruit	Kosrae	1/0	NA	NA	NA	NA		
Breadfruit	Societies	43/45	33.3	4.7	29	.1208		
Breadfruit	Cooks	7/11	50	29	17	.0912		
Breadfruit	Marquesas	7/9	0	14	17	.0790		
Breadfruit	Hawaii	3/1	0	33	NA	NA		
Breadfruit	Samoa	13/13	83.3	69	35	.1430		
Breadfruit	Tokelau*	16/27	66.7	62.5	27	.1406		
Breadfruit	Jamaica	0/4	NA	NA	2	.0119		
Breadfruit	Seychelles	0/4	NA	NA	1	.0057		

Estimates were determined for regions (shaded in gray) and island groups. Accession numbers of samples used in isozyme analyses are listed in Ragone (1991); samples used in AFLP analyses are listed in Zerega (2003) and Zerega et al. (2004).

\*Tokelau cultivars are all recent introductions of hybrid origin and were not included in the Polynesian region calculations.

Iso = isozyme, n = number of samples, % PES = percentage polymorphic enzyme systems, % UZ = percentage unique zymotypes, % PL = percentage polymorphic AFLP loci, G<sub>st</sub> = between-population differentiation, NA = not applicable because of small sample size.

cultivars from Fiji, the Solomon Islands, Vanuatu, Rotuma, Chuuk, Palau, the Mariana Islands, Pohnpei, Yap, Kiribati, Kosrae, the Society Islands, the Cook Islands, the Marquesas, Hawaii, and Samoa (table 10.1). Each individual was scored for the presence or absence of bands, and each unique pattern of bands identified for an enzyme system represents a unique isozyme phenotype. The combination of phenotypes for each individual over the six enzyme systems is the zymotype for that individual.

To summarize diversity in the regions of the Pacific, data from breadfruit cultivars were pooled together by island groups and by the regions Melanesia, western Polynesia, eastern Polynesia, and Micronesia. In order to determine levels of diversity in enzyme systems in breadfruit, the percentage of polymorphic enzyme systems was calculated (Menancio and Hymowitz, 1989; Ragone, 1991). Additionally, to assess the isozyme diversity of breadfruit within and between regions, the percentage of unique zymotypes was determined for each island and regional population (number of zymotypes in a population divided by total number of individuals in the population; Ragone, 1991).

A total of 45 different bands were scored across all six enzyme systems (9 for ACO, 12 for ADH, 4 for IDH, 8 for LAP, 3 for MDH, and 9 for PGM). Forty-four different isozyme phenotypes were scored across all six enzyme systems (18 for ACO, 7 for ADH, 2 for IDH, 7 for LAP, 4 for MDH, and 6 for PGM). When phenotypes from all six enzyme systems were combined for each individual, 90 unique zymotypes were identified. Although most zymotypes were narrowly distributed, one was found in 35% of individuals and was predominant among eastern Polynesian triploid cultivars. This will be called the Polynesian zymotype. All cultivars sampled from the Society Islands (except one), Hawaii, Marquesas, the Mariana Islands, and Kosrae had this Polynesian zymotype. It was also found to a lesser extent in the Cook Islands (57%), Pohnpei (31%), Palau (17%), Fiji (11%), Samoa (8%), and Chuuk (3.8%).

Breadfruit's closest relatives, *A. camansi* and *A. mariannensis*, exhibit high levels of diversity: 100% of the individuals sampled have unique zymotypes, and 100% (*A. camansi*) and 50% (*A. mariannensis*) of the enzyme systems investigated are polymorphic (table 10.1). Among breadfruit cultivars, levels of isozyme diversity range from extremely low to as high as or higher than those of the wild relatives. The percentage of polymorphic enzyme systems is equally high in Micronesia, Melanesia, and western Polynesia and lowest in eastern Polynesia. The percentage of unique zymotypes is highest in Melanesia, followed by western Polynesia, Micronesia,

and eastern Polynesia (table 10.1). These measures and the overwhelming dominance of a single zymotype in eastern Polynesia indicate that eastern Polynesian breadfruit cultivars are the least genetically diverse and probably originated from a much reduced gene pool. Interestingly, the percentage of unique zymotypes among breadfruit cultivars for each major region is lower than the percentage for most of the island groups in the region, indicating that the same zymotypes often are distributed between more than one island group.

Although the distribution of most of the isozyme phenotypes indicate no clear geographic patterns, MDH had one phenotype (A) common to *A. camansi* and to breadfruit in all of the Pacific islands in the study. Three additional phenotypes (B, C, and D) were restricted to *A. mariannensis* and Micronesian breadfruit (figure 10.3). This pattern is similar to the distribution of *A. camansi* and *A. mariannensis* AFLP markers and further supports the hypothesis that Melanesian and Polynesian breadfruit cultivars are derived from *A. camansi*, whereas Micronesian cultivars appear to be of hybrid origin.

#### AFLP Data

The AFLP technique has greater resolving power than isozymes because it samples across the entire genome, and in the current study AFLP data were able to differentiate between individuals with identical zymotypes. For genetic diversity estimates of breadfruit and wild relatives based on AFLP data, a total of 289 individuals were analyzed. These comprised the 254 samples described earlier, 4 breadfruit cultivars each from Jamaica and the Seychelles, and 27 cultivars from Tokelau (accessions listed in Zerega, 2003). The Tokelau cultivars are believed to be the result of hybridization between recently introduced *A. mariannensis* and diploid *A. altalis* cultivars (Ragone, 1991, 2001) and therefore were not included in the breadfruit origins discussion. Three AFLP primer pair combinations yielded 175 polymorphic markers across all 289 individuals (68 markers from *EcoRI-ACA/MseI-CTC*, 51 markers from *EcoRI-ACA/MseI-CAT*, and 56 markers from *EcoRI-AAG/MseI-CTG*). To summarize levels of diversity, breadfruit cultivars were pooled together by island groups and regional populations.

To determine the genetic diversity of breadfruit cultivars and wild relatives based on AFLP data, the percentage of polymorphic loci (% PL) and the Shannon index (Shannon and Weaver, 1949; Lewontin, 1972) were calculated using Popgene version 1.31 (Yeh et al., 1999). The Shannon index is

a diversity measure that reflects richness and distribution of genotypes in a population. It is calculated for each locus ( $\sum 1 \log^2 i$ , where  $i$  = the frequency of the presence or absence of the band), and the mean diversity is calculated as the average of index values over individual loci. The standard deviations for the Shannon index are not shown in table 10.1, but in all cases they are higher than the mean index because several loci were monomorphic in all populations and had a Shannon index of zero. Additionally, the  $G_{st}$  value was calculated (Hartl and Clark, 1989) to measure the proportion of the total genetic variance present in each subpopulation (e.g., the individual island groups) relative to the total genetic variance in the entire population (e.g., Melanesia, eastern and western Polynesia, and Micronesia). A high  $G_{st}$  value implies a high degree of differentiation between populations.

#### Comparison of Diversity Between Breadfruit and Its Closest Relatives

Levels of genetic diversity, as indicated by the percentage of polymorphic AFLP loci, for both *A. camansi* and *A. mariannensis* are as low as or lower than those for breadfruit cultivars from Polynesia, the least genetically diverse of the major Pacific regions. However, when compared with individual island groups, only Pohnpei has greater genetic diversity than *A. camansi*, whereas Fiji, the Marianas, and Samoa also have higher levels than *A. mariannensis*. The Shannon index for *A. mariannensis* is lower than that for breadfruit cultivars in any of the major Pacific regions, although it is higher than levels of diversity in breadfruit in most of the individual island groups. The Shannon index of genotypes among *A. camansi* individuals is greater than that found for the breadfruit cultivars from any of the major Pacific regions except Micronesia. These measures attest to the high levels of genetic diversity that exist among Pacific breadfruit cultivars throughout the islands of Oceania compared with their progenitor species. However, it must be pointed out that the full range of diversity for *A. camansi* and *A. mariannensis* was not represented because *A. mariannensis* from Palau and *A. camansi* from Irian Jaya (western New Guinea) and the Moluccas were not available. Additional sampling may reveal greater genetic diversity in these two species.

#### Breadfruit Genetic Diversity in Oceania

The diversity measures for Pacific island breadfruit cultivars indicate that Micronesia harbors the greatest levels of genetic diversity, followed by



Melanesia and then Polynesia. Interestingly, however, Polynesian cultivars are the most genetically differentiated (reflected by higher  $G_{st}$  values) (table 10.1). In other words, compared with other regions, a greater percentage of the genetic diversity in Polynesia is attributed to diversity within individual island groups. This may be explained by the fact that Polynesian cultivars are predominantly vegetatively propagated, which leads to a reduction in gene flow and lower genetic diversity than in the outcrossing cultivars in Melanesia and Micronesia. At the same time, vegetative propagation also increases differentiation between reproductively isolated individuals. Therefore, vegetative propagation in Polynesia appears to have contributed to a narrower genetic base than in other Pacific regions, but much of the existing diversity is unique to specific island groups. This may help explain the occurrence of hundreds of cultivar names in many of the island groups in Polynesia (Wester, 1924; Wilder, 1928; Handy et al., 1991; Ragone, 1997). In order to further investigate how genetic diversity is partitioned between breadfruit cultivars, a nested analysis of molecular variance (Excoffier et al., 1992) was conducted using Arlequin software version 2.000 (Schneider et al., 2000). Breadfruit diversity was examined between regions, between island groups within regions, and within island groups. By far the largest percentage of the total variance (74.92%) was accounted for within island groups (table 10.2), indicating that individual islands throughout Oceania represent important repositories of breadfruit genetic diversity.

Based on these results, the genetic diversity of breadfruit appears to depend on mode of reproduction. Melanesian and Micronesian cultivars exhibit the highest levels of genetic diversity based on both isozyme and AFLP data. In Melanesia breadfruit comprises primarily seeded, diploid, outcrossing individuals (figure 10.5b, c), which are propagated by seed. In

Table 10.2 Analysis of Molecular Variance Based on AFLP Markers from Breadfruit

Source of Variation	df	Sum of Squares	Variance Components	% of Total Variance	p Value
Between regions	3	239.938	1.21652	14.20	<.001
Between island groups within regions	13	184.306	0.93300	10.88	<.001
Within island groups	188	1194.503	6.42206	74.92	<.001

Degrees of freedom (df) are equal to the number of samples minus one.

Micronesia, seeded, outcrossing diploids also occur, and many Micronesian cultivars are of hybrid origin (Fosberg, 1960; Ragone, 2001; Zerega et al., 2004). Thus sexual reproduction and hybridization are responsible for higher levels of genetic diversity throughout these regions. Polynesian, particularly eastern Polynesian cultivars, exhibit the lowest levels of diversity based on both isozyme and AFLP data. In these regions, diploid few-seeded (western Polynesia) and triploid, seedless (eastern Polynesia) cultivars are overwhelmingly predominant (figure 10.5b, c), and propagation is vegetative. Thus genetic diversity in these areas would result primarily from the occurrence and subsequent human selection of desirable somatic mutations.

#### Diversity Among Non-Pacific Breadfruit

Cultivars from the islands of Jamaica and the Seychelles have the lowest levels of genetic diversity (table 10.1). This is not surprising because only a limited number of cultivars were ever introduced outside the Pacific, effectively creating a genetic bottleneck (Leakey, 1977; Ragone, 1997). For example, Bligh introduced approximately 600 plants representing only five different breadfruit cultivars to the islands of St. Vincent and Jamaica in 1792. These were subsequently spread throughout the Caribbean (Powell, 1973; Leakey, 1977). A single cultivar, *kele kele*, brought by the French from Tonga in 1796 was the ancestor of all seedless breadfruit trees distributed throughout the French tropical colonies (Leakey, 1977; Rouillard and Gueho, 1985). All the breadfruit trees in West Africa are also believed to have stemmed from a single introduction (Smith et al., 1992). This lack of genetic diversity outside the Pacific makes these regions especially susceptible to disease and emphasizes the importance of conserving the diversity of Pacific island breadfruit.

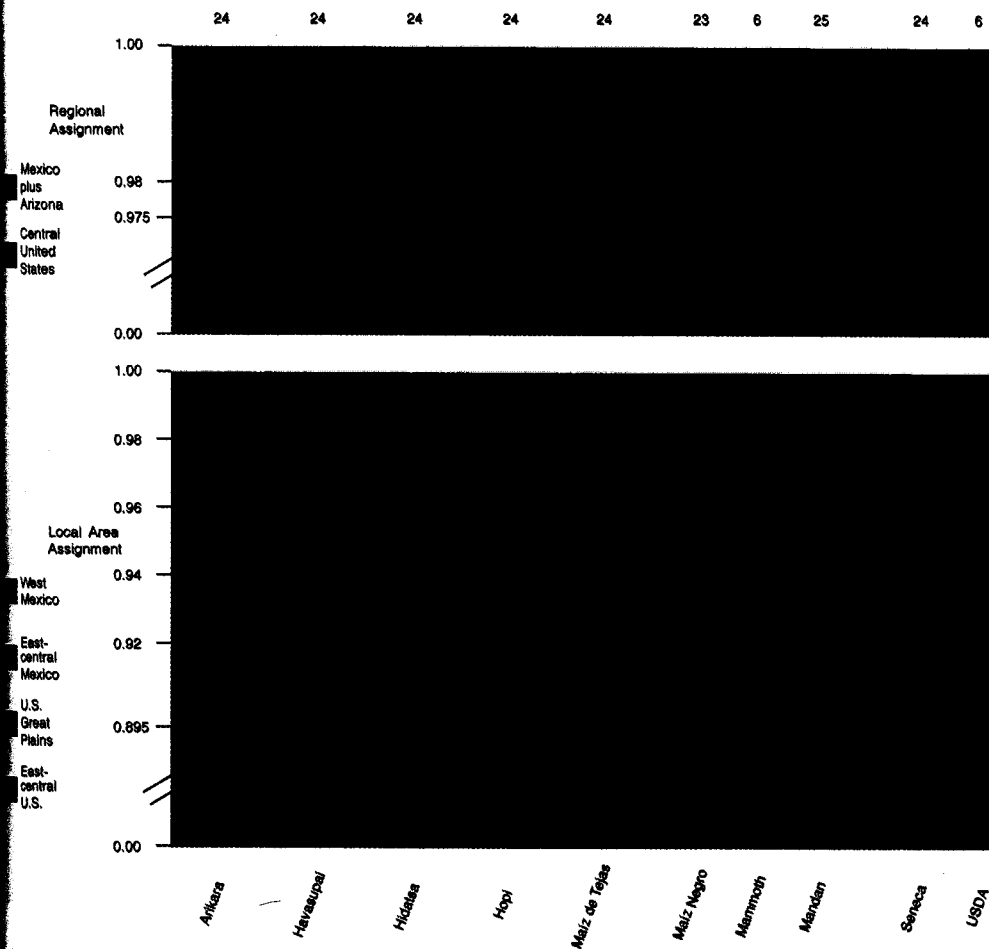
#### Human-Mediated Dispersal of Breadfruit

##### Human Migration and Breadfruit Dispersal in Melanesia and Polynesia

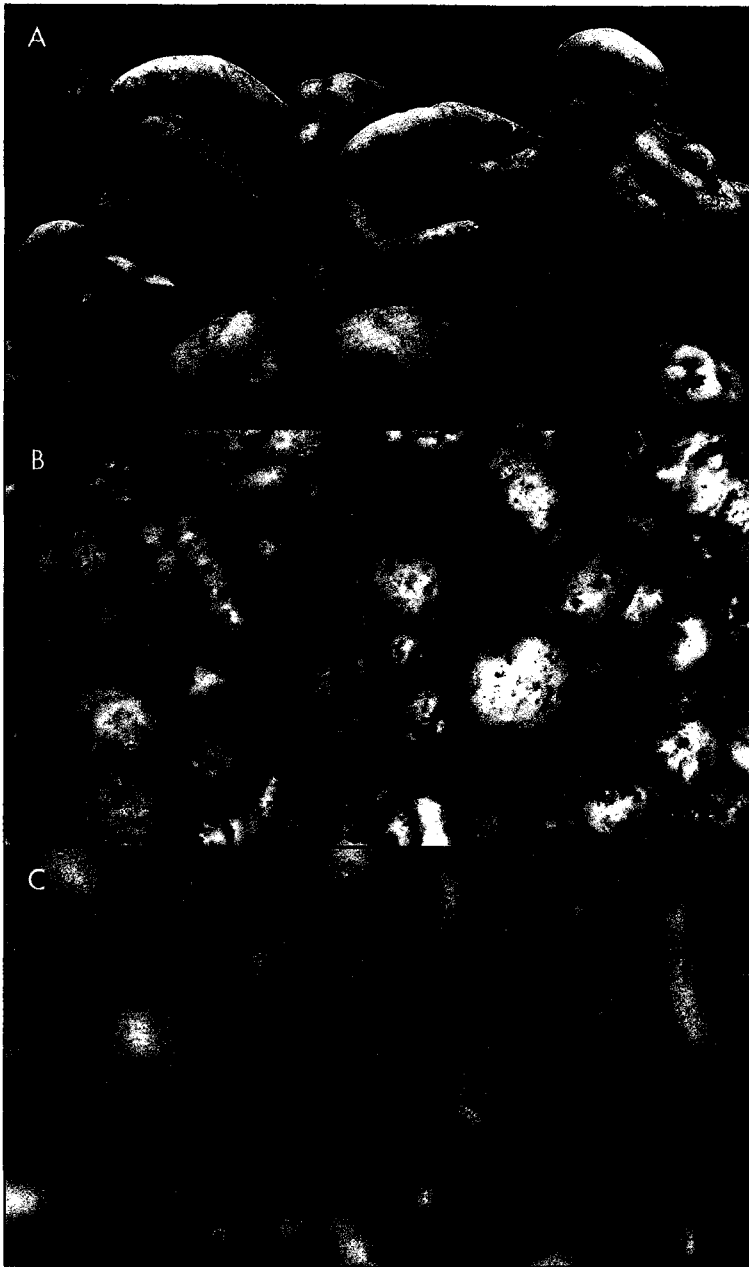
Long-distance breadfruit movement through the Pacific islands had to be human mediated because seeds are short-lived, and many cultivars are seedless. Therefore, evidence about human migrations in the Pacific based on linguistics, archaeology, anthropology, and genetics provides a working hypothesis that can be tested against molecular evidence from breadfruit.

Oceania consists of many culturally and linguistically diverse islands, and their settlement was not necessarily a simple event. This being said, scholars from several diverse disciplines generally agree that Polynesia represents a monophyletic entity and was settled via the north coast of New Guinea and then through island Melanesia within the last 4000 years by the Lapita people, a group known for their distinctive pottery and excellent seafaring skills (Kirch and Hunt, 1988; Spriggs, 1989; Intoh, 1997; Lum and Cann, 1998, 2000; Kirch, 2000; Gibbons, 2001). The Lapita are believed to have originated from somewhere in island Southeast Asia, but the exact location from which these Austronesian-speaking people came and how extensively they integrated with the Melanesians who had already been living in New Guinea and the Solomon Islands for more than 40,000 years are still debated (Diamond, 1988; Terrell, 1988; Lum and Cann, 1998; Richards et al., 1998; Kirch, 2000).

Lebot (1999) has demonstrated that several Pacific island crops (banana, *Musa* spp.; sugarcane, *Saccharum* sp.; yam, *Dioscorea alata*; and taro, *Colocasia esculenta*) probably were domesticated in New Guinea or western Melanesia and that genetic diversity decreases from the west (Melanesia) to the east (Polynesia) among cultivars of both taro and kava (*Piper methysticum*) (Lebot, 1992). This is also true for breadfruit, as demonstrated by the isozyme and AFLP data discussed earlier. If it is assumed that the region of origin is the region with the highest genetic variability, these findings correlate well with an eastward colonization through New Guinea and island Melanesia, and into Polynesia. As people sailed east into Polynesia to settle uninhabited islands, they would have been able to take only a subset of a crop's genetic diversity with them, causing the gene pool to decrease with each successive colonization event. In the case of breadfruit, most Melanesian and Polynesian breadfruit cultivars appear to be derived from *A. camansi*, a native New Guinea species. New Guinea, the Bismarck Archipelago, and the Solomon Islands are considered part of "near" rather than "remote" Oceania (Green, 1991) because they are all geographically close and were settled in the late Pleistocene (ca. 40,000 years ago) before the advent of the Austronesian-speaking Lapita people (ca. 3500–5000 years ago; Kirch, 2000). Consequently, the short-lived seeds, cuttings, or young plants of *A. camansi* may have been transported from their native New Guinea by pre-Lapita, non-Austronesian-speaking humans as far east as the Solomon Islands. Human selection of desirable traits gave rise to the domesticated *A. altivilis*, but the continued sexual reproduction of plants would explain the dominance of seeded, diploid cultivars in these islands.



**PLATE 2.4** Results of the domesticated *H. annuus* genotypic cluster assignment. Each domesticated individual's genome is represented by a thin vertical line that is partitioned into colored segments in proportion to the estimated membership in each of the wild source clusters. Cultivars are separated with black lines, with names below and sample sizes above.



**PLATE 13.1** Representative landraces **(A)** from the Andes (from Graves, 2001) and **(B)** from Chile (courtesy of Andres Contreras, Universidad Austral de Chile) and **(C)** modern cultivars (USDA Agricultural Research Magazine image gallery, [www.ars.usda.gov/is/graphics/photos/](http://www.ars.usda.gov/is/graphics/photos/)).

However, when the Lapita people arrived and ventured on longer ocean voyages eastward into the more distant unsettled islands of Melanesia and Polynesia in remote Oceania, a shift to vegetative propagation probably would have been necessary to facilitate survival on such long journeys. In fact, the Lapita people are known for their dependence on vegetatively propagated crops such as bananas, taro, yam, sugarcane, kava, and breadfruit (Barrau, 1963; Lebot, 1992; Kirch, 2000). This shift to vegetative propagation would have made long-distance transportation of breadfruit and other crops possible and increased the chances of few-seeded or seedless cultivars originating (through accumulated somatic mutations and meiotic defects) and persisting (through human selection). For example, in regions where vegetative propagation and sexual reproduction both occurred, diploid gametes arising from nondisjunction in meiosis, possibly caused by somatic mutation defects, could have joined with normal haploid gametes to produce triploid seedless cultivars. Indeed, it is on the periphery of near Oceania (eastern Solomon Islands and Vanuatu) where few-seeded diploid cultivars begin to appear and in western Polynesia where diploid seedless and few-seeded as well as triploid seedless cultivars become more common (Ragone, 1997). Seedless triploid cultivars were then preferentially propagated and dispersed eastward (figure 10.6), transforming breadfruit into a staple starch crop in Polynesia.

#### Human Migration and Breadfruit Dispersal in Micronesia

Breadfruit cultivars found in Micronesia include triploid *A. camansi*-derived “eastern Polynesian” type breadfruit in addition to hybrid cultivars bearing the genetic imprint of both *A. camansi* and *A. mariannensis*. This raises the questions, “From where was the Polynesian type cultivar introduced, and how and where did hybridization in Micronesia occur?”

Because there is no direct evidence of a Polynesian migration into Micronesia, the presence of Polynesian type breadfruit in Micronesia might be explained by trade following European contact. It has been suggested that the Spanish may have introduced the Polynesian type triploid breadfruit into the Philippines in the 1600s (Jarrett, 1959b). Despite its use as a food plant, there was no mention of it by de Morga (1971) in the Philippines in the early 17th century even though de Morga was acquainted with breadfruit through correspondences with Quiros (Markham, 1904). However, breadfruit was mentioned in Camel’s (1704) list of Philippine plants in the early 1700s. Therefore, it is possible that the Spanish distributed the

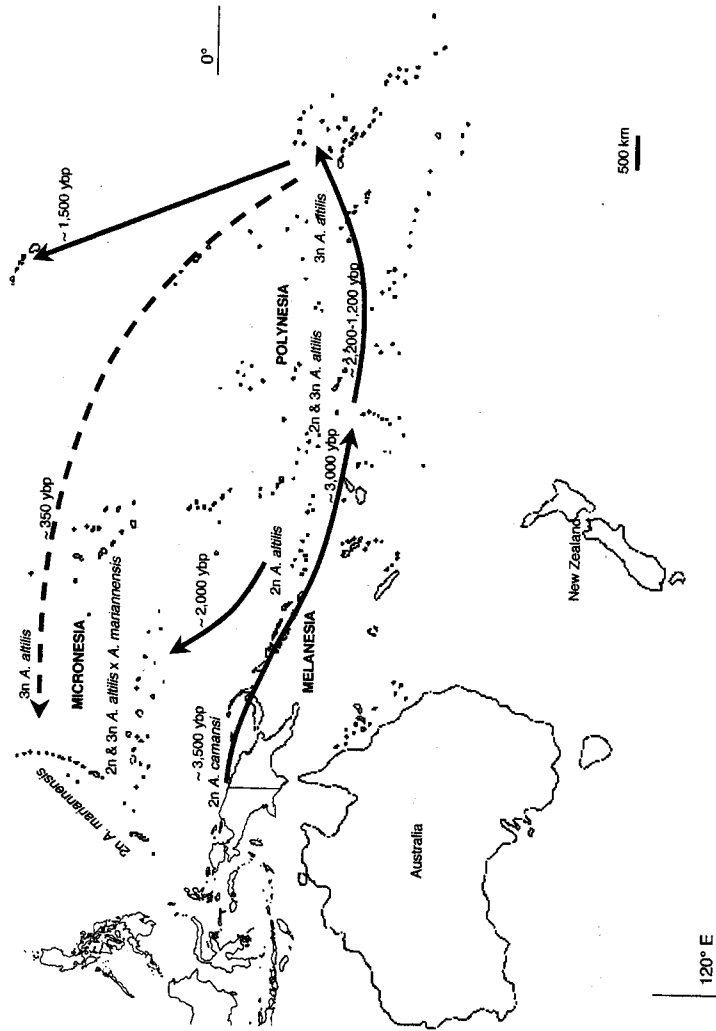


FIGURE 10.6 Map of Oceania with proposed human-mediated breadfruit dispersal routes. Arrows indicate general direction of migrations and are simplified from actual migration routes. Times are estimates and are given in years before present (ybp) (from Kirch, 2000). Species and ploidy levels found within regions are indicated. The dashed arrow represents a post-European contact route.

Polynesian breadfruit into both Micronesia and the Philippines to help provision their colonies.

Regarding the question of breadfruit hybrids in Micronesia, Fosberg (1960) proposed that hybridization and subsequent introgression between introduced triploid sterile Polynesian cultivars and native diploid *A. mariannensis* was occurring in the Mariana Islands. He suggested that this accounted for the great variability in Micronesian cultivars with shared morphological characters of both *A. altilis* and *A. mariannensis*. However, this hypothesis is highly unlikely because triploids very rarely make it through meiosis to successfully produce viable gametes. An alternative hypothesis is that diploid *A. camansi*-derived breadfruit was introduced into the range of *A. mariannensis*, allowing the two species to hybridize. Subsequently, varying degrees of introgression and human selection have led to the diversity of cultivars unique to Micronesia. This hypothesis is supported by another source of evidence that diploid *A. altilis* and *A. mariannensis* can hybridize because recent introductions of the two species in Tokelau have led to fertile hybrids (Ragone, 1991, 2001). The Micronesian hybrids comprise fertile and sterile diploids and sterile triploids (Ragone 2001). These triploids arose from a separate event than the seedless autotriploids in Polynesia and probably result from hybrid diploid gametes (through nondisjunction in meiosis) joining with normal haploid gametes from other diploid hybrids, *A. altilis*, or *A. mariannensis*. An alternative explanation for the presence of *A. camansi* and *A. mariannensis* markers in Micronesian breadfruit is that these two species hybridized with one another. However, the ranges of the two species do not overlap, and there is no evidence that they have ever overlapped (Zerega et al., 2004).

How does our knowledge of human migrations in Micronesia relate to the hypothesis about the origin of hybrid Micronesian breadfruit outlined above? The human settlement of the culturally and linguistically heterogeneous islands of Micronesia is more complex than that of Polynesia. It probably was settled from several directions at different times, and based on evidence from linguistics, archaeology, and genetics, several nonexclusive hypotheses have been proposed. These include migrations from New Guinea into Palau and Yap (Lum and Cann, 2000), independent colonizations of the Mariana Islands and Yap from Southeast Asia (Kirch, 2000; Lum and Cann, 2000), and a direct (or indirect through the Kiribati archipelago) northerly Lapita migration from somewhere between the Bismarck Archipelago and the southeast Solomons–Vanuatu region into central-eastern Micronesia (Caroline Islands [including Chuuk, Kosrae, Pohnpei],

Kiribati, and the Marshall Islands) (Lebot and Lévesque, 1989; Petersen, 1995; Kirch, 2000). Subsequent secondary migrations also occurred among the islands of Micronesia (Kirch, 2000; Lum and Cann, 2000).

It is unlikely that *A. camansi* was introduced into Micronesia from New Guinea because there are no historical accounts of its presence in Micronesia, and it grows on only a few Micronesian islands today as the result of recent introductions (Ragone, 2001). However, a northerly Lapita migration (transporting diploid *A. camansi*-derived breadfruit) from the southeast Solomons-Vanuatu region into central-eastern Micronesia, followed by subsequent human migrations and trading within Micronesia (Kirch, 2000; Lum and Cann, 2000), could have brought diploid *A. camansi*-derived breadfruit into the range of wild *A. mariannensis* (Mariana Islands and Palau), allowing the two species to hybridize (figure 10.6; Zerega et al., 2004). There has been debate about whether a northerly Lapita migration into Micronesia occurred directly into the high islands of the Carolines or indirectly via island hopping through the atolls of the Kiribati archipelago (Petersen, 1995). Because breadfruit cultivars without *A. mariannensis* traits do not grow well in harsh atoll conditions (Ragone, 1988), a human migration successfully transporting breadfruit probably was direct across open water as opposed to going through the low atolls of Kiribati, where purely *A. camansi*-derived cultivars would have fared poorly. Genetic and cultural evidence from kava (*Piper methysticum*), another cultivated Pacific plant, also suggests a direct migration (Lebot and Lévesque, 1989; Petersen, 1995). Such a direct route from Melanesia into Micronesia may have been reciprocal because *A. mariannensis*-diagnostic markers are also present in some breadfruit cultivars in Vanuatu and eastward into Polynesia (figure 10.3). Thus, a small percentage of breadfruit cultivars with *A. mariannensis* markers could have subsequently been dispersed into Polynesia with the eastward Lapita migration.

### Conclusions

Two species (*A. camansi* and *A. mariannensis*) and at least two different events (vegetative propagation coupled with human selection in Melanesia and Polynesia and introgressive hybridization in Micronesia) were involved in the origins of breadfruit. Thousands of years of cultivation and selection of breadfruit have led to a wealth of morphological diversity and unique breadfruit cultivars suited to different purposes and environments. Genetic erosion is evident in non-Pacific regions, where only a limited

number of cultivars were introduced. Today genetic erosion is also a concern in many areas of the Pacific. Because of urbanization and the ease of obtaining and preparing introduced foods, the importance of traditional foods such as breadfruit has diminished and endemic island cultivars have been lost. This is exacerbated by global climate change and rising sea levels, which threaten the very existence of some Pacific islands and the breadfruit cultivars unique to them. However, there is a growing interest in reducing food imports, more fully using locally grown crops, and encouraging young people to learn and perpetuate traditional cropping systems. As a result, the potential exists for breadfruit to once again become a much more widely grown and used tropical crop. Despite thousands of years of evolution in domestication, breadfruit research and commercial utility are still in their infancy. Additional research to improve the future potential and conservation of breadfruit is under way, including the development of a morphological descriptor list to identify cultivars and in-depth yield studies. Additional projects on pollination biology, development of breadfruit food products with a long shelf life suitable for a commercial market, and the collection of cultivars from underrepresented areas for deposit in both ex situ living gene banks and in situ conservation collections will all contribute to the future use and conservation of breadfruit.

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### References

- Aalbersberg, W. G. L., C. E. A. Lovelace, K. Madhoji, and S. V. Parkinson. 1988. Davuke, the traditional Fijian method of pit preservation of staple carbohydrate foods. *Ecology of Food and Nutrition* 21: 173-180.

- Andrews, L. 1990. Breadfruit varieties in the Windward Islands. *Tropical Fruit Newsletter* 1: 3–4.
- Atchley, J. and P.A. Cox. 1985. Breadfruit fermentation in Micronesia. *Economic Botany* 39: 326–335.
- Barrau, J. 1963. *Plants and the Migrations of Pacific Peoples*. Bishop Museum Press, Honolulu, HI, USA.
- Bligh, W. 1792. *A Voyage to the South Sea, Undertaken by Command of His Majesty, for the Purpose of Conveying the Bread-Fruit Tree to the West Indies, in His Majesty's Ship the Bounty, commanded by Lieutenant William Bligh*. George Nicol, London, UK.
- Brantjes, N. B. M. 1981. Nectar and the pollination of breadfruit, *Artocarpus altilis* (Moraceae). *Acta Botanica Neerlandica* 30: 345–352.
- Camel, J. G. 1704. Appendix. In J. Ray (ed.), *Historia Plantarum*, Vol. 3, 52. S. Smith and B. Walford, London, UK.
- Coenen, J. and J. Barrau. 1961. The breadfruit tree in Micronesia. *South Pacific Bulletin* 11: 37–39, 65–67.
- de Morga, A. 1971. *Sucesos de las Islas Filipinas*. Hakluyt Society, London, UK.
- Diamond, J. M. 1988. Express train to Polynesia. *Nature* 336: 307–308.
- Dumont d'Urville, M. J. 1832. Notice sur les îles du Grand Océan et sur l'origine des peuples qui le habitent. *Société de Géographie Bulletin* 17: 1–21.
- Excoffier, L., P. Smouse, and J. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics* 131: 479–491.
- Fosberg, F. R. 1960. Introgression in *Artocarpus* in Micronesia. *Brittonia* 12: 101–113.
- Gibbons, A. 2001. The peopling of the Pacific. *Science* 291: 1735–1737.
- Graham, H. D. and E. Negron de Bravo. 1981. Composition of the breadfruit. *Journal of Food Science* 46: 535–539.
- Green, R. C. 1991. Near and remote Oceania: Disestablishing "Melanesia" in culture history. In A. Pawley (ed.), *Man and a Half: Essays in Pacific Anthropology and Ethnobiology in Honour of Ralph Bulmer*, 491–502. Polynesian Society, Auckland, NZ.
- Handy, E. S. C., E. G. Handy, and M. K. Pukui. 1991. *Native Planters in Old Hawaii. Their Life, Lore, and Environment*. Bishop Museum, Honolulu, HI, USA.
- Hartl, D. L. and A. G. Clark. 1989. *Principles of Population Genetics*, 2nd ed. Sinauer Associates, Sunderland, MA, USA.
- Hasan, S. M. Z. and A. R. Razak. 1992. Parthenocarpy in seedless breadfruit (*Artocarpus incircus* (Thumb.) L.). *Acta Horticulturae* 321: 648–652.
- Intoh, M. 1997. Human dispersal into Micronesia. *Anthropological Science* 105: 15–28.
- Jarrett, F. M. 1959a. Studies in *Artocarpus* and allied genera, I. General considerations. *Journal of the Arnold Arboretum* 40: 1–29.
- Jarrett, F. M. 1959b. Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. *Journal of the Arnold Arboretum* 40: 113–155, 327–368.
- Kirch, P. V. 2000. *On the Road of the Winds: An Archaeological History of the Pacific Islands Before European Contact*. University of California Press, Berkeley, CA, USA.
- Kirch, P. V. and T. L. Hunt. 1988. Radiocarbon dates from the Mussau Islands and the Lapita colonization of the Southwest Pacific. *Radiocarbon* 30: 161–169.
- Leakey, C. L. A. 1977. *Breadfruit Reconnaissance Study in the Caribbean Region*. CIAT/InterAmerican Development Bank, Cali, Colombia.
- Lebot, V. 1992. Genetic vulnerability of Oceania's traditional crops. *Experimental Agriculture* 28(3): 309–323.
- Lebot, V. 1999. Biomolecular evidence for plant domestication in Sahul. *Genetic Resources and Crop Evolution* 46: 619–628.
- Lebot, V., and J. Lévesque. 1989. The origin and distribution of kava. *Allertonia* 5: 223–280.
- Lewontin, R. C. 1972. The apportionment of human diversity. *Evolutionary Biology* 6: 381–398.
- Lum, J. K. and R. L. Cann. 1998. mtDNA and language support a common origin of Micronesians and Polynesians in island Southeast Asia. *American Journal of Physical Anthropology* 105: 109–119.
- Lum, J. K. and R. L. Cann. 2000. mtDNA lineage analyses: Origins and migrations of Micronesians and Polynesians. *American Journal of Physical Anthropology* 113: 151–168.
- Markham, C. 1904. *The Voyages of Pedro Fernandez de Quiros 1595 to 1606*. Hakluyt Society, London, UK.
- Marte, R. 1986. Nontraditional fruit crops in the Windward Islands. *Proceedings Interamerican Society Tropical Horticulture* 30: 15–24.
- Menancio, D. I. and T. Hymowitz. 1989. Isozyme variation between diploid and tetraploid cytotypes of *Glycine tabacina* (Labill.) Benth. *Euphytica* 42: 79–87.
- Momose, K., A. Hatada, R. Yamaoka, and T. Inoue. 1998. Pollination biology of the genus *Artocarpus*, Moraceae. *Tropics* 7: 165–172.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.
- Petersen, G. 1995. The complexity of power, the subtlety of kava. *Canberra Anthropology* 18: 34–60.
- Powell, D. 1973. *The Voyage of the Plant Nursery*, H.M.S. Providence, 1791–1793. Institute of Jamaica, Kingston, Jamaica.
- Purseglove, J. W. 1968. *Artocarpus altilis*. In J. W. (ed.), *Tropical Crops* (2), *Dicotyledons*, 377–384. Longman, London, UK.
- Ragone, D. 1988. *Breadfruit Varieties in the Pacific Atolls*. Integrated Atoll Development Project, UNDP, Suva, Fiji.
- Ragone, D. 1991. *Collection, Establishment, and Evaluation of a Germplasm Collection of Pacific Island Breadfruit*. Ph.D. dissertation, University of Hawaii, Honolulu, HI, USA.
- Ragone, D. 1997. *Breadfruit, Artocarpus altilis* (Parkinson) Fosberg, *Promoting the Conservation and Use of Underutilized and Neglected Crops*, 10. International Plant Genetic Resources Institute, Rome, Italy.
- Ragone, D. 2001. Chromosome numbers and pollen stainability of three species of Pacific island breadfruit (*Artocarpus*, Moraceae). *American Journal of Botany* 88: 693–696.
- Richards, M., S. Oppenheimer, and B. Sykes. 1998. mtDNA suggests Polynesian origins in eastern Indonesia. *American Journal of Human Genetics* 63: 1234–1236.
- Roberts-Nkrumah, L. B. 1993. Breadfruit in the Caribbean: A bicentennial review. *Extension Newsletter Department of Agriculture University of the West Indies (Trinidad and Tobago)* 24: 1–3.
- Rouillard, G. and J. Gueho. 1985. History of the horticultural, medicinal, and economic plants of Mauritius. *Revue Agricole et Sucrière de l'île Maurice* 64: 151–167.
- Sakai, S., M. Kato, and H. Nagamasu. 2000. *Artocarpus* (Moraceae)—gall midge pollination mutualism mediated by a male-flower parasitic fungus. *American Journal of Botany* 87: 440–445.
- Schneider, S., D. Roessli, and L. Excoffier. 2000. *Arlequin ver. 2.000: A Software for Population Genetics Data Analysis*. Genetics and Biometry Laboratory, University of Geneva, Switzerland.
- Shannon, C. E. and W. Weaver. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, IL, USA.
- Smith, N. J. H., J. T. Williams, D. L. Plucknett, and J. P. Talbot. 1992. *Tropical Forests and Their Crops*, 296–303. Comstock Publishing Associates, Ithaca, NY, USA.

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## Genetic Relationship Between *Dioscorea alata* L. and *D. nummularia* Lam. as Revealed by AFLP Markers

The greater yam, *Dioscorea alata* L., is the most widely cultivated species of yam in the tropics. It is grown for its starchy tubers that are harvested from 6–9 months after planting. Its origin has been a long-standing enigma of Oceanian ethnobotany and is still a subject of debate (Barrau, 1956; Bourret, 1973; Hahn, 1991; Degras, 1993). This chapter attempts to clarify its taxonomic status and position within section *Enantiophyllum* using amplified fragment length polymorphism (AFLP) markers. Additionally, a brief review of traditional uses and folk classification in Vanuatu, Melanesia, and cytogenetic research is also presented and considered in light of historical data to address the geographic distribution and dispersal of edible yams in Oceania.

### Taxonomic Classification

Edible yams are twining vines that annually develop thickened tubers at the stem bases, which serve as storage organs to carry the plant through a period of dry season dormancy. At the onset of the rainy season, tubers begin to sprout, and new plants are produced for the next growing period. Stems are sometimes armed and twine either to the right or left according to species.

- Spriggs, M. 1989. The dating of island Southeast Asia Neolithic: An attempt at chronometric hygiene and linguistic correlation. *Antiquity* 63: 587–613.
- Sunarto, A. T. 1981. Fertility test of *Artocarpus altilis*. *Berita Biologi* 2: 118.
- Terrell, J. 1988. History as a family tree, history as an entangled bank: Constructing images and interpretations of prehistory in the South Pacific. *Antiquity* 62: 642–657.
- Vos, P., R. Hogers, M. Bleeker, M. Rijans, T. Van de Lee, M. Hornes, A. Frijters, J. Pot, J. Peleman, M. Kuiper, and M. Zabeau. 1995. AFLP: A new technique for DNA fingerprinting. *Nucleic Acids Research* 23: 4407–4414.
- Wester, P. J. 1924. The seedless breadfruits of the Pacific archipelagos. *Philippine Agricultural Review* 17: 24–39.
- Wilder, G. P. 1928. *Breadfruit of Tahiti*. Bishop Museum Bulletin 50. Bishop Museum, Honolulu, HI, USA.
- Yeh, F. C., T. Boyle, Y. Rongce, Z. Ye, and J. M. Xiyang. 1999. *Popgene* version 1.31, Microsoft Windows-based freeware for population genetic analysis. [www.ualberta.ca/~fyeh/](http://www.ualberta.ca/~fyeh/).
- Zerega, N. J. C. 2003. *Molecular Phylogenetic and Genome-Wide Analyses of Artocarpus (Moraceae): Implications for the Systematics, Origins, Human-Mediated Dispersal, and Conservation of Breadfruit*. Ph.D. dissertation, New York University, New York, NY, USA.
- Zerega, N. J. C., D. Ragone, and T. J. Motley. 2004. Complex origins of breadfruit: Implications for human migrations in Oceania. *American Journal of Botany* 91: 760–766.