

**COLLECTION, ESTABLISHMENT, AND EVALUATION
OF A GERMPLASM COLLECTION OF
PACIFIC ISLAND BREADFRUIT**

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ABSTRACT

Approximately 400 accessions of breadfruit (*Artocarpus altilis* (Parkin.) Fosberg, *A. mariannensis* Trecul, and *A. camansi* Blanco) were collected from 17 Pacific Island groups (Fiji, Rotuma, Solomon Islands, Vanuatu, Belau, Kiribati, Mariana Islands, Marshall Islands, Pohnpei, Truk, Yap, Cook Islands, Marquesas, Samoa, Society Islands, Tokelau, and Tonga) for a germplasm collection. Micronesian accessions included interspecific hybrids between *A. mariannensis* and *A. altilis*. A total of 145 accessions were propagated and 185 trees of 135 accessions were added to a germplasm collection on Maui, Hawaii, at the Kahanu Gardens of the National Tropical Botanical Garden. The collection now consists of 226 trees of more than 100 cultivars from 17 island groups.

The collection was evaluated using gel electrophoresis. Six enzyme systems (ACO, ADH, IDH, LAP, MDH, and PGM) were polymorphic, and 204 accessions were reduced to 90 unique zymotypes using cluster analysis. Only 12 zymotypes occurred in more than one island group, and one, a Polynesian triploid cultivar (*A. altilis*) was found in 11 island groups in Polynesia and Micronesia. Seventy-four accessions were observed to have this zymotype. The greatest isozyme variation occurred in Melanesia with 71% of the accessions uniquely characterized. Micronesia and Western Polynesia had relatively high rates of zymotypic variation with 59% and 51% variation, respectively. Only two zymotypes were found in Eastern Polynesia.

Chromosome numbers for *A. camansi* and *A. mariannensis* are reported here for the first time as $2n = 56$. Counts of $2n = 56$ and $2n = 84$ were observed for *A. altilis*. Most seeded cultivars of *A. altilis* had counts of $2n = 56$, but seedless diploid cultivars were also observed. The majority of interspecific hybrids were seedless with counts of $2n = 56$. Triploid interspecific hybrids were also observed.

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PREFACE

Every portion of the breadfruit tree has yielded materials useful to islanders, but it is principally important as a source of carbohydrates. Breadfruit is found on most of the inhabited Pacific islands, and its significance as a food crop varies with location. In Micronesia, it is a major source of food in Kiribati, Kosrae, Marshall Islands, Pohnpei, Truk, and Yap. This is particularly true on the atolls where breadfruit is the main subsistence crop along with *Cyrtosperma*, pandanus, and coconuts. It is only of marginal importance in Belau and the Mariana Islands.

Breadfruit is grown and utilized throughout the South Pacific, but traditional crops such as *Colocasia*, *Dioscorea*, and *Ipomoea* are of greater importance in the Cook Islands, Fiji, New Guinea, Society Islands, Solomon Islands, and Tonga. Breadfruit is still a significant food in the eastern Solomon islands, Vanuatu, Marquesas, and Samoa, and on the atolls of Tokelau and Tuvalu. Nevertheless, the use of breadfruit is declining in many islands, and genetic erosion is occurring.

The objectives of this study include:

- 1) The systematic survey and collection of breadfruit cultivars throughout the Pacific Islands.
- 2) The establishment of a safe, permanent germplasm collection in Hawaii that adequately represents the genetic diversity of this crop.
- 3) The characterization of the collection with respect to variation in isozyme content, chromosome number, and major morphological features.

CHAPTER I

LITERATURE REVIEW

Traditional importance of breadfruit

Breadfruit has long been an important staple crop in the Pacific Islands where it is part of an agricultural complex well adapted to island environments. This crop complex included cultigens such as coconuts (*Cocos*), taro (*Colocasia*, *Alocasia*, and *Cyrtosperma*), sweet potatoes (*Ipomoea*), bananas (*Musa*), yams (*Dioscorea*), sugarcane (*Saccharum*), *Pandanus*, *Terminalia*, *Inocarpus*, and *Cordyline*, with the dominating species varying from island to island.

Melanesia

In Melanesia, wild breadfruit is still an important component of the subsistence economy in lowland areas of New Guinea. Breadfruit seeds are a valued food in New Guinea and are widely collected (Barrau 1958b; Massal and Barrau 1954; Sorenson and Gajdusek 1969). Gathered seeds are sold in village markets in some areas providing an important source of income for women (E. Cox, personal communication, 1986). The majority of harvested trees grow wild in the forest, however, seeded trees are occasionally semi-cultivated by seed gatherers who transplant seedlings to other areas in the forest and to village areas (Croft 1987).

Breadfruit is found throughout the Solomon Islands but the greatest diversity occurs in the Santa Cruz and Reef Islands, the easternmost groups. The fruits, and to a lesser extent, seeds, are a major subsistence food in the eastern islands, but breadfruit is of little importance in the western and central Solomon Islands. Most cultivars are seeded and selection of seedlings is a common practice. Seedlings are allowed to grow until they bear fruit. The fruit is then sampled, and the tree is cut down if not of desired quality. If

the seedling has qualities which are desired, it is given an appropriate name and multiplied by vegetative propagation. Breadfruit is equally important in Vanuatu, formerly known as the New Hebrides, especially in the Banks Islands. Seeds from roasted or boiled fruits are eaten, but the fruit is of greater value. Breadfruit is still widely grown and used in Rotuma, and the Lau and Yasewa Groups of Fiji.

Polynesia

In western Polynesia, breadfruit is an important staple food crop. In Samoa, trees are found growing around residences in all villages, and numerous cultivars are grown in small plantations with other crops such as bananas, taro, and other root crops. Root crops are the primary staple foods in Tonga, but breadfruit is found in most villages. Tonga has fewer cultivars of breadfruit than Samoa, and six cultivars are common to both groups.

In eastern Polynesia, the northern coral atolls of the Cook Islands have few cultivars of breadfruit, but breadfruit trees are numerous in the southern group. Breadfruit was previously an important staple crop in Mangareva and the Austral, Marquesas, and Society Groups; it was of prime importance in the Marquesas. Breadfruit was of local importance in some areas of the Hawaiian Islands, but taro and other crops were more widely grown.

Micronesia

Breadfruit is a major crop in the atolls of the Caroline Islands, Marshall Islands, Tokelau, Kiribati, and Tuvalu, where it is the main staple food along with fish, coconut, and pandanus, and it is the predominant tree in the villages. Seedless breadfruit remains the most important staple crop in Truk and its use has been well-documented (Hall and Peltzer 1946; LeBar 1964; Murai et al. 1958). On the high volcanic islands of Truk, Pohnpei, and Kosrae, it is the most important crop in season, and the islands are renowned for their abundance and diversity of breadfruit.

While breadfruit played an important role in the subsistence economies of most of Micronesia, it was of limited importance in Guam, the Mariana Islands, and Belau. The few breadfruit cultivars found in Belau reflect its relative unimportance in the diet of these islands, where root crops such as *Cyrtosperma* predominate. Of particular interest is the widespread abundance of a seeded breadfruit, known as **meduuliou**, a major component of the native forest in the uplifted, limestone islands. It is rarely found on Belau's northern volcanic islands. In pre-European times, **meduuliou** was an important mainstay for the southern islands of Anguar, Kayangel, and Peleliu (McKnight 1964). One of the earliest accounts of Belau, written in the 1670s, documented the use of pit-fermentation to preserve abundant harvests for later use (Jacobs 1980).

Nutritional value of breadfruit

Breadfruit is typically roasted or boiled, and occasionally fried as chips. It is an important source of calories, being high in carbohydrates, but low in fats and protein (Miller 1948-1950; Graham and Bravo 1981; Wooten and Tumalii 1984). Murai et al. (1958) examined the nutritional values of 11 different breadfruit cultivars from the Pacific islands. They concluded that when enough breadfruit is eaten daily to provide most of the caloric needs, it is a good source of phosphorus, iron, calcium, ascorbic acid (vitamin C), and the B vitamins: thiamine, niacin, and riboflavin. Breadfruit is not a good source of vitamin A, which must be obtained from pandanus, other fruits, green, leafy vegetables, or animal sources (e.g., fish livers).

Compared to cooked, unpolished white rice and enriched wheat flour, which are replacing breadfruit and other traditional carbohydrate foods, breadfruit is a better source of calcium, riboflavin, niacin, phosphorus, and ascorbic acid (Thomas and Corden 1977; South Pacific Commission 1983). A study of the nutritional value of breadfruit seeds showed that they are a good source of protein, 8%, and are low in fat, 3-5%, compared to nuts such as peanuts or almonds which contain 50-60% fat (Murai et al. 1958). Breadfruit seeds contain more protein, calcium, phosphorus, iron, and niacin, and less fat and

carbohydrates than chestnuts. They are a poor source of ascorbic acid. Approximately 40 seeds are required to yield 100 grams of edible portion. The nutrient composition of fresh, roasted, and boiled fruits, and fresh and cooked seeds are provided in the following table.

Table 1.1. Proximate composition of boiled seeds, and fresh, roasted, boiled, and pit-fermented breadfruit per 100 grams edible portion.

		Method of preparation				
		Fresh	Roasted	Boiled	Preserved	Seeds
Water	%	69.1	65.7	70.6	67.6	61.9
Food energy	cal	121.0	133.0	115.0	130.0	156.0
Protein	g	1.3	1.5	1.1	1.4	7.94
Carbohydrate	g	28.1	31.4	27.4	29.4	38.2
Fat	g	0.4	0.3	0.3	0.9	4.68
Calcium	mg	23.2	23.0	16.6	18.8	48.3
Phosphorus	mg	47.2	59.6	32.6	30.6	89.4
Iron	mg	0.63	0.96	0.38	0.56	0.13
Thiamine	mg	0.09	0.08	0.08	0.02	0.08
Riboflavin	mg	0.06	0.08	0.06	0.08	1.84
Niacin	mg	1.28	1.42	0.67	0.91	1.9
Vitamin C	mg	8.7	1.9	3.1	6.5	1.9

Adapted from *Some Tropical South Pacific Island Foods* (Murai et al. 1958).

Storage and preservation methods

Since the breadfruit season on the atolls and some high islands is typically limited to three or five months, islanders developed several methods of preservation to extend its availability. Most common was the preparation of fermented, preserved breadfruit, known as **ma** or **masi** in Polynesia (Atchley and Cox 1985; Cox 1980; Handy 1923) **bwiru** in the Marshall Islands, **apot** in the Caroline Islands (Massal and Barrau 1954; Murai et al. 1958) and **madrai** in Fiji (Parkinson 1984; Seeman 1865-1873). Fermented breadfruit is still made every season in Truk, Pohnpei, and on most atolls in the Marshall and Caroline Islands. It is only occasionally made, on a very small scale, in the Marquesas and Samoa.

Mature and ripe fruits are peeled, cored, and halved and allowed to soften; this is achieved in the atolls by soaking the fruits in the lagoon for one to two days. The softened fruits are placed into a leaf-lined pit and covered with leaves, a layer of soil, and rocks (Figure 1.1). After two to three weeks, the fermented breadfruit pulp is ready for use; it is always washed and cooked before being eaten. Fermented breadfruit can be stored for one to two years in the pit, and the leaves are replaced as needed during the storage period.



Figure 1.1. Breadfruit fermentation pit

General uses of the breadfruit tree

In addition to its importance as a carbohydrate food source, the breadfruit tree has provided Pacific islanders with myriad useful materials. The tall-growing, straight-trunked trees provide a light-weight timber used for construction of buildings, canoes, and miscellaneous items such as fishing floats and carvings. The bark provides fiber for cordage and tapa cloth. The young shoots, bark, and latex are all used medicinally, and the latex is also used as an adhesive, especially for caulking canoes. In addition to providing shade, breadfruit leaves are used to wrap foods for cooking. Mature fruits, seeds, and leaves provide fodder for pigs and other animals.

A comprehensive account of the ethnobotany of breadfruit is beyond the scope of this study, and many of the formerly important uses are no longer practiced due to the availability of modern materials and foods. Detailed accounts of the importance and use of breadfruit are provided for Polynesia (Buck 1930, 1938; Henry 1928; Ragone in press; Wilder 1928) and Micronesia (LeBar 1964; Catala 1957; Lawrence 1964; MacKenzie 1964; McKnight 1964; Massal and Barrau 1954).

Present status of breadfruit

Changing Pacific subsistence economies

The importance of breadfruit in the Pacific has diminished in the past 50 years, and a number of cultivars have disappeared or are becoming rare. As Pacific islanders become more westernized and shift from a traditional subsistence economy to a cash economy, more people migrate from the outer islands to population centers (Thaman 1983). For example, 80% of the population of the Society Islands now lives in the town of Papeete.

Breadfruit trees are still numerous on the outer islands, but cultivation and use of breadfruit and other traditional crops is decreasing in the population centers. Urban households depend heavily on imported foods as busy work schedules don't allow for the often time-consuming task of gathering and preparing traditional foods. Urban

households may have one or two breadfruit trees, but these are generally limited to the most common cultivars (R. Brotherson; M. Guerin, personal communication, 1987). Older residents are still knowledgeable about the uses and cultivation of different cultivars, food preservation methods, and other information, however, post-World-War-II generations often know very little about their traditional crops and cropping systems.

Effects of storms and drought

The genetic erosion of breadfruit can be attributed to two main factors: the changes in traditional lifestyles outlined above and storm damage. Breadfruit trees are prone to damage from high winds and the accompanying salt spray and intrusion of salt water into the water table during severe storms. The low-lying atolls have been repeatedly inundated by storm-generated tides, resulting in uprooting or destruction of numerous breadfruit trees (Kerr 1976; Visher 1925). Hurricane damage has resulted in the destruction of trees in the Marshall Islands (Blumenstock et al. 1961; Hatheway 1953; Wiens 1957, 1962). Tokelau, the Tuamotus, Ulithi, and other atolls in the western Caroline Islands suffered considerable damage in 1987.

During the past decade, the high islands of Fiji, Guam, Saipan, Samoa, the Solomon Islands, Truk, and Vanuatu also experienced destructive storms. For example, as much as 100% of the breadfruit crop and was lost in Samoa in 1990 by Hurricane Ofa. Five hurricanes during 1985 destroyed trees on Fiji, and breadfruit has been replaced by other foods on the main island of Viti Levu.

Droughts also affect the breadfruit crop, and prolonged droughts have resulted in the destruction of trees in the Micronesian atolls. The southern islands of Kiribati are especially susceptible to periodic droughts in Kiribati (Luomala 1958; Wiens 1962). Droughts have also caused damage to trees in Guam, Pohnpei, Samoa, and other high islands. Droughts and storms have destroyed trees in the Tuamotus, and tsunami damage, wind, and attrition have taken their toll in the Marquesas (T. Pakeha; A. Tamarii, personal communication, 1987).

Other factors are also involved in the dwindling of breadfruit. A seeded breadfruit in the Mariana Islands known as **dugdug**, was a major component of the native forest, but deforestation due to fires during and after World War II has drastically decreased its numbers. Severe typhoons have also contributed to its decline. Only Rota still has large areas of this species.

Breadfruit diseases

Breadfruit trees are relatively free of diseases and insect pests. In the 1960s, however, there was concern that breadfruit trees in Micronesia were being decimated by a problem known as 'Pingelap disease'. Die-back on many islands, in particular, Guam and the Caroline atolls was extensive (Zaiger and Zentmyer 1966). A subsequent survey by Trujillo (1971) determined that there was no single pathological cause of this die-back. Rather, it was considered to be the result of a combination of typhoon damage, drought, aging of the trees, salinity, and other environmental factors. This problem has recently been observed in several Caribbean Islands (L. Roberts-Nkrumah, personal communication, 1990).

Problems with fruit rot have been reported as early as the 1930s (Hatheway 1957). Trujillo (1971) and Gerlach and Salevao (1984) have shown that the fruit can be affected by *Phytophthora*, *Colletotrichum* (anthracnose), and *Rhizopus* (soft rot), but these can be controlled by prompt harvest of mature fruits and removal of diseased fruits. Fruit rot was a problem especially on rough-skinned cultivars in Pohnpei, Truk, and Western Samoa during the 1987-1988 breadfruit season (J.E. Wilson, personal communication, 1989).

The need for germplasm conservation

Replanting has not kept pace with the losses incurred throughout the Pacific by drought, storm damage, attrition by age, and other factors. This has resulted in a decrease in both numbers of trees and cultivars. The need to preserve and study this valuable crop was first recognized on a regional basis in the 1950s when the South Pacific Commission

began a widespread collection of cultivars (Barrau 1958a). More recently, the International Board for Plant Genetic Resources (IBPGR) recommended that collection and preservation of breadfruit germplasm be given the highest priority rating of A1 (A - indigenous resources high; 1 - national need high) (Hazelman 1981).

The purpose of the present study was to conduct a systematic survey and collection of breadfruit cultivars from the Pacific Islands and establish a safe, permanent germplasm collection in Hawaii. Hawaii is outside of the major cyclonic region of the Pacific and only rarely experiences a hurricane of the severity often experienced elsewhere in the Pacific. A main function of the collection is to ensure that traditional cultivars will be maintained, with the goal of reintroduction for local production and consumption.

Taxonomy and Geographic Distribution

Genus description

Breadfruit is a member of the genus *Artocarpus* which contains about 50 species of trees that grow in the hot, moist regions of the southeast Asian tropics and in the Pacific islands (Jarrett 1959a; Purseglove 1968). Many species are important components of the primary and secondary rainforest in Southeast Asia (Primack 1985). This genus belongs to the Moraceae family and is characterized by the presence of a white, milky latex and the unique fruit structure, the syncarp, a specialized type of compound fruit (Jarrett 1976). Some species are locally valuable as timber trees, while breadfruit, champedak (*A. integer* (Thunberg) Merrill, and jackfruit (*A. heterophyllus* Lamarck) are grown for their fruits. All three are basically diploid with $2n=2x=56$, but triploidy does occur in seedless breadfruit cultivars (Barrau 1976).

There are two species of breadfruit in the Pacific Islands, *Artocarpus altilis* (Parkinson) Fosberg and *A. mariannensis* Trecul, as well as possible hybrids. A third species, *A. camansi* Blanco, is found further west. Distribution of breadfruit in the Pacific is shown in Figure 1.2.

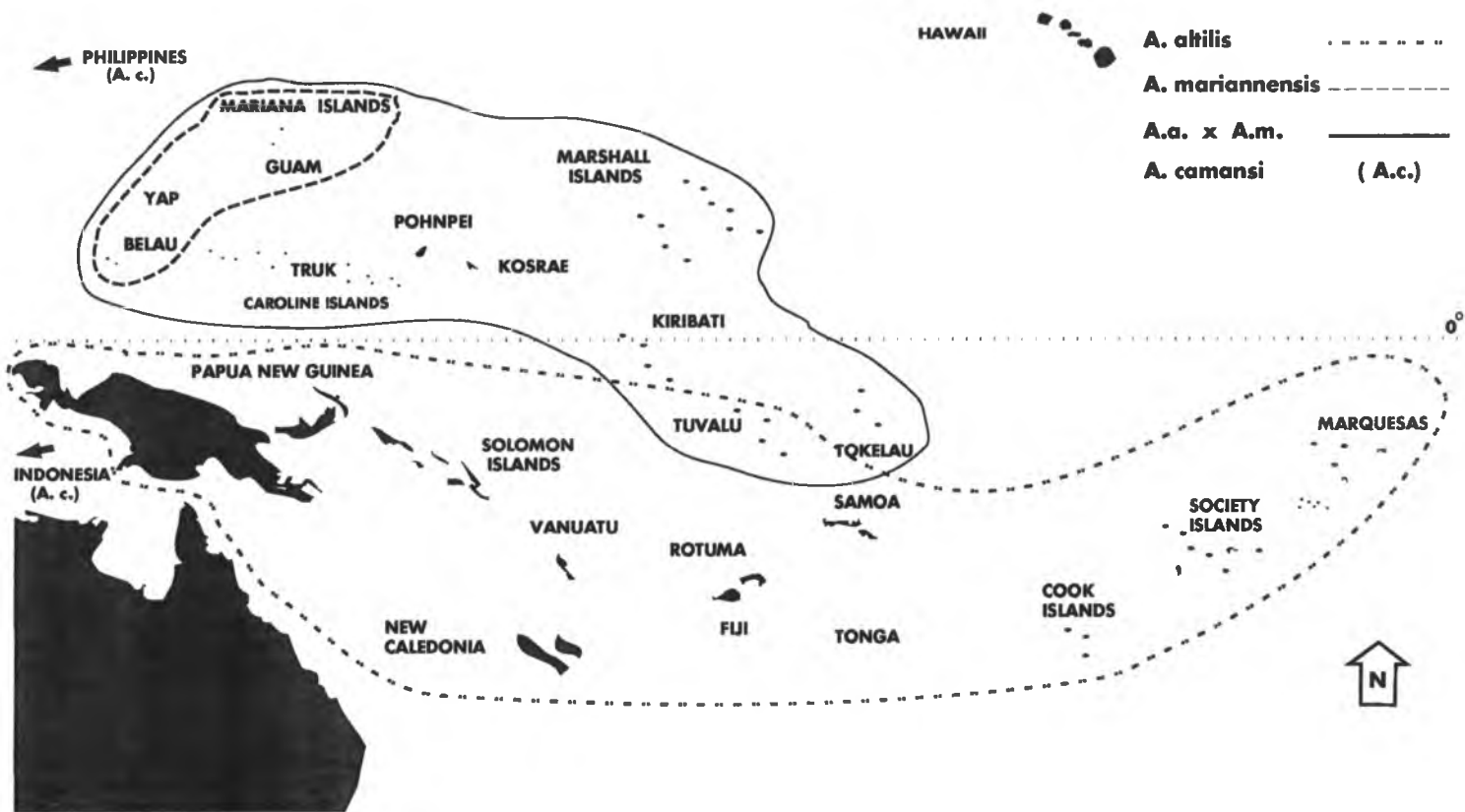


Figure 1.2. Distribution of *Artocarpus* in the Pacific

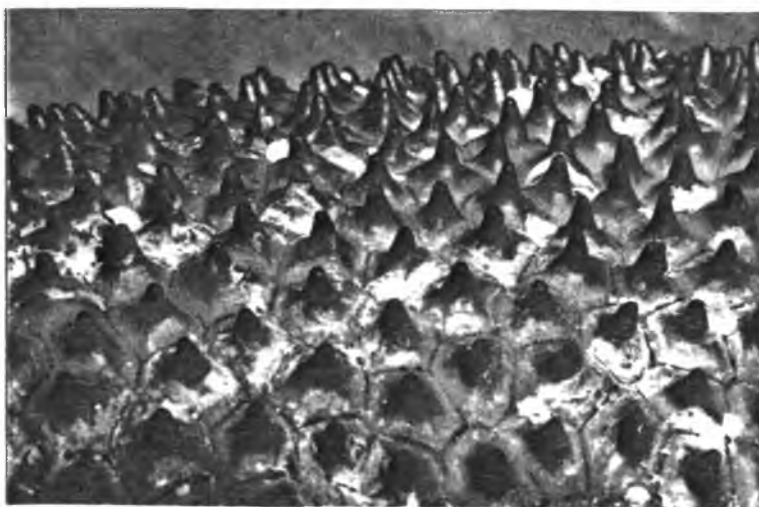


Figure 1.3. *Artocarpus camansi* and closeup of fruit

Distribution and description of *Artocarpus camansi*

A spiny, seeded breadfruit (Figure 1.3) similar to *A. altilis* is found in New Guinea, island Southeast Asia, and the Philippines. Rumphius saw it wild in several of the Sunda Islands (Indonesia) in the early 1600s and described the narrowly conical processes on what he called **soccus granosus** (de Candolle 1908). Sonnerat (1776) provided detailed illustrations of this species, seen in New Guinea, and considered it to be breadfruit, or **rimas**. It was described as a distinct species, *Artocarpus camansi* Blanco, by Blanco in 1837 and by Fernandez-Villar in 1880 (Quisumbing 1940). Both described *A. camansi* as indigenous to the Philippines. Merrill (1912, 1918) disagreed, noting that while the tree is common in cultivation, it did not occur in the wild in the Philippines, and was undoubtedly an introduced plant. He also concluded that it was not a separate species, but was a form of *A. communis*.

Jarrett (1959b) thought that it had been introduced to the Philippines from New Guinea or the Moluccas and grouped it under *A. communis*. Quisumbing (1940, 1951) considered *A. camansi* a separate species endemic to the Philippines, and surmised that it was closely related to, but specifically distinct, from the ancestor of Polynesian breadfruit. For the remainder of this dissertation, the spiny, seeded form will be referred to as *A. camansi* to distinguish it from the other types of seeded breadfruit.

European voyagers in the late 1700s and 1800s introduced *A. camansi* to other tropical areas where it is now widespread, especially in the Caribbean, parts of Central and South America, and coastal West Africa (Bligh 1976; Leakey 1977; Merrill 1914; Sonnerat 1776; Standley and Steyermark 1946). *Artocarpus camansi* is rarely seen in the South Pacific with the exception of a few trees in Western Samoa, Tahiti, and the Marquesas which were introduced in the past 35 years. It is not found anywhere in Micronesia.

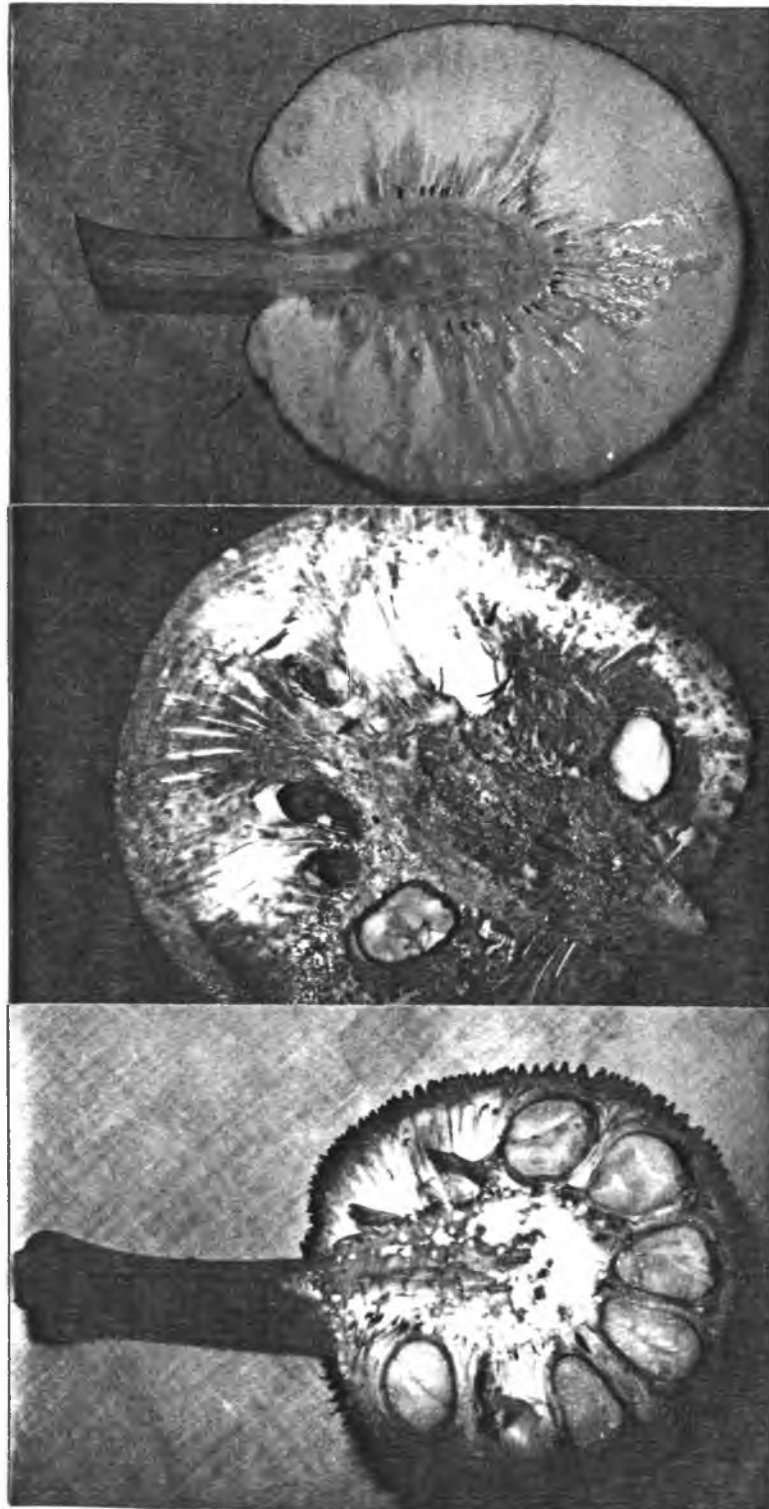


Figure 1.4. Variation of seed number in breadfruit

Distribution and description of *Artocarpus altilis*

Based on a type specimen of a seedless Tahitian breadfruit, Fosberg (1941) determined that the correct name for breadfruit was *Artocarpus altilis* (Parkinson) Fosberg, which replaced *A. incisus* Thunberg, *A. communis* J.R. & G. Forster, and other synonyms such as *Sitodium altile* Parkinson. Jarrett (1959a, 1959b) published an extensive monograph of the genus *Artocarpus*, but acknowledged that her treatment of breadfruit was preliminary and very conservative, based on the limited nature of herbarium material, most of it sterile, which was the subject of her study. She considered breadfruit a natural, but variable species, that has been greatly modified by the actions of humans. Jarrett (1959a) rejected the validity of the binomial *A. altilis* and concluded that the correct name for breadfruit was *A. incisus*. Later in her monograph (Jarrett 1959b), however, she decided that *A. communis* was the appropriate name.

Whereas *A. mariannensis* and *A. camansi* are always seeded, there are both seeded and seedless forms of *A. altilis*. The seeded form of *A. altilis* appears to be indigenous in New Guinea, where it is a dominant member of alluvial forests in lowland areas. It is one of the first species to appear on the tops of frequently flooded levee banks of rivers (Clunie 1978; Paijmans 1976). Seeded *A. altilis* trees grow widely scattered in the forest due, in part, to their dispersal by birds, fruit bats, and other arboreal mammals which feed on the flesh and drop the large seeds (Jarrett 1976; Primack 1985). Outside of New Guinea, *A. altilis* occurs only in cultivation, although long-abandoned plantations are often mistaken for wild trees.

The distribution of seeded forms of *A. altilis* beyond New Guinea reflects the movements of humans through the Pacific islands. Seeded forms are most common in the western South Pacific with numerous seeded and some few-seeded cultivars found in the eastern Solomon islands and Vanuatu. Murray (1894) recorded the names of 65 cultivars from one island in Vanuatu. (see Appendix A for cultivar names from 28 Pacific island groups). Seeded and few-seeded forms (few-seeded cultivars usually have from one to

several normal or aborted seeds) (Figure 1.4) are found as far east as Samoa and an occasionally one-seeded cultivar is known from both the Society Islands and the Marquesas (Wilder 1928). Seeded and few-seeded breadfruit cultivars are found in Samoa, and an early visitor, Wilkes (1845), stated that there were twenty cultivars. No seeded *A. altilis* are found in any of the Micronesian islands and they have not been distributed beyond Oceania.

The greatest diversity of seedless cultivars (Figures 1.5-1.7) occurs in eastern Polynesia and parts of the Caroline Islands (Wilder 1928; Barrau 1957). The eastern Polynesian islands are renowned for the abundance and diversity of breadfruit cultivars. Thirty-one names were recorded from the Marquesas (Jardin 1862). Early accounts by the first missionaries to the Society Islands noted that names of almost 50 cultivars were known (Ellis 1967). Names or descriptions for 34 seedless Marquesan cultivars were recorded by Christian (1910). The diversity of seedless cultivars in eastern Polynesia led many authors to believe breadfruit to be native to those islands, a misconception still found in the literature (Atchley and Cox 1985).

Seedless cultivars also occur together with seeded and few-seeded types in the western Polynesian islands, especially Fiji, Tonga, and Samoa (Seeman 1865-1873; Wilkes 1845). The few seedless cultivars found in the Santa Cruz Islands in eastern Melanesia are presumed to be introductions from Polynesia, possibly from the nearby Polynesian outlier islands of Tikopia and Anuta. Seedless cultivars were also introduced to the Solomon Islands by the South Pacific Commission in the 1950s (Barrau 1958a, 1959b). Seedless cultivars were brought to Papua New Guinea from Samoa by missionaries in the nineteenth century (Barrau 1957).

A few seedless cultivars typical of Polynesia are found throughout the northern Pacific islands from the Marshall Islands in the east to Guam, Yap, and Belau in the west. Dampier (1729) was the first to document the use of breadfruit in the Mariana Islands, and he noted that the fruit was seedless. Christian (1897, 1899) recorded 56 cultivar names for Pohnpei and Yap, and provided descriptions for many of these.

The dissemination of seedless breadfruit by Europeans is well-documented. Captain Bligh's efforts are the best known due to his failed attempt to take Tahitian breadfruit to the Caribbean on H.M.S. Bounty (Bligh 1792). A later voyage was much more successful, and in 1792 he introduced more than 600 breadfruit plants to the islands of Jamaica and St. Vincent (Bligh 1976). The French introduced a seedless cultivar from Tonga collected on the expedition of La Perouse to Martinique and Cayenne in the early 1790s (Leakey 1977). The Portuguese may have made a direct introduction of seedless cultivars to Brazil from other sources, possibly the Maldives (Leakey 1977).

The Spanish introduced the seedless breadfruit, **rima**, to the Philippines from Guam in the 17th century (Wester 1924). Seedless breadfruit reached Penang in 1802 and Malacca in 1836 (Burkill 1935). It was introduced to Madagascar in 1901 (Moreuil 1971). Breadfruit grows throughout the humid forest zone of Africa and was introduced to Congo Africa in the late 1800s, possibly earlier (Miracle 1967).

Distribution and description of *Artocarpus mariannensis*

The seeded breadfruit (**dugdug**) common to Micronesia is a different species than seeded breadfruit in the South Pacific and elsewhere (Figure 1.8). Trecul described *A. mariannensis* Trecul in 1847 from a specimen collected in the Mariana Islands by Gaudichaud in 1819 (Jarrett 1959b). Fosberg recognized *A. mariannensis* Trecul as the valid name of a seeded taxon endemic to the high islands of the western north Pacific and suggested that it was involved in introgression with *A. altilis* in Micronesia (Fosberg 1960). Although Jarrett (1959b) was aware of Fosberg's hypothesis of introgression between *A. altilis* and *A. mariannensis* in Micronesia, she felt that there was not enough evidence to consider *A. mariannensis* as a separate species or even subspecies. Consequently, she grouped *A. mariannensis* Trecul under *A. communis*. *Artocarpus altilis* (Parkinson) Fosberg, and *A. mariannensis* Trecul are accepted by most taxonomists as valid names and will be used in this dissertation.

Dugdug grows wild on the uplifted rock islands of Belau and on the limestone ridges of Guam and the Northern Mariana Islands (Fosberg 1960; Coenan and Barrau 1961). Native fruit bats have contributed to its dispersal. It is cultivated throughout the islands of Micronesia and south into Kiribati, Tuvalu, and Tokelau, and is well adapted to the calcareous soils of coral atolls and the limestone areas of high or raised islands. Ray's *Historia Plantarum*, published in 1704, describes **dugdug marianorum**, a tree introduced to the Philippines from Guam by the Spanish (Wester 1924). **Dugdug** has not been distributed beyond the northern Pacific Islands.

Distribution and description of *A. altilis* x *A. mariannensis* hybrids

Most of the cultivars of breadfruit in Micronesia east of the Mariana Islands exhibit characteristics of both *A. altilis* and *A. mariannensis*, suggesting that they are natural hybrids (Fosberg 1960). *Artocarpus altilis* characters include deeply dissected and numerous leaf lobes, white hairs on the upper veins, and denser fruits with a greater degree of fusion between the perianths of adjacent flowers. *Artocarpus mariannensis* often contributes conical, flattened perianth disks to the fruit and reddish hairs on the lower veins. The range of variation in interspecific hybrids is shown in Figures 1.9-1.10.

Artocarpus mariannensis and the putative hybrids are more tolerant of salinity than *A. altilis* and grow well on atoll soils (Catala 1957; Coenan and Barrau 1961; McKnight 1960), which probably has contributed to their distribution throughout the low-lying Micronesian atolls. The trees occurring on atolls generally reach a greater stature than those found growing on the high Micronesian islands (Fischer and Fischer 1970).



Figure 1.5. Variation in leaf and fruit shapes of *Artocarpus altilis*



Figure 1.6. Variation in leaf and fruit shapes of *Artocarpus altilis*

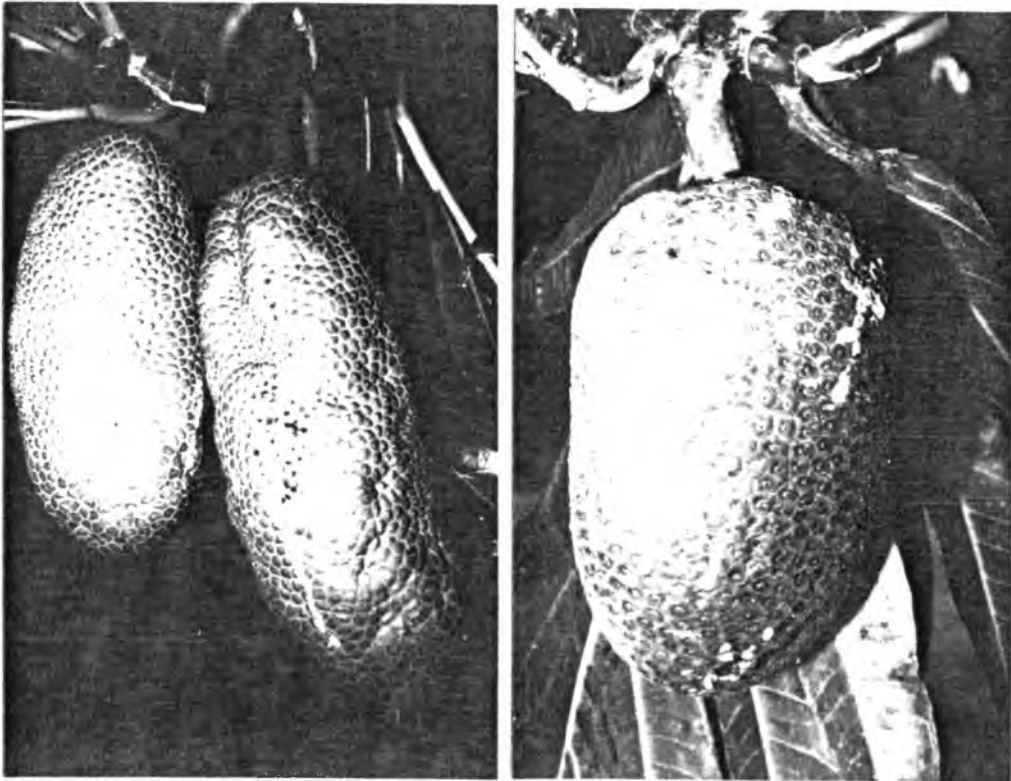


Figure 1.7. Variation in fruit shape and surface of *Artocarpus altilis*



Figure 1.8. Leaves and fruit of *Artocarpus mariannensis*

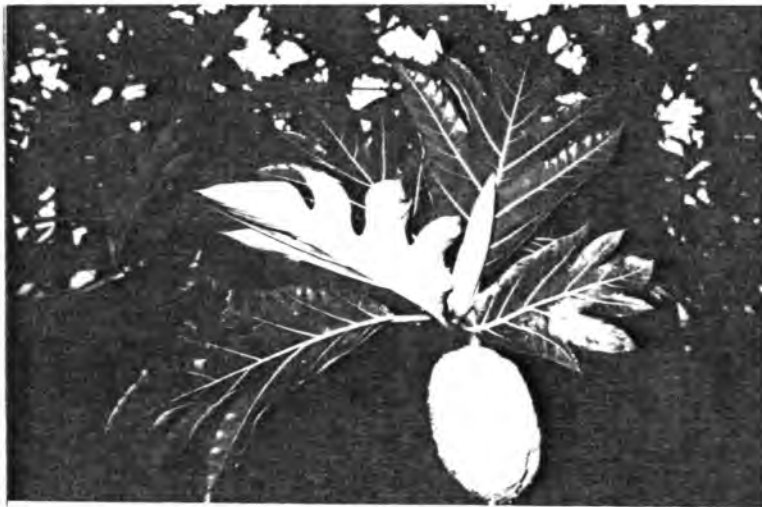


Figure 1.9. Variation in leaf and fruit shapes of *A. mariannensis* and *A. altilis* hybrids

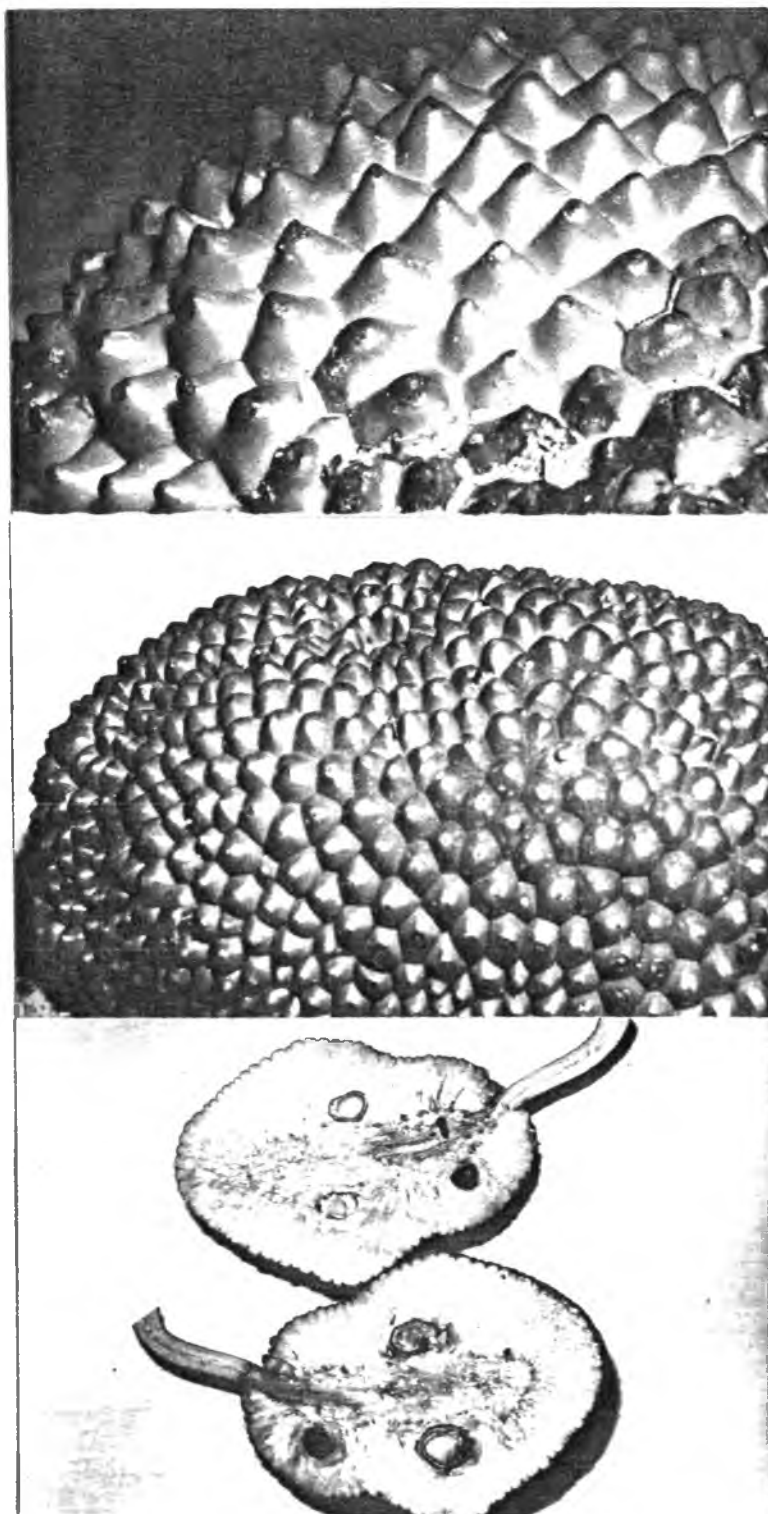


Figure 1.10. Variation in fruits of *A. mariannensis* and *A. altilis* hybrids

Morphology

Description of trees and leaves

Breadfruit trees are large, attractive, and evergreen, reaching heights of 15 to 20 meters (Figure 1.11). The tree has smooth, light-colored bark, and the trunk may be as large as 1.2 meters in diameter, occasionally growing to a height of 4 meters before branching. Branches are sparsely hairy, with pronounced leaf and stipule scars and lenticels. Latex is present in all parts of the tree.



Figure 1.11. Mature breadfruit tree

The leaves are subtended by two, large deciduous stipules which enclose the terminal bud. They are up to 15 cm long at maturity, caducous with the unfolding of the leaves, leaving a scar encircling the twig. There is striking variation in leaf outline and dissection. The leaves are broadly obovate to broadly ovate in outline, varying in size and shape even on the same tree. Juvenile leaves on young trees and new shoots of mature trees are typically larger and more hirsute. Blade texture is subcoriaceous to coriaceous with the upper side dark green, typically glossy. The underside is dull with an elevated midrib and main veins.

Leaf dissection of *A. altitlis* ranges from almost entire with only slight lobing to deeply pinnately lobed with sinuses from $\frac{2}{3}$ to $\frac{4}{5}$ of the distance from margin to midrib, or deeper (see Figure 1.5 - 1.6). Leaves are sometimes glabrous, but more usually sparsely pale pubescent, especially on the midrib and veins. The leaves of *A. camansi* are pinnately lobed with sinuses cut half way to the midrib. They are densely pubescent on upper and lower surfaces, midribs and veins. The leaves of *A. mariannensis* are generally smaller, broadly obovate to broadly elliptic in outline (see Figure 1.8). The leaf base is cuneate and leaves are entire or have a few lobes with sinuses cut less than half way to the midrib. Lobing occurs mostly in the distal third or half of the leaf. The upper surface of the leaf is glossy and glabrous. The midrib and veins on the lower surface are conspicuously brown appressed-hirsute.

Description of inflorescences

Inflorescences are axillary and monoecious, with the staminate inflorescence originating first. Staminate inflorescences are club-shaped, up to 6 cm wide and 30 cm long (Figure 1.12). The thick, spongy axis is covered by numerous minute flowers. Each flower consists of a reduced tubular perianth enclosing a single stamen with a two-locular anther on a thick filament. In young flowers, the perianth has a narrow opening, but at anthesis its lobes are widely separated, and the anther is exerted above the perianth (Sharma 1965a).

Pistillate inflorescences are globose to cylindrical, stiffly upright on stout peduncles (Figure 1.12). Numerous flowers are fused together on a thickened rachis forming a syncarpium. The ovary is two-loculed with a narrow style. The ovary and style usually remain free, while distal portions of the perianth fuse forming a five to seven-sided disk. This disk ranges from almost flat with an areolate surface to prominently umbonate; two to three strap-shaped, reflexed stigmas protrude from the disk. The entire syncarp is 5 cm or more in diameter at anthesis, becoming greatly enlarged in the mature fruit.

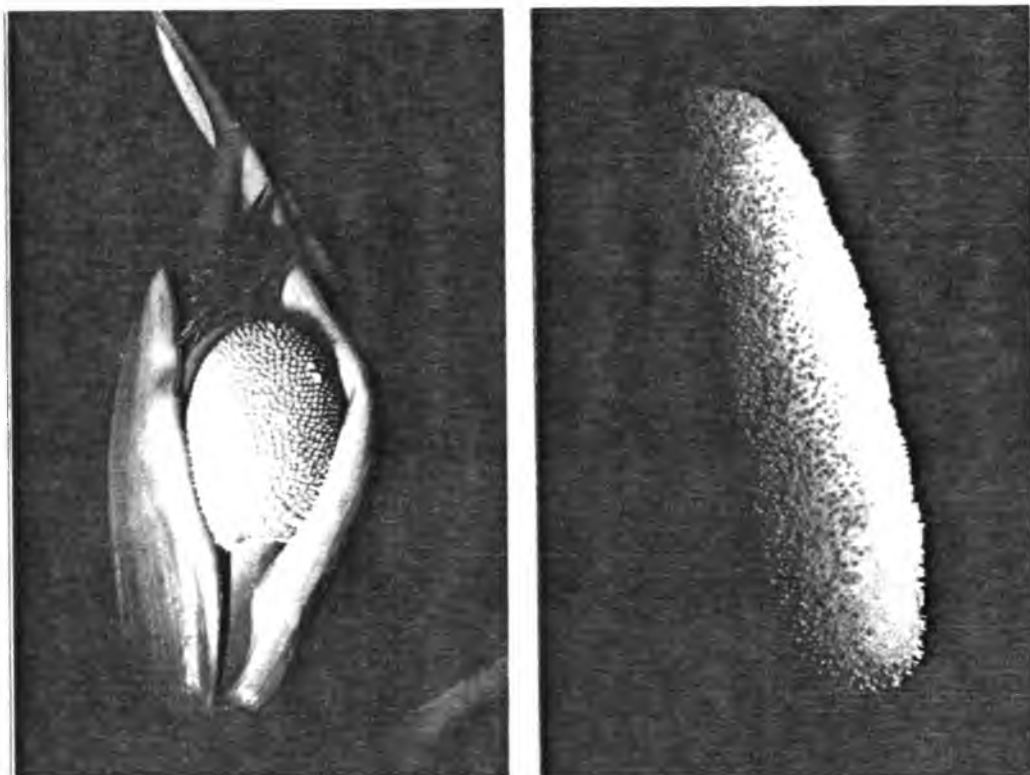


Figure 1.12. Female and male inflorescences of breadfruit

Description of fruit

The fruit is a highly specialized structure, a syncarp, composed of 1500-2000 flowers attached to the fruit axis or core (Jarrett 1976; Sharma 1965b). The core contains numerous latex tubes and large vascular bundles which discolor rapidly upon cutting, due to oxidative enzyme activity. The bulk of the fruit is formed from the persistent perianth of each flower. The perianths fuse together except at the base, forming a cavity which contains the true fruit and its enclosed ovule and seed (Reeve 1974). As the fruit develops this area grows vigorously and becomes fleshy at maturity, forming the edible portion of the fruit. The rind is usually stained with latex exudations at maturity.

The fruits of *A. altilis* are oblong to globose ranging from 10 to 20 cm in diameter. The yellowish-green rind is areolate or marked with attenuate or conical, acute processes, up to 3 mm long and 5 mm across at the base (see Figures 1.5-1.7). The creamy white or pale yellow flesh is soft and pulpy when mature, surrounding a spongy core.

Fruits of *A. mariannensis* are cylindrical or asymmetrically shaped with yellow flesh (see Figure 1.8). The perianth disks of the dark green rind are conical when immature, becoming flattened on top when mature. The degree of fusion of the perianths of this species appears to be more similar to *A. heterophyllous* (jackfruit) than *A. altilis*. Adjacent flowers fuse at the middle region of the perianths, leaving the lower and upper parts free from each other (Moncur 1985).

The fruits of *A. camansi* are spiny, being covered with narrowly conical, elongate processes, 5-12 mm long with elongated stigmas (see Figure 1.3). Seeds are numerous, ranging from as few as 12 to as many as 151 per fruit (Bennett and Nozzollilo 1988; Negron de Bravo et al. 1983; Quijano and Arango 1979).

Breadfruit seeds are thin-walled, subglobose or obovoid, irregularly compressed, 1-2 cm thick, embedded in the pulp. Seeds have little or no endosperm, no period of dormancy, and germinate immediately. They are not able to withstand desiccation.

History of breadfruit collections in the Pacific Islands

Regional survey and collection by the South Pacific Commission

While many cultivar names and descriptions have been reported, little work has been done to compare and describe cultivars from different islands. The South Pacific Commission (SPC) recognized the need to study this important crop and began a systematic collection of breadfruit cultivars in 1958 (Barrau 1958a, 1959a). Over 160 trees were described and collected from American and Western Samoa, New Guinea, Niue, Rotuma, Tonga, and Vanuatu (Parham 1966). His publication does not cover collections made by the South Pacific Commission in the Cook and Society Islands or Micronesia.

Propagating materials from this regional survey were sent to Fiji, Tahiti, and Western Samoa for comparative trials (Coenan and Barrau 1961). The fate of these cultivars provides a good lesson in the difficulties of establishing and maintaining a germplasm collection. The Fiji Department of Agriculture established a plant introduction station at Naduruloulou, Viti Levu, in 1936 (Parham 1967). The South Pacific Commission decided in 1949 to have this station serve as a regional introduction station, and provided funds and propagating material (Barrau 1959b).

Fiji Department of Agriculture Plant Introduction records from 1956-1961 show that 69 *Artocarpus* accessions were received from Kiribati, Pohnpei, Rotuma, Society Islands, Tuvalu, and Western Samoa. A small arboretum was planted with breadfruit and other economic trees, but only a few breadfruit trees were still growing at the station in 1985. The Fiji Department of Agriculture also surveyed and described 55 local cultivars, but none were collected or planted (Koroveibau 1966). Many of these cultivars can no longer be found (D. Koroveibau, personal communication, 1987).

Establishment of a regional collection in Western Samoa

The Western Samoa Department of Agriculture (WS Dept. Ag.) established a plant introduction station at Nafanua, Upolu, in 1956 (Parham 1959). A project was begun

to grow and study local and introduced breadfruit cultivars to determine which cultivars: (1) bear year-round, (2) are high yielding, (3) have overlapping periods of maturity, and (4) thrive on coral-atoll soils (WS Dept. Ag. 1964).

Over 300 accessions of breadfruit were received by Nafanua by 1964 (WS Dept. Ag. 1956, 1959-1962, 1964). A collection of 26 Samoan cultivars was planted in the late 1950s and regional collections were established at other sites in the country in 1964-65. The main collection was established at Vailima, Upolu, when 109 trees from 11 island groups were planted. This collection slowly declined, with 54 trees remaining in 1968 decreasing to 41 trees from nine island groups in the early 1970s (WS Dept. Ag. 1968, 1972). The collection continued to decline to a total of 30 trees in 1985 and even fewer, 26, remained in 1987. The other collections fared no better. Of the 44 trees from Vanuatu and the Society Islands planted at Alafua College, now the University of the South Pacific, all but four were razed during construction on the campus. Salafai High School, Savaii, received a small collection of ten trees from six island groups, only two trees remain. The status of eight trees planted on private land is unknown.

Other than brief mention in the Department of Agriculture Annual Reports cited above, no information on the regional collections in Samoa was published. Annual reports for 1965-1967 are not available. South Pacific Commission records show that SPC never received a report documenting the establishment and status of these collections (B. Flores, personal communication, 1985). Fortunately, the Western Samoan Department of Agriculture was able to provide me with copies of the original planting maps for all the collections. These maps, as well as plant introduction records, copies of original SPC survey forms, and visits to the collection sites in 1985 and 1987, allowed me to piece together the history of these collections. Introduction records for 1956, 1959-62 and 1964 show that 251 accessions from 13 island groups were received.

Collections in other Pacific Islands

Agriculture departments in other areas of the Pacific have also established collections. More than 30 cultivars from the Temotu Province were planted at the Tenaru Research Sub-station on Guadalcanal, Solomon Islands, in the early 1980s (Solomon Islands Dept. Ag. 1982). These are poorly growing and have been little documented.

Polynesian and Micronesian cultivars were distributed throughout Micronesia due to the efforts of the South Pacific Commission (Barrau 1958a). There are now three collections in Micronesia. The Pohnpei Agriculture Station at Kolonia has a collection of 20 Truk cultivars planted in 1955. These trees are healthy and bearing, but there is no documentation available (A. Lorens, personal communication, 1987). Kosrae Agriculture Station at Lelu has a collection of local and introduced South Pacific cultivars, many of which are identified and all are thriving (C. Phillips, personal communication, 1987). Local and introduced cultivars have been planted in Tarawa, Kiribati (R. Williams, personal communication, 1985).

Collections in Hawaii

Cultivars from several South Pacific island groups were introduced into Hawaii in the 1920s, but no collection was established. The Hawaii Agricultural Experiment Station (HAES) began propagating the Hawaiian cultivar in 1921 (HAES 1921), and in a few years had produced 400 trees for distribution to island residents (HAES 1924). G.P. Wilder of the Bishop Museum sent cultivars from Samoa, the Society Islands, and Tonga to HAES for propagation (HAES 1926, 1927, 1929). A total of 50 cultivars were sent, but fewer than half were successfully propagated and distributed in Hawaii (HAES 1929, 1931).

A collection of breadfruit was established in Hawaii in the 1970s by the National Tropical Botanical Garden (NTBG), formerly Pacific Tropical Botanical Garden (PTBG). NTBG made plans to establish a definitive collection of breadfruit and breadnuts as well as closely related species (Theobald 1976). An expedition to the Society Islands resulted

in the collection of 52 cultivars from five islands (Perlman 1977). NTBG also received cultivars from the Caribbean, Cook Islands, Kiribati, Pohnpei, Seychelles, Tonga, and Western Samoa (Herbst 1973; PTBG 1978, 1981).

A few cultivars were planted in the Lawai Gardens on the island of Kauai and 34 were planted at Kahanu Gardens in Hana, Maui. This 126-acre site is at sea level and has fertile, well-drained soils in a very high rainfall area (PTBG 1973). Mature trees of the Hawaiian cultivar of breadfruit were present at the site, and the first Pacific Island cultivars were planted at Kahanu Gardens in 1978. Five cultivars from Western Samoa and two from the Society Islands were established (PTBG 1979). Twenty-three cultivars from the Society Islands were planted the following year. In the early 1980s, three cultivars from Pohnpei and two from the Caribbean were added to the collection. In 1988, 33 trees of 29 cultivars were flourishing and bearing fruit (Figure 1.13).



Figure 1.13. Breadfruit collection at Kahanu Gardens, Hana, Maui

Summary of collections

The wide ranging efforts and extensive efforts of the South Pacific Commission to establish a permanent regional collection were unsuccessful. Although several local breadfruit collections have been established in the Solomon Islands, Pohnpei, and Truk, little, if any, work has been done to document or evaluate these valuable collections. The need to establish a permanent germplasm collection of cultivars from the Pacific islands is greater now than in the early post-World-War-II years when collection efforts were first begun. The many and varied breadfruit cultivars in the Pacific islands need to be documented and collected for a permanent germplasm collection. Such a collection will ensure that the diversity of this valuable crop will be available for future use by Pacific islanders and others in the tropical areas of the world.

CHAPTER II

COLLECTION AND ESTABLISHMENT OF GERMPLASM

Introduction

The objective of collecting a representative sample of breadfruit germplasm raised the question of how many cultivars of breadfruit exist in the Pacific. This is a difficult question to answer. Pacific islanders are keen observers and describers of the natural world and an elaborate system of folk taxonomy is used to distinguish between and assign names to different cultivars. Distinctions are based on bearing season, fruit shape, flesh color, presence of seeds, cooking or storage qualities of the fruit, tree form, leaf shape and horticultural requirements.

Many western visitors to the Pacific islands carefully documented customs, rituals, agricultural practices, food preparation and other aspects of island life. A careful examination of these accounts provides much information on the uses and importance of breadfruit on different islands. Often, only a list of vernacular names was recorded, although some authors provided descriptions of the different cultivars, details of seasonality, storage and uses of the tree or fruit.

The problem of using these lists of names to determine how many cultivars there actually are is compounded by the difficulties the authors faced in transcribing vernacular names into English, or another western language. In addition, the amount of information available about an island in the form of ethnographies, ship logs and other accounts varies from island to island.

The lack of recorded names cannot always be construed as indicating few breadfruit cultivars; rather it often reflects the lack of documentation for that island. Much

information exists for islands such as the Marquesas, Tahiti, Pohnpei and Samoa. Where multiple lists can be found, a comparison of names can help determine which names are likely to be valid by virtue of occurring on more than one list. Despite the inadequacies inherent in attempting to correlate actual number of cultivars with recorded names, these lists are an invaluable starting point in implementing a comprehensive collection of this important crop.

Breadfruit trees are traditionally propagated from root cuttings or shoots. The roots of the tree are exserted, growing on or slightly below the surface of the ground. A root will often produce a shoot, if it is cut or damaged, and islanders intentionally wound roots to induce shoot production. When the shoot is 0.5 to 0.75 m high and has developed its own root system, it is removed by cutting the root 10 to 15 cm on either side of the shoot.

Care is taken to avoid damaging the new root system, and the top of the shoot is usually removed before planting, cutting it at an angle. The shoot is planted in a hole, into which organic material, such as compost, seaweed, or dried manure, is placed. After planting, it is carefully tended, shaded from the hot sun and protected from pigs, chickens and other animals.

Root cuttings can also be propagated, and this is a useful method for trees that have no root shoots. The time of collection of roots is the most important factor for successful propagation. It is best to collect roots during the dormant season immediately preceding, or at the beginning of, the renewal of growth when carbohydrate stores in roots are highest. The dormant period begins immediately after the ripening of the crop and lasts for two to three months (Pope 1929; Wester 1920).

Roots of 1.5 to 6 cm in diameter are cut into sections from 12 to 30 cm long. These are placed in clean, washed sand or potting media and kept moist (Otanés and Ruiz 1956; Pope 1926, 1929). Best results are obtained when the roots are placed horizontally below the surface of the medium, instead of diagonally with the upper few centimeters exposed to the air. The percentage of rooting ranges from 80 to 85%, and

cuttings are large enough to transplant from the propagating bed in 3 to 5 months (HAES 1921, 1932; Pope 1929, n.d.).

These traditional methods of propagation, while effective and easily done, are relatively slow. Many experiments have been conducted using vegetative material instead of roots to provide faster results. Grafting and air-layering have been attempted (Moti and Chaturveill 1976; Rowe-Dutton 1976; Russell 1953). Air-layering is one method which has shown good results and is widely practiced in Tokelau (Ragone 1988).



Figure 2.1. Traditional method of airlayering

Branches 5 to 15 cm, and occasionally up to 30 cm, in diameter are prepared for air-layering by removing a strip of bark 2.5 to 5 cm wide around the circumference of the branch. Compost, mulch or other organic media is wrapped around this area and held in place with a tightly-tied copra bag (Figure 2.1). After two to six months, roots develop and grow through the bag, and new shoots may grow from above the wounded area. The branch is then cut just below the new roots and planted in a hole containing organic materials. Depending on the size of the air-layered branch, the tree will fruit in 3 to 4 years. Airlayers are most frequently made on branches that have previously borne fruit as the airlayer will bear fruit as soon as 1 to 2 years after planting.

Another method which promised to facilitate propagation of breadfruit is the use of stem cuttings under intermittent mist (Hamilton et al. 1982; Lopez 1975; Muzik 1948). With this method, leafless stem cuttings were treated with rooting hormone and placed under intermittent mist. After 10 weeks, 95% of the cuttings had produced sufficient root and shoot growth to be transplanted into larger containers. They were ready for planting in the field after 4 months (Hamilton et al. 1982). Lopez (1975) removed newly developed shoots from root cuttings grown in sand. These stem cuttings were treated with rooting hormone and placed under intermittent mist. After 4 weeks they were transplanted into larger containers and were ready for field planting in 6 months. The percentage of rooting using this method was not provided.

Materials and Methods

Collection of breadfruit

Collection of breadfruit germplasm in the Pacific Islands occurred in two phases for this study. The first phase in 1985 covered the Cook Islands, Tokelau, Tonga and Western Samoa. Funding for the first phase was provided by the South Pacific Agricultural Development Project (SPRAD) at the University of Hawaii and the National Tropical Botanical Garden. The second phase in 1987 covered Belau, Fiji, Guam, Kiribati, Kosrae, Marquesas, Marshall Islands, Pohnpei, Rota, Saipan, Society Islands, Solomon

Islands, Truk, Western Samoa and Yap. The International Board for Plant Genetic Resources (IBPGR) and the United States Department of Agriculture (USDA) provided plant exploration grants for phase two.

In Polynesia, collections of local cultivars were made in Western Samoa on the islands of Savaii and Upolu. In addition, cultivars from the Cook Islands, Fiji, Pohnpei, Rotuma, Society Islands, Solomon Islands and Vanuatu were collected from the South Pacific Commission's regional breadfruit collection at Vailima, Upolu. Tongan cultivars were collected from Tongatapu and Vava'u. Cook Islands breadfruit was collected on Aitutaki, Mangaia and Rarotonga, although three accessions were not traditional cultivars, but were introduced from Samoa and Tahiti in the past 30 years. Fifty-three accessions were collected from the Society Islands of Moorea, Raiatea, Tahaa and Tahiti. One accession was introduced from Rotuma and two were introductions from Indonesia or the Philippines. A similar accession was collected in the Marquesas on the island of Nuku Hiva, along with traditional cultivars. Seeds or root cuttings were collected on the Tokelau atolls of Fakaofu and Nukunonu.

In Micronesia, two species were collected in Belau on Babelthuap, Koror and Peleliu. One accession was an introduction from Yap. Collections were made from Yap proper, but I was unable to visit the outer islands of Yap because a hurricane had recently damaged most of the breadfruit trees and other crops on the island of Ulithi. Two species were also collected from Guam, Rota and Saipan in the Mariana Islands. Collections were made from the high islands of Pohnpei and Truk (Dublon, Fefan, Moen, and Uman), and the Truk atolls of Losap and Nama. Atoll cultivars were also collected from Tarawa in Kiribati. Kosrae and the Marshall Islands were visited, but no accessions were collected.

In Melanesia, collections were made on the Fijian islands of Viti Levu, Rabi, and Nacula and Vuaki in the Yasewa Group. Collections were made on Malaita in the Solomon Islands. Unfortunately, it was not possible to collect any propagating material from the Santa Cruz and Reef Islands. In early 1987, the government of the Temotu

Province which has jurisdiction for these islands, banned the collection of propagating material from any crop or economic plant grown in the province. While permission was granted for me to visit these islands, and transportation and assistance provided with the documentation and description of cultivars, I was forbidden to collect and remove any propagating material.

Planning and executing a successful collecting expedition involved contacting local Departments of Agriculture and making arrangements to work with their staff, especially extension agents. The Department usually was able to issue any permits required to collect and export plant materials from the country. They also inspected the collected materials and issued the phytosanitary certificates requested by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (APHIS). Most importantly, they provided well-informed local guides who served as interpreters and helped obtain permission from the landowner to collect fruits, herbarium specimens and propagating material. Collecting expeditions were also facilitated by the Yap Institute for Natural Sciences, the University of Guam Herbarium, Marquesas Service de l'Economie Rurale and Jardin Botanique de Tahiti.

Collecting trips were scheduled during the hot, rainy season when the majority of cultivars bear fruit. Collections were made during this time to facilitate identification of cultivars using fruit as well as vegetative characters. It is difficult, if not impossible, to identify a cultivar using only vegetative characters.

The starting point of each collecting expedition was compiling a list of names for each island. This list was shown to island residents who were asked to: verify if the names were valid and provide a definition of the name; provide a location for each cultivar; describe how it was used and what, if anything, made the cultivar special. In this manner, lists were revised and names were often deleted due to synonymy (the same cultivar may have different names in different villages or districts) and additional names were recorded. An effort was made to locate and collect materials from at least one tree of each cultivar on the revised list.

Field preparation of propagating material

The method employed by Hamilton et al. (1982) was modified for this study. Branches 3 to 5 cm in diameter were cut into 30 to 40 cm lengths and the leaves were removed. The cuttings were prepared for shipment by soaking in a Benlate slurry for 20 minutes and draining off excess water. Both ends of each cutting were dipped into melted paraffin wax to seal it. The stem cuttings were then wrapped in newspaper and placed in a plastic bag for shipping. Due to the constraints of field collecting, cuttings were not prepared as described above until 4 to 5 hours after collection of branches.

The collection of propagating material focused on roots. Relatively straight roots, 3 to 5 cm in diameter, with numerous, well-defined adventive buds were selected for propagation. These were cut into sections 20 to 30 cm long and scrubbed to remove all soil. After soaking in a Benlate slurry for 20 to 30 minutes, they were drained to remove excess water, wrapped in newspaper and placed in plastic bags for shipping. Seeds were also collected from seed-bearing trees. They were washed to remove all pulp, soaked in a Benlate slurry for 10 minutes, drained and then stored in slightly dampened newspaper in plastic bags.

Propagating materials were then shipped by air to Hawaii. After inspection by APHIS, the materials were placed in post-entry quarantine for one year at the Magoon Horticultural Facility of the University of Hawaii, in Honolulu, Hawaii. The USDA Clonal Germplasm Repository in Waiakea, Hawaii, received stem cuttings from selected cultivars for their collection.

Propagation procedures

In the greenhouse, the basal ends of the stem cuttings were cut at an angle above the paraffin seal and dipped in a commercial rooting compound, Rootone, containing 0.8% 1-naphtheleneacetic acid. They were set upright in 4-inch pots in an artificial medium consisting of sphagnum peat moss: perlite: medium grade vermiculite on a greenhouse bench under intermittent mist. An interval of 1 to 2 weeks, occasionally

3 weeks, occurred between collection of propagating material and insertion into the mist bed.

Most roots were planted within 2 weeks after collection in the field, but cuttings from French Polynesia were planted 5 weeks after collection. Roots were prepared for planting by cutting into 15 cm long sections and placed horizontally in trays of sphagnum peat moss: perlite: vermiculite and kept moist. The trays were kept in a greenhouse with 30% shade and additional shade of 30% was placed over the top of the benches. After 3 to 4 weeks, shoots began to develop from the adventive buds (Figure 2.2). There was sufficient shoot and root growth to transplant the cuttings into 15-cm pots after 1 to 3 months. They were transplanted into 7.5 liter pots after 2 to 3 months and were ready for field planting in 6 to 9 months.

Seeds were soaked in a Benlate slurry for 10 minutes and germinated in trays of vermiculite. They were transplanted into larger containers as outlined above.



Figure 2.2. Shoot developing from a section of root

Field planting

The Kahanu Gardens of the National Tropical Botanical Garden was selected as the site of the permanent germplasm collection. With its well-drained soils and annual rainfall of 1900 mm, this site is well suited to growing breadfruit, as evidenced by the existing breadfruit collection. Four field plantings were made in February and July, 1989, March 1990 and July 1991 (NTBG 1990; Ragone 1989). Accessions were randomly planted in holes 0.6 m deep and 0.6 m wide spaced 13 meters apart. Approximately 15 to 30 cm of topsoil and 20 grams of 10:10:10 NPK fertilizer were added to the bottom of each hole. Additional topsoil and soil from the original hole were used to fill the hole around each rootball. Trees were watered as needed after planting.

Results and Discussion

Field collection of germplasm

Field expeditions in 1985 and 1987 resulted in the collection of propagating material from 355 accessions of *A. altitls*, *A. mariannensts* and interspecific hybrids from 19 island groups. Forty-four additional accessions from Guam, Indonesia, Marshall Islands, Philippines, Pohnpei, Solomon Islands, and Truk were received during 1988-1989 resulting in a total of 399 accessions from 20 island groups (Table 2.1). In addition, leaf samples for gel electrophoresis were received for 10 accessions from Pohnpei and 21 from Truk. Table 2.2 provides detailed information for all accessions including a description, locality, vernacular name, and whether it was successfully propagated.

Establishment in greenhouse

Propagating materials in the form of seeds, stem cuttings or root cuttings were collected. Only 145 of the total 399 accessions have been successfully grown. Propagation by stem cuttings was very unsuccessful with none of 83 accessions rooting. Within 1 to 2 weeks, each cutting began to soften and rot, the bark slipped off the stem and the cuttings died in less than a month. Two (203, 207) of 18 accessions were

successfully propagated at the USDA Clonal Repository, Waiakea. It is apparent that while propagation by stem cuttings yielded good rooting percentages with materials which were immediately treated and placed into rooting beds, it is not a viable method for materials which are collected in the field and then shipped long distances to a propagation facility.

Roots provided a greater rate of success with 115 of 300 accessions (38%) propagated. The low propagation rate for root cuttings was mainly due to the collection of roots during the fruiting season when carbohydrate stores were low. The best propagation rate was achieved with seeds. Seeds were collected from 43 accessions, and 31 (72%) were successfully propagated. The disadvantage of using seeds is that the resulting seedlings are not clones of the parent tree as is the case with vegetatively propagated materials.

Establishment of permanent collection

A total of 185 trees of 135 accessions from 17 island groups were added in 1989-1991 to the permanent field collection located at the Kahanu Gardens. Two trees died and were replaced with duplicates. The collection now consists of 226 trees of 164 accessions from 18 island groups. More than 50 duplicate accessions were sent to the Lawai Gardens of the National Tropical Botanical Garden on Kauai to establish a backup collection at a second site. In addition to collections at NTBG, the USDA Clonal Germplasm Repository at Waiakea, Hawaii has received 20 accessions. A comprehensive list of all accessions growing at the National Tropical Botanical Garden is provided in Appendix B.

Kahanu Gardens now contains the largest and most comprehensive collection of breadfruit in the world. Additional collecting work needs to be conducted in New Guinea, Solomon Islands and Vanuatu to ensure a greater diversity of seeded forms of *A. altilis* in the collection. *Artocarpus mariannensis* and interspecific hybrids from Kosrae, the Marshall Islands, Truk and Yap also need better representation to complete

the collection. It is envisioned that once the trees in the collection reach fruiting age, yield and nutritional studies, morphological description, and further genetic work will be conducted.

Table 2.1. Number of breadfruit accessions collected, number propagated, and the percentage successfully established.

Island	Number collected	Number propagated	Percent established
Indonesia/Philippines	5	5	100
Melanesia	89	27	30
Fiji	49	8	16
Rotuma	6	6	100
Solomon Islands	19	7	37
Vanuatu	15	6	40
Micronesia	145	42	29
Belau	6	6	100
Kiribati	4	2	50
Mariana Islands	9	4	44
Marshall Islands	2	0	0
Pohnpei	62	16	26
Truk	49	11	22
Yap	13	3	23
Polynesia	160	71	44
Cook Islands	24	4	17
Marquesas	16	8	50
Samoa	37	14	38
Society Islands	51	26	51
Tokelau	27	19	70
Tonga	5	0	0
Total	399	145	36

Table 2.2. Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
PHILIPPINES				
Luzon	531	Camansi	Yes	Yes
Oahu	546	Pakok	Yes	Yes
Tahiti	282	Unnamed	Yes	Yes
INDONESIA				
Marquesas	221	Mei kakano	Yes	Yes
Raiatea	261	Huero ninamu	Yes	Yes
Bali	540	Sukun	Yes	Yes
MELANESIA				
Fiji				
Viti Levu	138	Kulu dina	No	No
Viti Levu	139	Kulu ni Samoa	Yes	No
Viti Levu	140	Kulu ni Samoa	Yes	No
Viti Levu	141	Balekana	No	No
Viti Levu	142	Kulu mabomabo	No	No
Viti Levu	143	Samoa type	Yes	No
Viti Levu	144	Samoa type	Yes	No
Yasewa Islands	145	Kulu balekana	No	No
Yasewa Islands	146	Samoa type	Yes	No
Yasewa Islands	147	Samoa type	Yes	Yes
Yasewa Islands	148	Kulu vailei	No	No
Yasewa Islands	149	Kulu dina	No	No
Yasewa Islands	150	Uto du	No	No
Yasewa Islands	151	Kulu votovoto	No	No
Rabi	152	Te mai keang	Yes	No
Rabi	153	Te mai wea	Yes	No
Rabi	154	Unknown	Yes	No
Rabi	155	Tu bukiraro	No	No
Rabi	156	Te mai kora	Yes	No
Viti Levu	157	Kasabalau	Yes	No
Viti Levu	158	Buco ni Samoa	Yes	No
Viti Levu	159	Samoa type	Yes	No
Viti Levu	160	Uto matalotu	Yes	No
Viti Levu	161	Matavude	Yes	No
Viti Levu	162	Uto levulevu	Yes	No
Viti Levu	163	Koqu	No	No
Viti Levu	428	Uto dina	No	Yes
Viti Levu	464	Samoa type	Yes	Yes

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Viti Levu	465	Buco ni Samoa	Yes	No
Viti Levu	467	Samoaan type	Yes	No
Viti Levu	468	Samoaan type	Yes	Yes
Viti Levu	476	Karawa dina	Yes	No
Viti Levu	477	Samoaan type	Yes	No
Viti Levu	478	Unknown	Yes	No
Viti Levu	480	Buco dina	No	No
Viti Levu	482	Uto lolo	No	Yes
Viti Levu	483	Uto dina	No	No
Viti Levu	484	Koqu	No	No
Viti Levu	485	Uto dina	No	No
Viti Levu	486	Uto vula	Yes	Yes
Viti Levu	487	Uto vula	Yes	No
Viti Levu	488	Uto ni viti	Yes	Yes
Viti Levu	489	Karawa	Yes	Yes
Viti Levu	490	Uto sore	Yes	No
Viti Levu	491	Uto sui	No	No
Viti Levu	492	Votovoto	No	No
Viti Levu	493	Buka-o	No	No
Viti Levu	494	Votovoto	No	No
Viti Levu	495	Uto samoa	Yes	Yes
Rotuma				
Upolu, Samoa	121	Pulupulu	Yes	Yes
Upolu, Samoa	127	Karawa	Yes	Yes
Upolu, Samoa	136	Ulufiti	Yes	Yes
Tahaa, Societies	243	Ro'otuma	Yes	Yes
Upolu, Samoa	427	Furau	Yes	Yes
Upolu, Samoa	439	Rauulu	Yes	Yes
Solomon Islands				
Upolu, Samoa	123	Toro	Yes	Yes
Malaita	164	Unknown	Yes	No
Malaita	165	Unknown	Yes	No
Malaita	166	Unknown	Yes	Yes
Malaita	167	Kekene	Yes	No
Malaita	168	Rausimi	Yes	No
Malaita	169	Abareba	Yes	Yes
Malaita	170	Abareba	Yes	No
Malaita	171	Unknown	Yes	No
Malaita	172	Abareba	Yes	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Upolu, Samoa	426	Kukumutasi	Yes	Yes
Upolu, Samoa	436	Bulo2	Yes	Yes
Upolu, Samoa	437	Tehelewa	Yes	Yes
Upolu, Samoa	438	RoveA	Yes	No
Reef Islands	535	Unknown	Yes	No
Reef Islands	536	Unknown	Yes	No
Reef Islands	537	Unknown	Yes	No
Reef Islands	538	Unknown	Yes	No
Reef Islands	539	Unknown	Yes	Yes
Upolu, Samoa	442	Malapatau	Yes	No
Upolu, Samoa	443	Manang	Yes	Yes
Upolu, Samoa	444	Goot	Yes	No
Upolu, Samoa	445	Malphang	Yes	Yes
Upolu, Samoa	446	Daliu	Yes	No
Upolu, Samoa	447	Willicocome	Yes	No
Wallis	518	Aveloloa	Yes	No
Wallis	519	Puou	Yes	Yes
Vate	520	Mele1	Yes	No
Vate	521	Mele2	Yes	No
Vate	522	Siviri1	Yes	No
Vate	523	Siviri3	Yes	Yes
Vate	524	Tepeanmbi	Yes	No
Vate	525	Tedailir	Yes	Yes
Vate	526	Forari2	Yes	Yes
Vate	527	Forari1	Yes	No
Vate	528	Siviri2	Yes	Yes
MICRONESIA				
Belau				
Koror	286	Meriaur	No	Yes
Koror	288	Ebechad	No	Yes
Babeldaob	289	Ebechad	No	Yes
Babeldaob	290	Midolab	No	Yes
Babeldaob	291	Errud	No	Yes
Peleliu	292	Chebiei	Yes	Yes

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Mariana Islands				
Guam	307	Lemae	No	No
Guam	308	Lemae	No	No
Guam	309	Dugdug	Yes	Yes
Saipan	310	Lemae	Yes	No
Saipan	311	Lemae	Yes	Yes
Saipan	312	Dugdug	No	No
Rota	313	Dugdug	Yes	Yes
Rota	314	Lemae	No	Yes
Kiribati				
Tarawa	036	Te mai	Yes	Yes
Tarawa	421	Te bukiraro	No	Yes
Tarawa	422	Motiniwae	No	No
Tarawa	423	Te mai	Yes	No
Kosrae				
Kosrae	410	Mos n wa	No	Yes
Marshall Islands				
Majuro	498	Bukurol	No	No
Majuro	499	Betaaktak	No	No
Pohnpei				
Pohnpei	364	Lukielel	No	No
Pohnpei	365	Lipet	No	Yes
Pohnpei	366	Mei tol	No	No
Pohnpei	367	Mei uhpw	No	Yes
Pohnpei	368	Mein mesehl	No	No
Pohnpei	369	Mein kalak	No	No
Pohnpei	370	Mein we	No	No
Pohnpei	371	Lokiamwas	No	No
Pohnpei	372	Mei aroape	No	No
Pohnpei	373	Mein pohnsakar	No	Yes
Pohnpei	374	Mei toahid	No	Yes
Pohnpei	375	Mein patak	No	No
Pohnpei	376	Mei woke	No	No
Pohnpei	377	Letemp	No	No
Pohnpei	378	Tahitian type	No	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Pohnpei	379	Mei kole	Rare	No
Pohnpei	381	Mei sei	No	No
Pohnpei	382	Mein tehid en mei sarek	No	No
Pohnpei	383	Pwumpwupu	No	No
Pohnpei	384	Mei mwed	No	No
Pohnpei	385	Mei kole	Yes	Yes
Pohnpei	386	Mein pwahr	No	Yes
Pohnpei	387	Nahnmwal	No	Yes
Pohnpei	388	Mein puht	No	Yes
Pohnpei	389	Mei se	No	No
Pohnpei	390	Mei kalak	No	No
Pohnpei	391	Mei ketieu	No	No
Pohnpei	392	Mei ohpop	No	No
Pohnpei	393	Mei kuet	No	No
Pohnpei	394	Mei pwet	No	No
Pohnpei	395	Mei pwuhleing	No	No
Pohnpei	398	Mei oang	No	No
Pohnpei	399	Mei kalak en kosrae	No	No
Pohnpei	400	Mei muhle	No	No
Pohnpei	401	Mei tol en lapar	No	No
Pohnpei	402	Mei kapas	No	No
Pohnpei	403	Mei kuli	Yes	No
Pohnpei	404	Mei kuli	Yes	No
Pohnpei	405	Mei saip	No	Yes
Pohnpei	406	Mein peimwas	No	No
Pohnpei	407	Mein lingkarahk	No	No
Pohnpei	408	Mein koit	No	No
Pohnpei	448	Mein patak	No	No
Pohnpei	499	Mein uwe	No	No
Pohnpei	500	Mei weke	No	No
Pohnpei	501	Mei arephe	No	Yes
Pohnpei	502	Mei kalak	No	Yes
Pohnpei	503	Mei mesehl	No	No
Pohnpei	504	Mei koid	No	No
Pohnpei	506	Nahnmwal	No	No
Pohnpei	507	Letemp	No	No
Pohnpei	508	Lukual	No	No
Pohnpei	509	Mei tol	No	Yes

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Pohnpei	510	Mei sei	No	Yes
Pohnpei	511	Mei lipet	No	Yes
Pohnpei	512	Mei tehid	No	Yes
Pohnpei	513	Mei pwet	No	No
Pohnpei	514	Mei ketieu	No	No
Pohnpei	515	Mei peimwas	No	No
Pohnpei	516	Mei kole	Yes	No
Pohnpei	529	Mein kole	Yes	Yes
Truk				
Moen	315	Annumur	No	No
Moen	316	Uwanaw	No	No
Moen	317	Mei koch	No	No
Moen	318	Mei nipis	No	No
Moen	319	Epinauo	No	No
Moen	320	Sewan	No	Yes
Moen	321	Nesoso	No	No
Moen	322	Mei on	No	Yes
Moen	323	Penno	No	No
Moen	324	Nipouch	No	No
Moen	325	Mesimech	No	No
Moen	326	Mei chon	No	Yes
Moen	327	Winiko	No	No
Uman	328	Mei ter	No	No
Uman	329	Nepopo	No	Yes
Uman	330	Achapar	No	No
Uman	331	Faine	No	Yes
Uman	332	Sewan	No	No
Uman	333	Mei nifa	No	No
Uman	334	Kisengei	No	No
Uman	335	Neapar	No	No
Uman	336	Affo	No	No
Uman	338	Abiraw	No	No
Uman	339	Mein fanam	No	No
Uman	340	Aniken	No	No
Dublon	341	Ennim	No	No
Dublon	342	Mura	No	No
Dublon	343	Mesekai	No	No
Dublon	344	Chonoor	No	No
Dublon	345	Senian	No	No
Fefan	347	Nenian	No	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Fefan	348	Ammech	No	No
Fefan	349	Ropo	No	No
Fefan	350	Irra	No	No
Losap	351	Mei koeng	Yes	Yes
Nama	353	Aniken	No	No
Nama	354	Mei koeng	Yes	Yes
Nama	355	Mein fanal	No	No
Nama	356	Lepopo	No	No
Nama	357	Bwikelew	Yes	No
Nama	358	Achapar	No	No
Nama	359	Leluku	No	No
Nama	360	Lepeito	No	No
Nama	361	Weang	Yes	No
Nama	362	Bochon	No	No
Nama	363	Mei chocho	Yes	Yes
Uman	532	Neonata	No	No
Uman	533	Oniunio	No	No
Uman	534	Neachen	No	Yes
Yap				
Yap	287	Unknown	No	Yes
Yap	293	Chaguy	No	No
Yap	294	Magyang	No	No
Yap	295	Manyor	No	No
Yap	296	Yupof	No	No
Yap	297	Yuluwach	No	No
Yap	298	Yunguluw	Yes	No
Yap	299	Tagfay	No	No
Yap	300	Yutuy	Yes	No
Yap	301	Luthar	Yes	Yes
Yap	302	Yoareb	No	No
Yap	303	Yuley	No	Yes
Yap	304	Fanam	No	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
POLYNESIA				
Cook Islands				
Mangaia	078	Patea	No	No
Mangaia	079	Pa'i	No	No
Mangaia	080	Enua	No	No
Mangaia	081	Tahitian	Yes	No
Mangaia	082	Enua	No	No
Mangaia	083	Patea	No	No
Aitutaki	085	Patea	No	No
Aitutaki	086	Maori	No	No
Aitutaki	087	Tahitian	Yes	No
Aitutaki	088	Maori	No	No
Aitutaki	089	Tahitian	Yes	No
Aitutaki	090	Patea	No	No
Aitutaki	096	Pae'a	No	Yes
Rarotonga	102	Toto	No	No
Rarotonga	103	Atu	No	Yes
Rarotonga	104	Tavake	No	No
Rarotonga	105	Morava	No	No
Upolu, Samoa	429	Enua	No	No
Upolu, Samoa	433	Enua	No	Yes
Upolu, Samoa	434	CI8	No	No
Upolu, Samoa	435	Enua	No	Yes
Marquesas				
Nuku Hiva	216	Mei puou	No	Yes
Nuku Hiva	217	Mei tookaha	No	No
Nuku Hiva	219	Mei koopupu	No	No
Nuku Hiva	220	Mei kiiahi	No	Yes
Nuku Hiva	222	Mei maoi	No	Yes
Nuku Hiva	223	Mei kauhiva	No	Yes
Nuku Hiva	224	Mei puau	No	Yes
Nuku Hiva	225	Mei aukape	No	No
Nuku Hiva	226	Mei kuuhaa	No	No
Nuku Hiva	227	Mei aukohe	No	No
Nuku Hiva	228	Mei tatahamau	No	No
Nuku Hiva	229	Mei patuki	No	No
Nuku Hiva	230	Mei aueka	No	Yes
Nuku Hiva	231	Mei kopumoko	No	Yes
Nuku Hiva	232	Mei konini	No	No
Nuku Hiva	234	Mei kakano	Rare	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Samoa				
Upolu	002	Maopo	No	No
Upolu	003	Puou	Yes	No
Upolu	007	Aveloloa	Yes	Yes
Upolu	009	Ulu e'a	No	No
Savaii	013	Manua	No	Yes
Savaii	014	Ma'a lau maopo	No	No
Savaii	019	Ulu sina	No	Yes
Upolu	022	Fefelo	Yes	No
Upolu	031	Faisaka	Yes	No
Aitutaki, Cooks	092	Unnamed	Yes	Yes
Aitutaki, Cooks	095	Niue	Yes	Yes
Rarotonga, Cooks	100	Niue	Yes	Yes
Upolu	109	Gutufagu	Yes	No
Upolu	110	Ulu e'a	No	Yes
Upolu	137	Ma'a	Yes	No
Upolu	451	Ulu salega	No	No
Upolu	452	Ulu tala	Yes	No
Upolu	453	Puou	Yes	Yes
Upolu	457	Fatu	Yes	No
Upolu	458	Maopo	No	No
Upolu	459	Momolega	Yes	No
Upolu	460	Ulu tala	Yes	No
Upolu	461	Aveloloa	Yes	No
Upolu	462	Ma'afala	Yes	No
Savaii	469	Manua	No	Yes
Savaii	470	Fa'a fia puou	Yes	No
Savaii	471	Ulu peti	Yes	No
Savaii	472	Mase'e	Yes	Yes
Upolu	475	Sagosago	Yes	Yes
Upolu	541	Ulu e'a	No	Yes
Upolu	542	Ulu e'a	No	No
Society Islands				
Moorea	200	Maire	No	Yes
Moorea	204	Pua'a	No	Yes
Moorea	205	Atiati	No	No
Moorea	206	Aravei	No	No
Moorea	207	Puero	No	No
Moorea	208	Tuutou	No	No
Moorea	210	Mahoi	No	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Moorea	211	Tuutou	No	No
Moorea	213	Paparu	No	No
Moorea	214	Maire	No	No
Tahaa	235	Huero	Rare	No
Tahaa	236	Hamo	No	Yes
Tahaa	237	Afara	No	No
Tahaa	238	Fafa'i	No	Yes
Tahaa	240	Orava	No	No
Tahaa	241	Patara	Rare	Yes
Tahaa	242	Atara	No	No
Tahaa	244	Puave	No	No
Tahaa	245	Piipiia	No	Yes
Tahaa	246	Peti	No	No
Tahaa	247	Otea	No	No
Tahaa	248	Ouo	No	Yes
Tahaa	249	Oatiati	No	No
Tahaa	250	Opiha	No	No
Tahaa	251	Teahimatoa	No	Yes
Tahaa	252	Tapehaa	No	No
Tahaa	253	Araarahaari	No	Yes
Tahaa	254	Huehue	No	No
Tahaa	255	Pua	No	Yes
Raiatea	256	Huero	Rare	Yes
Raiatea	257	Puurea	No	Yes
Raiatea	258	Tuutou,taatoe	No	Yes
Raiatea	259	Tuutou,auena	No	Yes
Raiatea	260	Tuutou,ooa	No	Yes
Raiatea	262	Mamaha	No	Yes
Raiatea	263	Manehe	No	Yes
Raiatea	264	Ioio	No	Yes
Raiatea	265	Paeataratara	No	No
Raiatea	266	Aue	No	Yes
Raiatea	267	Unknown	No	Yes
Raiatea	268	Apu	No	Yes
Raiatea	269	Anahonaho	No	Yes
Raiatea	270	Ahani	No	No
Raiatea	271	Opotopoto	No	No
Raiatea	272	Apuapua	No	Yes
Raiatea	273	Vaipaere	No	No

Table 2.2. (Continued) Collection sites, accession number, name, degree of seediness, and propagation success for 399 breadfruit accessions.

Island of Origin	Accession Number	Local Name	Seeds Present	Plants Grown
Tahiti	280	Havana	No	No
Tahiti	283	Rare	No	No
Upolu, Samoa	430	Aravei	No	No
Upolu, Samoa	432	Havana tara	No	No
Tokelau				
Nukunonu	040	Ulu afa	Yes	Yes
Nukunonu	041	Ulu afa	Yes	Yes
Nukunonu	042	Ulu afa	Yes	No
Nukunonu	043	Ulu hamoa	Yes	Yes
Nukunonu	044	Ulu afa	Yes	Yes
Nukunonu	045	Ulu afa	Yes	Yes
Nukunonu	046	Ulu afa elise	Yes	Yes
Nukunonu	047	Ulu elise	Yes	No
Nukunonu	048	Ulu afa	Yes	Yes
Nukunonu	049	Ulu afa hamoa	Yes	Yes
Nukunonu	050	Ulu afa elise	Yes	No
Nukunonu	051	Ulu afa	Yes	Yes
Nukunonu	052	Ulu afa	Yes	Yes
Nukunonu	053	Ulu afa elise	Yes	Yes
Nukunonu	054	Ulu afa hamoa	Yes	Yes
Nukunonu	055	Ulu afa elise	Yes	No
Nukunonu	056	Ulu afa	Yes	Yes
Nukunonu	057	Ulu afa	Yes	Yes
Nukunonu	058	Ulu afa	Yes	Yes
Nukunonu	059	Ulu hamoa	Yes	Yes
Fakaofu	060	Ulu elise	Yes	No
Fakaofu	061	Ulu afa	Yes	Yes
Fakaofu	062	Ulu hamoa	Yes	No
Fakaofu	063	Ulu elise	Yes	Yes
Fakaofu	064	Ulu hamoa	Yes	No
Fakaofu	065	Ulu elise	Yes	Yes
Fakaofu	066	Ulu elise	Yes	No
Tonga				
Nukualofa	067	Loutoka	Yes	No
Nukualofa	071	Kea	No	No
Vava'u	075	Kaunonou	No	No
Vava'u	076	Mase'e	Yes	No
Vava'u	077	Vahivahi	Yes	No

CHAPTER III

EVALUATION OF BREADFRUIT USING GEL ELECTROPHORESIS

Introduction

No systematic evaluation of breadfruit has been previously attempted, with the exception of grouping by gross morphological characters, in particular, vegetative characters. Several authors have provided general descriptions of cultivars for different island groups but few attempted to quantify the characters.

Vernacular names are typically based on morphological traits such as shape of the leaves, fruits, and to a lesser extent, the texture of the fruit epidermis and the presence or absence of seeds. Parham (1966) grouped cultivars based on 12 leaf shapes, four general fruit shapes, presence of hairs on midrib of lower surface of leaf, presence or absence of seeds, and texture of the fruit epidermis. He acknowledged that many cultivars did not fit the general patterns and that the same tree could have leaves of several different types. Leaf shape appeared to be the most variable, and he concluded that leaf shape did not appear to be correlated with the other three characters.

Koroveibau (1966) attempted to describe and compare Fijian cultivars using the same characters as Parham, however he reduced the number of leaf types to eight. Sasuke (1953) characterized Pohnpeian cultivars on the basis of 12 different leaf types. No statistical analysis of characters was conducted in any of these studies.

Using morphological traits to characterize breadfruit cultivars is difficult due to the great variability in leaves and fruits exhibited within a single clone, which obscures variability between clones. Variation is often continuous, and it is difficult to make comparisons between individuals. The fruits of different clones vary in shape, color of flesh and epidermis, size and shape of core, presence or absence of seeds, degree of

latex production and discoloration when the fruit is cut, and length of the peduncle and its insertion into the fruit. Leaf shape varies in the number of lobes, degree of dissection, and shape of the apex and base. Color and texture of the lamina are often variable, as is the color, length, and location of hairs.

Much of the variability within a clone can be attributed to developmental factors. For example, skin texture often becomes smoother as the fruit matures due to the abscission of the stigma as the fruit approaches maturity. Leaf characters, particularly lobe number and degree of dissection, often varies on an individual tree. This variability is due, in part, to the differences between new shoots and mature branches. The leaves of juvenile trees and new shoots on mature trees are often larger, more deeply dissected, and more hirsute than those of mature trees. In addition to these developmental factors, environmental factors play a role in the range of variation present in an individual.

Therefore, a systematic evaluation of breadfruit germplasm based solely on field-collected morphological data is not possible for the following reasons: 1) small sample size - often only one or two leaves for each accession were collected, and mature fruits were absent; 2) different ages and condition of the trees surveyed; and 3) different environmental conditions under which the trees were grown. Without an adequate sample size it is difficult to obtain a statistically valid measure of mean phenotype for individual clones, hence, it is not possible to accurately estimate differences between clones. Detailed measurements of morphological characters can be conducted once trees planted in the permanent germplasm collection have become established.

Most phenotypic characters are controlled by many genes which may have different individual effects. These quantitative characters are often strongly influenced by environmental factors. Consequently, it is difficult to determine the genetic component of morphological variation and assign genotypes to phenotypes.

The use of isozymes as genetic markers for cultivar and hybrid identification is a useful tool for evaluating germplasm collections (Byrne & Littleton 1988; Torres 1983; Yndgaard and Hoskuldsson 1985). The identification of fruit tree cultivars is often a

difficult task due to their long juvenile period and the large size of the trees. Isozyme analysis often provides a means to identify these trees when still in juvenile, or even, seedling stages, obviating the need to grow them to maturity. Isozyme analysis therefore circumvents some of the problems of cultivar identification based on morphological characters.

Isozymes are multiple forms of an enzyme having the same catalytic specificity (Kephart 1990). Electrophoresis detects the differences in enzymes on the basis of differences in their net electrostatic charges, manifested in the rate of migration of each enzyme in an electrical field. The resulting banding patterns of enzymes (zymogram) on a supporting gel matrix are treated as phenotypes. Charge differences result from changes in amino acid sequences which result from mutations in the nucleotide sequences of the structural genes (Gottlieb 1971). The correlation between genotype and phenotype due to the colinearity of amino acid and nucleotide sequences makes electrophoresis a useful tool for studying genetic variation.

Gottlieb (1977) detailed several of the advantages of using electrophoresis to study genetic variability. When a number of enzymes are examined they can be evaluated with more precision and objectivity than highly complex morphological features; problems of *a priori* character weighting do not occur because all enzymes are accorded equal value in similarity matrices; and electrophoretic evidence is precise and directly quantifiable in terms of numbers and kinds of enzymes studied which, is seldom possible with morphological characters.

Other advantages include: 1) The convenience of using any of several available tissues, such as seeds, leaves or stems; 2) rapidity and repeatability of results; and 3) the efficiency and economy of the procedure, especially in studies of intraspecific variability (Kephart 1990).

This procedure is not without its disadvantages. Redundancy in the genetic code means that approximately 30% of amino acid substitutions may not result in differences in charge and consequently, mobility of enzymes. This results in an underestimate of the

actual amount of genetic difference between taxa (Gottlieb 1977). Also, banding patterns can be complex and difficult to correctly interpret.

The complexity of banding patterns depends on several factors. Most isozymes of a single gene (allozymes) are codominantly inherited resulting in a single band for homozygotes and multiple bands for heterozygotes (Gottlieb 1977). More complex patterns arise from proteins composed of more than one polypeptide and/or coded by two or more loci. Polyploid species often produce complicated banding patterns as the addition of genomes increases the number of gene loci and isozymes (Gottlieb 1982). The genetic basis of observed patterns should be verified by isozyme analysis of progeny arrays from controlled crosses or other formal genetic studies (Kephart 1990). Isozyme phenotypes without a genetic interpretation, however, can be useful for identifying cultivars. Zymotypic information can also be analyzed using cluster analysis to get some idea of genetic relationships.

To use isozyme techniques successfully for cultivar identification, the levels of isozyme polymorphism must be wide enough to differentiate among the cultivars, yet each cultivar should be predominantly monomorphic. In addition, careful selection of the isozyme systems to be studied will enhance their usefulness. It is best to use systems that have been genetically and biochemically characterized in other plant species and exhibit little or no environmentally induced variation (Weeden and Lamb 1985).

In the past decade, numerous isozyme studies have been conducted on crop plants. While perennial tree crops such as almonds (Cerezo et al. 1989), apple (Weeden and Lamb 1985), and plums (Byrne and Littleton 1988), have been studied, fewer studies have been conducted on tropical fruit crops such as banana (Jarret and Litz 1986a, 1986b) and pineapple (DeWald et al. 1988). The identification of breadfruit cultivars by their isozyme patterns has not been reported. This study examined a wide array of breadfruit accessions from the Pacific islands, Indonesia, and the Philippines. The objectives were to describe the isozyme banding patterns of breadfruit and determine their usefulness in identifying cultivars and in examining relationships between different accessions.

Materials and Methods

A total of 204 breadfruit accessions from 19 island groups were surveyed for this study. Table 3.1 lists the number of accessions electrophoresed for each island group. Of these, 155 accessions were grown in the shadehouse at the Magoon Horticultural Facility of the University of Hawaii at Manoa, Honolulu. Eighteen samples were obtained from established trees at the Kahanu Gardens of the National Tropical Botanical Garden. Thirty one samples were received as leaf samples from the Micronesian islands of Truk and Pohnpei.

Table 3.1. Geographical origins of 204 accessions electrophoresed

Origin	Number of Accessions
Indonesia/Philippines	5
Melanesia	28
Solomon Islands	7
Vanuatu	6
Fiji	9
Rotuma	6
Micronesia	79
Belau	6
Mariana Islands	4
Yap	3
Truk	26
Pohnpei	37
Kosrae	1
Kiribati	2
Polynesia	92
Tokelau	16
Samoa	19
Cook Islands	4
Society Islands	43
Marquesas	7
Hawaii	3

Nineteen enzyme systems were assayed using a variety of buffer systems, and histidine citrate, pH 6.5, was found to be most consistently useful. Leaf samples consisted of a section of basal lobe of the second totally expanded leaf. Newly expanded leaves were not sampled, since these rapidly turned brown. Leaf samples were immersed in water overnight to enhance alcohol dehydrogenase activity. Comparison of soaked and non-soaked leaves showed no difference in the staining and resolution of the other enzyme systems.

Approximately 1 cm² of leaf material from each sample was placed in a well in a plexiglass grinding block that was kept cool with crushed ice. Each sample was thoroughly ground with a glass rod using three drops of modified Bousquet's extraction buffer (Bousquet et al. 1987). Immediately after grinding, 4mm x 13mm wicks of Whatman 3MM chromatography paper were placed into each well to absorb the crude extracts. The wicks were removed, lightly blotted, and loaded into a transverse slice cut into 12.5% starch gels.

Electrophoresis was conducted at 4 C and a tray of crushed ice was placed on each gel. A histidine citrate buffer, pH. 6.5, was used. The gel buffer was 0.016 M histidine (free base) and 0.002 M citric acid (anhydrous); the tray buffer consisted of 0.065 M histidine and 0.007 M citric acid. The origin was placed towards the cathodal end. After 20 minutes, the power was turned off and the wicks were removed from the gels. Gels were then run at a constant 200 V for six hours at 40-50 mA.

After the electrophoretic run, the gels were sliced into seven slabs. The bottom six slices were used, and the thin top slice was discarded, since it produced a strongly distorted pattern when stained. Staining solutions of enzymes were prepared immediately before the end of each gel run. The procedures of Soltis et al. (1983) were used for aconitase (ACO), alcohol dehydrogenase (ADH), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malic dehydrogenase (MDH), and phosphoglucumutase (PGM). Gel slices were immersed in the staining solutions with the top surface upward. All gels

except LAP were stained in the dark at 37 C until bands appeared. Stained gels were immediately scored, photographed, and fixed in a solution of 1 acetic acid: 5 water: 5 methanol.

Bands (electromorphs) were numbered for identification from fastest to slowest migrating. The band with the greatest anodal migration was designated as 1; bands with slower migration rates received progressively higher numerical designations. Each accession was scored for the absence or presence of bands. Each band was treated as one variable. If a band was present it was scored 1, if absent 0. Using this scoring method, 45 variables were created: 9 for ACO, 12 for ADH, 4 for IDH, 8 for LAP, 3 for MDH, and 9 for PGM. The results provided a qualitative classification (typical banding patterns) as well as a quantitative classification (banding pattern frequencies).

Two methods by Menancio and Hymowitz (1989) were used to summarize the enzyme variability of breadfruit accessions within each island group.

1. % PES= percent polymorphic enzyme systems (an enzyme is considered polymorphic when more than one type of pattern is observed).

2. Mean number of patterns per enzyme system (the arithmetic mean of the number of patterns over all enzyme systems). The maximum P possible in this study is 7.3.

Statistical analysis of the data was performed using a taxonomical computer program NTSYS, version 1.21 (Applied Biostatistics Inc. Setauket, NY). A similarity matrix utilizing Jaccard's coefficient was compiled from the data and cluster analysis (UPGMA) was used to reveal the patterns of isozyme variation within the collection. Hierarchical clustering analysis utilizing UPGMA clustering is the most frequently used form of analysis in numerical phenetics (Duncan & Baum 1981). Principal components analysis was also performed on the correlation matrix to confirm the results obtained through the dendrogram. No interpretation of the genetic significance of the banding patterns was attempted.

Results

Malic enzyme exhibited no polymorphism, producing only a single darkly stained band. Several other enzyme systems [6-phosphogluconate dehydrogenase (6PGD), glutamate dehydrogenase (GDH), shikimate dehydrogenase (SKDH), and phosphoglucisomerase (PGI)] exhibited polymorphism, but the banding patterns were faint or blurred and difficult to consistently score. Consequently, these systems did not produce results useful to characterizing the accessions. Six enzyme systems (ACO, ADH, IDH, LAP, MDH, PGM) produced sharp and well-resolved polymorphic banding patterns that could be used to distinguish among the accessions. The inheritance of isozymes studied in breadfruit is still unknown and the description of the accessions on the basis of their allozymes cannot be made from this study. It is possible, however, to differentiate between breadfruit accessions and to characterize genetic variation based on phenotypic banding patterns.

Considerable polymorphism in isozyme phenotype was observed among the accessions examined, and the different banding patterns were identified by letters (Table 3.2) lists the isozyme banding patterns obtained for each accession.. The most variable isozyme system was ACO with 18 banding patterns observed. The other enzyme systems all exhibited polymorphism with seven patterns each for ADH and LAP, six patterns for PGM, four for MDH, and two well-defined banding patterns for IDH. The distribution of the different isozyme banding patterns by geographic area is presented in Table 3.3.

Table 3.2. Enzyme banding patterns (zymotype) for 204 breadfruit accessions by island group

Accession	Island Group	Collection Site	Local Name	Zymotype
221	Indonesia/PI	Nukuhiva	Mei kakano	IFABAB
261	Indonesia/PI	Raiatea	Huero ninamu	IGABAB
282	Philippines	Tahiti	unnamed	CEABAA
531	Philippines	Luzon	Camansi	CEADAA
546	Philippines	Oahu	Pakok	CBADAA
147	Fiji	Viti Levu	Samoaan	GBBBAB
428	Fiji	Upolu, Samoa	Uto dina	MBABAB
464	Fiji	Viti Levu	Samoaan	HBABAB
468	Fiji	Viti Levu	Samoaan	MBABAB
482	Fiji	Viti Levu	Uto lolo	LBBBAB
486	Fiji	Viti Levu	Uto vula	PBBBAB
488	Fiji	Viti Levu	Uto ni viti	MBACAB
489	Fiji	Viti Levu	Karawa	GBBBAB
495	Fiji	Viti Levu	Uto samoa	ECABAD
123	Solomon Islands	Upolu, Samoa	Toro	NCAGAC
166	Solomon Islands	Malaita	unnamed	DCABAB
169	Solomon Islands	Malaiti	Abareba	NCAFAB
426	Solomon Islands	Upolu, Samoa	Kukumu tasi	HBABAB
436	Solomon Islands	Upolu, Samoa	Bulo2	MBABAD
437	Solomon Islands	Upolu, Samoa	Tehelewa	PCABAD
539	Solomon Islands	Reef Islands	unknown	PBACAB
443	Vanuatu	Upolu, Samoa	Manang	PBACAB
445	Vanuatu	Upolu, Samoa	Malphang	GBABAB
523	Vanuatu	Vate	Siviri3	RCAEAD
525	Vanuatu	Vate	Tedailir	MCAEAB
526	Vanuatu	Vate	Forari2	FCABAB
528	Vanuatu	Vate	Siviri2	FCABAB
286	Belau	Koror	Meriaur	LBBBAB
288	Belau	Koror	Ebechad	JCBBAB
289	Belau	Babeldaob	Ebechad	JCBBAB
290	Belau	Babeldaob	Midolab	QCBBD
291	Belau	Babeldaob	Errud	JCBBAB
292	Belau	Peleliu	Chebiei	AABDD
036	Kiribati	Tarawa	Te mai	AABABB
421	Kiribati	Tarawa	Te bukiraro	HCBCDB
mos	Kosrae	Kosrae	Mos n wa	LBBBAB
309	Mariana Islands	Guam	Dugdug	AABDDF
311	Mariana Islands	Saipan	Lemae	LBBBAB
313	Mariana Islands	Rota	Dugdug	AABDDD
314	Mariana Islands	Rota	Lemae	LBBBAB
365	Pohnpei	Pohnpei	Lipet	HCBBBB

Table 3.2. (Continued) Enzyme banding patterns (zymotype) for 204 breadfruit accessions by island group

Accession	Island Group	Collection Site	Local Name	Zymotype
366	Pohnpei	Pohnpei	Mei toal	HBBDCB
367	Pohnpei	Pohnpei	Mei uhpw	LBBBAB
368	Pohnpei	Pohnpei	Meinmesehl	MBBDBB
370	Pohnpei	Pohnpei	Mein iwe	LBBBAB
372	Pohnpei	Pohnpei	Mei aroape	LBBBAB
373	Pohnpei	Pohnpei	Mein pohnsakar	NCBCDB
374	Pohnpei	Pohnpei	Mei tehid	LBBBAB
375	Pohnpei	Pohnpei	Mein patak	NCBBBB
379	Pohnpei	Pohnpei	Mei kole	NBBBAB
380	Pohnpei	Pohnpei	Mein serihseng	HCBBBB
381	Pohnpei	Pohnpei	Mei sei	IBBBBB
384	Pohnpei	Pohnpei	Mei mwed	NBBDDDB
385	Pohnpei	Pohnpei	Mei kole	NCBBAB
386	Pohnpei	Pohnpei	Mein pwahr	HCBBBB
387	Pohnpei	Pohnpei	Nahnmwal	NCBDBB
388	Pohnpei	Pohnpei	Mein pwuht	MBBBBB
389	Pohnpei	Pohnpei	Mei se	HBBDBB
390	Pohnpei	Pohnpei	Mei kalak	LBBBAB
396	Pohnpei	Pohnpei	Mei pwahr	ICBDDDB
405	Pohnpei	Pohnpei	Mei saip	LBBBAB
406	Pohnpei	Pohnpei	Mein peimwas	EBBDDDB
501	Pohnpei	Pohnpei	Mei arephe	ECBBBB
502	Pohnpei	Pohnpei	Mei kalak	LBBBAB
509	Pohnpei	Pohnpei	Mei tol	LBBBAB
510	Pohnpei	Pohnpei	Mei sei	LBBBAB
511	Pohnpei	Pohnpei	Lipet	HCBBBB
512	Pohnpei	Pohnpei	Mei tehid	LBBBAB
529	Pohnpei	Pohnpei	Mei kole	MCBDDDB
ako	Pohnpei	Pohnpei	Mei akohnd	ICBDDDB
kew	Pohnpei	Pohnpei	Mei kewelik	HBBDBB
kol	Pohnpei	Pohnpei	Mei kole	NCBBAB
pat	Pohnpei	Kahanu	Mein patak	NCBBBB
sap	Pohnpei	Pohnpei	Mein sapwehehk	MCBDBB
tam	Pohnpei	Pohnpei	Mei tamworok	NCBDAB
teh	Pohnpei	Kahanu	Mei tehid	LBBBAB
utu	Pohnpei	Pohnpei	Mei utuhnpei	MCBDBB
315	Truk	Moen	Annumur	EBBBDB
316	Truk	Moen	Uwanaw	NCBBBB
317	Truk	Moen	Mei koch	ECBBDB
318	Truk	Moen	Meinipis	ICBBDB
320	Truk	Moen	Sewan	HCBCBD

Table 3.2. (Continued) Enzyme banding patterns (zymotype) for 204 breadfruit accessions by island group

Accession	Island Group	Collection Site	Local Name	Zymotype
322	Truk	Moen	Meion	ICBCBB
326	Truk	Moen	Mei chon	LBBBAB
327	Truk	Moen	Winiko	ECBBDB
328	Truk	Uman	Meiter	HCBBAB
329	Truk	Uman	Nepopo	ICBBDD
331	Truk	Uman	Faine	ICBBCB
333	Truk	Uman	Meinifa	NCBBAB
336	Truk	Uman	Affo	NCBCBB
338	Truk	Moen	Abiraw	NABBDB
340	Truk	Uman	Eniken	MCBDDB
341	Truk	Dublon	Ennim	HCBBBB
342	Truk	Dublon	Mura	MCBBDB
348	Truk	Fefan	Emmech	MCBCDB
351	Truk	Losap	Meikoeng	HCBDDDB
354	Truk	Nama	Meikoeng	HABDCB
357	Truk	Nama	Bwikelew	NBBCDB
363	Truk	Nama	Meichocho	HABDDDB
532	Truk	Uman	Neonata	ECBDAB
533	Truk	Uman	Oniunio	NCBCDB
534	Truk	Uman	Neachen	MCBCDB
nou	Truk	Uman	Nounuka	ICBBBB
287	Yap	Koror	unnamed	QBBCCB
301	Yap	Yap	Luthar	KABBCE
303	Yap	Yap	Yuley	OBBCCB
096	Cook Islands	Aitutaki	Pae'a	LBBBAB
103	Cook Islands	Rarotonga	Atu	LBBBAB
433	Cook Islands	Upolu, Samoa	Enua	LBBBAB
435	Cook Islands	Upolu, Samoa	Enua	LBBBAB
530	Hawaii	Maui	Ulu	LBBBAB
ana	Hawaii	Kauai	unknown	LBBBAB
kah	Hawaii	Oahu	unknown	LBBBAB
216	Marquesas	Nuku Hiva	Mei puou	LBBBAB
220	Marquesas	Nuku Hiva	Mei kii ahi	LBBBAB
222	Marquesas	Nuku Hiva	Mei maoi	LBBBAB
223	Marquesas	Nuku Hiva	Mei kauhiva	LBBBAB
224	Marquesas	Nuku Hiva	Mei puau	LBBBAB
230	Marquesas	Nuku Hiva	Mei aueka	LBBBAB
231	Marquesas	Nuku Hiva	Mei kopumoko	LBBBAB
121	Rotuma	Upolu, Samoa	Pulupulu	MBBBAB
127	Rotuma	Upolu, Samoa	Karawa	MBACAB
136	Rotuma	Upolu, Samoa	Ulu fiti	HBABAB

Table 3.2. (Continued) Enzyme banding patterns (zymotype) for 204 breadfruit accessions by island group

Accession	Island Group	Collection Site	Local Name	Zymotype
243	Rotuma	Tahaa	Ro'otuma	PBADAB
427	Rotuma	Upolu, Samoa	Furau	HBABAB
439	Rotuma	Upolu, Samoa	Rauulu	PBADAB
007	Samoa	Upolu	Aveloloa	CDACAB
013	Samoa	Savaii	Manua	CDABAB
019	Samoa	Savaii	Ulu sina	CDADAB
092	Samoa	Aitutaki, Cooks	unknown	EBABAD
095	Samoa	Aitutaki, Cooks	Niue	EBABAD
100	Samoa	Rarotonga, Cooks	Niue	EBABAD
110	Samoa	Upolu	unknown	CDADAB
453	Samoa	Upolu	Puou	ECABAD
469	Samoa	Savaii	Manua	CDABAB
472	Samoa	Savaii	Mase'e	CBABAB
475	Samoa	Savaii	Sagosago	BBABAD
519	Samoa	Vanuatu - Wallis	Puou?	CCABAD
540	Samoa	Bogor	unknown	CGADAB
541	Samoa	Upolu	Ulu e'a	LBBBAB
maf	Samoa	Kahanu	Ma'afala	CBADAD
mom	Samoa	Kahanu	Momolega	GBABAB
puo	Samoa	Kahanu	Puou	ECABAD
uhp	Samoa	Pohnpei	Mei uhp en samoa	ECADAD
unk	Samoa	Kahanu	unknown	CDADAB
200	Society Islands	Moorea	Maire	LBBBAB
204	Society Islands	Moorea	Pua'a	LBBBAB
236	Society Islands	Tahaa	Hamo	LBBBAB
238	Society Islands	Tahaa	Fafai	LBBBAB
241	Society Islands	Tahaa	Patara	PCBBAB
245	Society Islands	Tahaa	Pii piia	LBBBAB
248	Society Islands	Tahaa	Ouo	LBBBAB
251	Society Islands	Tahaa	Teahimatoa	LBBBAB
253	Society Islands	Tahaa	Araarahaari	LBBBAB
255	Society Islands	Tahaa	Pua	LBBBAB
256	Society Islands	Raiatea	Huero	LBBBAB
257	Society Islands	Raiatea	Pu'urea	LBBBAB
258	Society Islands	Raiatea	Tuutou, taatoe	LBBBAB
259	Society Islands	Raiatea	Tuutou, auena	LBBBAB
260	Society Islands	Raiatea	Tuutou, ooa	LBBBAB
262	Society Islands	Raiatea	Mamaha	LBBBAB
263	Society Islands	Raiatea	Manehe	LBBBAB
264	Society Islands	Raiatea	Ioio	LBBBAB
265	Society Islands	Raiatea	Paea taratara	LBBBAB

Table 3.2. (Continued) Enzyme banding patterns (zymotype) for 204 breadfruit accessions by island group

Accession	Island Group	Collection Site	Local Name	Zymotype
266	Society Islands	Raiatea	Aue	LBBBAB
267	Society Islands	Raiatea	unnamed	LBBBAB
268	Society Islands	Raiatea	Apu	LBBBAB
269	Society Islands	Raiatea	Anahonaho	LBBBAB
272	Society Islands	Raiatea	Apuapua	LBBBAB
aar	Society Islands	Kahanu	A'arue	LBBBAB
afa	Society Islands	Kahanu	Afara	LBBBAB
aha	Society Islands	Kahanu	Ahani	LBBBAB
aip	Society Islands	Kahanu	Aipu'u	LBBBAB
faf	Society Islands	Kahanu	Fafai	LBBBAB
mah	Society Islands	Kahanu	Mahani	LBBBAB
ote	Society Islands	Kahanu	Otea	LBBBAB
pii	Society Islands	Kahanu	Pii piia	LBBBAB
por	Society Islands	Kahanu	Porohiti	LBBBAB
pua	Society Islands	Kahanu	Pua'a	LBBBAB
puu	Society Islands	Kahanu	Pu'upu'u	LBBBAB
rar	Society Islands	Kahanu	Rare	LBBBAB
roi	Society Islands	Kahanu	Roi ha'a	LBBBAB
tap	Society Islands	Kahanu	Tapeha'a	LBBBAB
ton	Society Islands	Kahanu	Toneno	LBBBAB
tuu	Society Islands	Kahanu	Tuutou	LBBBAB
unk	Society Islands	Kahanu	unknown	LBBBAB
whi	Society Islands	Kahanu	Caribbean white	LBBBAB
yel	Society Islands	Kahanu	Caribbean yellow	LBBBAB
040	Tokelau	Nukunonu	Ulu afa	CABABB
041	Tokelau	Nukunonu	Ulu afa	CABADB
043	Tokelau	Nukunonu	Ulu hamoa	AABABB
044	Tokelau	Nukunonu	Ulu afa	CABADB
045	Tokelau	Nukunonu	Ulu afa	AABACB
046	Tokelau	Nukunonu	Ulu afa	AABACB
048	Tokelau	Nukunonu	Ulu afa	CAAAAB
049	Tokelau	Nukunonu	Ulu afa	CABABB
051	Tokelau	Nukunonu	Ulu afa	AAAABB
052	Tokelau	Nukunonu	Ulu afa	CABADB
053	Tokelau	Nukunonu	Ulu afa	CABABB
054	Tokelau	Nukunonu	Ulu afa	CABBBB
056	Tokelau	Nukunonu	Ulu afa	CABADB
059	Tokelau	Nukunonu	Ulu hamoa	CABBAB
063	Tokelau	Fakaofu	Ulu elise	AABADB
065	Tokelau	Fakaofu	Ulu elise	CAAADB

Table 3.3. Distribution of individual enzyme banding patterns by geographic area

		Melanesia						Micronesia						Polynesia							
														West				East			
		IN	PI	SI	VT	FJ	RO	BE	MR	YP	TR	PO	KS	KR	TK	WS	CI	SO	MQ	HI	
ACO	A							1	2		1			1	5						
	B															1					
	C		3												11	10					
	D			1																	
	E					1					4	2				6					
	F				2																
	G				1	2										1					
	H			1		1	2				6	7		1							
	I	2									5	3									
	J							3													
	K									1											
	L					1		1	2			1	11	1			1	4	42	7	3
	M			1	1	3	2					4	5								
	N			2								6	9								
	O									1											
	P			2	1	1	2											1			
	Q							1		1											
	R				1																
ADH	A							1	2	1	3			1	16						
	B		1	3	2	8	6	1	2	2	2	20	1			8	4	42	7	3	
	C			4	4	1		4			21	17		1		4		1			
	D															6					
	E		2																		
	F	1																			
	G	1														1					
IDH	A	2	3	7	6	5	5								3	18					
	B					4	1	6	4	3	26	37	1	2	13	1	4	43	7	3	
LAP	A													1	14						
	B	2	1	4	3	8	3	5	2	1	13	23	1		2	12	4	43	7	3	
	C			1	1	1	1			2	8	1		1		1					
	D		2				2	1	2		5	13				6					
	E				2																
	F			1																	
	G			1																	
MDH	A	2	3	7	6	9	6	4	2		4	15	1		2	19	4	43	7	3	
	B							1			6	15		1	6						
	C									3	2	1			2						
	D							1	2		14	6		1	6						
PGM	A		3																		
	B	2		4	5	8	6	5	2	2	23	37	1	2	16	10	4	43	7	3	
	C			1																	
	D			2	1	1		1	1		2					9					
	E									1											
	F								1												

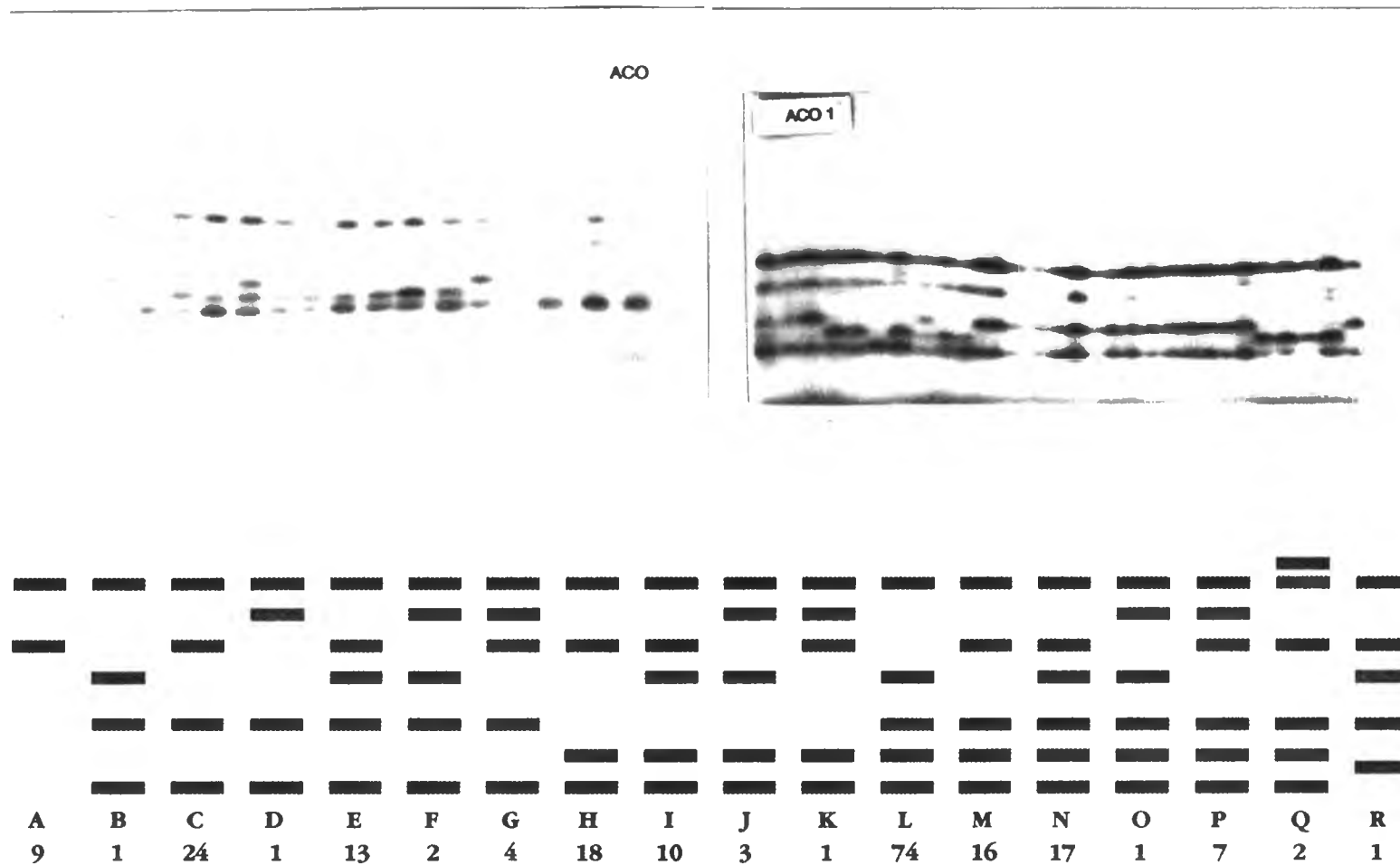


Figure 3.1. ACO banding patterns, photograph above and diagrammatic representation below with the number of accessions for each pattern

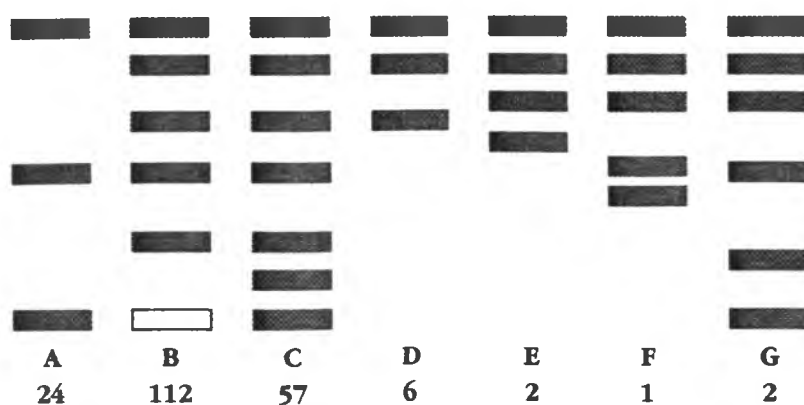
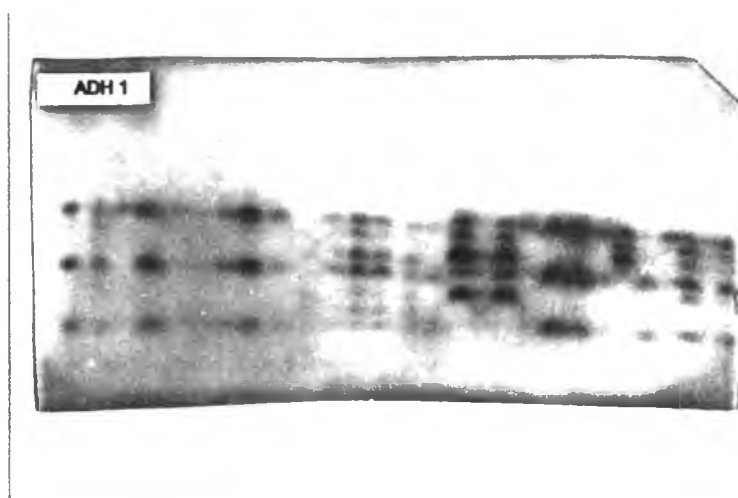


Figure 3.2. ADH banding patterns, photograph above and diagrammatic representation below with number of accessions for each pattern

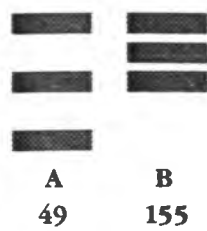
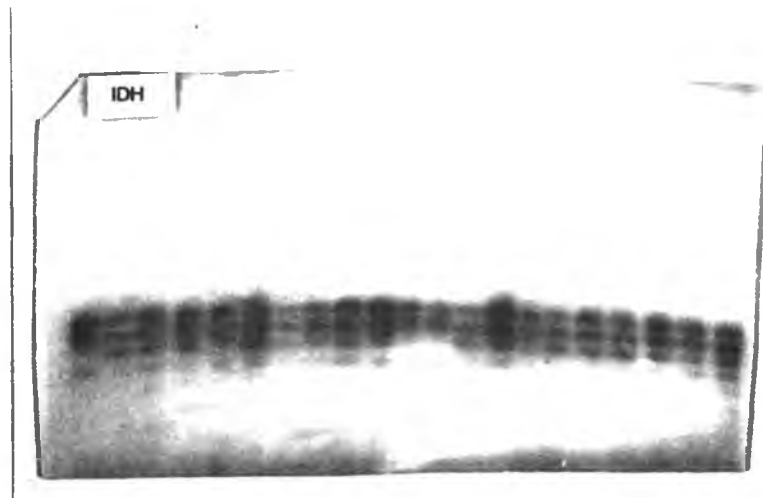


Figure 3.3. IDH banding patterns, photograph above and diagrammatic representation below with number of accessions for each pattern



Figure 3.4. Geographic distribution of IDH banding patterns A and B

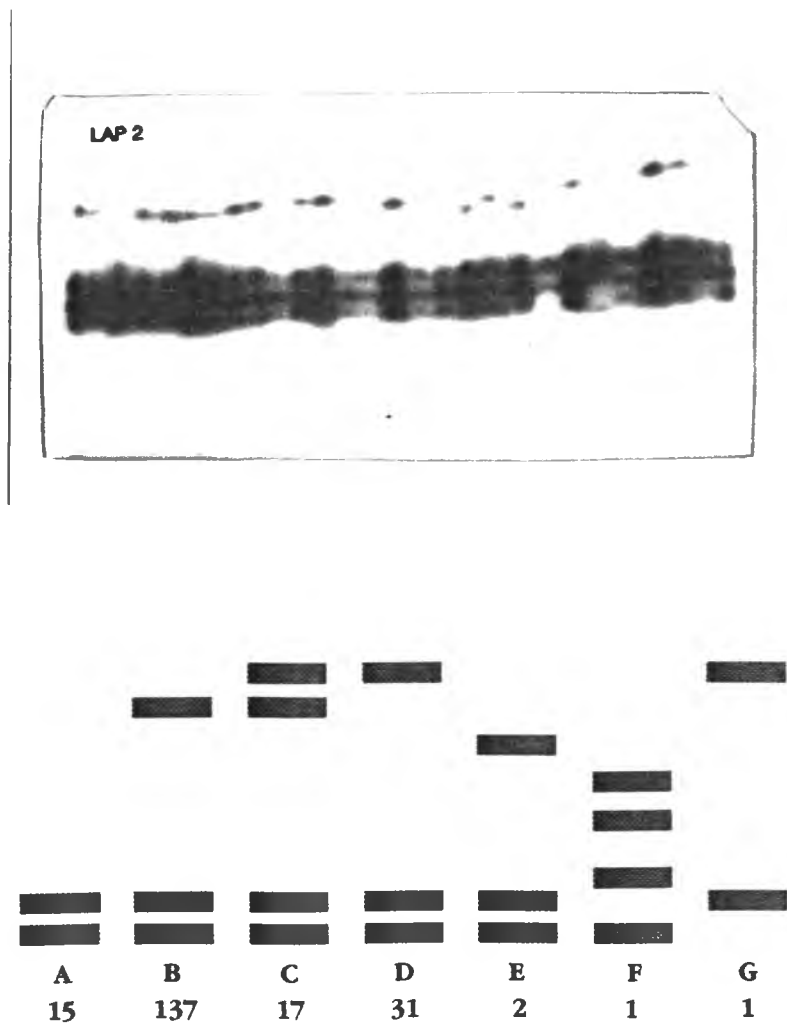


Figure 3.5. LAP banding patterns, photograph above and diagrammatic representation below with number of accessions for each pattern

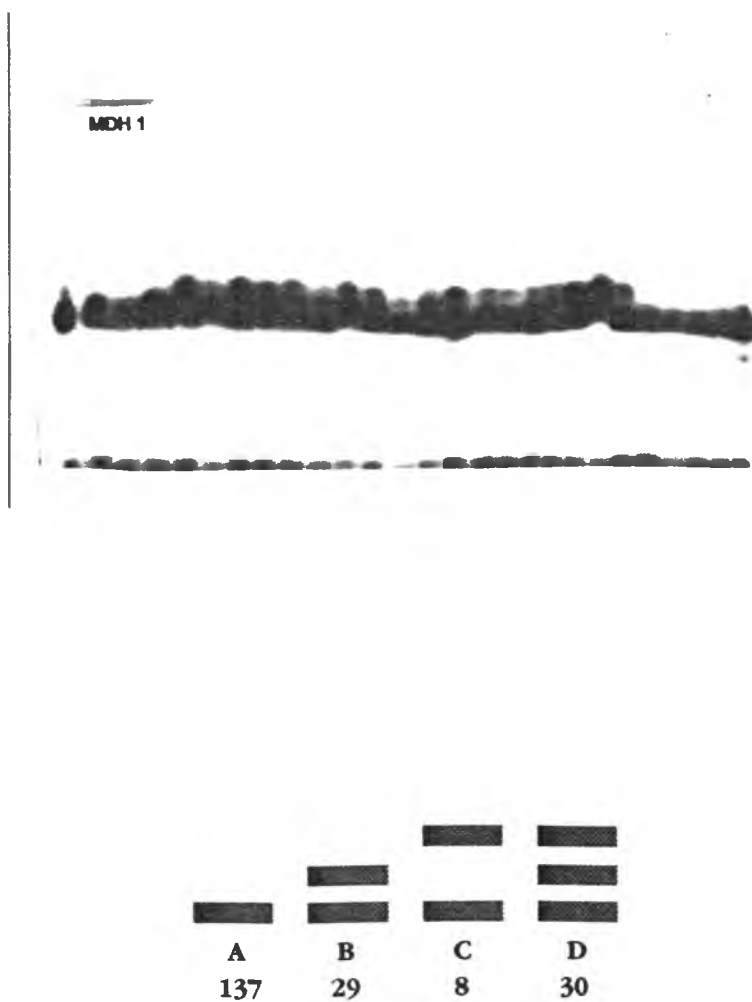


Figure 3.6. MDH banding patterns, photograph above and diagrammatic representation below with number of accessions for each pattern

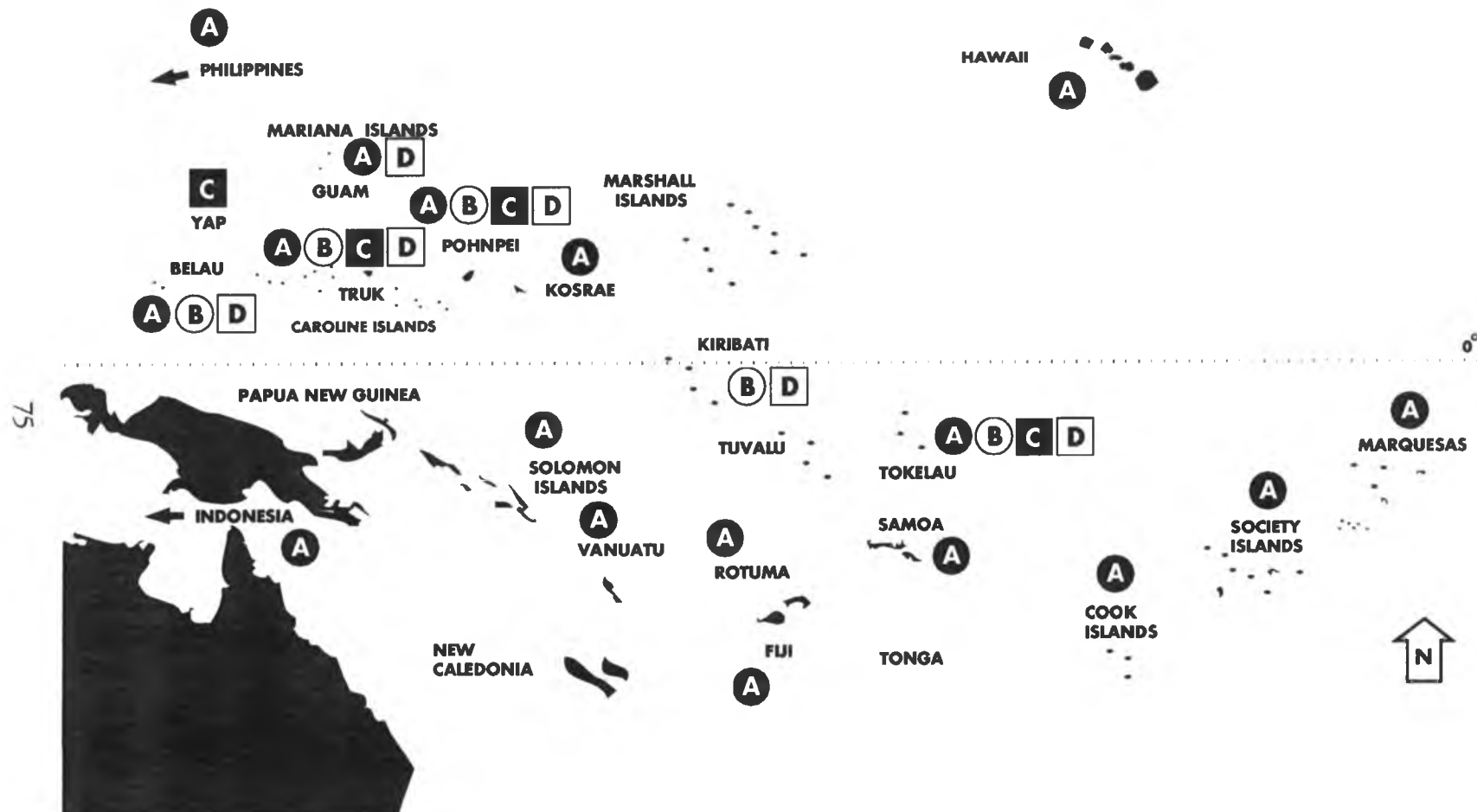


Figure 3.7. Geographic distribution of MDH banding patterns A, B, C, and D

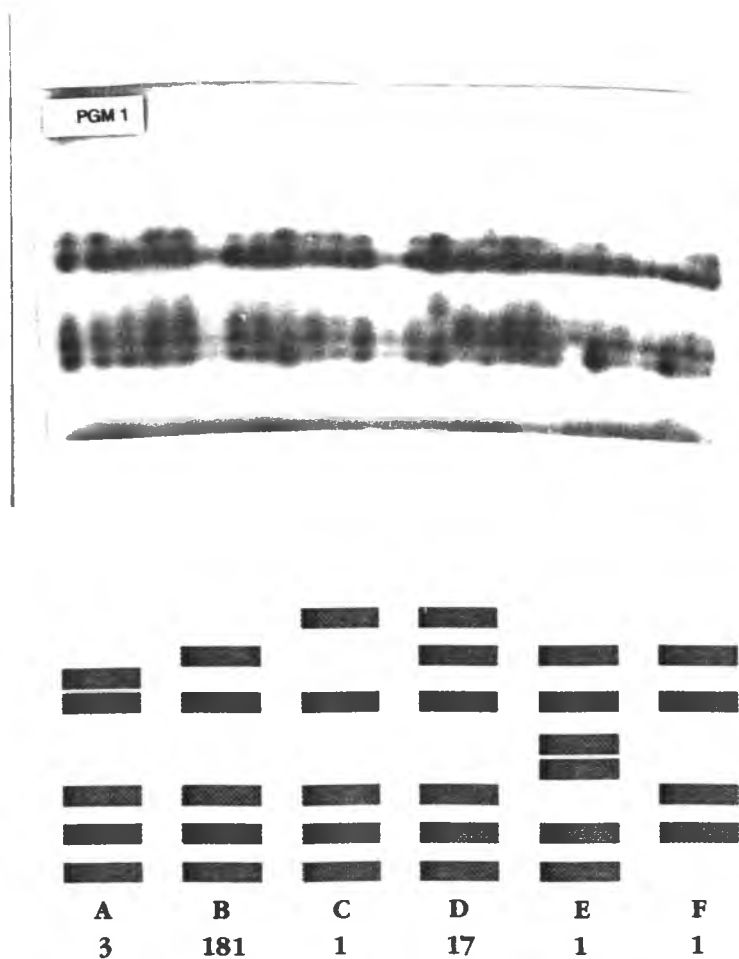


Figure 3.8. PGM banding patterns, photograph above and diagrammatic representation below with number of accessions for each pattern

Isozyme phenotypes and their geographic distribution

ACO

Aconitase exhibited the most variability with 18 patterns observed (Figure 3.1). ACO is a monomeric enzyme (Kephart 1990) and two distinct and well-resolved zones of ACO activity were seen. The most anodal zone, showed variation for bands 3, 4, and 5. Band 2 occurred in all patterns. The most anodal band (band 1) occurred in only two accessions (287, 290) from Belau and Yap. In the cathodal zone, variation was seen in bands 6 and 7. Band 8 occurred in only one accession (123) from the Solomon Islands, that also lacked band 9.

The most frequently occurring pattern (L) was seen in 74 accessions (36% of the accessions) from 11 island groups. All cultivars in the Cook Islands, Hawaii, and the Marquesas, and all but one cultivar in the Society Islands, displayed this pattern. The L pattern was also observed in 11 cultivars in Pohnpei, one in Truk, and three in western Micronesia.

Pattern C was second in frequency occurring in 24 accessions (12% of the accessions) from four island groups: Samoa, Tokelau, Indonesia, and the Philippines. Pattern C in the Tokelaus derives from a recent introduction of a Samoan cultivar, possibly **Aveloloa**. Also introduced into Tokelau from Tuvalu were *A. mariannensis* seedlings that show pattern A characterized by the absence of bands 6 and 7. This pattern is also found in four accessions from Kiribati (036), Marianas (309, 313), and Belau (292).

The next three most frequent patterns (H,M,N) were limited in distribution to Melanesia and Micronesia. They did not occur in any of the Polynesian islands. These three patterns were found in 51 accessions (25% of the accessions). Pattern M was observed in 16 accessions from six island groups. It was found in Melanesia, and the Micronesian islands of Pohnpei and Truk. Pattern N occurred in 17 accessions from the Solomons, Truk, and Pohnpei. Pattern H was observed in 18 accessions from the

Solomons, Fiji, Rotuma, Kiribati, Truk, and Pohnpei. Pattern P occurred in seven accessions and was limited to the western Pacific islands of Solomons, Vanuatu, Fiji, and Rotuma. A sixth accession from the Society Islands also displayed this pattern. Other unique banding patterns occurred in to Melanesia. Patterns R (523) and F (526, 528) were only found in Vanuatu.

Pattern E was found in 13 accessions from Fiji, Samoa, Pohnpei, and Truk. Four accessions from Fiji, Samoa and Vanuatu displayed pattern G. A single Samoan accession (475) exhibited pattern B. Accessions from Yap and Belau, with the exception of 286 with pattern L, all exhibited unique banding patterns. Three identical accessions (288, 289, 290) from Belau exhibited pattern J. Patterns K (301) and O (303) were observed in only one cultivar each. One cultivar each from Yap (287) and Belau (290) exhibited pattern Q.

ADH

Alcohol dehydrogenase was polymorphic with seven banding patterns observed (Figure 3.2). ADH is a dimeric enzyme and the products of various loci interact to produce interallelic and interlocus heterodimers (Hancock 1982). A probable heterodimer band (band 7), darker stained and located between the most anodal (band 1) and cathodal (band 12) bands was observed in patterns A, B, C, and G. Another probable heterodimer band located at band 2 was intermediate between bands 1 and 3 in patterns D, E, F, and G. Band 1 was detected in all zymotypes. Many bands stained faintly and were difficult to photograph, except for bands 4 and 7. Fainter staining in leaf tissue may be related to the function of ADH (Mowrey & Werner 1990). It is an inducible enzyme produced under anaerobic conditions or when the tissue is under stress. Leaf tissue would not normally experience anaerobic conditions and would not require high levels of the enzyme.

Three patterns (B,C,A) accounted for 95% of the accessions. Pattern B was observed most frequently, occurring in 112 accessions from all island groups except Indonesia, Kiribati, and Tokelau. Pattern C accounted for 58 accessions from nine island

groups. The third most frequently observed pattern (A) was observed in 24 accessions and is characteristic of *A. mariannensis* and some interspecific hybrids. It occurred in eight Micronesian accessions from Belau, Yap, Marianas, and Truk, and 16 Tokelau accessions. Three patterns (E,F,G) were unique to accessions from Indonesia and the Philippines. Six Samoa accessions exhibited pattern D.

IDH

Isocitrate dehydrogenase showed the least polymorphism with only two banding patterns observed (Figure 3.3). Figure 3.4 shows the distribution of IDH patterns by island group. This enzyme is a dimer (Kiang & Gorman 1985) and apparent heterodimer bands intermediate between bands 1 and 4 in pattern A and bands 1 and 3 in pattern B were observed. Pattern B was observed in 76% of the collection occurring in 155 accessions. It was found in all island groups in Micronesia. Its westernmost limit in the South Pacific was the islands of Fiji and Rotuma, and it was distributed throughout all island groups eastwards. Pattern A occurred in 49 accessions. It was found in the Philippines, Indonesia, Melanesia, and as far east as Samoa and Tokelau. The only overlap of these two patterns occurred in Fiji, Rotuma, and Samoa.

LAP

Seven banding patterns were observed for LAP (Figure 3.5), a typically monomeric enzyme (Kephart 1990). Pattern B accounted for the variability of 67% of the accessions occurring in 137 accessions from all islands groups except the Philippines and Kiribati. Patterns A, C, and D accounted for another 31% of the variability occurring in 63 accessions. Pattern A was restricted to 15 accessions from Tokelau and Kiribati. It only occurred in conjunction with pattern A of ADH that is characteristic of *A. mariannensis* and certain apparent interspecific hybrids.

A total of 17 accessions displayed pattern C and it was observed in 11 Micronesian accessions. Its range in the South Pacific lies from the Solomons in the west to Samoa in the east. It was found in a single accession each from the Solomons,

Vanuatu, Fiji, and Rotuma and two accessions from Samoa. It was not found in eastern Polynesia. Pattern E was observed in two accessions from Vanuatu. Patterns F and G were unique to one accession each, both from the Solomons.

MDH

Four banding patterns were observed for MDH (Figure 3.6). Figure 3.7 shows the distribution of patterns by island group. MDH has been reported as a dimeric enzyme (Byrne & Littleton 1989) and a possible heterodimer band (1) was observed in patterns C and D. The heterodimer band was intermediate in distance to the most cathodal band, 1, and a very faint anodal band that was only occasionally observed. This faint, anodal band was not numbered. Band 3 in all patterns was very darkly stained, and was slightly narrower in pattern A than in the other three patterns.

Pattern A is characteristic of *A. attilis* and occurred in 137 accessions from all island groups except Yap and Kiribati. Patterns B, C, and D did not occur anywhere in Melanesia and Polynesia and are characteristic of *A. mariannensis* and interspecific hybrids in Micronesia.

PGM

Seven banding patterns were observed for PGM (Figure 3.8), a monomeric enzyme (Jarret and Litz 1986). Two patterns accounted for 97% of the variability observed for this enzyme. Pattern B was observed in 181 (89%) accessions from all island groups except the Philippines. Pattern D was found in 17 accessions from Melanesia, Samoa, and three island groups in Micronesia. Three accessions from the Philippines exhibited pattern A. The remaining patterns were unique to one accession each: C from the Solomons, E from Yap, and F from the Marianas.

Geographic patterns of isozyme variability

Truk showed the highest variation among the 19 island groups with a total of 19 patterns observed out of a possible 44 (Table 3.4). Five of the six enzyme systems were polymorphic with IDH being monomorphic. Pohnpei, Belau, and the Marianas also

showed relatively high levels of variation reflecting the heterogeneity resulting from the occurrence of both *A. altilis* and *A. mariannensis*, and possible interspecific hybridization between these two species in Belau and Pohnpei. The Solomons, Fiji, and Samoa also exhibited the relatively high levels of heterogeneity expected from an outcrossing species.

Table 3.4. Pattern of isozyme variation in 204 accessions of *Artocarpus altilis*, *A. mariannensis* and interspecific hybrids from 19 Pacific island groups.

Island Group	Number of Accessions	%ESP ^a	P ^b
Truk	26	83.3	3.2
Samoa	19	83.3	2.8
Fiji	9	83.3	2.5
Belau	6	83.3	2.5
Marianas	4	83.3	2.0
Pohnpei	37	66.7	2.8
Indonesia/PI	5	66.7	2.7
Solomons	7	66.7	2.7
Vanuatu	6	66.7	2.3
Tokelau	16	66.7	2.0
Yap	3	66.7	1.8
Kiribati	2	66.7	1.7
Rotuma	6	50.0	1.8
Societies	43	33.3	1.3
Cook Is.	4	0	1.0
Marquesas	7	0	1.0
Hawaii	3	0	1.0
Kosrae	1	0	1.0

^a Percentage of enzyme systems that are polymorphic.

^b Mean number of isozyme banding patterns per enzyme system.

The lowest levels of variability were observed in eastern Polynesia, with all enzyme systems monomorphic in the Cook Islands, Marquesas, and Hawaii. In the Society Islands, only one accession of the total 43 exhibited any polymorphism, seen in two systems, ACO and ADH. The low levels of polymorphism in enzyme systems in eastern Polynesia is due to the seedless, clonal nature of these accessions. The lack of variability for Kosrae is not reflective of the true diversity for this island. It has many cultivars in common with Pohnpei, which had a PES of 66.7. and P of 2.8. Only one accession from Kosrae, apparently of Polynesian origin, was analyzed by electrophoresis. Additional materials need to be sampled to determine how much variation exists among cultivars from this island.

These formulas provide a useful estimate of variability in enzyme systems analogous to commonly used measures of genetic diversity, where %PES = proportion of loci polymorphic and p^b = mean number alleles/loci.

A comparison of the number of unique zymotypes for five major island groups is shown in Table 3.5. The 204 accessions surveyed were reduced to 90 unique zymotypes (isozyme phenotypes) (Table 3.6). The order used in this paper is ACO, ADH, IDH, LAP, MDH, PGM. Only 12 of the 90 zymotypes occurred in more than one island group. Of these, one (LBBBAB) had the greatest distribution, occurring in 11 areas. The others occurred in two, or rarely, three areas.

Table 3.5 Distribution of zymotypes by island group

Group	Number of accessions	Number of zymotypes	% unique zymotypes
Indonesia/PI	5	5	100
Melanesia	28	20	71.0
Micronesia	79	47	59.5
Polynesia	92	*24	26.0
West	45	23	51.0
East	57	2	3.5

* While a total of 24 zymotypes occur in Polynesia, one zymotype, LBBBAB, occurs in both western and eastern Polynesia.

Table 3.6. Distribution of 90 unique zymotypes by geographic area

MICRONESIA		MELANESIA		POLYNESIA	
Belau (4)		Fiji (7)		Cook Islands (1)	
AABDDDB	LBBBAB	ECABAD	MBABAB	LBBBAB	
JCBABAB	QCBBBD	GBBBAB	MBACAB	Hawaii (1)	
Kiribati (2)		HBABAB	PBBBAB	LBBBAB	
AABABB	HCBCDB	LBBBAB		Marquesas (1)	
Kosrae (1)		Rotuma (4)		LBBBAB	
LBBBAB		HBABAB	MBBBAB	Samoa (13)	
		MBACAB	PBADAB	BBABAD	CGADAB
Mariana Islands (3)		Solomon Islands (7)		CBABAB	EBABAD
AABDDD	LBBBAB	DCABAB	NCAGAC	CBADAD	ECABAD
AABDDF		HBABAB	PBACAB	CCABAD	ECADAD
Pohnpei (19)		MBABAD	PCABAD	CDABAB	GBABAB
EBBDDDB	MCBDBB	NCAFAB		CDACAB	LBBBAB
ECBBBB	MCBDDDB	Vanuatu (5)		CDADAB	
HBBDBB	NBBBAB	FCABAB	PBACAB	Society Islands (2)	
HBBDCB	NBBDDDB	GBABAB	RCAEAD	LBBBAB	PCBBAB
HCBBBB	NCBBAB	MCAEAB		Tokelau (10)	
IBBBBB	NCBBBB	INDONESIA/PI (5)		AAAABB	CAAADB
ICBDDDB	NCBCDB	CBADAA	IFABAB	AABABB	CABABB
LBBBAB	NCBDAB	CEABAA	IGABAB	AABACB	CABADB
MBBBBB	NCBDBB	CEADAA		AABADB	CABBAB
MBBDBB				CAAAAB	CABBBB
Truk (24)					
EBBDBB	ICBBDD				
ECBBDB	ICBCBB				
ECBDAB	LBBBAB				
HABDCB	MCBBDB				
HABDDDB	MCBCDB				
HCBBAB	MCBDDDB				
HCBBBB	NABBDB				
HCBCBD	NBBCDB				
HCBDDB	NCBBAB				
ICBBBB	NCBBBB				
ICBBCB	NCBCBB				
ICBBDB	NCBCDB				
Yap (3)					
KABBCE	QBBCCB				
OBBCCB					

Numbers within brackets designate the number of zymotypes for that island.
Highlighted zymotypes are those that occur in more than one island group.

The greatest isozyme variation occurred in Melanesia, with 71% of the accessions uniquely characterized. A relatively high level of zymotypic variation occurred in Micronesia, with 59% of the accessions uniquely characterized. While 26% of the Polynesian accessions were unique, the variation predominantly occurred in western Polynesia. Fifty-one percent of western Polynesian accessions are uniquely characterized compared to eastern Polynesia, where the only zymotypic variation is limited to one of 43 accessions collected in the Society Islands.

Multivariate analysis of isozyme data

A dendrogram resulting from cluster analysis is shown in Figure 3.9. Table 3.7 lists enzymatic formula, island of origin, and information on chromosome number, seeds, and hybrid characters for each accession. The accessions in the two largest clusters were closely related with an average of 71% of their electromorphs in common. The 40 accessions within cluster I shared at least 76% of their electromorphs in common. The largest group (cluster II) contained 134 accessions, 66% of total analyzed. Accessions within this group had at least 79% of their electromorphs in common. One accession from the Solomon Islands was uniquely characterized in cluster III with an average of only 67% of its electromorphs in common with clusters I and II.

Cluster IV contained 23 accessions from western Micronesia, and the atoll islands of Truk, Kiribati, and Tokelau with an average of 79% of their electromorphs in common. The one accession from Yap (301) in cluster V was uniquely characterized and most closely associated with cluster IV. These two clusters had an average of 64% of their electromorphs in common with the first three clusters. Clusters VI and VII contained only five accessions from Indonesia and the Philippines. These few accessions were the most dissimilar to the rest of the accessions, having less than 60% of their electromorphs in common.

Cluster I contains 24 different zymotypes for 40 accessions. The geographic distribution of this group was limited to Melanesia and Samoa. Only *A. altilis* was represented in this group. The largest group of 134 accessions (cluster II) contained 43

different zymotypes. This group displayed the greatest geographical distribution with 14 island groups represented. Within this cluster, 74 accessions were monomorphic for the six enzyme systems studied, with a zymotype of LBBBAB. This zymotype (25) is unique to typically seedless cultivars characteristic of eastern Polynesia and was observed in accessions from all the Polynesian islands, as well as the Micronesian islands of Belau, Marianas, Kosrae, Truk, and Pohnpei. No accessions from Melanesia, Tokelau, Kiribati, or Yap were observed to have this zymotype. Within cluster II, both *A. altitis* and interspecific hybrids between this species and *A. mariannensis* were represented.

Cluster IV contained 23 accessions with 16 different zymotypes. Three accessions of *A. mariannensis* from Belau and the Mariana Islands occurred in this group. This group also contained all 16 Tokelau accessions and accessions from Kiribati and Truk that are interspecific hybrids most closely related to *A. mariannensis*. The geographic distribution of each cluster is shown in Figure 3.10.

The grouping of zymotypes by cluster analysis is supported by the results provided by principle components analysis (Figure 3.11). Additional relationships between accessions, however, can be elucidated from these plots. Within cluster II, zymotype 25 (LBBBAB) is closely grouped with two zymotypes from Fiji, one from Rotuma, and one from Pohnpei. This group appears to be closer to the Micronesian accessions in cluster II than to the Melanesian and Polynesian accessions in cluster I.

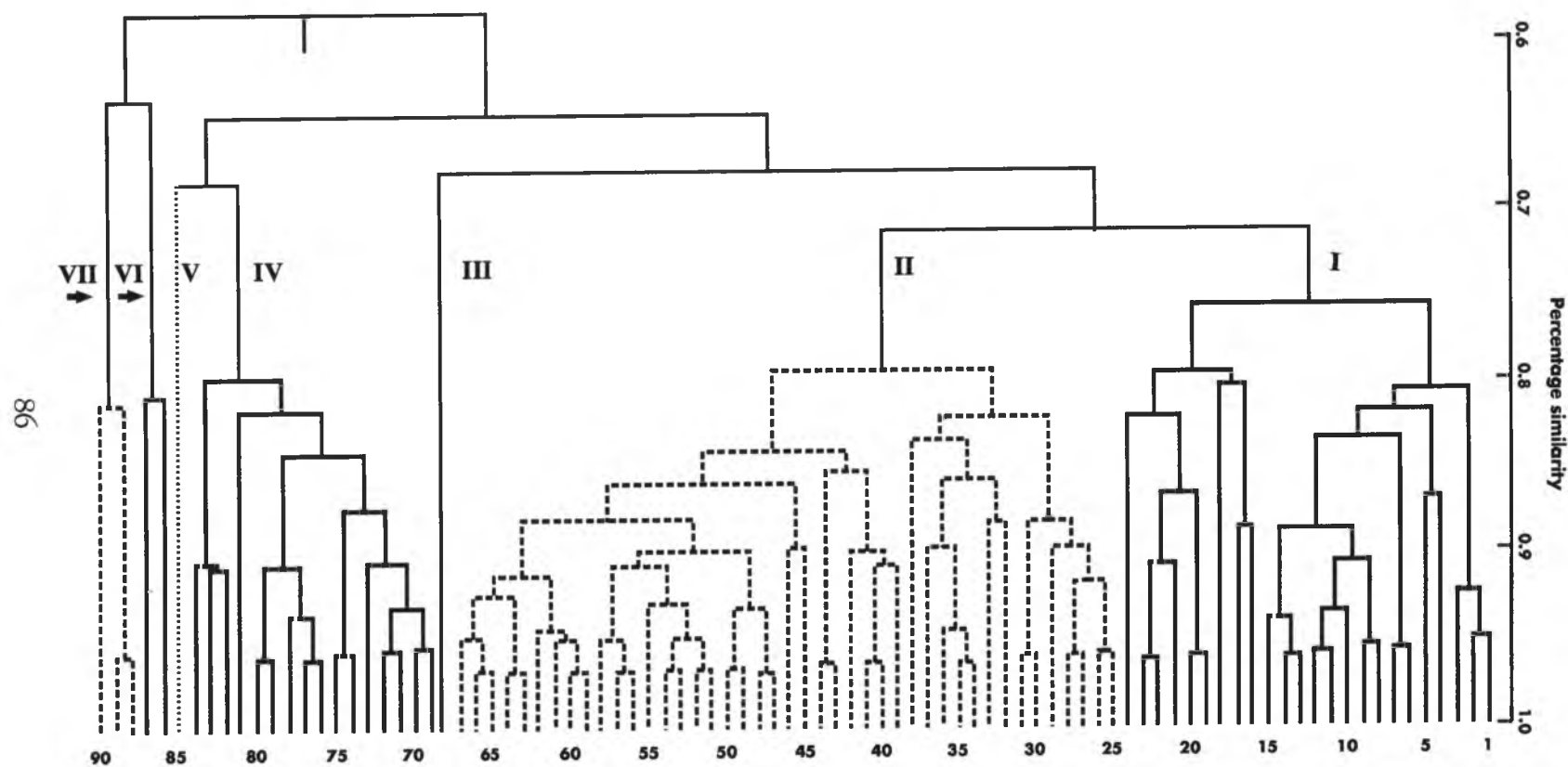


Figure 3.9. Dendrogram produced by cluster analysis of 204 breadfruit accessions.
(Numbers beneath the dendrogram correspond to identification numbers in Table 3.7)

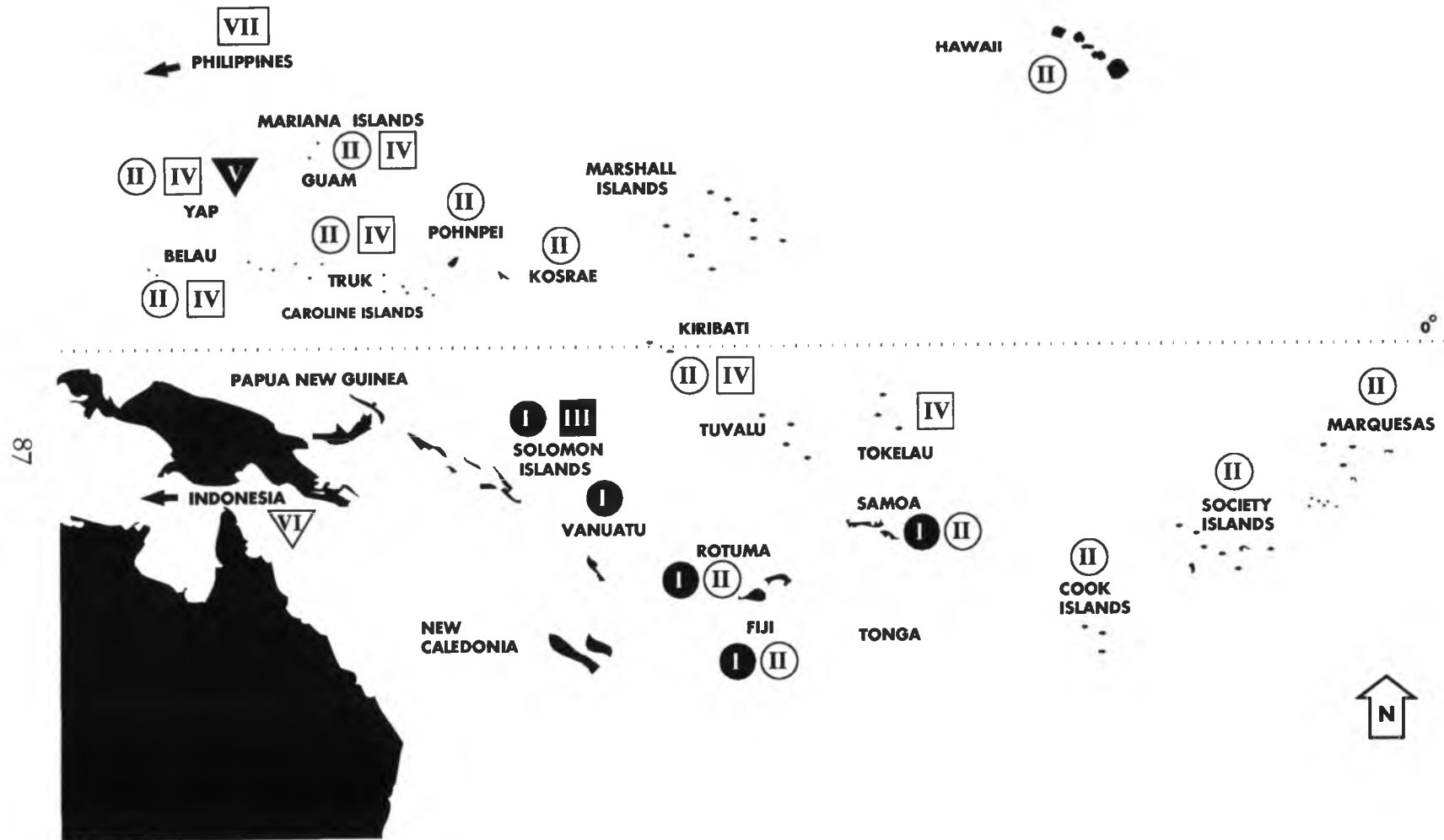


Table 3.10. Geographic distribution of clusters based on dendrogram

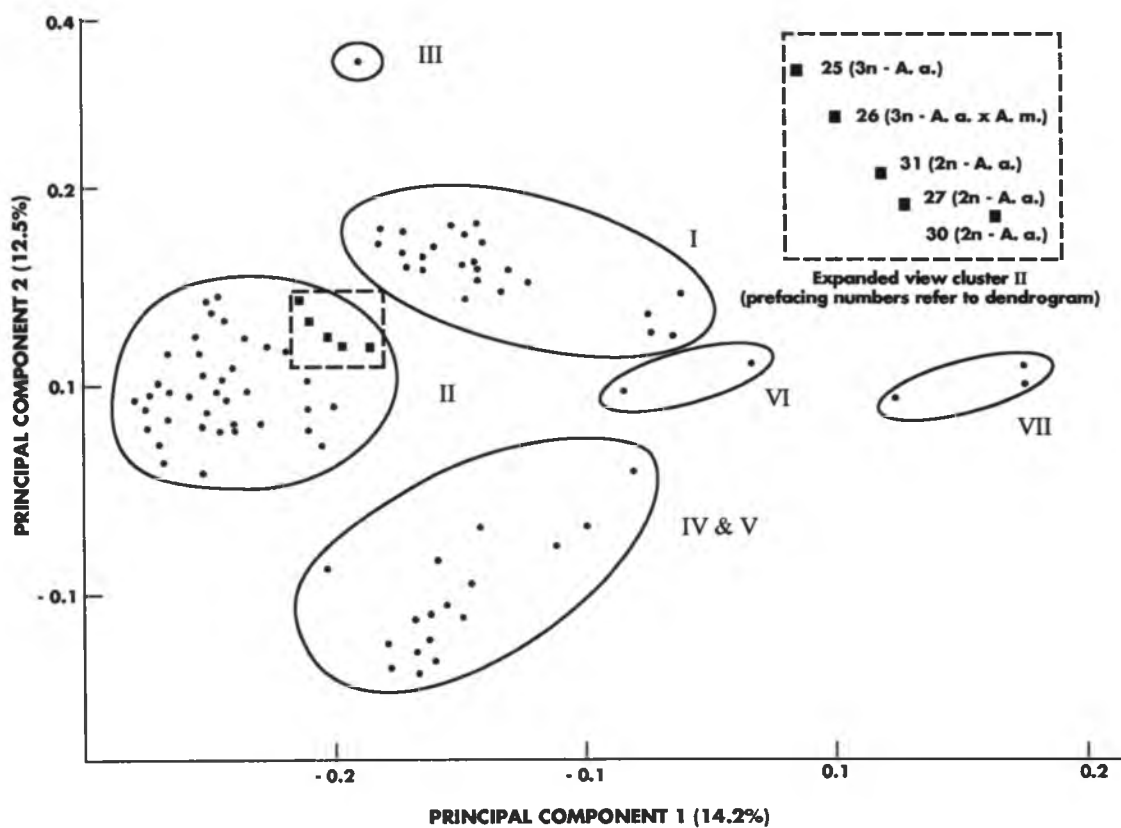


Table 3.11. Principal components analysis of the 204 breadfruit accessions with an expanded view of part of Cluster II

Discussion

There are several advantages to using isozyme analysis to evaluate and characterize a germplasm collection. In general, isozyme analysis provides a means of quickly and easily amassing data for characters used to produce a classification. In this case, 45 character states (electromorphs) were obtained from six enzyme systems. Rating the accessions for presence or absence of the electromorphs (presence is coded as 1 and absence as 0) was easier than rating them for often continuously variable morphological characters. In addition, the observed isozyme banding patterns provided a useful tool to identify cultivars and clarify relationships between cultivars.

Enough enzyme polymorphism existed within the six enzyme systems of ACO, ADH, IDH, LAP, MDH, and PGM to adequately characterize the germplasm collection; however, a genetic interpretation of the banding patterns cannot be determined without examining segregating seedling populations of the three species. Two systems, ACO and ADH, were especially useful for differentiating among accessions, because of the high levels of polymorphism in the systems. MDH was very useful in characterizing accessions, because three of its four patterns (B,C,D) were observed to occur only in *A. mariannensis* and interspecific hybrids. These three patterns were not observed in typical Melanesian and Polynesian cultivars. Pattern A occurs in *A. altalis* and some interspecific hybrids.

IDH showed the least polymorphism with only two banding patterns observed, however, its geographic distribution provided useful information that will be discussed later in this chapter. The remaining two systems, LAP and PGM, had high levels of polymorphism with 8 and 7 banding patterns, respectively. They were not as useful as the other systems, however, in characterizing the accessions, since one banding pattern in LAP accounted for 67% of the variability and one pattern in PGM accounted for 88% of the variability observed in the collection.

The results from using isozyme banding patterns to identify cultivars included:

1. When the same cultivar name applied to trees from several different regions, isozyme analysis offered an independent check of relationship.
2. Unknown or misidentified cultivars could be properly identified, and it was often possible to determine from which islands these originated.

Cultivar identification

Examples of same-name cultivars that were observed to have the same zymotype included **Manua** (013/469) in Samoa, **Ebechab** (288/289) from Belau, and **Mein patak** (375/pat) and **Lipet** (365/511) from Pohnpei. Two Samoan accessions (453/puo) and a Fijian accession identified as **Uto Samoa** (495) had the same zymotype, and were shown to be the cultivar **Puou**. In contrast, a fourth accession (519) introduced to Vanuatu from Wallis or Futuna, and identified as **Puou**, had a slightly different zymotype than the Samoan cultivar. Based on its zymotype, it can not be definitively identified as **Puou**. Two Pohnpeian accessions identified as **Mei pwahr** (386/396), had different zymotypes and morphotypes. These were collected in two different villages, indicating that the same name may be used for different cultivars in different villages or districts.

Several unknown or misidentified cultivars could be identified based on their zymotype matching that of named cultivars. A good example of this is the three accessions, 092, 095, and 100, collected in the Cook Islands, but recognized as introductions from other Polynesian islands. Two of these, 095 and 100, were given the same name, **Niue**, but while 092 was considered to be an introduction from Tahiti, it proved to have the same zymotype as the other two. These three accessions were most closely related to other accessions in Samoa, and differed in only one enzyme system from a very similar Samoan cultivar **Sagosago** (475). Two unknown Samoan accessions, 110 and an unidentified tree in the Kahanu collection, were shown to have the same zymotype as the Samoan cultivar **Ulu sina** (019).

An unknown Solomon cultivar (539) had the same zymotype as **Manang** (443) from Vanuatu. A Fijian cultivar (428) was misidentified as **Uto dina**. The name **Uto dina** means 'true breadfruit' which is always seedless. It had the same zymotype as a seeded 'Samoan' type. This accession was collected in the Vailima breadfruit collection in Western Samoa, and was probably misidentified. A similar situation applies to another cultivar from that collection. A Rotuman cultivar (127) identified as **Karawa** does not have the same zymotype as the same-named Fijian cultivar (489). Either the same name is used for two different cultivars in these two islands, or the Rotuman cultivar was misidentified in the Vailima collection.

An accession collected in a botanical garden in Tahiti (282) was shown to be most similar to two accessions from the Philippines (531 and 546). Two similar accessions (221 and 261) were also recent introductions, but it is unknown whether they originated in Indonesia or the Philippines. Accession 540 was grown from a seed collected from a few-seeded Pacific Island cultivar growing in a botanic garden in Indonesia. The banding patterns for five enzyme systems for this accession were most similar to those found in Samoan cultivars, suggesting that this cultivar originated from that island. The presence in this cultivar of pattern G of ADH, which was not found in the Pacific islands, indicates that the parent tree was cross-pollinated by pollen from a seeded Indonesian tree.

Since isozyme analysis was conducted on most of the accessions prior to their planting in the Kahanu Gardens, it should be possible to accurately identify those trees that lost their labels in transit, and are not currently identified or labeled.

Although isozyme analysis proved to be used in characterizing the collection as described above, this method has its limitations. Zymotypes can not be used to distinguish triploids from diploids, since no zymotype is uniquely triploid. In addition to the triploid cultivars with zymotype LBBBAB, three other zymotypes (NBBBAB, QBBCCB, and QCBBD) in the collection were observed to be triploid cultivars. In every case where a triploid had a certain banding pattern (ACO L,N,Q; ADH B,C; IDH B; LAP B,C; MDH A,B,C; and PGM B,D), there was also a diploid with this pattern.

While isozyme analysis readily distinguished breadfruit clones of basically different genetic background, it was not sufficient to resolve somatic mutants selected within clones on the basis of morphological differences. There were 74 accessions that were observed to have the same zymotype (LBBBAB). These accessions exhibit a diverse range of fruit and leaf characters, more than would be expected from a single zymotype in natural populations. Leaf indentation ranges from almost entire to very deeply lobed, and fruit shape, flesh, and skin texture show great variation. The range of morphological variation is as great as, or exceeds, that of seeded breadfruit found in Melanesia and western Polynesia where 44 zymotypes were observed for 65 accessions. It is likely that accessions with this zymotype all derived from an original seedless, triploid cultivar by human selection of somatic mutations occurring in the vegetatively propagated clone.

Seventeen other zymotypes (see Table 3.7 for accessions with the same dendrogram number) that were observed to have from two to as many as five accessions for the same zymotype may also be the result of somatic mutations. Morphological or other characters will have to be assessed for all zymotypes with multiple accessions to further characterize these cultivars.

Cultivar relationships

Zymotypes were also useful in elucidating relationships between cultivars. There were many Micronesian accessions in cluster II which, based on isozyme phenotypes (MDH B,C,D) and morphological characters (fruit surface and presence of red hairs), appear to be interspecific hybrids between *A. altilis* and *A. mariannensis*. Cluster IV contained *A. mariannensis* from western Micronesia, and closely related interspecific hybrids from the coral atolls of Tokelau. The large number of unique zymotypes found in Micronesia (60%) and Tokelau (62%) is to be expected from the hybrid nature of many of these accessions.

Cluster and principle components analyses show that seedless, triploid cultivars of *A. altilis* appear to be most closely related to three diploid accessions of *A. altilis*

(zymotypes 27, 30, 31), and the interspecific hybrids all found in cluster II. Triploid *A. altilis* cultivars occur in Micronesia, but diploid cultivars are not found there. This suggests that the interspecific hybrids found in cluster II may have resulted from hybridization between *A. mariannensis* and triploid cultivars of *A. altilis*. The separation of interspecific hybrids into two clusters (II and IV) shows that the triploids were not involved in interspecific hybridization in cluster IV, and the hybrids in this group originated from another source.

Support for the involvement of triploid *A. altilis* in interspecific hybridization and introgression with *A. mariannensis* is found in comparing the distribution of the two banding patterns for IDH. Pattern B is found in all accessions in Micronesia, including putative hybrids, and in the triploid *A. altilis* from eastern Polynesia. Except for the three accessions from Fiji and Rotuma found in cluster II, only the A pattern is found in *A. altilis* in western Polynesia and Melanesia. Thus, if hybridization had occurred, it would be difficult to explain the absence of the A pattern in all of Micronesia, had the *A. altilis* present been a typical Melanesian/Polynesian diploid *A. altilis*.

In contrast, cluster IV was more variable with the occurrence of IDH patterns A and B. All of the accessions in this cluster were also observed to have ADH pattern A, compared to cluster II where only ADH patterns B and C were observed. These accessions, mostly cultivars from atoll islands, appear more closely related to *A. mariannensis* and it appears that there was little backcrossing and introgression with *A. altilis*.

MDH is another enzyme system that provides clues to interspecific hybridization in Micronesia. Pattern A is the only form throughout the south Pacific, from western Melanesia to eastern Polynesia. Patterns B, C, and D only occur in Micronesia and are

characteristic of *A. mariannensis* and most interspecific hybrids. Pattern A, however, is also found in several Micronesian accessions which have morphological traits more characteristic of *A. mariannensis* than *A. altilis*. How hybridization between seedless, triploid *A. altilis* and seeded *A. mariannensis* occurred, and other questions concerning this interspecific hybridization will be discussed further in Chapter V.

The cluster analysis showed that 90% of the accessions from Melanesia and Samoa have unique zymotypes and are closely related. The high genetic variability shown by these accessions is expected since seeded, diploid cultivars predominate in these islands. The unique zymotype of one accession from the Solomon Islands (169), that fell into its own cluster (III), may not be as anomalous as it appears.

Accessions from Melanesia, especially New Guinea, are under-represented in the germplasm collection. Seeded breadfruit grows wild only in New Guinea, and possibly the Bismarck Archipelago, and was carried to other Pacific islands and cultivated by humans. The diversity of breadfruit in the other Melanesian islands probably does not represent the total diversity found in wild populations in New Guinea. Accession 169 may be a component of a much more variable group, and extensive collecting needs to be conducted in New Guinea, the Bismarcks, the Solomon Islands, and Vanuatu to compare these materials to the existing collection.

A Yapese accession in cluster III that was most dissimilar to the rest of Micronesian accessions parallels the problems of insufficient sampling in Melanesia. Additional materials from Yap proper and the outlying atolls of the Caroline Islands need to be collected and assessed. These, and the Polynesian outliers of Nukuoro and Kapingimarangi, may be important bridges in the distribution of breadfruit through Micronesia and from the South Pacific into Micronesia. Widespread collection and analysis of cultivars from Melanesia and the Micronesian atolls may show relationships between cultivars in these two areas that is not evident in the materials examined in this study.

Inadequate sampling also affects estimates of variability in Indonesia and the Philippines. This group had the least in common with the rest of the germplasm collection, sharing fewer than 60% of its zymotypes in common with all other accessions. While this small sample is not large enough to make definitive conclusions about these materials, the cluster and principal components analyses suggest that these accessions may indeed be a separate but closely related species to *A. altilis* described as *A. camansi*. Widespread sampling within its range will be required to determine if morphological and zymotypic variation on these islands is dissimilar from, or overlaps, with that of Pacific island breadfruit.

In conclusion, isozyme analysis proved to be a valuable tool in characterizing this breadfruit germplasm collection. Only 90 zymotypes were observed in the approximately 200 accessions analyzed. From the point-of-view of long-term conservation of genetic diversity in breadfruit, the extensive germplasm collection of almost 300 trees at the National Tropical Botanical Garden could be reduced to 90 representatives of the unique zymotypes to reduce the amount of land and labor required to maintain this permanent collection of large fruit trees.

This is not recommended, however, since reducing the germplasm collection to a single representative of each zymotype, while capturing the isozyme variability sampled in the collection, would not conserve the numerous and diverse cultivars that have developed from somatic mutations affecting morphological and horticultural traits. The many cultivars selected and maintained by humans over years, and possibly, centuries of cultivation, reflect the importance of this crop to Pacific island cultures. Maintaining the entire collection ensures that these culturally important cultivars will be conserved.

Table 3.7. Dendrogram number, origin, zymotype, chromosome number, and presence of *A. mariannensis* characters for 204 breadfruit accessions

Dendrogram	Accession	Island	Zymotype	2n	<i>A. mariannensis</i>		
					Seeds	Fruit	Hairs
Cluster I							
1	007	Samoa	CDACAB	56	yes	-	-
2	013	Samoa	CDABAB	56	no	-	-
2	469	Samoa	CDABAB		no	-	-
3	019	Samoa	CDADAB	56	yes	-	-
3	110	Samoa	CDADAB	56	few	-	-
3	unk	Samoa	CDADAB		yes	-	-
4	maf	Samoa	CBADAD	56	yes	-	-
5	540	Samoa	CGADAB		yes	-	-
6	092	Samoa	EBABAD		few	-	-
6	095	Samoa	EBABAD	56	few	-	-
6	100	Samoa	EBABAD		few	-	-
7	475	Samoa	BBABAD		yes	-	-
8	mom	Samoa	GBABAB		yes	-	-
8	445	Vanuatu	GBABAB		yes	-	-
9	472	Samoa	CBABAB		yes	-	-
10	464	Fiji	HBABAB	56	yes	-	-
10	136	Rotuma	HBABAB		yes	-	-
10	427	Rotuma	HBABAB		yes	-	-
10	426	Solomon Islands	HBABAB	56	yes	-	-
11	428	Fiji	MBABAB		yes	-	-
11	468	Fiji	MBABAB		yes	-	-
12	436	Solomon Islands	MBABAD		yes	-	-
13	488	Fiji	MBACAB		yes	-	-
13	127	Rotuma	MBACAB		yes	-	-
14	539	Solomon Islands	PBACAB		yes	-	-
14	443	Vanuatu	PBACAB	56	yes	-	-
15	243	Rotuma	PBADAB		yes	-	-
15	439	Rotuma	PBADAB	56	yes	-	-
16	123	Solomon Islands	NCAGAC	56	yes	-	-
17	uhp	Samoa	ECADAD		no	-	-
18	523	Vanuatu	RCAEAD		yes	-	-
19	166	Solomon Islands	DCABAB		yes	-	-
20	526	Vanuatu	FCABAB	56	yes	-	-
20	528	Vanuatu	FCABAB		yes	-	-
21	437	Solomon Islands	PCABAD		yes	-	-
22	495	Fiji	ECABAD		yes	-	-
22	453	Samoa	ECABAD	56	few	-	-
22	puo	Samoa	ECABAD		yes	-	-
23	519	Samoa	CCABAD		yes	-	-
24	525	Vanuatu	MCAEAB		yes	-	-

Table 3.7. (Continued) Dendrogram number, origin, zymotype, chromosome number, and presence of *A. maritannensis* characters for 204 breadfruit accessions

					<i>A. mariannensis</i>		
Dendrogram	Accession	Island	Zymotype	2n	Seeds	Fruit	Hairs
Cluster II							
25	286	Belau	LBBBAB	84	no	-	-
25	096	Cook Islands	LBBBAB	84	no	-	-
25	103	Cook Islands	LBBBAB	84	no	-	-
25	433	Cook Islands	LBBBAB	84	no	-	-
25	435	Cook Islands	LBBBAB		no	-	-
25	482	Fiji	LBBBAB		no	-	-
25	530	Hawaii	LBBBAB	84	no	-	-
25	ana	Hawaii	LBBBAB		no	-	-
25	kah	Hawaii	LBBBAB		no	-	-
25	mos	Kosrae	LBBBAB		no	-	-
25	311	Mariana Islands	LBBBAB	84	no	-	-
25	314	Mariana Islands	LBBBAB		no	-	-
25	216	Marquesas	LBBBAB	84	no	-	-
25	220	Marquesas	LBBBAB	84	no	-	-
25	222	Marquesas	LBBBAB	84	no	-	-
25	223	Marquesas	LBBBAB		no	-	-
25	224	Marquesas	LBBBAB		no	-	-
25	230	Marquesas	LBBBAB		no	-	-
25	231	Marquesas	LBBBAB		no	-	-
25	367	Pohnpei	LBBBAB		no	-	-
25	370	Pohnpei	LBBBAB	84	no	-	-
25	372	Pohnpei	LBBBAB	84	no	-	-
25	374	Pohnpei	LBBBAB	84	no	-	-
25	390	Pohnpei	LBBBAB		no	-	-
25	405	Pohnpei	LBBBAB		no	-	-
25	502	Pohnpei	LBBBAB		no	-	-
25	509	Pohnpei	LBBBAB		no	-	-
25	510	Pohnpei	LBBBAB		no	-	-
25	512	Pohnpei	LBBBAB		no	-	-
25	teh	Pohnpei	LBBBAB		no	-	-
25	541	Samoa	LBBBAB	84	no	-	-
25	200	Society Islands	LBBBAB		no	-	-
25	204	Society Islands	LBBBAB		no	-	-
25	236	Society Islands	LBBBAB	84	no	-	-
25	238	Society Islands	LBBBAB		no	-	-
25	245	Society Islands	LBBBAB		no	-	-
25	248	Society Islands	LBBBAB		no	-	-
25	251	Society Islands	LBBBAB		no	-	-
25	253	Society Islands	LBBBAB		no	-	-
25	255	Society Islands	LBBBAB		no	-	-
25	256	Society Islands	LBBBAB	56	rare	-	-
25	257	Society Islands	LBBBAB		no	-	-
25	258	Society Islands	LBBBAB		no	-	-
25	259	Society Islands	LBBBAB		no	-	-
25	260	Society Islands	LBBBAB		no	-	-

Table 3.7. (Continued) Dendrogram number, origin, zymotype, chromosome number, and presence of *A. maritannensis* characters for 204 breadfruit accessions

					<i>A. maritannensis</i>		
Dendrogram	Accession	Island	Zymotype	2n	Seeds	Fruit	Hairs
Cluster II (continued)							
25	262	Society Islands	LBBBAB		no	-	-
25	263	Society Islands	LBBBAB		no	-	-
25	264	Society Islands	LBBBAB		no	-	-
25	265	Society Islands	LBBBAB		no	-	-
25	266	Society Islands	LBBBAB		no	-	-
25	267	Society Islands	LBBBAB		no	-	-
25	268	Society Islands	LBBBAB	84	no	-	-
25	269	Society Islands	LBBBAB		no	-	-
25	272	Society Islands	LBBBAB	84	no	-	-
25	aar	Society Islands	LBBBAB		no	-	-
25	afa	Society Islands	LBBBAB		no	-	-
25	aha	Society Islands	LBBBAB		no	-	-
25	aip	Society Islands	LBBBAB		no	-	-
25	faf	Society Islands	LBBBAB		no	-	-
25	mah	Society Islands	LBBBAB		no	-	-
25	ote	Society Islands	LBBBAB		no	-	-
25	pil	Society Islands	LBBBAB		no	-	-
25	por	Society Islands	LBBBAB		no	-	-
25	pua	Society Islands	LBBBAB		no	-	-
25	puu	Society Islands	LBBBAB		no	-	-
25	rar	Society Islands	LBBBAB		no	-	-
25	roi	Society Islands	LBBBAB		no	-	-
25	tap	Society Islands	LBBBAB		no	-	-
25	ton	Society Islands	LBBBAB		no	-	-
25	tuu	Society Islands	LBBBAB		no	-	-
25	unk	Society Islands	LBBBAB		no	-	-
25	whi	Society Islands	LBBBAB		no	-	-
25	yel	Society Islands	LBBBAB		no	-	-
25	326	Truk	LBBBAB	84	no	-	-
26	379	Pohnpei	NBBBAB	84	rare	+	+
27	121	Rotuma	MBBBAB		yes	-	-
28	388	Pohnpei	MBBBBB		no	-	+
29	381	Pohnpei	IBBBBB		no	-	-
30	147	Fiji	GBBBAB	56	few	-	-
30	489	Fiji	GBBBAB	56	yes	-	-
31	486	Fiji	PBBBAB		yes	-	-
32	287	Yap	QBCCCB	84	no	-	-
33	366	Pohnpei	HBBDCB		no	+	+
34	357	Truk	NBBCDB		rare	+	+
35	384	Pohnpei	NBDDDB		no	+	+
36	406	Pohnpei	EBDDDB		no	+	+
37	368	Pohnpei	MBBDBB		no	-	-
38	303	Yap	OBCCCB	56	no	+	+
39	241	Society Islands	PCBBAB		rare	-	-
40	328	Truk	HCBBAB		no	-	-

Table 3.7. (Continued) Dendrogram number, origin, zymotype, chromosome number, and presence of *A. mariannensis* characters for 204 breadfruit accessions

Dendrogram	Accession	Island	Zymotype	2n	<i>A. mariannensis</i>		
					Seeds	Fruit	Hairs
Cluster II (continued)							
41	385	Pohnpei	NCBBAB	56	rare	+	+
41	koi	Pohnpei	NCBBAB		yes	+	+
41	333	Truk	NCBBAB	56	no	+	+
42	288	Belau	JCBAB		no	+	-
42	289	Belau	JCBAB		no	+	-
42	291	Belau	JCBAB		no	+	-
43	532	Truk	ECBDAB		no	*	*
44	tam	Pohnpei	NCBDAB		no	*	*
45	290	Belau	QCBBD	84	no	-	-
46	320	Truk	HCBCBD		no	-	-
47	315	Truk	EBBDB		no	+	+
48	373	Pohnpei	NCBCDB	56	no	-	+
48	533	Truk	NCBCDB		no	*	*
49	317	Truk	ECBDB		no	+	+
49	327	Truk	ECBDB		no	+	+
50	501	Pohnpei	ECBBB		no	-	-
51	375	Pohnpei	NCBBB	56	no	+	-
51	pat	Pohnpei	NCBBB		no	+	-
51	316	Truk	NCBBB		no	+	+
52	336	Truk	NCBCB		no	+	+
53	322	Truk	ICBCB	56	no	+	+
54	nou	Truk	ICBBB		no	+	*
55	365	Pohnpei	HCBBB	56	no	*	+
55	380	Pohnpei	HCBBB		no	+	-
55	386	Pohnpei	HCBBB		no	+	+
55	511	Pohnpei	HCBBB		no	*	+
55	341	Truk	HCBBB		no	+	+
56	318	Truk	ICBDB		no	+	*
57	329	Truk	ICBDD		no	+	+
58	331	Truk	ICBBC	56	no	+	+
59	529	Pohnpei	MCBDD		yes	+	+
59	340	Truk	MCBDD		no	+	+
60	348	Truk	MCBCD		no	+	+
60	534	Truk	MCBCD		no	*	*
61	421	Kiribati	HCBCD		no	+	+
62	342	Truk	MCBDB		no	+	+
63	351	Truk	HCBDDB		yes	+	+
64	396	Pohnpei	ICBDDB		no	+	+
64	ako	Pohnpei	ICBDDB		no	*	*
65	387	Pohnpei	NCBDB		no	+	-
66	sap	Pohnpei	MCBDB		no	*	*
66	utu	Pohnpei	MCBDB		no	*	*
67	389	Pohnpei	HBBDB		no	+	+
67	kew	Pohnpei	HBBDB		no	*	*

Table 3.7. (Continued) Dendrogram number, origin, zymotype, chromosome number, and presence of *A. mariannensis* characters for 204 breadfruit accessions

Dendrogram	Accession	Island	Zymotype	2n	<i>A. mariannensis</i>		
					Seeds	Fruit	Hairs
Cluster III							
68"	169	Solomon Islands	NCAFAB		yes	-	-
Cluster IV							
69	036	Kiribati	AABABB		yes	+	+
69	043	Tokelau	AABABB		yes	+	+
70	063	Tokelau	AABADB		yes	+	+
71	040	Tokelau	CABABB		yes	+	+
71	049	Tokelau	CABABB		yes	+	*
71	053	Tokelau	CABABB		yes	+	+
72	041	Tokelau	CABADB	56	yes	+	+
72	044	Tokelau	CABADB		yes	+	+
72	052	Tokelau	CABADB		yes	+	+
72	056	Tokelau	CABADB		yes	+	+
73	045	Tokelau	AABACB		yes	+	+
73	046	Tokelau	AABACB		yes	+	+
74	054	Tokelau	CABBBB		yes	+	+
75	059	Tokelau	CABBAB		yes	*	+
76	292	Belau	AABDDDB	56	yes	+	+
77	313	Mariana Islands	AABDDD		yes	+	+
78	309	Mariana Islands	AABDDF	56	yes	+	+
79	354	Truk	HABDCB		yes	+	+
80	363	Truk	HABDDDB	56	yes	+	+
81	338	Truk	NABBDB		no	+	+
82	048	Tokelau	CAAAAB		yes	+	+
83	065	Tokelau	CAAADB		yes	+	+
84	051	Tokelau	AAAABB		yes	+	+
Cluster V							
85	301	Yap	KABBCE	56	yes	+	+
Cluster VI							
86	221	Indonesia/PI	IFABAB		yes	-	-
87	261	Indonesia/PI	IGABAB		yes	-	-
Cluster VII							
88	282	Philippines	CEABAA	56	yes	-	-
89	531	Philippines	CEADAA	56	yes	-	-
90	546	Philippines	CBADAA		yes	-	-

+ *A. mariannensis* characters present

- *A. mariannensis* characters absent

* Information not available

CHAPTER IV CYTOLOGICAL ANALYSIS OF BREADFRUIT COLLECTION

Introduction

Little cytological work has been done on the genus *Artocarpus*, much less on the many cultivars of Pacific Island breadfruit. As a genus, *Artocarpus* appears to be tetraploid with respect to the basic number of 14 that occurs widely in the Moraceae. All the species for which counts have been reported (*A. chaplasha*, *A. gomezianus*, *A. heterophyllus*, and *A. lakoocha*) show a chromosome number of $2n = 56$ (Hans 1972; Mehra & Gill 1974). There is no evidence that the diploid number of 28 occurs in this genus.

The haploid number of breadfruit is considered to be 28 with seeded breadfruit being diploid ($2n = 4x = 56$) and seedless breadfruit being triploid ($2n = 6x = 84$) (Barrau 1976; Jarrett 1959b). These numbers are based on counts by Janaki-Ammal in *Chromosome Atlas of Flowering Plants* (Darlington and Wylie 1955) of $2n = 56$ for a seeded *A. communis*, and counts by Nishiyama and Kondo (1942) of $2n = 54$ for seeded and $2n = 81$ for seedless *A. communis*. The latter authors acknowledge that their counts are suspect due to the poor preparations of their material. The purpose of this study was to determine the chromosome numbers of *A. altilis*, *A. mariannensis*, and *A. camansi* and to clarify the genetic basis of seed abortion and sterility in breadfruit.

Breadfruit trees are normally cross-pollinated, with the small, powdery pollen grains spread by the wind (Brantjes 1981; Jarrett 1959b). Pollen is shed 10 to 15 days after the emergence of the inflorescence for a period of about four days. Female flowers are receptive three days after the emergence of the inflorescence from the bracts and open in

successive stages with basal flowers opening first. Flowering appears to be highly synchronized between branches of a tree, and the tree as a whole alternates anthesis of the pistillate and staminate inflorescences. This second-order dichogamy produces a second-order dioecy, making self-pollination unlikely (Brantjes 1981). Trees are not synchronized with each other, so mutual cross-pollination is possible.

The fruit is a highly specialized structure, a syncarp (Jarrett 1976). The perianths of individual flowers fuse together except at the base, forming a cavity which contains the true fruit and its enclosed ovule and seed (Reeve 1974). As the fruit develops, this area grows vigorously and becomes fleshy at maturity, forming the edible portion of the fruit.

Seedless cultivars may lack developed ovules or may have numerous abortive seeds surrounding the core. Few-seeded cultivars usually have one or several normal or aborted seeds. Since many cultivars of breadfruit are seedless it has been inferred that fruit development is due to parthenocarpy, but there is little experimental evidence of this (Barrau 1976). Singh et al. (1967) showed that seedless fruit will set without pollination, but the resulting fruits were smaller than normal. They concluded that pollination produces stimulative parthenocarpy rather than fertilization. Others noted, however, that unfertilized fruits develop normally (Schwartz 1966).

Seedlessness in breadfruit has been attributed to sterility due to triploidy (Barrau 1976; Jarrett 1959b; Simmonds 1979). Triploid plants principally arise from the fusion of an unreduced $2n$ gamete, usually the egg, and a reduced n gamete (Harlan and DeWet 1980; Moore 1976). Unreduced $2n$ gametes occur widely, although sporadically, due to environmental and genetic factors. They are probably produced occasionally in most individuals and are a common occurrence in many fruit crops. Most of the $2n$ gametes in fruit crops have been reported in the female gametophyte due to aposporous egg formation, which often occurs in conjunction with parthenogenesis (Sanford 1983). Apospory essentially bypasses the meiotic process since a diploid embryo sac is mitotically derived from a somatic cell of the nucellus or chalaza.

Factors affecting infertility in triploid plants include 1) abortion of gametes due to multivalent formation and unequal division of chromosomes during meiosis, and 2) abortion of embryos due to embryo/ endosperm imbalance. Most triploids are sterile or nearly sterile because random distribution of chromosomes to the spindle poles will rarely produce balanced haploid or diploid products capable of further normal development (Dyer 1979).

Each set of homologous chromosomes in a triploid can associate to form a trivalent which, depending on their orientation at metaphase, unevenly segregate during meiosis. The formation of bivalents and univalents is more prevalent, and these result if one of the chromosomes does not form appropriate chiasmata or if the small size of the chromosomes precludes complete pairing. Univalents irregularly segregate or lag on the spindle and are thus excluded from the nuclei. Consequently, irregular disjunction of univalents and trivalents results in unbalanced (aneuploid) gametes ranging from $x+1$ to $2x-1$, with a subsequent reduction in fertility (Moore 1976; Sanford 1983).

Genetic factors in the endosperm also play an important role in the fertility of triploids. If the normal 2 maternal:1 paternal ratio in the genomic constitution of the endosperm is altered, the seed will tend to abort or be ill-formed or undeveloped (Sanford 1983; Simmonds 1979).

While sterility in triploids is common and presents a barrier to sexual reproduction, it is by no means absolute. Moore (1976) commented that the sterility of triploids is frequently overestimated, and detailed how fertility in triploids can be maintained. At metaphase, trivalents can independently orient in several ways, and numerically balanced gametes (x and $2x$) can be produced in the infrequent event that trivalents orient to give a 2:1 segregation to the poles. Jarrett (1959b) surmised that diploid or triploid progeny could arise from triploid seedless breadfruit cultivars if an occasional viable haploid or diploid gamete is produced.

More commonly, triploids form aneuploid gametes, and these may combine with normal gametes to produce aneuploid progeny. A tolerance for aneuploidy among

progeny is one mechanism which allows for limited triploid fertility, and several authors (Dyer 1979; Sanford 1983; Simmonds 1979) have discussed how a tolerance of aneuploidy can occur. Generally, aneuploidy has less effect if a single or small chromosome is involved, and a gain is more easily tolerated than a loss of a chromosome. The specific effect of the gene(s) carried on the chromosome involved is also important. Many polyploids are tolerant of aneuploidy due to the buffering effects of additional genomes which lessen the deleterious effects of a loss or addition of chromosomes. Thus, some fertility in triploids can often be observed.

Jarrett (1959b) also suggested that the failure of breadfruit to set seed may be due to genetic factors other than polyploidy. Since breadfruit trees are propagated by vegetative means, each cultivar is a clone within which the primary source of variation is presumably somatic mutation. Repeated vegetative propagation of breadfruit clones permits the accumulation of somatic mutations affecting reproductive fertility which may be deleterious in nature, but which are maintained and perpetuated as curiosities or useful variants by human selection.

Materials and Methods

A collection of approximately 200 breadfruit accessions from 18 island groups growing at the Magoon Horticultural Facility of the University of Hawaii was used in this study. Fifty-one accessions, representing each island group in the collection, were surveyed, selecting seedless, seeded, and few-seeded accessions randomly. After isozyme analysis of 204 accessions, additional counts were made to verify that accessions of the same zymotype had the same chromosome count. Particular attention was given to obtaining chromosome counts for those accessions with unique isozyme banding patterns.

Chromosome counts were based on meristematic cells obtained from root tips from three sources: seeds; roots growing from 15-cm-long sections of mature roots; or from airlayers made on the stems of potted plants approximately 2 cm in diameter and

less than 1 meter in height (Figure 4.1). Roots from all three sources were prepared in the same manner. Root tips of 3-4 mm length were excised and pretreated in a saturated solution of paradichlorobenzene (PDB) at room temperature for two hours and fixed in Carnoy's fluid (3:1 of 95% ethanol and glacial acetic acid) for 24 hours at 37 C before hydrolysis in 1N HCl for seven minutes at 60 C. The root tips were stained in Feulgens solution for 1 1/2 hours at room temperature, and slide preparations were made by squashing root meristems in a drop of 2% acetocarmine stain and Hoyer's solution. Chromosome numbers were determined from cells at mitotic metaphase using a Zeiss phase contrast microscope. Documentation was made with camera lucida drawings and photomicrographs were taken with Kodak Technical Pan film at X1000 magnification.

Pollen fertility was assessed by observing the percentage of pollen grains that stained uniformly with acetocarmine. At least 500 pollen grains from each accession were scored.



Figure 4.1. Roots growing on an air-layered shoot

Results and Discussion

Chromosome numbers

Chromosome numbers determined for 51 accessions are summarized in Table 4.1. A total of 31 accessions were observed to have somatic chromosome numbers of 56 and 20 accessions had a somatic number of 84 (Figure 4.2).

The chromosome number for *Artocarpus mariannensis* (accessions 292 and 309), reported here for the first time, is $2n = 56$. The report of $2n = 54$ by Nishiyama and Kondo (1942) for a seeded breadfruit from the island of Rota in the Northern Mariana Islands was probably erroneous. They identified their specimen as *A. communis*, but since seeded forms of this species are not known to occur in the Mariana Islands, the count was probably based on *A. mariannensis*. The chromosome number for *A. camansi* (accessions 282 and 531), also reported for the first time, is $2n = 56$.

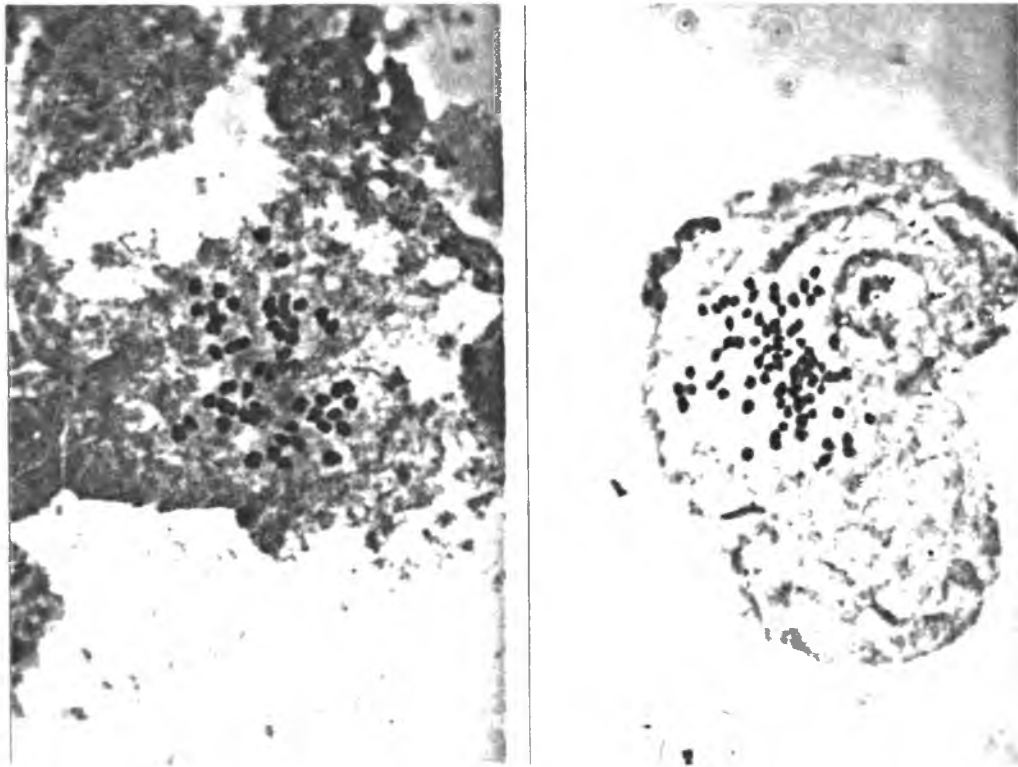


Figure 4.2. Photomicrographs of *Artocarpus altilis* chromosomes at mitotic metaphase

Thirteen seeded cultivars of *A. altilis* were verified to have counts of $2n = 56$. Counts of $2n = 56$ were also obtained for accession 256 from the Society Islands that produces fruits that occasionally yield one or two viable seeds. Two seedless cultivars (013 and 095 from Samoa) were also observed to have counts of $2n = 56$. Counts of $2n = 56$ were observed for three seeded cultivars from Tokelau and Micronesia (041 from Tokelau, 301 from Yap, and 363 from Truk). Another seven Micronesian accessions (303, 322, 331, 333, 365, 373, and 375), with counts of $2n = 56$, were seedless. Based on morphological characters and isozyme phenotypes, these accessions are putative crosses between *A. mariannensis* and *A. altilis*.

Chromosome counts of $2n = 84$ were obtained for 20 accessions. These accessions were all seedless with the exception of accession 379 from Pohnpei which has fruits that rarely contain one or two seeds. This cultivar, and two triploid seedless Micronesian cultivars (287 from Yap and 290 from Belau), are also putative crosses between *A. altilis* and *A. mariannensis*.

Pollen stainability

While it is likely that unreduced female gametes occur in breadfruit, it cannot be determined from the cytological data whether they were present in the materials analyzed. Possible unreduced pollen grains were observed in *A. mariannensis* (Figure 4.3). The degree of pollen stainability for seeded, few-seeded, and seedless accessions is shown in Table 4.2. These initial studies show that the degree of seediness in breadfruit cultivars is correlated with pollen stainability.

Triploid cultivars have the lowest pollen stainability, averaging from 6 to 16%, and the pollen grains are typically malformed, clumped and poorly stained (Figure 4.4). These facts were previously noted by Tri Sunarto (1981), who showed that a seeded form had the highest pollen grain stainability (99%), while a few-seeded form had medium stainability (45%), and a seedless form had low stainability (6%). Thus pollen sterility may be one factor contributing to seedlessness in certain forms.

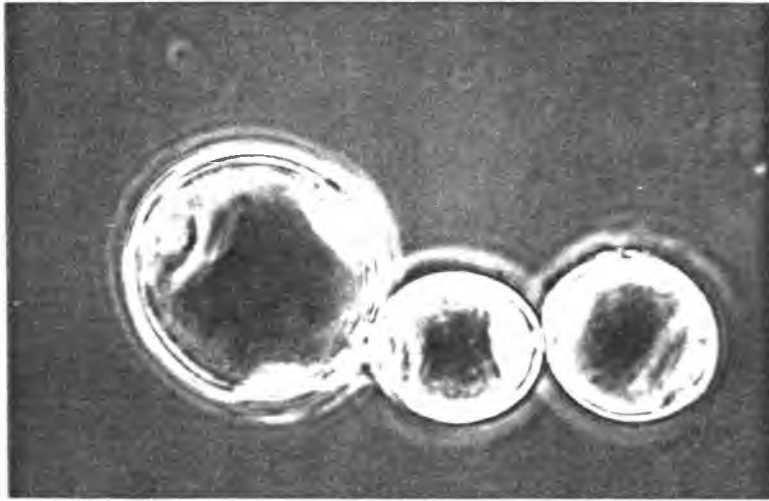


Figure 4.3. Photomicrograph of an unreduced pollen grain of *Artocarpus mariannensis*

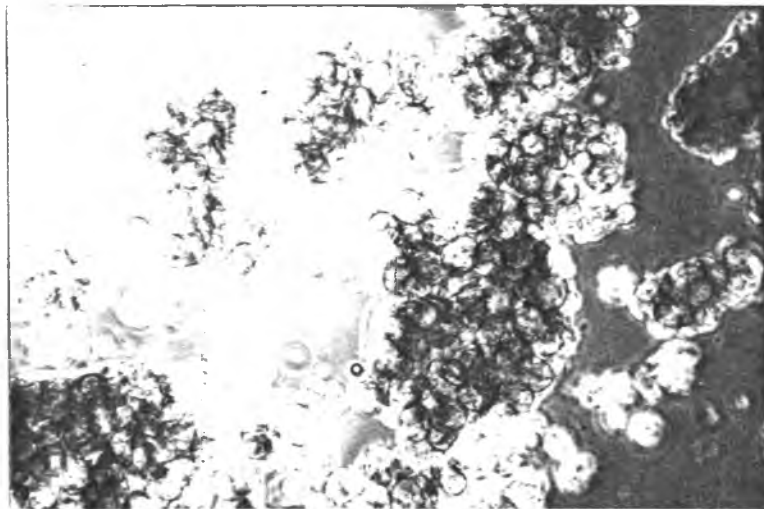


Figure 4.4 Photomicrograph of pollen of triploid cultivar of *Artocarpus altilis*

Table 4.1. Species, provenance, accession numbers, chromosome counts, and degree of seediness for 51 accessions of breadfruit

Species	Provenance	Accession No.	$2n^a$	Fertility
<i>A. camansi</i>	Philippines	282	56	normal
	Philippines	531	56	normal
<i>A. mariannensis</i>	Belau	292	56	normal
	Mariana Islands	309	56	normal
<i>A. altilis</i>	Solomon Islands	123	56	normal
	Solomon Islands	426	56	normal
	Vanuatu	443	56	normal
	Vanuatu	526	56	normal
	Fiji	147	56	partial
	Fiji	464	56	normal
	Fiji	489	56	normal
	Rotuma	439	56	normal
	Belau	286	84	sterile
	Mariana Islands	311	84	sterile
	Truk	326	84	sterile
	Pohnpei	370	84	sterile
	Pohnpei	372	84	sterile
	Pohnpei	374	84	sterile
	Samoa	007	56	normal
	Samoa	maf	56	normal
	Samoa	013	56	sterile
	Samoa	019	56	normal
	Samoa	095	56	sterile
	Samoa	110	56	partial
	Samoa	453	56	partial
	Samoa	541	84	sterile
	Cook Islands	096	84	sterile
	Cook Islands	103	84	sterile
	Cook Islands	433	84	sterile
	Marquesas	216	84	sterile
	Marquesas	220	84	sterile
	Marquesas	222	84	sterile
	Society Islands	256	56	partial
	Society Islands	236	84	sterile
	Society Islands	268	84	sterile
	Society Islands	272	84	sterile
	Hawaii	530	84	sterile

Table 4.1. (Continued) Species, provenance, accession numbers, chromosome counts, and degree of seediness for 51 accessions of breadfruit

Species	Provenance	Accession No.	2n	Fertility
<i>A. altilis</i> x <i>A. mariannensis</i>				
	Belau	290	84	sterile
	Yap	301	56	normal
	Yap	303	56	sterile
	Yap	287	84	sterile
	Truk	322	56	sterile
	Truk	331	56	sterile
	Truk	333	56	sterile
	Truk	363	56	normal
	Pohnpei	379	84	partial
	Pohnpei	365	56	sterile
	Pohnpei	373	56	sterile
	Pohnpei	375	56	sterile
	Pohnpei	385	56	partial
	Tokelau	041	56	normal

^a - Chromosome counts are approximate, and in the case of diploids with reduced fertility, the possibility of aneuploidy is not ruled out.

Table 4.2. The degree of pollen stainability for seeded, few-seeded, and seedless breadfruit

Degree of seediness	Species	Accession	2n	Pollen stainability (%)
Many	A.m.	292	56	96
	A.a.	maf	56	92
	A.m.	313	na [*]	91
	A.c.	531	56	91
Few	A.a.	453	56	78
	A.a.	147	56	71
	A.a.	110	56	67
None	A.a. x A.m.	290	84	16
	A.a.	541	84	7
	A.a	mos	na	6

A.m. = *A. mariannensis*, A.a = *A. altilis*, A.c. = *A. camansi* * na - not available

Seedless cultivars

Seedlessness in breadfruit has been attributed to sterility due to triploidy (Jarrett 1959b; Barrau 1976), and this seems to be the case for those cultivars with a somatic number of 84. In areas such as eastern Polynesia, where the majority of cultivars are seedless triploids, little viable pollen is produced, and breadfruit cultivars with seeds are so unusual that the presence of a sporadic seed is denoted in the cultivar name, as in **mei kole** of Pohnpei, meaning “with a seed.” A similar appellation occurs in the Society Islands where numerous triploid cultivars are known, and a rare seed-bearing triploid cultivar is so designated by its name, **huero**, again meaning “with a seed.”

Triploidy obviously can not account for reduced fertility among diploid cultivars. Reduced seed number in some diploid cultivars is probably a byproduct of the practice of clonally propagating these plants using root shoots or sections of roots. Repeated vegetative propagation allows mutations deleterious to sexual reproduction to accumulate, disrupting normal meiosis and resulting in reduced fertility and decreased number of seeds. This mechanism best explains the partial or complete sterility of *A. altitlis* diploids in the South Pacific region (accessions 013, 147, 110, 453).

Seedless diploid cultivars are also found in the North Pacific in Micronesia. All of these appear to be interspecific hybrids between *A. mariannensis* and *A. altitlis*, based primarily on shared morphological characters. Seven (64%) of the 11 putative diploid hybrids from Micronesia were seedless or had reduced fertility. The hybrid nature of Micronesian diploids may be largely responsible for their sterility, as with many other interspecific hybrids, in which insufficient homology between genomes results in meiotic abnormalities, embryo lethality, or disruption of normal embryo/endosperm relations (Simmonds 1979; Stebbins 1971).

In Micronesia, where *A. mariannensis* produces abundant pollen, some of the hybrids may derive from crosses between diploid *A. mariannensis* and triploid *A. altitlis*

clones, which have overlapping distributions. The hybrid progeny of such crosses would have additional sterility problems resulting from aneuploidy or sterility mutations derived from the triploid *A. altalis* parent.

The relatively large number of chromosomes ($2n = 56$ and $2n = 84$) in breadfruit could serve to buffer clones against more deleterious effects of aneuploidy. As supporting evidence of this, the Tahitian accession (256) in this germplasm collection was reported to be a seedling of the triploid **huero**. Its somatic number was observed to be $2n = ca56$, demonstrating that seedless, triploid cultivars can produce an occasional viable seed if a fertile pollen source is available. It is also significant that the seedling is semi-sterile.

The chromosome data, however, does not show that any of the 51 cultivars sampled were aneuploids. The large number and small size of their chromosomes, especially triploid cultivars, made it difficult to discern whether aneuploid cultivars of breadfruit do indeed exist. A more detailed and extensive examination of the germplasm collection may show the presence of aneuploid cultivars.

CHAPTER V

HISTORY OF DOMESTICATION OF BREADFRUIT IN OCEANIA

The cytological, and especially the isozyme analyses, facilitated the identification and characterization of cultivars, and the determination of relationships between cultivars. Questions about the origin of few-seeded and seedless forms and interspecific hybrids still remain unanswered. This chapter will examine the origin and distribution of breadfruit in a cultural and geographic context, and attempt to answer these questions.

Early origins in the Western South Pacific

Indo-Malayan region

Breadfruit is an ancient domesticated cultigen, but the long-held supposition that it was first domesticated in the Indo-Malayan region (Barrau 1976; Jarrett 1959b; Kirch 1985) may be inaccurate. *Artocarpus camansi*, or "breadnut," is the only form of breadfruit, as defined by Jarrett (1959b), growing wild to the west of New Guinea. The fruit pulp of *A. camansi* and other indigenous *Artocarpus* species is a source of food for birds and arboreal mammals which are responsible for their seed dispersal (Primack 1985). *Artocarpus camansi* seeds are eaten boiled or roasted in the Moluccas (Jarrett 1959b), but it is otherwise unimportant to the human population. The cultivation and distribution of *A. camansi* and seedless cultivars of breadfruit in island southeast Asia may be a relatively recent event, possibly occurring in the past few hundred years.

The earliest description of *A. camansi* (**soccus granosus**) in this area was in the mid-1600s (de Candolle 1908). A possible seedless type was also described. In an early, detailed account of the breadfruit, Ellis (1775) said that although both types are reported to grow in the East Indies, Captain Cook only observed the seeded form. He

continued that another early, but unnamed, visitor to this area said that the local breadfruit was much inferior to that found in the South Seas, and did not think them the same.

Burkill (1935) stated that throughout the Malay islands, only the seeds of *Artocarpus* are eaten, and only one seedless type is found in this widespread island group. He also noted that an earlier author, Crawford, who visited Java in the early 1800s, suggested that the Javanese had recently obtained seedless breadfruit while trading in the Moluccas. In the early 1790s, Captain Bligh (1976) acquired specimens of the local, wild, seeded form in Timor for transport to the Caribbean. He also introduced seedless Tahitian cultivars to St. Helena.

New Guinea

Purseglove's (1968) contention that breadfruit was first domesticated in Melanesia (New Guinea to Fiji) may be more accurate. The coastal strand and lowland vegetation in New Guinea, and associated islands such as the Bismarck Archipelago, would have been extensive at the time of man's arrival and may have included many of the taxa still used there today, including breadfruit (Powell 1976). It is likely that breadfruit was first domesticated in these areas,

Breadfruit is now cultivated in village areas of New Guinea, but the majority of trees grow wild in the forest. Wild breadfruit, both *A. altilis* and *A. camansi*, is an important component of the subsistence economy in lowland areas (Conroy & Bridgeland 1950; Paijmans 1976). Both the fruit pulp and the seeds are eaten in some varieties, while in others only the seeds are edible, since the flesh is tough and stringy (Croft 1987; Oomen & Malcolm 1958).

Breadfruit is not as important in the highlands since it does not occur naturally at higher elevations, although it may be cultivated at elevations up to 1550 meters (Powell 1976). That cultivation of breadfruit in the mountains is a recent practice is indicated by visitors such as Lam (1945), who noted that breadfruit was not found in the

mountains. The importance of breadfruit seeds as an early subsistence food has not yet been documented by archaeological research, although Bulmer (1964) inferred that prehistoric pestles and mortars from lower montane areas of New Guinea were used to grind seeds and nuts.

Melanesia

The origin of Oceanic breadfruit is linked to the movements of a group of people comprising the Lapita Cultural Complex. The Lapita moved eastward into Melanesia from 1600 to 500 B.C. (Kirch 1985, 1987, 1990; Pawley and Green 1984). Whether the Lapita culture moved out of southeast island Asia into this area, or was an indigenous Melanesian development is still debated; however, thorough archaeological research is providing a clear picture for their movements eastwards (Allen 1984; Bellwood 1987; Bower 1987; Kirch 1985, 1990; Spriggs 1984).

The discovery of remains of seeds of 24 species, found in an early Lapita coastal site in Mussau in the Bismarck Archipelago, provided support for the theory that the Lapita were early agriculturists who carried a full complement of crops with them (Kirch 1988, 1989). On the other hand, these seeds may indicate instead the subsistence use of species already present and growing wild. Whether vegetative propagation of breadfruit was developed by the Lapita or borrowed from Papuan people already residing on these islands is unknown. In any event, the Lapita were no strangers to vegetative propagation as evidenced by their complement of cultigens, including taro, sugarcane, yams, and bananas (Barrau 1965; Bellwood 1979) which required this method of propagation.

Wild breadfruit trees do not ordinarily produce root shoots, since it is not a viable reproductive mode in the close competition of a tropical forest ecosystem (Yen 1987). The first cultivated breadfruits were transplanted seedlings from the forest, or more likely, plants grown from gathered seeds. Cultivated breadfruit trees have developed under very different ecological conditions of light and competition than their forest brethren. Breadfruit roots are typically exserted or grow slightly below the surface of the

ground; damage to the root often induces a shoot to develop at the site of the wound. It is likely that the vegetative mode of propagation developed from the chance injury to roots of a cultivated tree. Root shoots, which could be removed and planted elsewhere, would have provided an alternative, faster method of propagation than seeds. Also, vegetative propagation would have preserved desirable horticultural qualities of specific genotypes resulting from early selection efforts in a highly variable out-crossing population.

The Lapita moved quickly through the western Pacific and settled islands from New Britain to Samoa in about 300 years (Bellwood 1987; Kirch 1985, 1990). Communities in western and central Melanesia, where islands could be seen or reached by a few days sail, maintained contacts and trade networks with one another (Allen 1984; Bellwood 1979; Kirch 1985, 1990; Terrell 1986). The relative ease of interisland travel facilitated the transfer of cultigens, including breadfruit. Seeded cultivars indigenous to New Guinea and the Bismarck Archipelago are now widely distributed throughout the western South Pacific islands. Lapita sites in Melanesia, typically in coastal or low-lying areas, correspond with the occurrence of breadfruit cultivars. No sites have yet been found in the western and central Solomons (Bellwood 1979; Kirch 1985, 1990) where wild breadfruit does not occur, and cultivated breadfruit is of little importance.

In contrast, the greater distances across open ocean made it difficult for Lapita settlements in eastern Melanesia to maintain contacts with the homeland communities. The eastern Lapita islands became isolated from their western counterparts, and became the ancestral population for Polynesians (Bellwood 1987; Kirch 1985, 1987, 1990). As distances increased between islands, the type of propagative material would have to change because seeds quickly lose their viability (Jarrett 1959a; Purseglove 1968), and seedlings would be difficult to transport and keep alive during longer voyages.

The shift to vegetative propagation of breadfruit would have a great impact on its distribution and cultivation, and profound implications for its cultivators. It would allow for transportation over greater distances and ultimately increase the chances of few-

seeded or seedless cultivars originating. The development of fruits with reduced fertility and reduced seed number resulted in a shift from utilizing this species as a nut crop (breadnut) in western Melanesia to primarily a fruit crop (breadfruit) eastwards.

It was probably in the eastern islands of Santa Cruz and Vanuatu, especially the Banks Islands, where breadfruit was first extensively cultivated and selected (see page 14). Numerous seeded and few-seeded cultivars are found there. The importance of breadfruit in the subsistence economies of these islands would ensure that if a true seedless breadfruit had appeared here, it would have been extensively propagated and distributed, resulting in many more seedless cultivars than are now found in western Melanesia.

Origin of seedless breadfruit

Western Polynesia

The paucity of triploid cultivars in Melanesia points to its origin further east in western Polynesia where few-seeded and seedless cultivars occur with seeded types in many islands, especially Fiji, Tonga, and Samoa. The 850-km water gap between eastern Melanesia and western Polynesia precluded the two-way contact possible further west, and the cultural and geographic isolation of Lapita people in Fiji and western Polynesia ensured that this important horticultural development remained unknown in western Melanesia in prehistoric times.

The first triploid cultivar probably derived from reduced and unreduced gametes (see Chapter IV) provided by few-seeded or seeded cultivars. An alternate possibility, suggested by the isozyme data, specifically the distribution of the IDH B pattern (see page 72), suggests that the triploid may have originated from a cross between *A. altilis* and *A. mariannensis*. It must be noted, however, that widespread collection and analysis of cultivars from Melanesia and the Micronesian atolls must be made before this is shown to be the case. If the IDH B phenotype does not occur in Melanesian *A. altilis*, it would provide evidence for the involvement of *A. mariannensis* as the B allele donor in the origin of the triploid "Polynesian" seedless clone.

All of western Polynesia (Tonga, Samoa, and nearby atolls of Tokelau, Tuvalu, Uvea, Wallis, and Futuna) was settled by 1000 B.C. (Bellwood 1987; Kirch 1984, 1990). Interisland contacts between Fiji, Tonga, and Samoa were maintained (Terrell 1986), permitting the distribution of this unique seedless breadfruit. Many of the same cultivars are found in Tonga, Samoa, Tuvalu, and Futuna. Futuna, in particular, has many cultivars in common with Tonga and Samoa including **Aveloloa**, **Fau**, **Kea**, **Maopo**, **Puou**, and **Talatala**. **Aveloloa** is the only cultivar found in all four island groups. **Mase'e**, **Maopo**, and **Ma'afala** occur in Tonga and Samoa, while the latter cultivar is also found in Tuvalu. All of these cultivars have seeds with the exception of triploid **Maopo**.

The western Polynesian islands are geologically and biotically less diverse than the Melanesian islands. With a limited native flora and fauna available for exploitation, colonizers were especially dependent upon marine resources and introduced cultigens (Bellwood 1979; Kirch 1985, 1990). The complex of fruit and nut trees important in the subsistence of eastern Melanesia (Yen 1974) was reduced primarily to a dependence on breadfruit, especially few-seeded and seedless cultivars.

The genetic base of cultigens transported to these islands, and islands further east, was limited. The amount and diversity of food stocks carried on a colonizing canoe was limited by the restricted range of plant materials initially available, space constraints, and the ability of the cultigen to survive long journeys with limited fresh water (Beggerly 1976). Survival on an unknown island with varying climate, soil, and rainfall conditions would be enhanced if small stocks of many different cultigens were carried.

Once the initial cultivars became established, repeated vegetative propagation of the established trees would have occurred to multiply the limited resource. In addition, seeds from cultivars with seeds probably would have been planted to further increase the number of trees. Selected seedlings then would have been vegetatively propagated along with seedless types. This cycle of establishment and vegetative propagation would have been repeated for generations.

Somatic mutations in existing clones and creation of new clones from selected seedlings resulted in some new cultivars unique to each island. If enough trees became established to provide an ample supply of food, trees with undesired fruit qualities could be removed, and only those trees with desired fruit characters or other traits would be preserved and perpetuated. The need to carefully husband their scarce and precious resources would have restricted selection against less-desirable cultivars. Even today, there exist certain Polynesian cultivars with poor fruit quality that are used only if nothing else is available.

Eastern Polynesia

Settlement dates for eastern Polynesia are still uncertain, but range from as early as 200 B.C. for the Marquesas and Society Islands to approximately A.D. 500 for Hawaii; scant information is available for the Cook Islands, Tuamotus or Australs (Bellwood 1987; Kirch 1985, 1986). It is likely that with continued archaeological research, much earlier settlement dates will be ascertained for these island groups (Bellwood 1987; Kirch 1986). The 2,000 to 3,000 km of open ocean separating western from eastern Polynesia kept interisland contacts to a minimum, and long-distance voyaging in Polynesia ceased by A.D. 1,000 (Keegan and Diamond 1987). Eastern Polynesia was probably settled by the same basic population (from western Polynesia), and the homogeneity of Polynesians in race and culture reflects their being derived from a small group of initial colonizers (Bellwood 1987).

Seedless cultivars, along with some seeded cultivars, were transported east into eastern Polynesia, and westward and north to the outlier islands. **Maopo** is also found in the Society Islands as 'Rowdeah' (**Rare autia**) (Bligh 1792), in Fiji as **Uto lolo** (Seeman 1863-1873), and it is known as **Mei aukape** on Nuku Hiva in the Marquesas. Numerous cultivars are found by the same, or very similar names, in the Marquesas and Society Islands, and to a lesser degree, in the Cook Islands (see Appendix A). One particular triploid cultivar, known as **Ulu e'a** in Samoa, is recognized as a very old cultivar in the Marquesas, Society Islands, and Cook Islands where it is known as **Maoui, Maohi, Maori**

or **Maore** (Christian 1910; Hugenin 1902; Ragone 1987; Wilder 1931). **Maore** is also found in the outlier island of Anuta (Yen 1973a). It is the only cultivar to reach Hawaii where it has no specific name other than **Ulu**. Its widespread distribution and antiquity suggests that this may be one of the earliest, if not the original, seedless triploid cultivars.

Effect of selection on genetic diversity

The genetic diversity of breadfruit in the south Pacific decreases from west to east mirroring the cultural diversity of the Lapita. The results of isozyme analysis (see Table 3.5) show that breadfruit cultivars from Melanesia are genetically diverse, with different zymotypes observed for 71% of the accessions. This level of diversity is expected of a seeded, outcrossing crop. The decreasing, but still relatively high level of genetic diversity seen in western Polynesia (51% of accessions have different zymotypes) reflects the genetic base inherent in the initial cultigens transported from Melanesia and that arising from subsequent sexual recombination between seeded cultivars. It parallels the cultural diversity of this area. The cultural uniformity of eastern Polynesia has its counterpart in the homogeneity of breadfruit cultivars; only two different zymotypes were observed and 96% were seedless, triploid accessions.

The combined effects of human and natural selection on crop genetic diversity were severe and cumulative in the Pacific. As humans moved eastwards onto increasingly isolated islands, the genetic diversity of cultigens tended to decrease. Availability of space and selection of cultigens based on their ability to travel would seriously constrain the number of cultivars which could be selected for transport. Another important factor in crop diversity in the Pacific, is whether or not the introduced cultigens could become established on a new island. The limited stock of cultivars initially introduced in each island would result in a bottleneck or founder effect and its concomitant narrow genetic base (Simmonds 1979).

Selection and cultivation of crop plants always involves a conscious decision to keep certain progeny. The isozyme homogeneity of cultivars in eastern Polynesia suggests that the existence of a seedless, triploid cultivar had an overriding significance in

determining future selection in this crop. The chance occurrence of a truly seedless breadfruit would have important ramifications for islanders dependent on this crop. Each fruit would yield a greater proportion of edible portion and the production of **ma**, pit-fermented breadfruit, for long term storage would be enhanced. The importance of **ma** production in Polynesia, especially the Marquesas, would be a critical element in a preference for seedless cultivars.

Although the effect of human selection within the triploid cultivar does not show up at the isozyme level, the tremendous morphological diversity within a single isozyme phenotype illustrates the power of human selection to capitalize on observable variation within the original stock. The importance of this seedless, triploid breadfruit is signified by the numerous cultivars in the Marquesas and Society Islands, and its widespread distribution beyond Polynesia to Micronesia.

Importance of breadfruit in Micronesia

Micronesia consists of nearly 3,000 islands having a combined area of 3,100 square kilometers scattered across the central Pacific between longitudes 135 to 175 E and latitudes 18 N to 3S. The western islands (Marianas, Belau, Yap) are volcanic or uplifted limestone from submerged reefs. Eastern Micronesia is comprised of atolls; except Truk, Pohnpei, and Kosrae in the Caroline islands. While archaeological and linguistic information explaining the migrations of the Lapita people and the settlement of the south Pacific is fairly clear, the picture for Micronesia is less so. A review of Micronesian prehistory by Craib (1983) details how little archaeological research has been conducted in Micronesia, especially on the atolls, until recently. The ephemeral nature of the material culture on atolls has made it difficult to determine dates of occupation or find evidence for interaction between atolls and high islands (Davidson 1967).

Western Micronesia

Most theories of the origins and movements of islanders in Micronesia are based on linguistic models (Ayres & Haun 1977; Craib 1983; Pawley and Ross 1990; Schutler

and Marck 1975). The languages of the western groups are Indonesian types, while the remaining languages are classed as nuclear Micronesian, and are related to those from eastern Melanesia (southeastern Solomons, Banks Islands, and Vanuatu). The linguistic model is that Micronesia was settled from different directions at different times.

The western high islands were settled from the west about 4,000 years ago (Craib 1983). Recent work led Masse (1990) to estimate that Belau was settled from Indonesia relatively late in the culture history of Micronesia: no earlier than the beginning of the first millennium, and as late as A.D 200 to 400. In comparison, the Marianas were settled around 1,000 B.C. from the Philippines. It is obvious that more archaeological research is needed to provide a clearer picture of the prehistory of this region.

Atolls and Eastern Micronesia

The eastern islands were settled approximately 2,000 years ago through movements of people from Melanesia into the eastern Carolines, Marshalls, and Kiribati with eventual westward expansion from these areas (Craib 1983; Tyron 1984). Triploid cultivars did not exist in Melanesia, so they could not have been introduced into Micronesia by the early Lapita colonizers. Tuvalu and Kiribati are considered the traditional interface between Polynesia and Micronesia (Bellwood 1987), and **Mos n wa** in Kosrae, **Mejenwe** in the Marshall islands, **Mein uwe** in Pohnpei, and **Mai uea** in Kiribati, all appear to be the same cultivar and the names are cognate to the Samoan **Uhu e'a**.

Craig (1983) acknowledged that settlement patterns outside of western Micronesia appear more complex than the linguistic model suggests. He saw no clear archaeological evidence for movement from eastern Melanesia. Recent papers by Petersen (1991) and Ayres (1990) argue that Pohnpei was directly settled from eastern Melanesia, not the eastern atolls. Coeval settlement dates of 2000 years ago are given for the Marshall Islands, Truk, Pohnpei, and Kosrae. They supplement the linguistic data with comparisons of cultigens found in Pohnpei/Kosrae and Melanesia, especially work done on kava (Lebot and Levesque 1989; Lebot et al. 1991), and note that these cultigens could not have survived island hopping through Kiribati and the Marshall Islands.

Settlement of western Caroline atolls may be as recent as 500 to 1000 years ago with the exception of Ulithi, possibly settled 1700 years ago (Craib 1983). Ayres (1990) contends that there is no evidence that people from the western high islands colonized the atolls before nuclear Micronesian speakers arrived from the east. Rather, the atolls were efficient barriers to eastward settlement by islanders adapted to islands which were biologically and geologically more diverse. He suggests that the Carolines were colonized by nuclear Micronesians after they adapted to atoll environments in the eastern atolls.

The multitudinous but little-studied atolls figure prominently in the prehistory of Micronesia. The ability of humans to successfully inhabit the different atolls depended on being able to adapt to often tenuous conditions. The severe environmental constraints found on atolls include poor soils, lack of water, destructive cyclonic storms, and a very limited native flora and fauna. Colonizers faced great difficulties in getting initial stocks of breadfruit and other cultigens established (Schattenburg 1976). Early communities presumably relied on marine resources and a very limited number of crops, primarily *Cyrtosperma*, breadfruit, pandanus, and coconuts (Alkire 1978; Barrau 1961; Bellwood 1979).

Within recent memory, numerous atolls have experienced severe storm damage to crops and the water supply, forcing islanders to evacuate. That many atoll settlements were impermanent is documented by legends, historic accounts, and recent archaeological evidence (Alkire 1978; Hezel 1983). For example, the earliest recorded dates for human habitation of atolls in the Mortlock Group of Truk were 400 to 500 B.C. (M. Graves, personal communication 1988). There is an 800-year gap in the archaeological record with no other sites recorded until A.D. 400. The absence of sites during this time may reflect inadequate archaeological sampling, or the temporary nature of habitation. The excavation of large-scale fermentation pits shows that the inhabitants were extensively exploiting breadfruit by A.D. 1300. Graves surmised that if breadfruit were available to the early inhabitants, they were unproductive cultivars or they did not know how to exploit them.

The prehistory of two Polynesian outliers in Micronesia was chronicled by Kirch (1984). Nukuoro and Kapingamarangi were settled directly or indirectly from Tuvalu by populations already well adapted to atoll life. Nukuoro was not colonized until A.D. 1500 to 1600. Kapingamarangi has been occupied for 1000 years, but due to its susceptibility to severe storms and droughts it was only sporadically occupied from approximately A.D. 1300 to 1700 (Alkire 1978; Kirch 1984).

Although breadfruit is now widely distributed throughout Micronesia, the impermanence of settlements in the atolls and limited archaeological evidence for the use of breadfruit, such as fermentation pits, limits our understanding of its prehistoric distribution. Since breadfruit is one of the first major crops destroyed by storms (Alkire 1978), many, if not all, early cultivars would disappear from atolls over time. We cannot correlate with certainty the prehistoric distribution of breadfruit with its contemporary distribution.

Origin of interspecific hybrids

Any discussion of the origin and distribution of breadfruit in Micronesia is complicated by the presence of two species, *A. altilis* and *A. mariannensis*. The majority of accessions appear to be hybrids between the two species, and cluster analysis suggests that triploid Polynesian cultivars with zymotype LBBBAB were involved in hybridization with *A. mariannensis*. This discussion will assume that cultivars with this phenotype are triploid forms of *A. altilis*. Cluster analysis of isozyme zymotypes also does not provide evidence for the involvement of seeded *A. altilis* in hybridization, with the exception of materials examined from Tokelau. How did the seedless Polynesian form reach Micronesia and how was it involved in hybridization with *A. mariannensis*? The latter question is easier to address.

Fosberg (1960) speculated that although seedless cultivars of *A. altilis* are largely sterile, they may produce viable pollen which may have fertilized female flowers of *A. mariannensis*. Barrau (1961) and Stone (1970) also endorsed this viewpoint. Conversely, pollen from *A. mariannensis* may have fertilized seedless or few-seeded

cultivars of *A. altilis* (Fosberg 1960). While triploid cultivars may produce a few viable pollen grains, they are not very fertile plants since the anthers typically do not dehisce, and very little, if any, pollen is shed. In contrast, *A. mariannensis* produces abundant amounts of fertile pollen and pollen shed is so heavy that the leaves underlying male inflorescences are often dusted with a layer of pollen. Furthermore, a chance seed in a seedless cultivar would be such a novelty that it is more likely to be planted and grown; it would attract no special attention in seeded *A. mariannensis*.

Triploid cultivars have some degree of fertility, as described in Chapter IV, which helps explain the cytological and zymotypic diversity of cultivars in Micronesia. Excluding Tokelau, which will be discussed later, only a very few hybrid cultivars are seeded. The zymotypic diversity (60%) of seedless diploid cultivars is best accounted for by interspecific hybridization and backcrossing between the two species (Fosberg 1960). Even though triploids and hybrid diploids may have greatly reduced fertility, it is often adequate for backcrossing to either parent (Sanford 1983; Simmonds 1979).

It is unlikely that seedless hybrids would backcross to the Polynesian triploid, so further sexual crosses would probably involve seeded *A. mariannensis*. The progeny of backcrossing, could retain characters of the original triploid parent, including sterility genes or those that had arisen by somatic mutation (Jarrett 1959b). Many products of backcrossing and introgression are superior to either parent (Stebbins 1971), and cultivars with adaptability to atoll environments or other desired characters would have been selected and perpetuated.

Triploid hybrids probably originated by the same mechanisms as triploid *A. altilis*, but the source material differed. The hybrid nature of seedless Micronesian diploids would cause meiotic aberrations described for seedless diploid *A. altilis*. They would be able to produce an increased frequency of unreduced gametes, which on fusion with a reduced gamete would produce a triploid.

All of the seedless hybrids were found in cluster II based on their zymotypes (see Table 3.7). *Artocarpus mariannensis* and seeded hybrids from the atolls of Tokelau

and Kiribati grouped separately (cluster IV) from the hybrids elsewhere in Micronesia. It appears that the Polynesian triploid was not involved in introgression with *A. mariannensis*. Breadfruit was recently introduced to Tokelau, and as recently as the 1930s, none were growing on the island of Atafu (Hooper and Huntsman 1973; MacGregor 1937). Most breadfruit cultivars in Tokelau originated in Tuvalu, along with a few Samoan cultivars (MacGregor 1937; Lambert 1974). Tuvaluan materials were not examined during this study, but information from herbarium specimens at the Bishop Museum shows that most cultivars have hybrid characters and are seeded. Only one seedless cultivar was documented. All of the hybrids in Tokelau are seeded.

It can be surmised that hybridization probably occurred between seeded forms of *A. altilis* and *A. mariannensis*, or already existing hybrids. Seeded **Aveloloa** and **Ma'afala** are found both in Tokelau and Tuvalu. Since both parents are fertile, seeded forms (or one was a hybrid), there may have been enough homology between the two genomes so that the resulting progeny were fertile. The cluster analysis of isozyme zymotypes clearly shows that hybridization and introgression between *A. altilis* and *A. mariannensis* occurred in more than one island group, and that the Polynesian triploid was involved in some islands.

Distribution of breadfruit in Micronesia

How the Polynesian triploid reached Micronesia, and where and how it was brought together with *A. mariannensis* is difficult to address. The breadfruit cultivars analyzed were restricted to the Micronesian high islands, with only a few accessions from the atolls. It is suggestive that the few atoll cultivars studied appear not to be derived from the Polynesian triploid. The importance of the atolls in the cultural history of Micronesia poses intriguing questions. Extensive collection and analysis of atoll cultivars should provide clues.

Fosberg (1960) theorized that the initial hybridization could have taken place in the Marianas where the two species were first brought into contact. The absence of interspecific hybrids in the Mariana Islands where *A. mariannensis* grows wild, appears

to makes this unlikely. This is an excellent example of the problem of trying to infer the antiquity of breadfruit cultivars from cultivars now present on an island. Even though no hybrids were seen in the Marianas in 1987, Fosberg (1960) described several herbarium specimens of hybrids collected early in the century. Breadfruit was an important crop in the Marianas (Safford 1905), but its numbers have greatly reduced since World War II.

It is possible, but difficult to prove unless records can be found in Spanish archives, that the Spanish were responsible for introducing Polynesian breadfruit to Guam. The Spanish, regularly traversing the Pacific islands on the Acapulco-Manila sailing route during the 16th to 18th century, were responsible for the dissemination of many plants between the eastern and western hemispheres (Merrill 1914). They knew of seedless breadfruit since Quiros described Marquesan breadfruit in 1595 (Markham 1904; Yen 1973b). The Spanish probably introduced both species to the Philippines from Guam prior to A.D. 1700 (Wester 1924). It is possible that they had earlier introduced it to Guam to help provision their new colony. Trees would have been well established by the time Dampier (1729) documented the use of seedless breadfruit in the Marianas.

If interspecific hybridization first occurred in the Mariana Islands, the progeny could have readily been spread from there to the atolls. The presence of *A. mariannensis* and hybrids in Kiribati, Marshall and Caroline Islands attests to this (Fosberg 1960; Fosberg et al. 1979). *Artocarpus mariannensis* and hybrids are well adapted to atoll conditions (Catala 1957; Coenan and Barrau 1961; McKnight 1960). Its ability to grow on uplifted limestone and coral islands may have been a crucial factor in the now widespread distribution of hybrids in Micronesia.

A far-flung **sawei** exchange system that existed until the early 19th century provides well-documented evidence for long-term movements of people through the Caroline Islands (Bellwood 1979; Ayres 1990; Alkire 1978). The **sawei** allowed atoll dwellers to share scarce resources over vast distances and may help explain the contemporary distribution of breadfruit. It extended from Yap in the west through a chain of atolls to Namonuito 1100 km east. Tribute and gifts flowed at intervals of 2 to 3 years

from the outer atolls through Woleai and Ulithi to Yap. In exchange, gifts of high island produce were sent to the atolls (Alkire 1978; Bellwood 1979). Belau was the only island not tied into this trade network (Bellwood 1979; Hezel 1983), and it is unlikely that *A. mariannensis* entered the atolls from there. Woleai, an important link in the **sawei**, is renowned for its breadfruit cultivars, and the islanders had many connections with the Marianas (Alkire 1978; Hezel 1983). Carolinians travelled regularly to the Marianas until the late 1660s when Spanish missionaries established a colony; they resumed travelling there in 1787 (Hezel 1983). It is possible that the spread of breadfruit through Micronesia occurred in the last millennium.

Many questions about the origin and distribution of breadfruit in the Pacific Islands remain. Extensive collection and analyses of cultivars in Micronesia, especially the atolls, and western Melanesia should provide additional pieces to the puzzle of this important cultigen. The achievements of indigenous peoples in discovering, colonizing, and utilizing the limited resources available on many Pacific islands are truly impressive. Unfortunately, subsistence economies that have supported Pacific islanders for centuries, and in some cases millennia, are disappearing in a rapidly changing world. Maintenance of germplasm collections such as this one may ensure that the genetic diversity found in this crop is conserved and perpetuated.

APPENDIX A
VERNACULAR NAMES OF BREADFRUIT
FROM THE PACIFIC ISLANDS

More than 2,000 vernacular names were recorded for the following island groups:

Belau	Marquesas	Solomon Islands
Caroline Islands	New Guinea	Tokelau
Cook Islands	Niue	Tonga
Fiji	Pohnpei	Truk
Kiribati	Rotuma	Tuvalu
Kosrae	Samoa	Vanuatu
Mariana Islands	Society Islands Yap	
	Marquesas	

Local Name	Island	Author	Year
Balawa ni Viti	Fiji	Koroweibau	1966
Balekana	Fiji	Ragone	1991
Balekana dina	Fiji	Koroweibau	1966
Balekana ni Samoa	Fiji	Koroweibau	1966
Balekana ni Viti	Fiji	Koroweibau	1966
Bokasi	Fiji	Koroweibau	1966
Bokasi ni Samoa	Fiji	Koroweibau	1966
Buco dina	Fiji	Ragone	1991
Buco do	Fiji	Seeman	1865
Buco ne viti	Fiji	Koroweibau	1966
Buco ni Samoa	Fiji	Koroweibau	1966
Buco ni Samoa	Fiji	Ragone	1991
Buco ni Samoa	Fiji	Ragone	1991
Buco uvi	Fiji	Seeman	1865
Bucotabua utoga	Fiji	Seeman	1865
Buka-o	Fiji	Ragone	1991
Cikobia	Fiji	Koroweibau	1966
Dregadrega	Fiji	Seeman	1865
Gilipati	Fiji	Koroweibau	1966
Karawa	Fiji	Koroweibau	1966
Kasa balavu	Fiji	Koroweibau	1966
Kasabalau	Fiji	Ragone	1991
Koqo	Fiji	Koroweibau	1966
Koqu	Fiji	Ragone	1991
Kuku balekana	Fiji	Ragone	1991
Kulu dina	Fiji	Koroweibau	1966
Kulu dina	Fiji	Ragone	1991
Kulu levulevu	Fiji	Koroweibau	1966
Kulu mabomabo	Fiji	Koroweibau	1966
Kulu mabomabo	Fiji	Ragone	1991
Kulu ni Samoa	Fiji	Ragone	1991
Kulu raurau	Fiji	Koroweibau	1966
Kulu vailei	Fiji	Ragone	1991
Kulu vawiri	Fiji	Koroweibau	1966
Kulu votovoto	Fiji	Ragone	1991
Matavesi	Fiji	Seeman	1865
Matavude	Fiji	Koroweibau	1966
Matavude	Fiji	Ragone	1991
Samoa	Fiji	Ragone	1991
Savisavi	Fiji	Koroweibau	1966
Savisavi ni Viti	Fiji	Koroweibau	1966
Sici ni Samoa	Fiji	Koroweibau	1966
Sogasoga	Fiji	Koroweibau	1966
Te bukiraro	Fiji	Ragone	1991
Te mai keang	Fiji	Ragone	1991
Te mai kora	Fiji	Ragone	1991
Te mai wea	Fiji	Ragone	1991
Uto asalea	Fiji	Seeman	1865
Uto balavu	Fiji	Koroweibau	1966
Uto balekana	Fiji	Seeman	1865
Uto bokasi	Fiji	Seeman	1865
Uto buco**	Fiji	Seeman	1865
Uto dina	Fiji	Koroweibau	1966
Uto dina	Fiji	Seeman	1865
Uto dina	Fiji	Ragone	1991
Uto dina ni Samoa	Fiji	Koroweibau	1966
Uto drega	Fiji	Koroweibau	1966
Uto du	Fiji	Ragone	1991
Uto kalasai**	Fiji	Seeman	1865
Uto karokaro	Fiji	Koroweibau	1966

Local Name	Island	Author	Year
FJI			
Uto kasekasei	Fiji	Koroweibau	1966
Uto koqo	Fiji	Seeman	1865
Uto kuro	Fiji	Koroweibau	1966
Uto lolo	Fiji	Koroweibau	1966
Uto lolo	Fiji	Ragone	1991
Uto lolo (cokocoko)	Fiji	Seeman	1865
Uto maliva	Fiji	Seeman	1865
Uto matala	Fiji	Koroweibau	1966
Uto matalotu	Fiji	Ragone	1991
Uto me	Fiji	Koroweibau	1966
Uto ni viti	Fiji	Ragone	1991
Uto puaka	Fiji	Koroweibau	1966
Uto qio	Fiji	Seeman	1865
Uto rokouta	Fiji	Seeman	1865
Uto samoa	Fiji	Ragone	1991
Uto sasaloa	Fiji	Seeman	1865
Uto sore	Fiji	Seeman	1865
Uto sore	Fiji	Ragone	1991
Uto vaka sorena	Fiji	Seeman	1865
Uto vakasorena	Fiji	Koroweibau	1966
Uto vagele	Fiji	Koroweibau	1966
Uto varaqa	Fiji	Seeman	1865
Uto vono	Fiji	Seeman	1865
Uto votovoto	Fiji	Seeman	1865
Uto vula	Fiji	Ragone	1991
Uto wa	Fiji	Koroweibau	1966
Uto yalewa	Fiji	Koroweibau	1966
Utoloa	Fiji	Seeman	1865
Via loa	Fiji	Koroweibau	1966
Votovoto	Fiji	Koroweibau	1966
Votovoto	Fiji	Ragone	1991
Waisea	Fiji	Seeman	1865
Tabukiraro	Fiji (Rabi)	Koroweibau	1966
Tamai kora	Fiji (Rabi)	Koroweibau	1966
Temai kiang	Fiji (Rabi)	Koroweibau	1966
Temai po	Fiji (Rabi)	Koroweibau	1966
NEW GUINEA			
Aninta doea	New Guinea	WS Dept. Ag.	1960
Aninta satu	New Guinea	WS Dept. Ag.	1960
Daro	New Guinea	Parham	1965
Gog	New Guinea	Parham	1965
Guni	New Guinea	Parham	1965
Hakananogo	New Guinea	WS Dept. Ag.	1960
Iseisa	New Guinea	WS Dept. Ag.	1960
Kapiak	New Guinea	Parham	1965
Namlakes	New Guinea	Parham	1965
Obawn	New Guinea	WS Dept. Ag.	1960
Ouna	New Guinea	Parham	1965
ROTUMA			
Buco	Rotuma	WS Dept. Ag.	1964
Furau	Rotuma	WS Dept. Ag.	1960
Karawa	Rotuma	Ragone	1991
Karawa	Rotuma	WS Dept. Ag.	1964
Kaumaga	Rotuma	Fiji Dept. Ag.	1960
Kaumaja	Rotuma	Fiji Dept. Ag.	1960
Kaumanga	Rotuma	WS Dept. Ag.	1960
Koro	Rotuma	WS Dept. Ag.	1964
Maekora	Rotuma	WS Dept. Ag.	1964
Mahalu	Rotuma	WS Dept. Ag.	1960

Local Name	Island	Author	Year
ROTUMA			
Makeva	Rotuma	WS Dept. Ag.	1960
Makeva	Rotuma	Fiji Dept. Ag.	1960
Manoma	Rotuma	WS Dept. Ag.	1964
Manoma	Rotuma	Fiji Dept. Ag.	1960
Oreuniyavi	Rotuma	WS Dept. Ag.	1964
Pulpulu	Rotuma	Fiji Dept. Ag.	1960
Pulupulu	Rotuma	Ragone	1991
Pulupulu	Rotuma	WS Dept. Ag.	1960
Rauje ije	Rotuma	WS Dept. Ag.	1964
Raujeije	Rotuma	Fiji Dept. Ag.	1960
Raululu	Rotuma	WS Dept. Ag.	1960
Rauulu	Rotuma	Ragone	1991
Ro'otuma	Rotuma	Ragone	1991
Samantalhil	Rotuma	Fiji Dept. Ag.	1960
Ul Fiti	Rotuma	Fiji Dept. Ag.	1960
Ul Forau	Rotuma	Fiji Dept. Ag.	1960
Ul Rotuma	Rotuma	Fiji Dept. Ag.	1960
Ul Samop	Rotuma	Fiji Dept. Ag.	1960
Ulu fiti	Rotuma	Ragone	1991
Ulu fiti	Rotuma	WS Dept. Ag.	1964
Ulu samoa	Rotuma	WS Dept. Ag.	1964
Ulu semantefhil	Rotuma	WS Dept. Ag.	1960
Uto dina	Rotuma	WS Dept. Ag.	1964
Uto i Samoa	Rotuma	WS Dept. Ag.	1964
Raululu	Rotuma	Fiji Dept. Ag.	1960
SOLOMON ISLANDS			
Abareba	Solomon Islands	Ragone	1991
Aowewe	Solomon Islands	WS Dept. Ag.	1964
Arerere	Solomon Islands	WS Dept. Ag.	1964
Bara	Solomon Islands	WS Dept. Ag.	1964
Baura	Solomon Islands	WS Dept. Ag.	1964
Begoro	Solomon Islands	Jackson	1982
Bia bai	Solomon Islands	Ragone	1991
Bia banuoi	Solomon Islands	Ragone	1991
Bia bnowi	Solomon Islands	Jackson	1982
Bia ipoto	Solomon Islands	Jackson	1982
Bia kai	Solomon Islands	Ragone	1991
Bia kio	Solomon Islands	Jackson	1982
Bia kiyo	Solomon Islands	Ragone	1991
Bia kto	Solomon Islands	Jackson	1982
Bia lamanau	Solomon Islands	Jackson	1982
Bia lapewa	Solomon Islands	Jackson	1982
Bia lea	Solomon Islands	Jackson	1982
Bia leik	Solomon Islands	Jackson	1982
Bia mingi	Solomon Islands	Ragone	1991
Bia motomalo	Solomon Islands	Jackson	1982
Bia nadapo	Solomon Islands	Jackson	1982
Bia nakir	Solomon Islands	Jackson	1982
Bia namua	Solomon Islands	Jackson	1982
Bia nasokopa	Solomon Islands	Jackson	1982
Bia no	Solomon Islands	Jackson	1982
Bia papna	Solomon Islands	Jackson	1982
Bia po	Solomon Islands	Ragone	1991
Bia taki	Solomon Islands	Jackson	1982
Bia taluaki	Solomon Islands	Jackson	1982
Bia tamna leboi	Solomon Islands	Jackson	1982
Bia teli	Solomon Islands	Ragone	1991
Bia toki	Solomon Islands	Jackson	1982
Bia vango	Solomon Islands	Jackson	1982

Local Name	Island	Author	Year
Bia venga	Solomon Islands	Ragone	1991
Bia vengapo	Solomon Islands	Ragone	1991
Bia yibe	Solomon Islands	Ragone	1991
Biavenga napenyimibile	Solomon Islands	Ragone	1991
Blo lili	Solomon Islands	Jackson	1982
Blo na basil	Solomon Islands	Jackson	1982
Blo nasulu	Solomon Islands	Jackson	1982
Blo sopula	Solomon Islands	Jackson	1982
Blo tokoko	Solomon Islands	Jackson	1982
Blosi	Solomon Islands	Jackson	1982
Bulo belua	Solomon Islands	Ragone	1991
Bulo bosi	Solomon Islands	Ragone	1991
Bulo bota	Solomon Islands	Ragone	1991
Bulo bwaa	Solomon Islands	Ragone	1991
Bulo dena basil	Solomon Islands	Ragone	1991
Bulo dena bona	Solomon Islands	Ragone	1991
Bulo dena panuma	Solomon Islands	Ragone	1991
Bulo kai	Solomon Islands	Ragone	1991
Bulo kinapwa	Solomon Islands	Ragone	1991
Bulo kingoga	Solomon Islands	Ragone	1991
Bulo kiyeta	Solomon Islands	Ragone	1991
Bulo kiyivebu	Solomon Islands	Ragone	1991
Bulo kosa	Solomon Islands	Ragone	1991
Bulo laa	Solomon Islands	Ragone	1991
Bulo lili	Solomon Islands	Ragone	1991
Bulo momwala	Solomon Islands	Ragone	1991
Bulo mwala	Solomon Islands	Ragone	1991
Bulo nasulu	Solomon Islands	Ragone	1991
Bulo nede	Solomon Islands	Ragone	1991
Bulo nenu	Solomon Islands	Ragone	1991
Bulo niyia	Solomon Islands	Ragone	1991
Bulo nyimebele	Solomon Islands	Ragone	1991
Bulo olosi nunugo	Solomon Islands	Ragone	1991
Bulo pobo	Solomon Islands	Ragone	1991
Bulo santo**	Solomon Islands	Ragone	1991
Bulo si	Solomon Islands	Ragone	1991
Bulo siguo	Solomon Islands	Ragone	1991
Bulo tokoko	Solomon Islands	Ragone	1991
Bulo unage	Solomon Islands	Ragone	1991
Bulo uto	Solomon Islands	Ragone	1991
Bulo uto	Solomon Islands	Ragone	1991
Bulo utupua	Solomon Islands	Ragone	1991
Bulo vinage	Solomon Islands	Ragone	1991
Bulo wamwanugolilwo	Solomon Islands	Ragone	1991
Bulo wamwatekiye	Solomon Islands	Ragone	1991
Bulo wana	Solomon Islands	Ragone	1991
Bulo yau	Solomon Islands	Ragone	1991
Bulomemave na pevale	Solomon Islands	Ragone	1991
Bwa nyalo	Solomon Islands	Ragone	1991
Bwa nyive	Solomon Islands	Ragone	1991
Bwa yibe	Solomon Islands	Ragone	1991
Bwa yinyalo	Solomon Islands	Ragone	1991
Bwegoto	Solomon Islands	Ragone	1991
Dalegile	Solomon Islands	Ragone	1991
Denapanumao	Solomon Islands	Ragone	1991
Denyigi nupwagaa	Solomon Islands	Ragone	1991
Elado	Solomon Islands	Jackson	1982
Eyoladu	Solomon Islands	Ragone	1991
Fau	Solomon Islands	WS Dept. Ag.	1964
Gaapota	Solomon Islands	Ragone	1991

Local Name	Island	Author	Year
Goro	Solomon Islands	WS Dept. Ag.	1964
Guwnubu	Solomon Islands	Ragone	1991
Kekene	Solomon Islands	Ragone	1991
Keluna	Solomon Islands	Ragone	1991
Kikero	Solomon Islands	Ragone	1991
Kiyeta	Solomon Islands	Ragone	1991
Kukumu tasi	Solomon Islands	Ragone	1991
Kukumu tasi	Solomon Islands	WS Dept. Ag.	1964
Kukumutolu	Solomon Islands	WS Dept. Ag.	1964
Kurumulua	Solomon Islands	WS Dept. Ag.	1964
La'atu	Solomon Islands	Ragone	1991
La'atu po	Solomon Islands	Ragone	1991
Lagemuliaro	Solomon Islands	Jackson	1982
Lagemuliyato	Solomon Islands	Ragone	1991
Lumongi	Solomon Islands	Ragone	1991
Malapatau	Solomon Islands	Ragone	1991
Malawarawa	Solomon Islands	WS Dept. Ag.	1964
Melonadu	Solomon Islands	Ragone	1991
Mwaulela	Solomon Islands	Ragone	1991
Mwo oula	Solomon Islands	Ragone	1991
Na'au	Solomon Islands	Ragone	1991
Nabwe	Solomon Islands	Ragone	1991
Nado	Solomon Islands	Jackson	1982
Nado	Solomon Islands	Ragone	1991
Nado la nubwe	Solomon Islands	Jackson	1982
Nadola biavenga	Solomon Islands	Ragone	1991
Nadola bulobwaa	Solomon Islands	Ragone	1991
Nadola bulokingoga	Solomon Islands	Ragone	1991
Nadola kuli	Solomon Islands	Ragone	1991
Nadola lagemuliyato	Solomon Islands	Ragone	1991
Nadola nalenga	Solomon Islands	Ragone	1991
Nadola nebae	Solomon Islands	Ragone	1991
Nadola nobo	Solomon Islands	Ragone	1991
Nadola nubwa	Solomon Islands	Ragone	1991
Nadola nyigisi	Solomon Islands	Ragone	1991
Nadola topwalau	Solomon Islands	Ragone	1991
Nadola uliyegale	Solomon Islands	Ragone	1991
Naga nwopoyi	Solomon Islands	Ragone	1991
Nagadya	Solomon Islands	Ragone	1991
Nala	Solomon Islands	Ragone	1991
Nata	Solomon Islands	Ragone	1991
Natopwale	Solomon Islands	Ragone	1991
Nebe	Solomon Islands	Ragone	1991
Nigisi	Solomon Islands	Jackson	1982
Nobo	Solomon Islands	Jackson	1982
Nobo	Solomon Islands	Ragone	1991
Nobowa	Solomon Islands	Ragone	1991
Nogano poi	Solomon Islands	Jackson	1982
Noganopoyi	Solomon Islands	Ragone	1991
Nua nebi	Solomon Islands	Jackson	1982
Nuboa	Solomon Islands	Jackson	1982
Nuboa	Solomon Islands	Ragone	1991
Nugasa topulaka	Solomon Islands	Jackson	1982
Nugo nai	Solomon Islands	Jackson	1982
Nugonai	Solomon Islands	Ragone	1991
Nupwa negi	Solomon Islands	Ragone	1991
Nuwanebi	Solomon Islands	Ragone	1991
Nwana moyi	Solomon Islands	Ragone	1991
Nwanebi	Solomon Islands	Ragone	1991
Nwaneyo	Solomon Islands	Ragone	1991

Local Name	Island	Author	Year
SOLOMON ISLANDS			
Nwatoli*	Solomon Islands	Ragone	1991
Nwotu boua kuli	Solomon Islands	Ragone	1991
Nwoula	Solomon Islands	Ragone	1991
Nyigasa tepulaka	Solomon Islands	Ragone	1991
Nyigesianelo	Solomon Islands	Ragone	1991
Nyigisi	Solomon Islands	Ragone	1991
Nyike manubo	Solomon Islands	Ragone	1991
Nyike uto	Solomon Islands	Ragone	1991
Nyikele	Solomon Islands	Ragone	1991
Ogo	Solomon Islands	WS Dept. Ag.	1964
Otoo po	Solomon Islands	Ragone	1991
Raumatari	Solomon Islands	WS Dept. Ag.	1964
Rausimi	Solomon Islands	Ragone	1991
Rawa	Solomon Islands	WS Dept. Ag.	1964
Rove	Solomon Islands	WS Dept. Ag.	1964
Sibwa	Solomon Islands	Ragone	1991
Silikinebe	Solomon Islands	Ragone	1991
Talau yilavepo	Solomon Islands	Ragone	1991
Tapiyai	Solomon Islands	Ragone	1991
Tehelewa	Solomon Islands	WS Dept. Ag.	1964
Teulingiya	Solomon Islands	Ragone	1991
Tobola	Solomon Islands	Ragone	1991
Toka'a	Solomon Islands	Ragone	1991
Tomwaki	Solomon Islands	Ragone	1991
Toro	Solomon Islands	Ragone	1991
Toro	Solomon Islands	WS Dept. Ag.	1964
Tubiliya	Solomon Islands	Ragone	1991
Tulango	Solomon Islands	Ragone	1991
Uliyegale	Solomon Islands	Ragone	1991
Urimanai	Solomon Islands	WS Dept. Ag.	1964
Velepu	Solomon Islands	Ragone	1991
Visa	Solomon Islands	Jackson	1982
Visa	Solomon Islands	Ragone	1991
Waowao	Solomon Islands	WS Dept. Ag.	1964
Willicocome	Solomon Islands	Ragone	1991
Yalobeka	Solomon Islands	Ragone	1991
VANUATU			
Alututsori	Vanuatu	Nalo	1967
Anavturo	Vanuatu	Walter	1990
Ara ara	Vanuatu	Walter	1990
Baka	Vanuatu	Parham	1965
Bakol	Vanuatu	Walter	1990
Basis	Vanuatu	Walter	1990
Batkau	Vanuatu	Walter	1990
Bedbull	Vanuatu	WS Dept. Ag.	1964
Berepsopwa	Vanuatu	Walter	1990
Beta andum	Vanuatu	Murray	1894
Beta arbol	Vanuatu	Murray	1894
Beta basivir	Vanuatu	Murray	1894
Beta bawehe	Vanuatu	Murray	1894
Beta betaiye	Vanuatu	Murray	1894
Beta bwise	Vanuatu	Murray	1894
Beta dyu	Vanuatu	Murray	1894
Beta fane	Vanuatu	Murray	1894
Beta fanhor	Vanuatu	Murray	1894
Beta fira	Vanuatu	Murray	1894
Beta for	Vanuatu	Murray	1894
Beta hivil	Vanuatu	Murray	1894
Beta karo	Vanuatu	Murray	1894

Local Name	Island	Author	Year
Birin metan bo*	Vanuatu	Walter	1990
Biubulido ri	Vanuatu	Walter	1990
Bombouro	Vanuatu	Walter	1990
Bona	Vanuatu	Walter	1990
Bresa	Vanuatu	Walter	1990
Buvi	Vanuatu	Walter	1990
Bwingbwing	Vanuatu	Walter	1990
Chochota	Vanuatu	Walter	1990
Daliu	Vanuatu	WS Dept. Ag.	1964
Damame	Vanuatu	Walter	1990
Desmadum	Vanuatu	WS Dept. Ag.	1964
Dowon	Vanuatu	Walter	1990
Fan	Vanuatu	Walter	1990
Flefling	Vanuatu	Walter	1990
Gobi	Vanuatu	Walter	1990
Gonausu	Vanuatu	Walter	1990
Goot	Vanuatu	WS Dept. Ag.	1964
Gwasisi	Vanuatu	Walter	1990
Hargo	Vanuatu	WS Dept. Ag.	1964
Hati arara	Vanuatu	Walter	1990
Hortamalum	Vanuatu	Nalo	1967
Hortapul	Vanuatu	Nalo	1967
Kablabenruan	Vanuatu	Walter	1990
Kanaotau	Vanuatu	Parham	1965
Kanotao	Vanuatu	WS Dept. Ag.	1964
Kasau	Vanuatu	Walter	1990
Kaukakas	Vanuatu	Walter	1990
Kavekepahau	Vanuatu	Walter	1990
Kelefi	Vanuatu	Walter	1990
Kikibi	Vanuatu	Walter	1990
Kilikili	Vanuatu	WS Dept. Ag.	1964
Kut	Vanuatu	Parham	1965
Kutrok	Vanuatu	Parham	1965
Lahmoro	Vanuatu	Walter	1990
Lehula	Vanuatu	Walter	1990
Levhulu	Vanuatu	Walter	1990
Liemal	Vanuatu	Walter	1990
Liepwilina	Vanuatu	Walter	1990
Lihasmwe	Vanuatu	Walter	1990
Liholiho	Vanuatu	Walter	1990
Liolio	Vanuatu	Walter	1990
Liptultul	Vanuatu	Walter	1990
Lof	Vanuatu	Parham	1965
Lof	Vanuatu	Walter	1990
Lolmeme	Vanuatu	Walter	1990
Luko	Vanuatu	Walter	1990
Lum	Vanuatu	Walter	1990
MaRvoy	Vanuatu	Walter	1990
Malapatau	Vanuatu	WS Dept. Ag.	1964
Malhemb	Vanuatu	Walter	1990
Maliago	Vanuatu	Walter	1990
Malphang	Vanuatu	Ragone	1991
Malphang	Vanuatu	WS Dept. Ag.	1964
Malum	Vanuatu	Nalo	1967
Manang	Vanuatu	Ragone	1991
Manang	Vanuatu	WS Dept. Ag.	1964
Manhamb	Vanuatu	Walter	1990
Manvi	Vanuatu	Walter	1990
Maptibon	Vanuatu	Walter	1990
Matsoni	Vanuatu	Nalo	1967

Local Name	Island	Author	Year
Birin metan bo"	Vanuatu	Walter	1990
Biubulido ri	Vanuatu	Walter	1990
Bombouro	Vanuatu	Walter	1990
Bona	Vanuatu	Walter	1990
Bresa	Vanuatu	Walter	1990
Buvi	Vanuatu	Walter	1990
Bwingbwing	Vanuatu	Walter	1990
Chochota	Vanuatu	Walter	1990
Daliu	Vanuatu	WS Dept. Ag.	1964
Damame	Vanuatu	Walter	1990
Desmadum	Vanuatu	WS Dept. Ag.	1964
Dowon	Vanuatu	Walter	1990
Fan	Vanuatu	Walter	1990
Flefling	Vanuatu	Walter	1990
Gobi	Vanuatu	Walter	1990
Gonausu	Vanuatu	Walter	1990
Goot	Vanuatu	WS Dept. Ag.	1964
Gwasisi	Vanuatu	Walter	1990
Hargo	Vanuatu	WS Dept. Ag.	1964
Hati arara	Vanuatu	Walter	1990
Hortamalum	Vanuatu	Nalo	1967
Hortapul	Vanuatu	Nalo	1967
Kablabenruan	Vanuatu	Walter	1990
Kanaotau	Vanuatu	Parham	1965
Kanotao	Vanuatu	WS Dept. Ag.	1964
Kasau	Vanuatu	Walter	1990
Kaukakas	Vanuatu	Walter	1990
Kavekepahau	Vanuatu	Walter	1990
Kelefi	Vanuatu	Walter	1990
Kikibi	Vanuatu	Walter	1990
Kilikili	Vanuatu	WS Dept. Ag.	1964
Kut	Vanuatu	Parham	1965
Kutrok	Vanuatu	Parham	1965
Lahmoro	Vanuatu	Walter	1990
Lehula	Vanuatu	Walter	1990
Levhulu	Vanuatu	Walter	1990
Liemal	Vanuatu	Walter	1990
Liepwilina	Vanuatu	Walter	1990
Lihasmwe	Vanuatu	Walter	1990
Liholiho	Vanuatu	Walter	1990
Liolo	Vanuatu	Walter	1990
Liptultul	Vanuatu	Walter	1990
Lof	Vanuatu	Parham	1965
Lof	Vanuatu	Walter	1990
Lolmeme	Vanuatu	Walter	1990
Luko	Vanuatu	Walter	1990
Lum	Vanuatu	Walter	1990
MaRvov	Vanuatu	Walter	1990
Malapatau	Vanuatu	WS Dept. Ag.	1964
Malhemb	Vanuatu	Walter	1990
Maliago	Vanuatu	Walter	1990
Malphang	Vanuatu	Ragone	1991
Malphang	Vanuatu	WS Dept. Ag.	1964
Malum	Vanuatu	Nalo	1967
Manang	Vanuatu	Ragone	1991
Manang	Vanuatu	WS Dept. Ag.	1964
Manhamb	Vanuatu	Walter	1990
Manvi	Vanuatu	Walter	1990
Mapuibon	Vanuatu	Walter	1990
Matsoni	Vanuatu	Nalo	1967

Local Name	Island	Author	Year
Matualele"	Vanuatu	WS Dept. Ag.	1964
Melasur	Vanuatu	Parham	1965
Melewoke	Vanuatu	Walter	1990
Menonok	Vanuatu	Walter	1990
Merekwo	Vanuatu	Walter	1990
Memowonwon	Vanuatu	Walter	1990
Mialasuru	Vanuatu	Parham	1965
Minamon	Vanuatu	Parham	1965
Morghi	Vanuatu	Nalo	1967
NabRafpungoR	Vanuatu	Walter	1990
Nabosulu	Vanuatu	Walter	1990
Nafuliaka	Vanuatu	WS Dept. Ag.	1964
Nahoero'o	Vanuatu	Walter	1990
Naliu	Vanuatu	Parham	1965
Naliu	Vanuatu	Walter	1990
NamalhoR	Vanuatu	Walter	1990
Nambogolabwo	Vanuatu	Walter	1990
Nameruan	Vanuatu	Walter	1990
Nape'opore	Vanuatu	Walter	1990
Napele	Vanuatu	WS Dept. Ag.	1964
Napore	Vanuatu	Walter	1990
Naptam	Vanuatu	Parham	1965
Narawono	Vanuatu	WS Dept. Ag.	1964
Nasamel	Vanuatu	Walter	1990
Nasnof	Vanuatu	Parham	1965
NasobRu	Vanuatu	Walter	1990
Natekrei	Vanuatu	Walter	1990
Nateman	Vanuatu	Parham	1965
Natevui	Vanuatu	Walter	1990
Naur	Vanuatu	WS Dept. Ag.	1964
Navito'o	Vanuatu	Walter	1990
Nendango	Vanuatu	Walter	1990
Netalayban	Vanuatu	Walter	1990
Nevan	Vanuatu	Walter	1990
Ngaribus	Vanuatu	Walter	1990
Norawong	Vanuatu	Walter	1990
Numnumin	Vanuatu	Walter	1990
Numwel	Vanuatu	Walter	1990
Pakotau	Vanuatu	Parham	1965
Palupeka	Vanuatu	Nalo	1967
Paunagia	Vanuatu	WS Dept. Ag.	1964
Perlot	Vanuatu	Walter	1990
Permismis	Vanuatu	Walter	1990
Permorus	Vanuatu	Walter	1990
Permut	Vanuatu	Walter	1990
Perwawar	Vanuatu	Walter	1990
Pesuhi	Vanuatu	Nalo	1967
Petpulmei	Vanuatu	WS Dept. Ag.	1964
Puka	Vanuatu	Walter	1990
Pulut	Vanuatu	Nalo	1967
Qwalmat	Vanuatu	Walter	1990
Ra-usi	Vanuatu	Nalo	1967
Rakrakawul	Vanuatu	Walter	1990
Raulap	Vanuatu	Walter	1990
Raupwete	Vanuatu	Walter	1990
Rot	Vanuatu	Walter	1990
Sagwai	Vanuatu	Walter	1990
Sahper	Vanuatu	Walter	1990

Local Name	Island	Author	Year
Sario	Vanuatu	WS Dept. Ag.	1964
Sarinditi	Vanuatu	Walter	1990
Sebwek	Vanuatu	Walter	1990
Selbay	Vanuatu	Walter	1990
Semakul	Vanuatu	Walter	1990
Sevo	Vanuatu	Walter	1990
Sinopu	Vanuatu	WS Dept. Ag.	1964
Sinopu artou atau	Vanuatu	Parham	1965
Sinopu malakesa	Vanuatu	Parham	1965
Siskauni	Vanuatu	Walter	1990
Slaomiel	Vanuatu	Parham	1965
Snobo	Vanuatu	Walter	1990
Soloamiela	Vanuatu	WS Dept. Ag.	1964
Sorniu	Vanuatu	Walter	1990
Sulapil	Vanuatu	Nalo	1967
Sur	Vanuatu	Walter	1990
Taba	Vanuatu	Walter	1990
Tafra	Vanuatu	WS Dept. Ag.	1964
Talavose	Vanuatu	Walter	1990
Tamimeres	Vanuatu	Walter	1990
Tamot	Vanuatu	Walter	1990
Tanarau	Vanuatu	Nalo	1967
Tanaruma	Vanuatu	Walter	1990
Tangiran	Vanuatu	Walter	1990
Taraliplipu	Vanuatu	Nalo	1967
Taravanthi	Vanuatu	Nalo	1967
Tari wakli	Vanuatu	Walter	1990
Tchumtchum	Vanuatu	Walter	1990
Tedailir	Vanuatu	Ragone	1991
Teman	Vanuatu	WS Dept. Ag.	1964
Tenamanu	Vanuatu	Walter	1990
Tenenom	Vanuatu	Walter	1990
Teurangona	Vanuatu	Parham	1965
Tevila kasu	Vanuatu	Parham	1965
Tirip	Vanuatu	Walter	1990
Tsangan	Vanuatu	Walter	1990
Tseptso	Vanuatu	Walter	1990
Tuturer	Vanuatu	Walter	1990
Varivuno	Vanuatu	Nalo	1967
Veiatortor	Vanuatu	Nalo	1967
Vin bilan vi	Vanuatu	Walter	1990
Vovortornalabel	Vanuatu	Nalo	1967
Vunatavu	Vanuatu	Nalo	1967
Wabi	Vanuatu	Walter	1990
Wakmakur	Vanuatu	Parham	1965
Walk	Vanuatu	WS Dept. Ag.	1964
Watasiwol	Vanuatu	Walter	1990
Wawulang	Vanuatu	Walter	1990
Willicocame	Vanuatu	WS Dept. Ag.	1964
Wo	Vanuatu	Walter	1990
Wohata	Vanuatu	Walter	1990
Wokobo	Vanuatu	Walter	1990
Wolsu	Vanuatu	Walter	1990
Wometaden	Vanuatu	Walter	1990
Worspesuhi	Vanuatu	Nalo	1967
Wotanagwaru	Vanuatu	Walter	1990
Wotolbul	Vanuatu	Walter	1990
Wulewot	Vanuatu	Walter	1990
Wulkawan	Vanuatu	Walter	1990
Wushortahi	Vanuatu	Nalo	1967

Local Name	Island	Author	Year
MICRONESIA			
BELAU			
Chebechab	Belau	Coenan & Barrau	1961
Chebechab	Belau	McKnight	1964
Chebiei	Belau	Ragone	1991
Ebechad	Belau	Ragone	1991
Errud	Belau	Ragone	1991
Errud	Belau	McKnight	1964
Etelouch	Belau	McKnight	1964
Meduueliou	Belau	McKnight	1964
Meriaur	Belau	Ragone	1991
Meriaur	Belau	McKnight	1964
Midolab	Belau	Ragone	1991
Olekidel	Belau	McKnight	1964
CAROLINE ISLANDS			
Mai guiau	Carolines (Ifaluk)	Burrows & Spiro	1957
Mai mwarei	Carolines (Ifaluk)	Burrows & Spiro	1957
Mai rau	Carolines (Ifaluk)	Burrows & Spiro	1957
Mai vae	Carolines (Ifaluk)	Burrows & Spiro	1957
Mai vau	Carolines (Ifaluk)	Burrows & Spiro	1957
Mauli	Carolines (Ifaluk)	Burrows & Spiro	1957
Seuaiki	Carolines (Ifaluk)	Burrows & Spiro	1957
Tagumelin	Carolines (Ifaluk)	Burrows & Spiro	1957
Tro malo	Carolines (Ifaluk)	Burrows & Spiro	1957
Welige sol	Carolines (Ifaluk)	Burrows & Spiro	1957
Moai id	Carolines (Mokil)	Harrison & Albert	1977
Moai in Uhrek	Carolines (Mokil)	Harrison & Albert	1977
Moai in pahdak	Carolines (Mokil)	Harrison & Albert	1977
Moai joapwoahroak	Carolines (Mokil)	Harrison & Albert	1977
Moai kalak	Carolines (Mokil)	Harrison & Albert	1977
Moai ngeljouau	Carolines (Mokil)	Harrison & Albert	1977
Moai pa	Carolines (Mokil)	Harrison & Albert	1977
Moai si	Carolines (Mokil)	Harrison & Albert	1977
Moai soal	Carolines (Mokil)	Harrison & Albert	1977
Moai upw	Carolines (Mokil)	Harrison & Albert	1977
Achepar	Carolines (Pis/Losap)	Ragone	1991
Aniken	Carolines (Pis/Losap)	Ragone	1991
Bochon	Carolines (Pis/Losap)	Ragone	1991
Bwikilew	Carolines (Pis/Losap)	Ragone	1991
Chipwei	Carolines (Pis/Losap)	Ragone	1991
Etei	Carolines (Pis/Losap)	Ragone	1991
Fenal	Carolines (Pis/Losap)	Ragone	1991
Leluku	Carolines (Pis/Losap)	Ragone	1991
Lepeito	Carolines (Pis/Losap)	Ragone	1991
Lesoso	Carolines (Pis/Losap)	Ragone	1991
Mei chocho	Carolines (Pis/Losap)	Ragone	1991
Mei koeng	Carolines (Pis/Losap)	Ragone	1991
Mei or (Main oror)	Carolines (Pis/Losap)	Ragone	1991
Mein fenal	Carolines (Pis/Losap)	Ragone	1991
Meseu	Carolines (Pis/Losap)	Ragone	1991
Mweserang	Carolines (Pis/Losap)	Ragone	1991
Olumar	Carolines (Pis/Losap)	Ragone	1991
Fayinomw	Carolines (Puluwat)	Elbert	1972
Hariir	Carolines (Puluwat)	Elbert	1972
Hawaan	Carolines (Puluwat)	Elbert	1972
Kumuwwur	Carolines (Puluwat)	Elbert	1972
Leefe	Carolines (Puluwat)	Elbert	1972
Leeker	Carolines (Puluwat)	Elbert	1972
Leeyo	Carolines (Puluwat)	Elbert	1972
Lepeeeyre	Carolines (Puluwat)	Elbert	1972

Local Name	Island	Author	Year
CAROLINE ISLANDS			
Lesooso	Carolines (Puluwat)	Elbert	1972
Lewaar	Carolines (Puluwat)	Elbert	1972
Loworoor	Carolines (Puluwat)	Elbert	1972
Lukineme	Carolines (Puluwat)	Elbert	1972
Luukanimw	Carolines (Puluwat)	Elbert	1972
Maay ah	Carolines (Puluwat)	Elbert	1972
Maay fawu	Carolines (Puluwat)	Elbert	1972
Maayhoolap	Carolines (Puluwat)	Elbert	1972
Maaykooor	Carolines (Puluwat)	Elbert	1972
Maaylaar	Carolines (Puluwat)	Elbert	1972
Maaynikaraw	Carolines (Puluwat)	Elbert	1972
Maaynohook	Carolines (Puluwat)	Elbert	1972
Maaypwopw	Carolines (Puluwat)	Elbert	1972
Maaytaal	Carolines (Puluwat)	Elbert	1972
Maayraan	Carolines (Puluwat)	Elbert	1972
Mahaapwer	Carolines (Puluwat)	Elbert	1972
Mahaarool	Carolines (Puluwat)	Elbert	1972
Mahaawuu	Carolines (Puluwat)	Elbert	1972
Maharang	Carolines (Puluwat)	Elbert	1972
Reemoon	Carolines (Puluwat)	Elbert	1972
Rooyiyang	Carolines (Puluwat)	Elbert	1972
Tunawuw	Carolines (Puluwat)	Elbert	1972
Weeyiraan	Carolines (Puluwat)	Elbert	1972
Wenipwula	Carolines (Puluwat)	Elbert	1972
Wiliwil	Carolines (Puluwat)	Elbert	1972
Wuhap	Carolines (Puluwat)	Elbert	1972
Wurokaay	Carolines (Puluwat)	Elbert	1972
Yamehaapwut	Carolines (Puluwat)	Elbert	1972
Yinanefot	Carolines (Puluwat)	Elbert	1972
Aniken	Carolines (Satawan)	Ragone	1991
Aparet	Carolines (Satawan)	Ragone	1991
Elei	Carolines (Satawan)	Ragone	1991
Leluku	Carolines (Satawan)	Ragone	1991
Mai solap	Carolines (Satawan)	Ragone	1991
Mai ter	Carolines (Satawan)	Ragone	1991
Mei fanal	Carolines (Satawan)	Ragone	1991
Mei oror	Carolines (Satawan)	Ragone	1991
Meias	Carolines (Satawan)	Ragone	1991
Oeng	Carolines (Satawan)	Ragone	1991
Pochar	Carolines (Satawan)	Ragone	1991
Pukileu	Carolines (Satawan)	Ragone	1991
Lukuwal	Carolines (Stokes)	WS Dept. Ag.	1961
Mai n put	Carolines (Stokes)	WS Dept. Ag.	1961
Mammual	Carolines (Stokes)	WS Dept. Ag.	1961
MARIANA ISLANDS			
Dugdug	Guam	Coenan & Barrau	1961
Lemai	Guam	Coenan & Barrau	1961
Palada	Guam	Coenan & Barrau	1961
KIRIBATI			
Bukiraro	Kiribati	Sabatier	1971
Bukiraro	Kiribati	Fiji Dept. Ag.	1961
Mai keang	Kiribati	Fiji Dept. Ag.	1961
Mai kora	Kiribati	Fiji Dept. Ag.	1961
Mai rekereke	Kiribati	Sabatier	1971
Mai uea	Kiribati	Sabatier	1971
Te bukiraro	Kiribati	Catala	1957
Te bukiraro	Kiribati	Ragone	1991
Te keang ni makin	Kiribati	Catala	1957
Te mai	Kiribati	Catala	1957

Local Name	Island	Author	Year
KIRIBATI			
Te mai	Kiribati	Ragone	1991
Te mātarika	Kiribati	Catala	1957
Te motini wae	Kiribati	Catala	1957
Te motiniwae	Kiribati	Ragone	1991
KOSRAE			
Earkon	Kosrae	Safert	1919
Ek in ba	Kosrae	Safert	1919
Ek in fa	Kosrae	Safert	1919
Ek in lik	Kosrae	Safert	1919
Ek un lal	Kosrae	Safert	1919
Elwal wet	Kosrae	Lee	1976
Fok fas	Kosrae	Safert	1919
Fok in kapihn ohr	Kosrae	Lee	1976
Fok in kihsrihk	Kosrae	Lee	1976
Fok keke	Kosrae	Safert	1919
Fok kulo	Kosrae	Safert	1919
Fok kwekwe	Kosrae	Lee	1976
Fok sal	Kosrae	Safert	1919
Fok sesak	Kosrae	Safert	1919
Fokeke	Kosrae	Ragone	1991
Foksrusrak	Kosrae	Lee	1976
Foksrusrak	Kosrae	Ragone	1991
Ikunlal	Kosrae	Ragone	1991
Ikunlal	Kosrae	Lee	1976
Inohl	Kosrae	Lee	1976
Inol	Kosrae	Safert	1919
Inol aw	Kosrae	Ragone	1991
Inol wet	Kosrae	Ragone	1991
Lwactoh	Kosrae	Lee	1976
Mabon	Kosrae	Safert	1919
Mos fwel	Kosrae	Lee	1976
Mos in Kosa	Kosrae	Safert	1919
Mos in Kosra	Kosrae	Ragone	1991
Mos in kosra	Kosrae	Lee	1976
Mos in oa	Kosrae	Safert	1919
Mos in wa	Kosrae	Ragone	1991
Mos in wac	Kosrae	Lee	1976
Mos in wuht	Kosrae	Lee	1976
Mos yohlahp	Kosrae	Lee	1976
Pairkes	Kosrae	Safert	1919
Parkahs	Kosrae	Lee	1976
Parkas	Kosrae	Ragone	1991
Pataktak	Kosrae	Safert	1919
Popol	Kosrae	Ragone	1991
Popol	Kosrae	Lee	1976
Puhtaktuhk	Kosrae	Lee	1976
Puhtaktuhk fok sruhsra	Kosrae	Lee	1976
Putaktak	Kosrae	Ragone	1991
Safon	Kosrae	Safert	1919
Sra fon	Kosrae	Ragone	1991
Sra waseng	Kosrae	Ragone	1991
Sra waseng	Kosrae	Lee	1976
Srafohn	Kosrae	Lee	1976
Sruf	Kosrae	Ragone	1991
Sruf	Kosrae	Lee	1976
Suf	Kosrae	Safert	1919

Local Name	Island	Author	Year
Betakatok	Marshall Islands	Mason	1947
Bilbwillikkaj	Marshall Islands	Mason	1947
Bitakdak	Marshall Islands	Pollock	1970
Bukarel	Marshall Islands	Pollock	1970
Bukdol	Marshall Islands	MacKenzie	1964
Bukdol	Marshall Islands	WS Dept. Ag.	1961
Bukuroi	Marshall Islands	Ragone	1991
Bukuroi	Marshall Islands	Mason	1947
Bwilbwillkkaj	Marshall Islands	MacKenzie	1964
Kibwedoul	Marshall Islands	MacKenzie	1964
Kituro	Marshall Islands	MacKenzie	1964
Koturoro	Marshall Islands	Mason	1947
Lijimanwi	Marshall Islands	Mason	1947
Mabat	Marshall Islands	Abo et al.	1976
Mabat	Marshall Islands	MacKenzie	1964
Madak	Marshall Islands	Abo et al.	1976
Maddak	Marshall Islands	MacKenzie	1964
Madik	Marshall Islands	Abo et al.	1976
Madik	Marshall Islands	MacKenzie	1964
Maijokaar	Marshall Islands	MacKenzie	1964
Maikwe	Marshall Islands	Abo et al.	1976
Maikwe	Marshall Islands	MacKenzie	1964
Majiloklok	Marshall Islands	MacKenzie	1964
Majoklap	Marshall Islands	MacKenzie	1964
Majwaan	Marshall Islands	MacKenzie	1964
Makinono	Marshall Islands	Abo et al.	1976
Makinono	Marshall Islands	MacKenzie	1964
Makole	Marshall Islands	MacKenzie	1964
Makonono	Marshall Islands	Mason	1947
Makwole	Marshall Islands	Abo et al.	1976
Mamwe	Marshall Islands	Abo et al.	1976
Mamwe	Marshall Islands	MacKenzie	1964
Maron	Marshall Islands	Abo et al.	1976
Maron	Marshall Islands	MacKenzie	1964
Mateite	Marshall Islands	Mason	1947
Medak	Marshall Islands	MacKenzie	1964
Mejekolet	Marshall Islands	Pollock	1970
Mejelekelek	Marshall Islands	Mason	1947
Mejenwe	Marshall Islands	MacKenzie	1964
Mejidduul	Marshall Islands	Abo et al.	1976
Mejidduul	Marshall Islands	MacKenzie	1964
Mejokelap	Marshall Islands	Mason	1947
Mejwa	Marshall Islands	MacKenzie	1964
Mejwaan	Marshall Islands	Pollock	1970
Mejwaan	Marshall Islands	Coenan & Barrau	1961
Mejwaan	Marshall Islands	Abo et al.	1976
Mekinono	Marshall Islands	Pollock	1970
Meron	Marshall Islands	Pollock	1970
Metate	Marshall Islands	Pollock	1970
Metete	Marshall Islands	Abo et al.	1976
Metete	Marshall Islands	MacKenzie	1964
Nonnon	Marshall Islands	MacKenzie	1964
Petaaktak	Marshall Islands	Abo et al.	1976
Petaaktak	Marshall Islands	MacKenzie	1964

Local Name	Island	Author	Year
Amarepe	Pohnpei	Raynor	1989
Animwure	Pohnpei	Soucie	1978
Animwure	Pohnpei	Raynor	1989
Animwure	Pohnpei	Ragone	1991
Apil	Pohnpei	Christian	1897
Chai	Pohnpei	Christian	1897
Chaniak	Pohnpei	Christian	1897
En chak	Pohnpei	Christian	1897
En charak	Pohnpei	Christian	1897
En cherrichang	Pohnpei	Christian	1897
En kaualik	Pohnpei	Christian	1897
En kotokot	Pohnpei	Christian	1897
En machal	Pohnpei	Christian	1897
En monei	Pohnpei	Christian	1897
En paipai	Pohnpei	Christian	1897
En pakot	Pohnpei	Christian	1897
En par	Pohnpei	Christian	1897
En patak	Pohnpei	Christian	1897
En polle	Pohnpei	Christian	1897
En ponchakar	Pohnpei	Christian	1897
En put	Pohnpei	Christian	1897
En uaoutak	Pohnpei	Christian	1897
En uchar	Pohnpei	Christian	1897
Impak	Pohnpei	Christian	1897
Kalak	Pohnpei	Christian	1897
Katiu	Pohnpei	Christian	1897
Kirimwot	Pohnpei	Soucie	1978
Kirimwot	Pohnpei	Raynor	1989
Kirimwot	Pohnpei	Raynor	1989
Kirimwot	Pohnpei	Rehg & Sohl	1961
Kirimwot	Pohnpei	Ragone	1991
Koli	Pohnpei	Christian	1897
Kumar	Pohnpei	Christian	1897
Lehtemp	Pohnpei	Soucie	1978
Lehtemp	Pohnpei	Raynor	1989
Lehtemp	Pohnpei	Rehg & Sohl	1961
Letam	Pohnpei	Christian	1897
Letemp	Pohnpei	Sasuke	1953
Letemp (Lehtemp)	Pohnpei	Ragone	1991
Lipet	Pohnpei	Sasuke	1953
Lipet	Pohnpei	Soucie	1978
Lipet	Pohnpei	Kanehira	1931
Lipet	Pohnpei	Christian	1897
Lipet	Pohnpei	Raynor	1989
Lipet	Pohnpei	Ragone	1991
Liptet	Pohnpei	Rehg & Sohl	1961
Luhkual	Pohnpei	Soucie	1978
Luhkual	Pohnpei	Raynor	1989
Luhkual	Pohnpei	Raynor	1989
Luhkual	Pohnpei	Raynor	1989
Luhkual	Pohnpei	Raynor	1989
Lukiamwas	Pohnpei	Soucie	1978
Lukiamwas	Pohnpei	Ragone	1991
Lukiamwas	Pohnpei	Rehg & Sohl	1961
Lukielel	Pohnpei	Sasuke	1953
Lukielel	Pohnpei	Soucie	1978
Lukielel	Pohnpei	Rehg & Sohl	1961
Lukielel	Pohnpei	Ragone	1991
Lukual	Pohnpei	Christian	1897

Local Name	Island	Author	Year
Lukuwal	Pohnpei	Coenan & Barrau	1961
Lukuwal	Pohnpei	Sasuke	1953
Lukuwal	Pohnpei	Rehg & Sohl	1961
Lukuwal	Pohnpei	Fiji Dept. Ag.	1961
Lukwal	Pohnpei	Kanehira	1931
Ma up en salak	Pohnpei	Sasuke	1953
Mai anumol	Pohnpei	Sasuke	1953
Mai ele	Pohnpei	Kanehira	1931
Mai kalak	Pohnpei	Sasuke	1953
Mai kalak	Pohnpei	WS Dept. Ag.	1961
Mai kalak	Pohnpei	Fiji Dept. Ag.	1961
Mai kapeis	Pohnpei	Sasuke	1953
Mai katiya	Pohnpei	Sasuke	1953
Mai kipal	Pohnpei	Sasuke	1953
Mai kiyol	Pohnpei	Sasuke	1953
Mai kohleh	Pohnpei	Glassman	1952
Mai kole	Pohnpei	Sasuke	1953
Mai kulmot	Pohnpei	Sasuke	1953
Mai kuwat	Pohnpei	Sasuke	1953
Mai le	Pohnpei	Sasuke	1953
Mai lukeamas	Pohnpei	Sasuke	1953
Mai maka	Pohnpei	Kanehira	1931
Mai mule	Pohnpei	Sasuke	1953
Mai n nuwe	Pohnpei	WS Dept. Ag.	1961
Mai n nuwe	Pohnpei	Fiji Dept. Ag.	1961
Mai n patak	Pohnpei	WS Dept. Ag.	1961
Mai n patak	Pohnpei	Fiji Dept. Ag.	1961
Mai n put	Pohnpei	Fiji Dept. Ag.	1961
Mai ong	Pohnpei	Sasuke	1953
Mai owa	Pohnpei	Sasuke	1953
Mai pa	Pohnpei	Kanehira	1931
Mai pah	Pohnpei	Glassman	1952
Mai pean	Pohnpei	Kanehira	1931
Mai pehmasi	Pohnpei	Kanehira	1931
Mai petepet	Pohnpei	Sasuke	1953
Mai po	Pohnpei	Sasuke	1953
Mai poko	Pohnpei	Sasuke	1953
Mai pot malola	Pohnpei	Sasuke	1953
Mai potamp	Pohnpei	Sasuke	1953
Mai puilipuul	Pohnpei	Sasuke	1953
Mai puut	Pohnpei	Kanehira	1931
Mai saip	Pohnpei	Sasuke	1953
Mai sarak	Pohnpei	Kanehira	1931
Mai seu	Pohnpei	Sasuke	1953
Mai silisang	Pohnpei	Sasuke	1953
Mai tait	Pohnpei	Kanehira	1931
Mai takai	Pohnpei	Sasuke	1953
Mai tamwarok	Pohnpei	Soucie	1978
Mai tamwoarok	Pohnpei	Raynor	1989
Mai teit	Pohnpei	Coenan & Barrau	1961
Mai teit	Pohnpei	Sasuke	1953
Mai teit	Pohnpei	WS Dept. Ag.	1961
Mai teit	Pohnpei	Fiji Dept. Ag.	1961
Mai tempap	Pohnpei	Sasuke	1953
Mai temuwasil	Pohnpei	Sasuke	1953
Mai tiponue	Pohnpei	Sasuke	1953
Mai tol	Pohnpei	Sasuke	1953
Mai tol	Pohnpei	Kanehira	1931
Mai up	Pohnpei	Coenan & Barrau	1961
Mai up	Pohnpei	Sasuke	1953

Local Name	Island	Author	Year
Mai up	Pohnpei	WS Dept. Ag.	1961
Mai up	Pohnpei	Fiji Dept. Ag.	1961
Mai wake	Pohnpei	Sasuke	1953
Mai woke	Pohnpei	Sasuke	1953
Main apaop	Pohnpei	Sasuke	1953
Main patak	Pohnpei	Sasuke	1953
Main peimuas	Pohnpei	Sasuke	1953
Main pohnkeweneie	Pohnpei	Raynor	1989
Main ponsakal	Pohnpei	Sasuke	1953
Main put	Pohnpei	Sasuke	1953
Main puwal	Pohnpei	Sasuke	1953
Main salak	Pohnpei	Sasuke	1953
Main tampuet	Pohnpei	Sasuke	1953
Main uwe	Pohnpei	Sasuke	1953
Main wol	Pohnpei	Sasuke	1953
Mei ais	Pohnpei	Soucie	1978
Mei ais	Pohnpei	Raynor	1989
Mei akohndrok	Pohnpei	Raynor	1989
Mei arepe	Pohnpei	Soucie	1978
Mei arepe	Pohnpei	Raynor	1989
Mei arephe (aroape)	Pohnpei	Ragone	1991
Mei auleng	Pohnpei	Soucie	1978
Mei auleng	Pohnpei	Raynor	1989
Mei auleng	Pohnpei	Ragone	1991
Mei deipw	Pohnpei	Raynor	1989
Mei epil	Pohnpei	Soucie	1978
Mei epil	Pohnpei	Raynor	1989
Mei epil	Pohnpei	Ragone	1991
Mei kalak	Pohnpei	Soucie	1978
Mei kalak	Pohnpei	Ragone	1991
Mei kalak en kosrae	Pohnpei	Ragone	1991
Mei kalak en meiarepe	Pohnpei	Soucie	1978
Mei kalak en meiarepe	Pohnpei	Raynor	1989
Mei kalak en meikuet	Pohnpei	Soucie	1978
Mei kalak en meikuet	Pohnpei	Raynor	1989
Mei kalak en meiniwe	Pohnpei	Raynor	1989
Mei kalak en meinwe	Pohnpei	Soucie	1978
Mei kalak en meise	Pohnpei	Raynor	1989
Mei kalak en meisei	Pohnpei	Soucie	1978
Mei kapas	Pohnpei	Soucie	1978
Mei kapas	Pohnpei	Raynor	1989
Mei kapas	Pohnpei	Ragone	1991
Mei karat	Pohnpei	Raynor	1989
Mei katakot	Pohnpei	Soucie	1978
Mei katakot	Pohnpei	Raynor	1989
Mei katakot	Pohnpei	Ragone	1991
Mei katik	Pohnpei	Raynor	1989
Mei keke	Pohnpei	Raynor	1989
Mei ketieu	Pohnpei	Soucie	1978
Mei ketieu	Pohnpei	Raynor	1989
Mei ketieu	Pohnpei	Ragone	1991
Mei kewelik	Pohnpei	Soucie	1978
Mei kewelik	Pohnpei	Raynor	1989
Mei kewelik	Pohnpei	Ragone	1991
Mei kidi	Pohnpei	Soucie	1978
Mei kidi	Pohnpei	Raynor	1989
Mei kidi	Pohnpei	Ragone	1991
Mei kihmwer	Pohnpei	Raynor	1989
Mei kimwear	Pohnpei	Ragone	1991
Mei kimwer	Pohnpei	Soucie	1978

Local Name	Island	Author	Year
Mei kiol	Pohnpei	Soucie	1978
Mei kiol	Pohnpei	Raynor	1989
Mei kiol	Pohnpei	Ragone	1991
Mei kipal	Pohnpei	Soucie	1978
Mei kipal	Pohnpei	Raynor	1989
Mei kipal	Pohnpei	Ragone	1991
Mei kitik	Pohnpei	Soucie	1978
Mei kiuk	Pohnpei	Raynor	1989
Mei kituk	Pohnpei	Ragone	1991
Mei koid (koi)	Pohnpei	Ragone	1991
Mei kokehmwot	Pohnpei	Soucie	1978
Mei kole	Pohnpei	Raynor	1989
Mei kole	Pohnpei	Ragone	1991
Mei kolewmot	Pohnpei	Raynor	1989
Mei kuet	Pohnpei	Soucie	1978
Mei kuet	Pohnpei	Raynor	1989
Mei kuet	Pohnpei	Ragone	1991
Mei kuet in mei kalak	Pohnpei	Ragone	1991
Mei kuet in mein uwe	Pohnpei	Ragone	1991
Mei kuli	Pohnpei	Ragone	1991
Mei li	Pohnpei	Raynor	1989
Mei li	Pohnpei	Ragone	1991
Mei lingkarahk	Pohnpei	Raynor	1989
Mei lingkarahk	Pohnpei	Ragone	1991
Mei loangon	Pohnpei	Raynor	1989
Mei long	Pohnpei	Raynor	1989
Mei long	Pohnpei	Ragone	1991
Mei luhr	Pohnpei	Soucie	1978
Mei luhr	Pohnpei	Raynor	1989
Mei luhr	Pohnpei	Ragone	1991
Mei marahra	Pohnpei	Soucie	1978
Mei marahra	Pohnpei	Raynor	1989
Mei marahra	Pohnpei	Ragone	1991
Mei mesehl	Pohnpei	Ragone	1991
Mei moang	Pohnpei	Raynor	1989
Mei mong	Pohnpei	Ragone	1991
Mei muhle	Pohnpei	Raynor	1989
Mei muhle	Pohnpei	Ragone	1991
Mei mwed	Pohnpei	Soucie	1978
Mei mwed	Pohnpei	Raynor	1989
Mei mwed	Pohnpei	Ragone	1991
Mei oang	Pohnpei	Soucie	1978
Mei oang	Pohnpei	Raynor	1989
Mei oang	Pohnpei	Ragone	1991
Mei olodung	Pohnpei	Soucie	1978
Mei olodung	Pohnpei	Raynor	1989
Mei olodung	Pohnpei	Ragone	1991
Mei omp	Pohnpei	Raynor	1989
Mei pa	Pohnpei	Soucie	1978
Mei pa	Pohnpei	Raynor	1989
Mei pah	Pohnpei	Ragone	1991
Mei pahnie	Pohnpei	Raynor	1989
Mei pahie	Pohnpei	Raynor	1989
Mei peimwas	Pohnpei	Raynor	1989
Mei pikos	Pohnpei	Raynor	1989
Mei pkot	Pohnpei	Sasuke	1953
Mei poang	Pohnpei	Soucie	1978
Mei poang	Pohnpei	Raynor	1989
Mei pohnoulal	Pohnpei	Soucie	1978
Mei pohnoulal	Pohnpei	Ragone	1991

Local Name	Island	Author	Year
Mei pohntakai	Pohnpei	Raynor	1989
Mei puilipuil	Pohnpei	Soucie	1978
Mei puilipuil	Pohnpei	Raynor	1989
Mei puilipuil	Pohnpei	Ragone	1991
Mei pwahr	Pohnpei	Ragone	1991
Mei pwet	Pohnpei	Raynor	1989
Mei pwet	Pohnpei	Ragone	1991
Mei pwetepwet	Pohnpei	Soucie	1978
Mei pwetepwet	Pohnpei	Raynor	1989
Mei pwetepwet	Pohnpei	Ragone	1991
Mei pwiliet	Pohnpei	Soucie	1978
Mei pwiliet	Pohnpei	Raynor	1989
Mei pwiliet	Pohnpei	Ragone	1991
Mei pwuhleŋg	Pohnpei	Soucie	1978
Mei pwuhleŋg	Pohnpei	Raynor	1989
Mei pwuhleŋg	Pohnpei	Ragone	1991
Mei pwuht	Pohnpei	Raynor	1989
Mei pwuht en lmwahni	Pohnpei	Raynor	1989
Mei pwuht en sokehs	Pohnpei	Raynor	1989
Mei saip	Pohnpei	Soucie	1978
Mei saip	Pohnpei	Raynor	1989
Mei saip	Pohnpei	Ragone	1991
Mei sapwahpw	Pohnpei	Soucie	1978
Mei sapwahpw	Pohnpei	Raynor	1989
Mei sapwahpw	Pohnpei	Ragone	1991
Mei se	Pohnpei	Soucie	1978
Mei se	Pohnpei	Raynor	1989
Mei se	Pohnpei	Ragone	1991
Mei sei	Pohnpei	Soucie	1978
Mei sei	Pohnpei	Raynor	1989
Mei sei	Pohnpei	Ragone	1991
Mei serihseng	Pohnpei	Ragone	1991
Mei takai	Pohnpei	Raynor	1989
Mei tamwarok	Pohnpei	Ragone	1991
Mei tehid	Pohnpei	Soucie	1978
Mei tehid	Pohnpei	Raynor	1989
Mei tehid (toahid)	Pohnpei	Ragone	1991
Mei tehid en mei sarak	Pohnpei	Ragone	1991
Mei tek	Pohnpei	Raynor	1989
Mei tek	Pohnpei	Ragone	1991
Mei tempap	Pohnpei	Soucie	1978
Mei tempap	Pohnpei	Raynor	1989
Mei tempap	Pohnpei	Ragone	1991
Mei ti	Pohnpei	Soucie	1978
Mei ti	Pohnpei	Raynor	1989
Mei ti	Pohnpei	Ragone	1991
Mei tikapau	Pohnpei	Soucie	1978
Mei tikapau	Pohnpei	Raynor	1989
Mei tikapau	Pohnpei	Ragone	1991
Mei toal	Pohnpei	Soucie	1978
Mei toal	Pohnpei	Raynor	1989
Mei toal ehume katik	Pohnpei	Soucie	1978
Mei toal en lapar	Pohnpei	Raynor	1989
Mei toal en oarou	Pohnpei	Raynor	1989
Mei toal sohŋe katik	Pohnpei	Soucie	1978
Mei toantoal	Pohnpei	Raynor	1989
Mei tol (toal)	Pohnpei	Ragone	1991
Mei tol en lapar	Pohnpei	Ragone	1991
Mei tomworok	Pohnpei	Ragone	1991
Mei uhp	Pohnpei	Soucie	1978

Local Name	Island	Author	Year
Mei uhp	Pohnpei	Raynor	1989
Mei uhp en Samoa	Pohnpei	Raynor	1989
Mei uhpw	Pohnpei	Ragone	1991
Mei umpwei	Pohnpei	Raynor	1989
Mei upenserek	Pohnpei	Soucie	1978
Mei upenserek	Pohnpei	Raynor	1989
Mei upenserek	Pohnpei	Ragone	1991
Mei utuhnpei	Pohnpei	Raynor	1989
Mei wehwe	Pohnpei	Soucie	1978
Mei wehwe	Pohnpei	Raynor	1989
Mei weke	Pohnpei	Soucie	1978
Mei wid	Pohnpei	Soucie	1978
Mei woke	Pohnpei	Raynor	1989
Mei woke (weke)	Pohnpei	Ragone	1991
Meiais	Pohnpei	Rehg & Sohl	1961
Meiapaup	Pohnpei	Rehg & Sohl	1961
Meiarepe	Pohnpei	Rehg & Sohl	1961
Meikalak	Pohnpei	Rehg & Sohl	1961
Meikidi	Pohnpei	Rehg & Sohl	1961
Meikimwer	Pohnpei	Rehg & Sohl	1961
Meikole	Pohnpei	Soucie	1978
Meikole	Pohnpei	Rehg & Sohl	1961
Meikuwet	Pohnpei	Rehg & Sohl	1961
Meilwmahni	Pohnpei	Soucie	1978
Meimwed	Pohnpei	Rehg & Sohl	1961
Mein ahdor	Pohnpei	Raynor	1989
Mein ahndor	Pohnpei	Soucie	1978
Mein ahnoor	Pohnpei	Ragone	1991
Mein anihmwoll	Pohnpei	Raynor	1989
Mein anihnmwoll	Pohnpei	Soucie	1978
Mein anihnomwoll	Pohnpei	Ragone	1991
Mein anuhsar	Pohnpei	Raynor	1989
Mein enguhp	Pohnpei	Soucie	1978
Mein enguhp	Pohnpei	Raynor	1989
Mein enguhp	Pohnpei	Ragone	1991
Mein enimwure	Pohnpei	Raynor	1989
Mein ihmwed	Pohnpei	Raynor	1989
Mein ihwe	Pohnpei	Soucie	1978
Mein ihwor	Pohnpei	Raynor	1989
Mein impei	Pohnpei	Soucie	1978
Mein impei	Pohnpei	Raynor	1989
Mein impei	Pohnpei	Ragone	1991
Mein intoal	Pohnpei	Raynor	1989
Mein ipwidi	Pohnpei	Raynor	1989
Mein iwe	Pohnpei	Raynor	1989
Mein kalak	Pohnpei	Ragone	1991
Mein kohrari	Pohnpei	Raynor	1989
Mein lingkarahk	Pohnpei	Ragone	1991
Mein litokpwuri	Pohnpei	Raynor	1989
Mein mall	Pohnpei	Raynor	1989
Mein mesehl	Pohnpei	Soucie	1978
Mein mesehl	Pohnpei	Raynor	1989
Mein mesehl	Pohnpei	Ragone	1991
Mein muhle	Pohnpei	Soucie	1978
Mein mweli	Pohnpei	Raynor	1989
Mein mwelihtik	Pohnpei	Soucie	1978
Mein mwelihtik	Pohnpei	Raynor	1989
Mein mwelihtik	Pohnpei	Ragone	1991
Mein mwnakot	Pohnpei	Soucie	1978
Mein mwnakot	Pohnpei	Raynor	1989

Local Name	Island	Author	Year
Mein mwnakot	Pohnpei	Ragone	1991
Mein mwohne	Pohnpei	Raynor	1989
Mein mwohne	Pohnpei	Ragone	1991
Mein ohwa	Pohnpei	Raynor	1989
Mein padahk	Pohnpei	Rehg & Sohl	1961
Mein pahnwi	Pohnpei	Raynor	1989
Mein pakahk	Pohnpei	Soucie	1978
Mein pakahk	Pohnpei	Raynor	1989
Mein pakahk en meiniwe	Pohnpei	Raynor	1989
Mein patak	Pohnpei	Coenan & Barrau	1961
Mein patak (padahk)	Pohnpei	Ragone	1991
Mein peimwas	Pohnpei	Ragone	1991
Mein peimwas	Pohnpei	Rehg & Sohl	1961
Mein peipei	Pohnpei	Soucie	1978
Mein peipei	Pohnpei	Raynor	1989
Mein peipei	Pohnpei	Ragone	1991
Mein peisahle	Pohnpei	Soucie	1978
Mein peisahle	Pohnpei	Raynor	1989
Mein peisahle	Pohnpei	Ragone	1991
Mein pek	Pohnpei	Raynor	1989
Mein poakod	Pohnpei	Soucie	1978
Mein poakod	Pohnpei	Raynor	1989
Mein poakod	Pohnpei	Ragone	1991
Mein pohn pahn wi	Pohnpei	Ragone	1991
Mein pohnkeweneie	Pohnpei	Soucie	1978
Mein pohnkeweneie	Pohnpei	Ragone	1991
Mein pohnkoatoa	Pohnpei	Soucie	1978
Mein pohnkoatoa	Pohnpei	Raynor	1989
Mein pohnkoatoa	Pohnpei	Ragone	1991
Mein pohnle	Pohnpei	Soucie	1978
Mein pohnle	Pohnpei	Raynor	1989
Mein pohnoulal	Pohnpei	Raynor	1989
Mein pohnpahnwi	Pohnpei	Raynor	1989
Mein pohnsakar	Pohnpei	Soucie	1978
Mein pohnsakar	Pohnpei	Raynor	1989
Mein pohnsakar	Pohnpei	Ragone	1991
Mein pohnsakar	Pohnpei	Rehg & Sohl	1961
Mein pohtakai	Pohnpei	Soucie	1978
Mein pohtakai	Pohnpei	Ragone	1991
Mein pong (poang)	Pohnpei	Ragone	1991
Mein pwahr	Pohnpei	Soucie	1978
Mein pwahr	Pohnpei	Raynor	1989
Mein pwahr	Pohnpei	Ragone	1991
Mein pwahr	Pohnpei	Rehg & Sohl	1961
Mein pweimwas	Pohnpei	Soucie	1978
Mein pwuht	Pohnpei	Soucie	1978
Mein pwuht	Pohnpei	Rehg & Sohl	1961
Mein pwuht (puht)	Pohnpei	Ragone	1991
Mein pwuht en sohehs	Pohnpei	Soucie	1978
Mein sahref	Pohnpei	Rehg & Sohl	1961
Mein sakaresei	Pohnpei	Raynor	1989
Mein sakaresei	Pohnpei	Raynor	1989
Mein sanipwur	Pohnpei	Soucie	1978
Mein sanipwur	Pohnpei	Raynor	1989
Mein sapwehrek	Pohnpei	Soucie	1978
Mein sapwehrek	Pohnpei	Ragone	1991
Mein sapwerek	Pohnpei	Raynor	1989
Mein seinpwur	Pohnpei	Ragone	1991
Mein seniak	Pohnpei	Soucie	1978
Mein seniak	Pohnpei	Raynor	1989

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Mein seniak	Pohnpei	Ragone	1991
Mein serih seng	Pohnpei	Soucie	1978
Mein serih seng	Pohnpei	Ragone	1991
Mein seriseng	Pohnpei	Raynor	1989
Mein takai	Pohnpei	Soucie	1978
Mein tihnpopap	Pohnpei	Raynor	1989
Mein uhsar	Pohnpei	Soucie	1978
Mein uhsar	Pohnpei	Raynor	1989
Mein uhsar	Pohnpei	Ragone	1991
Mein utuhn	Pohnpei	Soucie	1978
Mein utuhn	Pohnpei	Raynor	1989
Mein utuhn	Pohnpei	Ragone	1991
Mein uwe (we)	Pohnpei	Ragone	1991
Mein weli	Pohnpei	Soucie	1978
Mein weli	Pohnpei	Ragone	1991
Mein wet	Pohnpei	Raynor	1989
Mein wol	Pohnpei	Soucie	1978
Mein wol	Pohnpei	Raynor	1989
Mein wol	Pohnpei	Ragone	1991
Meinmesehl	Pohnpei	Ragone	1991
Meinpwuten sokehs	Pohnpei	Rehg & Sohl	1961
Meinuwe	Pohnpei	Rehg & Sohl	1961
Meipa	Pohnpei	Rehg & Sohl	1961
Meipwiliet	Pohnpei	Rehg & Sohl	1961
Meipwuh leng	Pohnpei	Rehg & Sohl	1961
Meisaip	Pohnpei	Rehg & Sohl	1961
Meise	Pohnpei	Rehg & Sohl	1961
Meisei	Pohnpei	Rehg & Sohl	1961
Meiserih seng	Pohnpei	Rehg & Sohl	1961
Meitehid	Pohnpei	Rehg & Sohl	1961
Meiti	Pohnpei	Rehg & Sohl	1961
Meitoal	Pohnpei	Rehg & Sohl	1961
Meiuhpw	Pohnpei	Rehg & Sohl	1961
Meiweke	Pohnpei	Rehg & Sohl	1961
Men ihwer	Pohnpei	Soucie	1978
Nahnmwai	Pohnpei	Soucie	1978
Nahnmwai	Pohnpei	Ragone	1991
Nahnmwai	Pohnpei	Rehg & Sohl	1961
Nakont	Pohnpei	Christian	1897
Nanimal	Pohnpei	Kanehira	1931
Nanmwai	Pohnpei	Raynor	1989
Nanumal	Pohnpei	Christian	1897
Niuer	Pohnpei	Christian	1897
Nue	Pohnpei	Christian	1897
Nunmual	Pohnpei	Fiji Dept. Ag.	1961
Opohp	Pohnpei	Soucie	1978
Pa	Pohnpei	Christian	1897
Paimach	Pohnpei	Christian	1897
Paramitsu	Pohnpei	Soucie	1978
Ponpanui	Pohnpei	Christian	1897
Potopot	Pohnpei	Christian	1897
Pueteput	Pohnpei	Christian	1897
Pulang	Pohnpei	Christian	1897
Pwumpwum	Pohnpei	Soucie	1978
Pwumpwum	Pohnpei	Raynor	1989
Pwumpwupu	Pohnpei	Ragone	1991
Sangkamawahu	Pohnpei	Soucie	1978
Sangkamawahu	Pohnpei	Ragone	1991
Sangkamawahu	Pohnpei	Raynor	1989
Tahitian	Pohnpei	Ragone	1991

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POHNPEI			
Taik	Pohnpei	Christian	1897
Takai	Pohnpei	Christian	1897
Ti	Pohnpei	Christian	1897
Tol	Pohnpei	Christian	1897
Uaka	Pohnpei	Christian	1897
Utuhn pei	Pohnpei	Ragone	1991
Yong	Pohnpei	Christian	1897
Tikul nukuor	Pohnpei (Nukuoro)	Coenan & Barrau	1961
TOKELAU			
Mafala	Tokelau	Lambert	1974
Ulu afa	Tokelau	Lambert	1974
Ulu afa	Tokelau	Ragone	1991
Ulu ehile	Tokelau	Lambert	1974
Ulu elise	Tokelau	Ragone	1991
Ulu elise	Tokelau	WS Dept. Ag.	1959
Ulu hamoa	Tokelau	Lambert	1974
TRUK			
Abiraw	Truk	Raynor	1989
Achapar	Truk	Ragone	1991
Achapar	Truk	Elbert	1947
Aemaron	Truk	WS Dept. Ag.	1961
Affo	Truk	Ragone	1991
Affo	Truk	Raynor	1989
Ammech	Truk	Ragone	1991
Aniken	Truk	Ragone	1991
Annumur	Truk	Ragone	1991
Annumur	Truk	Raynor	1989
Apinauwa	Truk	Elbert	1947
Bochon	Truk	Ragone	1991
Bwikelew	Truk	Ragone	1991
Chifen	Truk	Elbert	1947
Chomon	Truk	Elbert	1947
Emmech	Truk	Raynor	1989
Eniken	Truk	Elbert	1947
Eniken	Truk	Raynor	1989
Eniken	Truk	WS Dept. Ag.	1961
Enim	Truk	Elbert	1947
Ennim	Truk	Ragone	1991
Ennim	Truk	Raynor	1989
Epinauo	Truk	Ragone	1991
Epirau	Truk	Elbert	1947
Faine	Truk	Ragone	1991
Faine	Truk	Elbert	1947
Faine	Truk	Raynor	1989
Faior	Truk	Elbert	1947
Faiton	Truk	Elbert	1947
Fakun	Truk	Elbert	1947
Fanpwosuk	Truk	Elbert	1947
Irra	Truk	Ragone	1991
Kisengei	Truk	Elbert	1947
Leluku	Truk	Ragone	1991
Lepeito	Truk	Ragone	1991
Letemp	Truk	Bascom	1946
Linet	Truk	Bascom	1946
Loki	Truk	Bascom	1946
Lokiamwas	Truk	Bascom	1946
Lokielel	Truk	Bascom	1946
Lokiepwet	Truk	Bascom	1946
Lukual	Truk	Bascom	1946

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Mai arapa	Truk	Bascom	1946
Mai chon	Truk	Useem	1946
Mai chon	Truk	Hall & Pelzer	1946
Mai kalak	Truk	Bascom	1946
Mai katieu	Truk	Bascom	1946
Mai kiol	Truk	Bascom	1946
Mai koch	Truk	Useem	1946
Mai koch	Truk	Hall & Pelzer	1946
Mai kole	Truk	Bascom	1946
Mai kuet	Truk	Bascom	1946
Mai li	Truk	Bascom	1946
Mai on	Truk	Useem	1946
Mai on	Truk	Hall & Pelzer	1946
Mai pa (Mai mat)	Truk	Bascom	1946
Mai patak	Truk	Bascom	1946
Mai pwet	Truk	Bascom	1946
Mai pwiliet	Truk	Bascom	1946
Mai sa	Truk	Bascom	1946
Mai taith	Truk	Bascom	1946
Mai ti	Truk	Bascom	1946
Mai tol	Truk	Bascom	1946
Mai up	Truk	Bascom	1946
Mai woke	Truk	Bascom	1946
Main kotakot	Truk	Bascom	1946
Main ponsakar	Truk	Bascom	1946
Main serisang	Truk	Bascom	1946
Main usar	Truk	Bascom	1946
Masae	Truk	Elbert	1947
Mei chon	Truk	Coenan & Barrau	1961
Mei chon	Truk	Ragone	1991
Mei chon	Truk	Elbert	1947
Mei chonun pwonapei	Truk	Elbert	1947
Mei choput	Truk	Elbert	1947
Mei fanang	Truk	Elbert	1947
Mei koch	Truk	Coenan & Barrau	1961
Mei koch	Truk	Ragone	1991
Mei koch	Truk	Elbert	1947
Mei koch chomon	Truk	Elbert	1947
Mei motou	Truk	Elbert	1947
Mei moutu (uninaf)	Truk	Elbert	1947
Mei nifa	Truk	Elbert	1947
Mei nipis	Truk	Elbert	1947
Mei on	Truk	Elbert	1947
Mei pwo	Truk	Elbert	1947
Mei pwoch	Truk	Elbert	1947
Mei sop	Truk	Elbert	1947
Mei ter	Truk	Elbert	1947
Mei ton	Truk	Elbert	1947
Meichocho	Truk	Ragone	1991
Meichon	Truk	WS Dept. Ag.	1961
Meicon	Truk	LeBar	1964
Meikipin	Truk	Raynor	1989
Meikoch	Truk	Raynor	1989
Meikoch	Truk	WS Dept. Ag.	1961
Meikoeng	Truk	Ragone	1991
Mein fanal	Truk	Ragone	1991
Meinifa	Truk	Raynor	1989
Meinipis	Truk	Ragone	1991
Meinipis	Truk	Raynor	1989
Meion	Truk	Raynor	1989

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Meiror	Truk	LeBar	1964
Meiter	Truk	LeBar	1964
Meiter	Truk	Ragone	1991
Memtol	Truk	Bascom	1946
Merip	Truk	Elbert	1947
Mesekai	Truk	Ragone	1991
Mesimech	Truk	Ragone	1991
Mesochon	Truk	Elbert	1947
Monuken	Truk	Elbert	1947
Mura	Truk	Ragone	1991
Mura	Truk	Raynor	1989
Murus	Truk	Elbert	1947
Nanumwal	Truk	Bascom	1946
Napar	Truk	Elbert	1947
Neachen	Truk	Raynor	1989
Neapar	Truk	Ragone	1991
Nei on	Truk	Elbert	1947
Nenian	Truk	Ragone	1991
Neonata	Truk	Ragone	1991
Neonata	Truk	Raynor	1989
Nepaso	Truk	Elbert	1947
Nepat	Truk	Elbert	1947
Nepopo	Truk	Ragone	1991
Nepopo	Truk	Raynor	1989
Neson	Truk	Elbert	1947
Nesoso	Truk	Ragone	1991
Nesoso	Truk	Elbert	1947
Newota	Truk	Elbert	1947
Nipouch	Truk	Ragone	1991
Nippuch	Truk	Elbert	1947
Nipweni	Truk	Elbert	1947
Niteikepar	Truk	Elbert	1947
Nonuka	Truk	Raynor	1989
Ofa	Truk	LeBar	1964
Ofa	Truk	WS Dept. Ag.	1961
Oneas	Truk	Elbert	1947
Ongi	Truk	Elbert	1947
Oniunio	Truk	Ragone	1991
Onommur	Truk	Elbert	1947
Onunio	Truk	Raynor	1989
Pompop	Truk	Bascom	1946
Pono	Truk	Elbert	1947
Ropo	Truk	Ragone	1991
Ropwo	Truk	Elbert	1947
Sawan	Truk	Useem	1946
Sawan	Truk	Elbert	1947
Sawan	Truk	Hall & Pelzer	1946
Senian	Truk	Ragone	1991
Sewan	Truk	Ragone	1991
Toch	Truk	Elbert	1947
Tuni	Truk	Elbert	1947
Unifitun	Truk	Elbert	1947
Unupeison	Truk	Elbert	1947
Uwanau	Truk	Elbert	1947
Uwanaw	Truk	Raynor	1989
Weang	Truk	Ragone	1991
Winiko	Truk	Ragone	1991
Winiko	Truk	Raynor	1989
Winiwin	Truk	Elbert	1947
Wolumar	Truk	WS Dept. Ag.	1961

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TUVALU			
Mei Funafuti	Tuvalu	Tuvalu Dept. Ag	1982
Mei aveloa	Tuvalu	Chambers (Bish)	1974
Mei aveloa	Tuvalu	Tuvalu Dept. Ag	1982
Mei butaritari	Tuvalu	Chambers (Bish)	1974
Mei faka Vaitupu	Tuvalu	Tuvalu Dept. Ag	1982
Mei falaua	Tuvalu	Chambers (Bish)	1974
Mei fuamaulalo	Tuvalu	Tuvalu Dept. Ag	1982
Mei laumaile	Tuvalu	Tuvalu Dept. Ag	1982
Mei maafala	Tuvalu	Tuvalu Dept. Ag	1982
Mei nanumanga	Tuvalu	Chambers (Bish)	1974
Mei nanumea	Tuvalu	Chambers (Bish)	1974
Mei pokeekee	Tuvalu	Chambers (Bish)	1974
Mei pokeke	Tuvalu	Tuvalu Dept. Ag	1982
Te bokene	Tuvalu	Fiji Dept. Ag.	1961
Te mai	Tuvalu	Fiji Dept. Ag.	1961
Te mazarika	Tuvalu	Fiji Dept. Ag.	1961
YAP			
Chaguy	Yap	Ragone	1991
Fanam	Yap	Ragone	1991
Fanum	Yap	Christian	1899
Foonam	Yap	Jensen	1977
Iaotathen	Yap	Christian	1899
Luathar	Yap	Christian	1899
Luthar	Yap	Ragone	1991
Maagayaang	Yap	Jensen	1977
Magyang	Yap	Ragone	1991
Mai nior	Yap	Christian	1899
Manyor	Yap	Ragone	1991
Meenyoer	Yap	Jensen	1977
Paaqaaw	Yap	Jensen	1977
Peau	Yap	Christian	1899
Pemathau	Yap	Christian	1899
Tagafei	Yap	Christian	1899
Tagfay	Yap	Ragone	1991
Tagfiy	Yap	Jensen	1977
Yaereb	Yap	Christian	1899
Yalqath	Yap	Jensen	1977
Yaolei	Yap	Christian	1899
Yaouat	Yap	Christian	1899
Yeotui	Yap	Christian	1899
Yoareb	Yap	Ragone	1991
Yooqriib	Yap	Jensen	1977
Yugoi	Yap	Christian	1899
Yuley	Yap	Ragone	1991
Yuluwach	Yap	Ragone	1991
Yungalu	Yap	Christian	1899
Yunguluw	Yap	Ragone	1991
Yupof	Yap	Ragone	1991
Yutuy	Yap	Ragone	1991
Yuubgil	Yap	Jensen	1977
Yuul'iy	Yap	Jensen	1977
Yuungluw	Yap	Jensen	1977
Yuut'uuy	Yap	Jensen	1977

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POLYNESIA			
COOK ISLANDS			
Amoa	Cook Islands	WS Dept. Ag.	1964
Aru	Cook Islands	WS Dept. Ag.	1964
Kaka	Cook Islands	WS Dept. Ag.	1964
Kuku oi	Cook Islands	WS Dept. Ag.	1964
Kuru atu	Cook Islands	Ragone	1991
Kuru atu	Cook Islands	Savage	1962
Kuru atu	Cook Islands	Wilder	1931
Kuru atu	Cook Islands	Cheeseman	1903
Kuru enua (Maori)	Cook Islands	Ragone	1991
Kuru koviri	Cook Islands	Ragone	1991
Kuru maori	Cook Islands	Savage	1962
Kuru maori	Cook Islands	Wilder	1931
Kuru maori	Cook Islands	Cheeseman	1903
Kuru morava	Cook Islands	Ragone	1991
Kuru niue	Cook Islands	Ragone	1991
Kuru oeoe	Cook Islands	Savage	1962
Kuru oi	Cook Islands	Ragone	1991
Kuru pa'i	Cook Islands	Ragone	1991
Kuru pae	Cook Islands	Buck	1927
Kuru pae'a (Patea)	Cook Islands	Ragone	1991
Kuru pateā	Cook Islands	Savage	1962
Kuru pateā	Cook Islands	Wilder	1931
Kuru pateā	Cook Islands	Buck	1927
Kuru peka	Cook Islands	Savage	1962
Kuru peka	Cook Islands	Ragone	1991
Kuru peka	Cook Islands	Wilder	1931
Kuru peti	Cook Islands	Ragone	1991
Kuru rotuma	Cook Islands	Buck	1927
Kuru taratara	Cook Islands	Savage	1962
Kuru taratara	Cook Islands	Ragone	1991
Kuru tartara	Cook Islands	Wilder	1931
Kuru tavake	Cook Islands	Ragone	1991
Kuru toto	Cook Islands	Ragone	1991
Maori	Cook Islands	WS Dept. Ag.	1964
Morava	Cook Islands	WS Dept. Ag.	1964
Patea	Cook Islands	Cheeseman	1903
Patea	Cook Islands	WS Dept. Ag.	1964
Puero	Cook Islands	WS Dept. Ag.	1964
Rare autia	Cook Islands	WS Dept. Ag.	1964
Tahitian	Cook Islands	Ragone	1991
Tahitian	Cook Islands	WS Dept. Ag.	1964
Tatara	Cook Islands	Cheeseman	1903
Toto	Cook Islands	WS Dept. Ag.	1964
OUTLIER ISLANDS			
Aregō	Fiji (Lau)	Fox	1974
Kekena	Fiji (Lau)	Fox	1974
Mbalekana	Fiji (Lau)	Thompson	1940
Mbutō	Fiji (Lau)	Thompson	1940
Miramira	Fiji (Lau)	Thompson	1940
Rau'ai	Fiji (Lau)	Fox	1974
Uto nitchina	Fiji (Lau)	Thompson	1940
Uto yalewa	Fiji (Lau)	Thompson	1940
Ave'aveloioa	Futuna	Burrows	1936
Kea	Futuna	Burrows	1936
Kuta	Futuna	Burrows	1936
Lautoko ma'opo	Futuna	Burrows	1936
Mei fau	Futuna	Burrows	1936
Mei laupakapaka	Futuna	Burrows	1936

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OUTLIER ISLANDS			
Puou	Futuna	Burrows	1936
Talatala	Futuna	Burrows	1936
Tikul dewed	Kapingimarangi	Coenan & Barrau	1961
Tikul kirinis	Kapingimarangi	Coenan & Barrau	1961
Tikul pawer	Kapingimarangi	Coenan & Barrau	1961
MARQUESAS			
Mei aeka	Marquesas	Wester	1924
Mei amoa	Marquesas	Jardin	1862
Mei au kohekohe	Marquesas	Ragone	1991
Mei aueka	Marquesas	Ragone	1991
Mei auena	Marquesas	Christian	1910
Mei aukape	Marquesas	Ragone	1991
Mei aukohe	Marquesas	Ragone	1991
Mei aukohi	Marquesas	Wester	1924
Mei autea	Marquesas	Christian	1910
Mei epau pipii	Marquesas	Jardin	1862
Mei euea	Marquesas	Jardin	1862
Mei fafaua	Marquesas	Wester	1924
Mei fafaua	Marquesas	Christian	1910
Mei haapuuu	Marquesas	Christian	1910
Mei hahaua	Marquesas	Jardin	1862
Mei haupahu	Marquesas	Wester	1924
Mei hetutu	Marquesas	Christian	1910
Mei hiitevai	Marquesas	Ragone	1991
Mei hinu	Marquesas	Christian	1910
Mei hoi	Marquesas	Ragone	1991
Mei hoi	Marquesas	Christian	1910
Mei huihui	Marquesas	Jardin	1862
Mei kakano	Marquesas	Ragone	1991
Mei kakano-koemohomoho	Marquesas	Christian	1910
Mei kauhiva	Marquesas	Jardin	1862
Mei kauhiva	Marquesas	Ragone	1991
Mei kavekave aheke	Marquesas	Jardin	1862
Mei kiekie	Marquesas	Jardin	1862
Mei kiekie koui	Marquesas	Wester	1924
Mei kihohaa	Marquesas	Jardin	1862
Mei kiihi	Marquesas	Ragone	1991
Mei kiitahi	Marquesas	Jardin	1862
Mei kipokipo	Marquesas	Jardin	1862
Mei koka	Marquesas	Christian	1910
Mei kokaupopoto	Marquesas	Jardin	1862
Mei kokipo	Marquesas	Wester	1924
Mei komanu	Marquesas	Jardin	1862
Mei komanu	Marquesas	Ragone	1991
Mei konini	Marquesas	Ragone	1991
Mei konini	Marquesas	Wester	1924
Mei koopupu	Marquesas	Jardin	1862
Mei koopupu	Marquesas	Ragone	1991
Mei koopupu	Marquesas	Wester	1924
Mei kootea	Marquesas	Jardin	1862
Mei kopumoko	Marquesas	Ragone	1991
Mei koufau	Marquesas	Christian	1910
Mei koui	Marquesas	Jardin	1862
Mei kuahe	Marquesas	Jardin	1862
Mei kuahe	Marquesas	Wester	1924
Mei kuanui	Marquesas	Ragone	1991
Mei kuhuvahaka	Marquesas	Jardin	1862
Mei kuu matuke	Marquesas	Jardin	1862
Mei kuuhaa	Marquesas	Jardin	1862

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Mei kuuhaa	Marquesas	Ragone	1991
Mei kuukou	Marquesas	Christian	1910
Mei kuutaa	Marquesas	Jardin	1862
Mei kuuvahane	Marquesas	Wester	1924
Mei kuuvahane	Marquesas	Christian	1910
Mei maie	Marquesas	Christian	1910
Mei maikiouhoi	Marquesas	Jardin	1862
Mei mamaitavaka	Marquesas	Wester	1924
Mei maoui	Marquesas	Ragone	1991
Mei maoui	Marquesas	Wester	1924
Mei maoui	Marquesas	Christian	1910
Mei mapua	Marquesas	Christian	1910
Mei moepua	Marquesas	Ragone	1991
Mei mohomoho	Marquesas	Christian	1910
Mei movai	Marquesas	Christian	1910
Mei oha	Marquesas	Jardin	1862
Mei orihu	Marquesas	Christian	1910
Mei otai	Marquesas	Christian	1910
Mei ouape	Marquesas	Christian	1910
Mei oukape	Marquesas	Jardin	1862
Mei ovai	Marquesas	Wester	1924
Mei pae'a	Marquesas	Ragone	1991
Mei paotu	Marquesas	Ragone	1991
Mei patiotio	Marquesas	Jardin	1862
Mei patuki	Marquesas	Ragone	1991
Mei patuki	Marquesas	Wester	1924
Mei pavai	Marquesas	Wester	1924
Mei pepeti	Marquesas	Wester	1924
Mei pihiti	Marquesas	Jardin	1862
Mei pimata	Marquesas	Ragone	1991
Mei pimata	Marquesas	Wester	1924
Mei piohe	Marquesas	Christian	1910
Mei pipi	Marquesas	Christian	1910
Mei pitaetae	Marquesas	Christian	1910
Mei pitake	Marquesas	Jardin	1862
Mei piti	Marquesas	Christian	1910
Mei pohata	Marquesas	Jardin	1862
Mei pohauta	Marquesas	Wester	1924
Mei puahi	Marquesas	Christian	1910
Mei puau	Marquesas	Jardin	1862
Mei puau	Marquesas	Ragone	1991
Mei puau	Marquesas	Wester	1924
Mei puero	Marquesas	Ragone	1991
Mei puou	Marquesas	Jardin	1862
Mei puou	Marquesas	Ragone	1991
Mei puou	Marquesas	Wester	1924
Mei pupupi	Marquesas	Christian	1910
Mei taakivao	Marquesas	Ragone	1991
Mei taataa	Marquesas	Wester	1924
Mei takaha	Marquesas	Christian	1910
Mei tapaa	Marquesas	Christian	1910
Mei tataatoetoe	Marquesas	Christian	1910
Mei tatahamau	Marquesas	Ragone	1991
Mei tavau	Marquesas	Jardin	1862
Mei tepavai	Marquesas	Ragone	1991
Mei teve	Marquesas	Christian	1910
Mei tioe	Marquesas	Christian	1910
Mei tona	Marquesas	Christian	1910
Mei tookaha	Marquesas	Ragone	1991
Mei tookaha	Marquesas	Wester	1924

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MARQUESAS			
Mei tuhavaka	Marquesas	Ragone	1991
Mei tutou	Marquesas	Wester	1924
Mei uea	Marquesas	Parham	1965
Mei uea	Marquesas	Christian	1910
Mei umeume	Marquesas	Ragone	1991
Mei vaeoaeota	Marquesas	Wester	1924
Mei vahakau	Marquesas	Ragone	1991
Mei vevee	Marquesas	Christian	1910
NIUE			
Mei fualahi	Niue	Parham	1965
Mei fualahi	Niue	McEwen	1970
Mei fualahi	Niue	Yuncker	1943
Mei luea	Niue	Yuncker	1943
Mei mafala	Niue	Parham	1965
Mei mafala	Niue	McEwen	1970
Mei mafala	Niue	Yuncker	1943
Mei maopo	Niue	McEwen	1970
Mei maopo	Niue	Yuncker	1943
Mei mase	Niue	Parham	1965
Mei mase	Niue	McEwen	1970
Mei mase	Niue	Yuncker	1943
Mei uluea	Niue	McEwen	1970
ROTUMA			
Loutoko nokonoko	Rotuma	Parham	1965
Ul Fiji	Rotuma	Churchward	1940
Ul Fiti	Rotuma	Parham	1965
Ul Rotuma	Rotuma	Churchward	1940
Ul Rotuma	Rotuma	Parham	1965
Ul Samoa	Rotuma	Parham	1965
Ul fupou	Rotuma	Churchward	1940
Ul kaumaja	Rotuma	Churchward	1940
Ul ma on hula	Rotuma	Churchward	1940
Ul mahalu	Rotuma	Churchward	1940
Ul mahalu	Rotuma	Parham	1965
Ul makeva	Rotuma	Churchward	1940
Ul makeva	Rotuma	Parham	1965
Ul pulpulu	Rotuma	Churchward	1940
Ul pulpulu	Rotuma	Parham	1965
Ul raujeiei	Rotuma	Parham	1965
Ul raululu	Rotuma	Churchward	1940
Ul raululu	Rotuma	Parham	1965
Vereagtiarmaoi	Rotuma	Parham	1965
SAMOA			
Asina	Samoa	Christophersen	1935
Aveloloa	Samoa	Christophersen	1935
Aveloloa	Samoa	Ragone	1991
Aveloloa	Samoa	WS Dept. Ag.	1956
Aveloloa	Samoa	Fiji Dept. Ag.	1956
Aveloloa	Samoa	Buck	1930
Aveloloa tenga	Samoa	Parham	1965
E'a	Samoa	Fiji Dept. Ag.	1956
Ea"	Samoa	Buck	1930
Fa'a fia puou	Samoa	Christophersen	1935
Faisaka	Samoa	Ragone	1991
Fatufala	Samoa	Christophersen	1935
Fatulasi	Samoa	WS Dept. Ag.	1959
Fau	Samoa	Fiji Dept. Ag.	1956
Fau	Samoa	Buck	1930
Fefelo	Samoa	Parham	1965

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Pefelo	Samoa	Ragone	1991
Pefelo	Samoa	WS Dept. Ag.	1960
Fia puou	Samoa	Parham	1965
Gutufagu	Samoa	Parham	1965
Gutufagu	Samoa	WS Dept. Ag.	1960
Ma'a	Samoa	WS Dept. Ag.	1960
Ma'a	Samoa	Buck	1930
Ma'a lau maopo	Samoa	Ragone	1991
Ma'afala	Samoa	Parham	1965
Ma'afala	Samoa	Christophersen	1935
Ma'afala	Samoa	Ragone	1991
Ma'afala	Samoa	WS Dept. Ag.	1956
Ma'afala	Samoa	Fiji Dept. Ag.	1956
Ma'afala	Samoa	Buck	1930
Ma'opo	Samoa	Parham	1965
Ma'opo kalou	Samoa	Parham	1965
Malali	Samoa	Christophersen	1935
Manu'a	Samoa	Buck	1930
Manua	Samoa	Ragone	1991
Manua	Samoa	Fiji Dept. Ag.	1956
Maopo	Samoa	Christophersen	1935
Maopo	Samoa	Ragone	1991
Maopo	Samoa	WS Dept. Ag.	1956
Maopo	Samoa	Fiji Dept. Ag.	1956
Maopo	Samoa	Buck	1930
Maopo vai	Samoa	Parham	1965
Mase	Samoa	Buck	1930
Mase'e	Samoa	Christophersen	1935
Mase'e	Samoa	Ragone	1991
Matatetele	Samoa	Parham	1965
Moamoa	Samoa	Christophersen	1935
Moamoafala	Samoa	Christophersen	1935
Moamoalega	Samoa	Parham	1965
Moamoalega	Samoa	WS Dept. Ag.	1959
Moamoalenga	Samoa	Christophersen	1935
Momolega	Samoa	Ragone	1991
Momolega	Samoa	Fiji Dept. Ag.	1956
Naioti	Samoa	Parham	1965
Naioti	Samoa	Fiji Dept. Ag.	1956
Ngutufangu	Samoa	Christophersen	1935
Nuimoli	Samoa	WS Dept. Ag.	1960
Peti	Samoa	WS Dept. Ag.	1960
Pousina	Samoa	Buck	1930
Poututono	Samoa	Buck	1930
Pungaleve	Samoa	Christophersen	1935
Puou	Samoa	Parham	1965
Puou	Samoa	Christophersen	1935
Puou	Samoa	Ragone	1991
Puou	Samoa	WS Dept. Ag.	1956
Puou	Samoa	Buck	1930
Puou salega	Samoa	Parham	1965
Puou singa	Samoa	Parham	1965
Puousina	Samoa	Buck	1930
Puoututono	Samoa	Buck	1930
Pupu tutunu	Samoa	Parham	1965
Sagosago	Samoa	Ragone	1991
Sangosango	Samoa	Buck	1930
Sanosano	Samoa	WS Dept. Ag.	1960
Tala	Samoa	Buck	1930
Tilipati	Samoa	Parham	1965

Local Name	Island	Author	Year
SAMOA			
Tui tu	Samoa	Christophersen	1935
Tuitu	Samoa	WS Dept. Ag.	1960
Ulu au	Samoa	Christophersen	1935
Ulu aveloloa	Samoa	Setchell	1924
Ulu avetutua	Samoa	Fiji Dept. Ag.	1956
Ulu e'a	Samoa	Parham	1965
Ulu e'a	Samoa	Setchell	1924
Ulu e'a	Samoa	Ragone	1991
Ulu e'a	Samoa	WS Dept. Ag.	1959
Ulu ea	Samoa	Christophersen	1935
Ulu elise	Samoa	Parham	1965
Ulu fatu	Samoa	Ragone	1991
Ulu fau	Samoa	Parham	1965
Ulu fau	Samoa	Christophersen	1935
Ulu fau	Samoa	Setchell	1924
Ulu fau	Samoa	WS Dept. Ag.	1960
Ulu ma'a	Samoa	Christophersen	1935
Ulu ma'a	Samoa	Ragone	1991
Ulu ma'a	Samoa	Fiji Dept. Ag.	1956
Ulu ma'a lau maopo	Samoa	Parham	1965
Ulu ma'a maopo	Samoa	Christophersen	1935
Ulu ma'afala	Samoa	Setchell	1924
Ulu mama	Samoa	Christophersen	1935
Ulu manu'a	Samoa	Christophersen	1935
Ulu manua	Samoa	Parham	1965
Ulu manua	Samoa	Setchell	1924
Ulu manua	Samoa	WS Dept. Ag.	1961
Ulu maopo	Samoa	Setchell	1924
Ulu masee	Samoa	Setchell	1924
Ulu peti	Samoa	Parham	1965
Ulu peti	Samoa	Christophersen	1935
Ulu puou	Samoa	Setchell	1924
Ulu puou sina	Samoa	Setchell	1924
Ulu salega	Samoa	Ragone	1991
Ulu sanasano	Samoa	Setchell	1924
Ulu sanosano	Samoa	Parham	1965
Ulu sina	Samoa	Parham	1965
Ulu sina	Samoa	Christophersen	1935
Ulu sina	Samoa	Ragone	1991
Ulu sina	Samoa	WS Dept. Ag.	1960
Ulu singa	Samoa	Parham	1965
Ulu tala	Samoa	Christophersen	1935
Ulu tala	Samoa	Ragone	1991
Ulu tala	Samoa	WS Dept. Ag.	1960
Ulu vale	Samoa	Christophersen	1935
Ulu valea	Samoa	Parham	1965
Ulu vasi	Samoa	Christophersen	1935
SOCIETY ISLANDS			
Kaire'u	Societies (Mangareva)	Buck	1938
Kouri	Societies (Mangareva)	Buck	1938
Kururutu	Societies (Mangareva)	Buck	1938
Kurutara	Societies (Mangareva)	Buck	1938
Mei kiri o'o'o'o	Societies (Mangareva)	Buck	1938
Mei kiri taratara	Societies (Mangareva)	Buck	1938
Nioi	Societies (Mangareva)	Buck	1938
No'u	Societies (Mangareva)	Buck	1938
Pipiri	Societies (Mangareva)	Buck	1938
Takave	Societies (Mangareva)	Buck	1938
Tamarega	Societies (Mangareva)	Buck	1938

Local Name	Island	Author	Year
Tane	Societies (Mangareva)	Buck	1938
Totara	Societies (Mangareva)	Buck	1938
Aano	Society Islands	Wester	1924
Aata	Society Islands	Petard	1986
Aata	Society Islands	Wilder	1928
Abuabua	Society Islands	Wester	1924
Afara	Society Islands	Ragone	1991
Afara	Society Islands	Petard	1986
Afara	Society Islands	Wilder	1928
Afara	Society Islands	Fiji Dept. Ag.	1960
Afatu	Society Islands	Bennett	1860
Ahani	Society Islands	Ragone	1991
Aipu'u	Society Islands	Henry	1928
Amae	Society Islands	Wilder	1928
Anahonaho	Society Islands	Ragone	1991
Anuana	Society Islands	Bennett	1860
Aoa	Society Islands	Wester	1924
Aoutia	Society Islands	Wilder	1928
Apini	Society Islands	Henry	1928
Apo'oahu	Society Islands	Henry	1928
Appeere	Society Islands	Bligh	1792
Apu	Society Islands	Ragone	1991
Apuapua	Society Islands	Petard	1986
Apuapua	Society Islands	Ragone	1991
Apuapua	Society Islands	Wilder	1928
Apuapua	Society Islands	WS Dept. Ag.	1964
Apuapua	Society Islands	Fiji Dept. Ag.	1960
Araoro	Society Islands	Henry	1928
Aravei	Society Islands	Ragone	1991
Aravei	Society Islands	Petard	1986
Aravei	Society Islands	Henry	1928
Aravei	Society Islands	Wilder	1928
Aravei	Society Islands	Bennett	1860
Aravei	Society Islands	WS Dept. Ag.	1964
Atiati	Society Islands	Petard	1986
Atiati	Society Islands	Ragone	1991
Atiati	Society Islands	Wilder	1928
Atiati	Society Islands	WS Dept. Ag.	1964
Atiati	Society Islands	Fiji Dept. Ag.	1960
Aue	Society Islands	Ragone	1991
Aume'e	Society Islands	Henry	1928
Aumure	Society Islands	Wester	1924
Autia	Society Islands	Wester	1924
Avei	Society Islands	Wester	1924
Avei	Society Islands	Henry	1928
Avei	Society Islands	Wilder	1928
Avei	Society Islands	WS Dept. Ag.	1964
Awanna	Society Islands	Bligh	1792
Buero	Society Islands	Bennett	1860
Emouti	Society Islands	Wilder	1928
Epea	Society Islands	Wilder	1928
Epiti	Society Islands	Wilder	1928
Epouhi	Society Islands	Wilder	1928
Ereroo	Society Islands	Bligh	1792
Ererua	Society Islands	Wilder	1928
Evete	Society Islands	Wilder	1928
Faara	Society Islands	Bennett	1860
Pafai	Society Islands	Ragone	1991
Pafatea	Society Islands	Wilder	1928
Para	Society Islands	Henry	1928

Local Name	Island	Author	Year
Fatai	Society Islands	Wilder	1928
Fati	Society Islands	Wilder	1928
Fei	Society Islands	WS Dept. Ag.	1964
Firikiki	Society Islands	Fiji Dept. Ag.	1960
Firititi	Society Islands	WS Dept. Ag.	1964
Ha'ama	Society Islands	Henry	1928
Hamo	Society Islands	Ragone	1991
Hamo	Society Islands	Wilder	1928
Haparu	Society Islands	Wilder	1928
Harare	Society Islands	Petard	1986
Harare	Society Islands	Wilder	1928
Hatara	Society Islands	WS Dept. Ag.	1964
Havae	Society Islands	Wilder	1928
Havana	Society Islands	Ragone	1991
Havana	Society Islands	Petard	1986
Havana	Society Islands	Henry	1928
Havana	Society Islands	Wilder	1928
Havana	Society Islands	Fiji Dept. Ag.	1960
Havana pataitai	Society Islands	Henry	1928
Havana taratara	Society Islands	WS Dept. Ag.	1964
Huehue	Society Islands	Henry	1928
Huero	Society Islands	Petard	1986
Huero	Society Islands	Wester	1924
Huero	Society Islands	Ragone	1991
Huero	Society Islands	Wilder	1928
Huero	Society Islands	WS Dept. Ag.	1964
Huero	Society Islands	Fiji Dept. Ag.	1960
Huha papae	Society Islands	Wilder	1928
Huhu papae	Society Islands	Petard	1986
Huhu papai	Society Islands	WS Dept. Ag.	1964
Huhupapai	Society Islands	Fiji Dept. Ag.	1960
Iofai	Society Islands	Bennett	1860
Ioio	Society Islands	Ragone	1991
Kauhiva	Society Islands	Fiji Dept. Ag.	1959
Kiko tao	Society Islands	WS Dept. Ag.	1964
Kikotao	Society Islands	Fiji Dept. Ag.	1959
Kuahe	Society Islands	Fiji Dept. Ag.	1959
Ma'aro'aro	Society Islands	Henry	1928
Mahani	Society Islands	Wester	1924
Mahani	Society Islands	Wilder	1928
Mahani	Society Islands	WS Dept. Ag.	1964
Mahani	Society Islands	Fiji Dept. Ag.	1960
Mahoi	Society Islands	Ragone	1991
Maire	Society Islands	Ragone	1991
Maire	Society Islands	Petard	1986
Maire	Society Islands	Bennett	1924
Maire	Society Islands	Henry	1928
Maire	Society Islands	Wilder	1928
Maire	Society Islands	WS Dept. Ag.	1964
Maire	Society Islands	Fiji Dept. Ag.	1960
Mamatea	Society Islands	Henry	1928
Manehe	Society Islands	Ragone	1991
Manina	Society Islands	Henry	1928
Maohi	Society Islands	Petard	1986
Maohi	Society Islands	Bennett	1924
Maohi	Society Islands	Wilder	1928
Maohi	Society Islands	WS Dept. Ag.	1964
Marea	Society Islands	Petard	1986
Marea	Society Islands	Wilder	1928
Matatea	Society Islands	Wilder	1928

Local Name	Island	Author	Year
Matateoa	Society Islands	Petard	1986
Mi-re	Society Islands	Bligh	1792
Momi	Society Islands	Wester	1924
O'iri	Society Islands	Henry	1928
Oa	Society Islands	Wester	1924
Ofatia	Society Islands	Bennett	1860
Ofea	Society Islands	Ragone	1991
Ohinuhinu	Society Islands	Wester	1924
Opiha	Society Islands	Bennett	1860
Opiha	Society Islands	Ragone	1991
Opiha	Society Islands	Wilder	1928
Opiha	Society Islands	WS Dept. Ag.	1964
Opiripiri	Society Islands	Wester	1924
Opotopoto	Society Islands	Ragone	1991
Orava	Society Islands	WS Dept. Ag.	1964
Oree	Society Islands	Bligh	1792
Otai	Society Islands	WS Dept. Ag.	1964
Otea	Society Islands	Bennett	1924
Otea	Society Islands	Ragone	1991
Otea	Society Islands	Henry	1928
Otea	Society Islands	Wilder	1928
Otea	Society Islands	WS Dept. Ag.	1964
Ouo	Society Islands	Ragone	1991
Ovai	Society Islands	Fiji Dept. Ag.	1959
Oviri	Society Islands	Bennett	1860
Pa'auara	Society Islands	WS Dept. Ag.	1964
Pa'i fe'e	Society Islands	Henry	1928
Pae fee	Society Islands	Petard	1986
Pae fee	Society Islands	Wilder	1928
Pae tauatia	Society Islands	Wilder	1928
Pae'a	Society Islands	Henry	1928
Paea	Society Islands	Petard	1986
Paea	Society Islands	Bennett	1924
Paea	Society Islands	Wilder	1928
Paea	Society Islands	WS Dept. Ag.	1964
Paea	Society Islands	Fiji Dept. Ag.	1960
Paea fee	Society Islands	WS Dept. Ag.	1964
Paea taratara	Society Islands	Ragone	1991
Paere	Society Islands	WS Dept. Ag.	1964
Paere	Society Islands	Fiji Dept. Ag.	1960
Pafai	Society Islands	Bennett	1860
Pafara	Society Islands	Bennett	1860
Pai ahuri	Society Islands	WS Dept. Ag.	1964
Paifee	Society Islands	Wester	1924
Panafara	Society Islands	Wester	1924
Paparu	Society Islands	Petard	1986
Paparu	Society Islands	Wester	1924
Paparu	Society Islands	Ragone	1991
Paparu	Society Islands	Fiji Dept. Ag.	1960
Parerau ohua	Society Islands	WS Dept. Ag.	1964
Pareva	Society Islands	WS Dept. Ag.	1964
Paru	Society Islands	Wilder	1928
Parupaparu	Society Islands	WS Dept. Ag.	1964
Patara	Society Islands	Wester	1924
Patara	Society Islands	Ragone	1991
Patea	Society Islands	Wester	1924
Patea	Society Islands	Henry	1928
Pateah	Society Islands	Bligh	1792
Patohora	Society Islands	WS Dept. Ag.	1964
Pavai	Society Islands	WS Dept. Ag.	1964

Local Name	Island	Author	Year
Pe'a	Society Islands	Ragone	1991
Peetia	Society Islands	Wilder	1928
Pehi	Society Islands	Bennett	1860
Pei	Society Islands	Petard	1986
Pei	Society Islands	Wilder	1928
Pei	Society Islands	WS Dept. Ag.	1964
Pei	Society Islands	Fiji Dept. Ag.	1960
Peiahuri	Society Islands	Bennett	1860
Pererau ohua	Society Islands	Henry	1928
Peti	Society Islands	Petard	1986
Peti	Society Islands	Wester	1924
Peti	Society Islands	Ragone	1991
Peti	Society Islands	Henry	1928
Peti	Society Islands	Wilder	1928
Peti pit	Society Islands	WS Dept. Ag.	1964
Piia	Society Islands	Wester	1924
Piipia	Society Islands	Fiji Dept. Ag.	1960
Piipia	Society Islands	Bennett	1860
Piri ati	Society Islands	Wilder	1928
Piriati	Society Islands	Petard	1986
Ponafara	Society Islands	Henry	1928
Porohiti	Society Islands	Wester	1924
Poru	Society Islands	Wester	1924
Pou marari	Society Islands	Wilder	1928
Pouponou	Society Islands	Wilder	1928
Poutia	Society Islands	Wilder	1928
Powerro	Society Islands	Bligh	1792
Pu'upu'u	Society Islands	Henry	1928
Pua	Society Islands	Ragone	1991
Pua'a	Society Islands	Ragone	1991
Pua'a	Society Islands	WS Dept. Ag.	1964
Puaa	Society Islands	Petard	1986
Puaa	Society Islands	Wester	1924
Puaa	Society Islands	Wilder	1928
Puaue	Society Islands	WS Dept. Ag.	1964
Puave	Society Islands	Ragone	1991
Puero	Society Islands	Ragone	1991
Puero	Society Islands	Wester	1924
Puero	Society Islands	Henry	1928
Puero	Society Islands	Wilder	1928
Puero	Society Islands	WS Dept. Ag.	1964
Puero	Society Islands	Fiji Dept. Ag.	1959
Puero ovili	Society Islands	Wilder	1928
Puero ovili	Society Islands	WS Dept. Ag.	1964
Puero oviri	Society Islands	Petard	1986
Pufatata	Society Islands	Wester	1924
Pupia	Society Islands	Wester	1924
Pureru	Society Islands	Wester	1924
Putu	Society Islands	Henry	1928
Putu	Society Islands	WS Dept. Ag.	1964
Puupuu	Society Islands	Wester	1924
Puvero	Society Islands	Wester	1924
Raiatea	Society Islands	WS Dept. Ag.	1964
Raoere menemene	Society Islands	WS Dept. Ag.	1964
Rapara	Society Islands	Henry	1928
Rare	Society Islands	Petard	1986
Rare	Society Islands	Bennett	1924
Rare	Society Islands	Ragone	1991
Rare	Society Islands	Henry	1928
Rare	Society Islands	Wilder	1928

Local Name	Island	Author	Year
Rare	Society Islands	WS Dept. Ag.	1964
Rare aumee	Society Islands	Wilder	1928
Rare auti'a	Society Islands	Henry	1928
Rare autia	Society Islands	Ragone	1991
Rare autia	Society Islands	Petard	1986
Rare autia	Society Islands	Wilder	1928
Rare autia	Society Islands	WS Dept. Ag.	1964
Rare autia	Society Islands	Fiji Dept. Ag.	1959
Rare pupure	Society Islands	WS Dept. Ag.	1964
Rau mae	Society Islands	Wester	1924
Rau mae	Society Islands	Wilder	1928
Rau min	Society Islands	Ragone	1991
Rau'mae	Society Islands	Henry	1928
Raumae	Society Islands	Bennett	1860
Raumae	Society Islands	WS Dept. Ag.	1964
Rautia	Society Islands	Bennett	1860
Rauvaravara	Society Islands	Wester	1924
Roru	Society Islands	Bennett	1860
Rotuma	Society Islands	Fiji Dept. Ag.	1960
Rowdeah	Society Islands	Bligh	1792
Taea	Society Islands	Henry	1928
Tao	Society Islands	Bennett	1860
Tao	Society Islands	Henry	1928
Tao	Society Islands	Wilder	1928
Tatara	Society Islands	Petard	1986
Tatara	Society Islands	Henry	1928
Tatara	Society Islands	Wilder	1928
Tatara	Society Islands	Bennett	1860
Tatara	Society Islands	WS Dept. Ag.	1964
Tatara	Society Islands	Fiji Dept. Ag.	1960
Taupaitaa	Society Islands	Wilder	1928
Temateoa	Society Islands	Fiji Dept. Ag.	1960
Ti ura	Society Islands	WS Dept. Ag.	1964
Tiatea	Society Islands	Wester	1924
Tiatea	Society Islands	Henry	1928
Toarau	Society Islands	Henry	1928
Toerau	Society Islands	Wester	1924
Tohe hava'e	Society Islands	Henry	1928
Tohe ti'apou	Society Islands	Henry	1928
Tohetupou	Society Islands	Wester	1924
Toutano	Society Islands	Wilder	1928
Tu'utou	Society Islands	WS Dept. Ag.	1964
Tutau	Society Islands	Ragone	1991
Tuutou	Society Islands	Wester	1924
Tuutou	Society Islands	Ragone	1991
Tuutou	Society Islands	Wilder	1928
Tuutou	Society Islands	Fiji Dept. Ag.	1960
Upuupuu	Society Islands	Wilder	1928
Uru huero	Society Islands	Henry	1928
Uru ma'ohi	Society Islands	Henry	1928
Uru maohi	Society Islands	Ragone	1991
Uru maore	Society Islands	Huguenin	1902
Uru maua	Society Islands	Ragone	1991
Uru moua	Society Islands	Wilder	1928
Uru ohinuhinu	Society Islands	Huguenin	1902
Uru otea	Society Islands	Huguenin	1902
Uru paiffee	Society Islands	Huguenin	1902
Uru panafara	Society Islands	Huguenin	1902
Uru patu	Society Islands	Huguenin	1902
Uru puero	Society Islands	Huguenin	1902

Local Name	Island	Author	Year
SOCIETY ISLANDS			
Uru pureru	Society Islands	Huguenin	1902
Uru puruhi	Society Islands	Huguenin	1902
Uru rare	Society Islands	Huguenin	1902
Uru raumae	Society Islands	Huguenin	1902
Uru rauvaravara	Society Islands	Huguenin	1902
Uru tatara	Society Islands	Huguenin	1902
Uru tiatea	Society Islands	Huguenin	1902
Uru tohetopou	Society Islands	Huguenin	1902
Ute ute	Society Islands	WS Dept. Ag.	1964
Vai paere	Society Islands	Petard	1986
Vai paere	Society Islands	Wilder	1928
Vaiotai	Society Islands	WS Dept. Ag.	1964
Vaipaere	Society Islands	Ragone	1991
Vaipaere	Society Islands	WS Dept. Ag.	1964
Vaka fenua	Society Islands	WS Dept. Ag.	1964
Vareau pura	Society Islands	WS Dept. Ag.	1964
OUTLIER ISLAND			
Akaumotu	Solomons (Anuta)	Yen	1973
Kanopatu	Solomons (Anuta)	Yen	1973
Konongapua	Solomons (Anuta)	Yen	1973
Maore	Solomons (Anuta)	Yen	1973
Maruru	Solomons (Anuta)	Yen	1973
Matavau	Solomons (Anuta)	Yen	1973
Mua	Solomons (Anuta)	Yen	1973
Puakauta	Solomons (Anuta)	Yen	1973
Sala	Solomons (Anuta)	Yen	1973
Tatinawa	Solomons (Anuta)	Yen	1973
Tekauariki	Solomons (Anuta)	Yen	1973
Tenga	Solomons (Anuta)	Yen	1973
Vaii	Solomons (Anuta)	Yen	1973
TONGA			
Aveloloa	Tonga	Parham	1965
Aveloloa	Tonga	Yunker	1959
Aveloloa	Tonga	WS Dept. Ag.	1960
Avenonou	Tonga	Yunker	1959
Kalou	Tonga	WS Dept. Ag.	1960
Kaunonou	Tonga	Ragone	1991
Kea	Tonga	Ragone	1991
Kea fatu	Tonga	Parham	1965
Kea fatu	Tonga	WS Dept. Ag.	1960
Kea kulufau	Tonga	Yunker	1959
Kea loutoka	Tonga	WS Dept. Ag.	1960
Kea ma'ama'a	Tonga	Parham	1965
Kea ma'ama'a	Tonga	Yunker	1959
Kea tala	Tonga	Parham	1965
Kea tala	Tonga	WS Dept. Ag.	1960
Kea tala vai	Tonga	WS Dept. Ag.	1960
Lautolo	Tonga	Yunker	1959
Loutoka	Tonga	WS Dept. Ag.	1960
Loutoka kaunonou	Tonga	WS Dept. Ag.	1960
Loutoka kulufau	Tonga	WS Dept. Ag.	1960
Loutoka laumoa	Tonga	WS Dept. Ag.	1960
Loutoka ma'ama'a	Tonga	WS Dept. Ag.	1960
Loutoka nokonoko	Tonga	WS Dept. Ag.	1960
Loutoka vahivahi	Tonga	WS Dept. Ag.	1960
Loutoko	Tonga	Parham	1965
Loutoko kaunounou	Tonga	Parham	1965
Loutoko kulufau	Tonga	Parham	1965
Loutoko loumoa	Tonga	Parham	1965

Local Name	Island	Author	Year
TONGA			
Loutoko vahivahi	Tonga	Parham	1965
Ma'afala	Tonga	WS Dept. Ag.	1960
Ma'afala kau'iki	Tonga	Parham	1965
Ma'afala kauiki	Tonga	WS Dept. Ag.	1960
Ma'afala kea	Tonga	Parham	1965
Ma'ofala	Tonga	Yuncker	1959
Maopo	Tonga	Yuncker	1959
Maopo vai	Tonga	WS Dept. Ag.	1960
Mase'e	Tonga	Ragone	1991
Puou	Tonga	Yuncker	1959
Puou maka	Tonga	Parham	1965
Puou vai	Tonga	Parham	1965
Puou vai	Tonga	WS Dept. Ag.	1960
Ulu sina	Tonga	WS Dept. Ag.	1960
Vahivahi	Tonga	Ragone	1991
Vahivahi	Tonga	Yuncker	1959

APPENDIX B
BREADFRUIT GERMPLASM COLLECTION
AT THE KAHANU GARDENS
OF THE NATIONAL TROPICAL BOTANICAL GARDEN

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
POLYNESIA				
Cook Islands		6		
Rarotonga	Atu	1	103	1989-1991
Rarotonga	Enua	1	433	1989-1991
Rarotonga	Enua	2	435*	1989-1991
Aitutaki	Paea	2	096	1989-1991
Hawaii		1		
Maui	Ulu	1	530	1960
Marquesas		7		
Nuku Hiva	Mei aueka	1	230	1989-1991
Nuku Hiva	Mei kauhiva	1	223	1989-1991
Nuku Hiva	Mei kii ahi	1	220	1989-1991
Nuku Hiva	Mei kopumoku	1	231	1989-1991
Nuku Hiva	Mei maoi	1	222	1989-1991
Nuku Hiva	Mei puau	1	224*	1989-1991
Nuku Hiva	Mei puou	1	216	1989-1991

Appendix B. (Continued) Breadfruit germplasm collection at the Kahanu Gardens
of the National Tropical Botanical Garden

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
Samoa		22		
Upolu	Aveloloa	1	007	1989-1991
Upolu	Ma'afala	1	-	1978
Savai'i	Manua	1	013	1989-1991
Savai'i	Manua	1	469	1989-1991
Savai'i	Mase'e	1	472	1989-1991
Upolu	Momolega	1	-	1978
Aitutaki	Niue	1	095*	1989-1991
Aitutaki	Niue	1	100	1989-1991
Upolu	Puou	1	-	1978
Upolu	Puou	1	453	1989-1991
Savai'i	Sagosago	2	475	1989-1991
Bali	Sukun	1	540*	1989-1991
Upolu	Ulu e'a	1	541*	1989-1991
Savai'i	Ulu sina	2	019	1989-1991
Upolu	Ulu tala	1	-	1978
Upolu	Unknown	1	-	1978
Upolu	Unknown	1	-	1989-1991
Upolu	Unknown	1	110	1989-1991
Aitutaki	Unnamed	2	092*	1989-1991
Society Islands		47		
Huahine	A'arue	1	-	1978
Moorea	Afara	1	-	1978
Moorea/Raiatea	Ahani	1	-	1978
Huahine	Aipu'u	1	-	1978
Raiatea	Anahonaho	1	269	1989-1991
Raiatea	Apu	2	268*	1989-1991
Raiatea	Apuapua	2	272	1989-1991
Tahaa	Araarahaari	1	253	1989-1991
Raiatea	Aue	2	266*	1989-1991
Raiatea	Fafai	2	-	1978
Raiatea	Fafai	1	238	1989-1991
Tahaa	Hamoia	1	236	1989-1991
Tahaa	Huehue	1	-	1978
Tahaa	Huehue	1	254	1989-1991
Raiatea	Huero	1	256	1989-1991
Raiatea	Ioio	1	264*	1989-1991
Moorea	Mahani	1	-	1978
Moorea	Maire	2	200	1989-1991
Raiatea	Mamaha	1	262*	1989-1991

Appendix B. (Continued) Breadfruit germplasm collection at the Kahanu Gardens
of the National Tropical Botanical Garden

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
Society Islands				
Tahaa	Ouo	1	248	1989-1991
Huahine	Otea	1	-	1978
Tahaa	Patara	1	241	1989-1991
Raiatea	Pii piia	1	-	1978
Tahaa	Pii piia	2	245*	1989-1991
Raiatea	Pua'a	1	-	1978
Moorea	Pua'a	1	204*	1989-1991
Moorea	Porohiti	1	-	1978
Huahine	Pu'upu'u	1	-	1978
Raiatea	Puurea	2	257	1989-1991
Tahiti	Rare	1	-	1978
Huahine	Roi ha'a	1	-	1978
Tahaa	Tapeha'a	1	-	1978
Tahaa	Teahimatoa	1	251*	1989-1991
Tahaa	Toneno	1	-	1978
Tahiti	Tuutou	1	-	1978
Raiatea	Tuutou, auena	1	259	1989-1991
Raiatea	Tuutou, ooa	1	260	1989-1991
Raiatea	Tuutou, taatoe	2	258*	1989-1991
	Unknown	1	-	1989-1991
Tokelau		28		
Nukunonu	Ulu afa	2	040	1989-1991
Nukunonu	Ulu afa	1	041	1989-1991
Nukunonu	Ulu afa	2	044*	1989-1991
Nukunonu	Ulu afa	2	045*	1989-1991
Nukunonu	Ulu afa	2	046	1989-1991
Nukunonu	Ulu afa	1	048*	1989-1991
Nukunonu	Ulu afa	1	049*	1989-1991
Nukunonu	Ulu afa	2	051*	1989-1991
Nukunonu	Ulu afa	1	052*	1989-1991
Nukunonu	Ulu afa	2	053*	1989-1991
Nukunonu	Ulu afa	1	054	1989-1991
Nukunonu	Ulu afa	1	056*	1989-1991
Nukunonu	Ulu afa	1	057	1989-1991
Nukunonu	Ulu afa	1	058	1989-1991
Fakaofu	Ulu afa	2	061	1989-1991
Fakaofu	Ulu elise	1	063*	1989-1991
Fakaofu	Ulu elise	2	065*	1989-1991
Nukunonu	Ulu hamoa	2	043	1989-1991
Fakaofu	Ulu hamoa	1	059*	1989-1991

Appendix B. Breadfruit germplasm collection at the Kahanu Gardens
of the National Tropical Botanical Garden.

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
MICRONESIA				
Belau		9		
Peleliu	Chebiei	1	292	1989-1991
Koror	Ebechad	1	288*	1989-1991
Babeldaob	Ebechad	1	289	1989-1991
Babeldaob	Errud	2	291	1989-1991
Babeldaob	Meraieur	2	286*	1989-1991
Babeldaob	Midolab	2	290	1989-1991
Kiribati		3		
Tarawa	Te bukiraro	2	421*	1989-1991
Tarawa	Te mai	1	036	1989-1991
Mariana Islands		7		
Rota	Dugdug	3	313	1989-1991
Saipan	Lemae	2	311*	1989-1991
Rota	Lemae	2	314*	1989-1991
Pohnpei		28		
Pohnpei	Lipet	1	365	1989-1991
Pohnpei	Lipet	3	511*	1989-1991
Pohnpei	Mei arephe	2	501	1989-1991
Pohnpei	Mei kalak	2	502*	1989-1991
Pohnpei	Mei kole	1	385	1989-1991
Pohnpei	Mei kole	1	529*	1989-1991
Pohnpei	Mei saip	2	405*	1989-1991
Pohnpei	Mei sei	2	510*	1989-1991
Pohnpei	Mei tehid	1	-	1980
Pohnpei	Mei tehid	2	374*	1989-1991
Pohnpei	Mei tehid	1	512*	1989-1991
Pohnpei	Mei tol	1	509	1989-1991
Pohnpei	Mei puht	1	388	1989-1991
Pohnpei	Mei uhpw	1	367	1989-1991
Pohnpei	Mein padahk	1	-	1980
Pohnpei	Mein pohnsakar	2	373*	1989-1991
Pohnpei	Mein pwahr	1	386	1989-1991

Appendix B. Breadfruit germplasm collection at the Kahanu Gardens
of the National Tropical Botanical Garden.

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
Pohnpei				
Pohnpei	Mein uwe	2	-	1980
Pohnpei	Nahnmwal	1	387*	1989-1991
Truk		11		
Uman	Faine	1	331	1989-1991
Nama	Mei chocho	1	363	1989-1991
Moen	Mei chon	1	326*	1989-1991
Losap	Mei koeng	1	351	1989-1991
Nama	Mei koeng	2	354	1989-1991
Moen	Mei on	2	322*	1989-1991
Uman	Neachen	1	534	1989-1991
Uman	Nepopo	1	329	1989-1991
Moen	Sewan	1	320	1989-1991
Yap		3		
Yap	Luthar	1	301*	1989-1991
Koror	Unknown	1	287	1989-1991
Yap	Yuley	1	303	1989-1991
MELANESIA				
Fiji		11		
Viti Levu	Karawa	1	489	1989-1991
Viti Levu	Samoaan type	1	147	1989-1991
Viti Levu	Samoaan type	2	464	1989-1991
Viti Levu/Vuaki	Samoaan type	2	468	1989-1991
Upolu	Uto dina	1	428	1989-1991
Viti Levu	Uto ni viti	1	488	1989-1991
Viti Levu	Uto samoa	1	495*	1989-1991
Viti Levu	Uto vula	1	486*	1989-1991
Rotuma		10		
Upolu	Furau	2	427	1989-1991
Upolu	Karawa	1	127	1989-1991
Upolu	Pulupulu	2	121*	1989-1991
Upolu	Rauulu	1	439	1989-1991
Tahaa	Ro'otuma	1	-	1978
Tahaa	Ro'otuma	1	243	1989-1991
Upolu	Ulu fiti	2	136	1989-1991

Appendix B. Breadfruit germplasm collection at the Kahanu Gardens
of the National Tropical Botanical Garden.

Island of origin Island where collected	Local Name	Number of tree	Accession Number	Year Planted
Solomon Islands		10		
Malaita	Abareba	1	169	1989-1991
Upolu	Bulo2	2	436	1989-1991
Upolu	Kukumu tasi	1	426*	1989-1991
Upolu	Tehelewa	2	437	1989-1991
Upolu	Toro	2	123	1989-1991
Guadacanal	Unknown	1	539	1989-1991
Malaita	Unnamed	1	166	1989-1991
Vanuatu		8		
Vate	Forari2	1	526	1989-1991
Upolu	Malphang	1	445	1989-1991
Upolu	Manang	2	443*	1989-1991
Wallis	Puou	1	519	1989-1991
Vate	Siviri2	1	528	1989-1991
Vate	Siviri3	1	523	1989-1991
Vate	Tedailir	1	525	1989-1991
CARIBBEAN		4		
Unknown	White type	3	-	1980
Unknown	Yellow type	1	-	1980
INDONESIA		4		
Tahiti	Unnamed	1	-	1978
Raiatea	Huero ninamu	1	261	1989-1991
Nuku Hiva	Mei kakano	2	221*	1989-1991
PHILIPPINES		2		
Luzon	Camansi	1	531	1989-1991
Oahu	Pakok	1	546	1989-1991
UNKNOWN		5	*	1989-1991

* Also planted at the Lawai Gardens on the island of Kauai

BIBLIOGRAPHY

- Abo, T, R. Bender, B.W. Capelle and A. deBrum. 1976. *Marshallese-English Dictionary*. University of Hawaii Press. Honolulu.
- Alkire, William H. 1978. *Coral Islanders*. AHM Publishing Corp. Arlington Heights, Illinois.
- Allen, Jim. 1984. In search of the Lapita homeland: reconstructing the prehistory of the Bismarck Archipelago. *Journal of Pacific History* 19(4):186-201.
- Atchley, Jennifer and Paul Alan Cox. 1985. Breadfruit fermentation in Micronesia. *Economic Botany* 39(3):326-335.
- Ayres, William S. 1990. Pohnpei's position in eastern Micronesian prehistory. *Micronesica*. *Recent Advances in Micronesian Archaeology*. Supplement 2:187-212.
- Ayres, William S. and Alan E. Haun. 1980. *Ponape Archaeological Survey: 1977 Research*. *Micronesian Archaeological Survey*. Historic Preservation Office. Report No. 1. Trust Territory of Pacific Islands. Saipan.
- Barrau, Jacques. 1957. L'arbre de pain en Oceanie. *Journal D'agriculture Tropicale et de Botanique Appliquee* 3/4:117-123.
- _____. 1958a. SPC plant introduction service steadily expands. *South Pacific Bulletin* 8(3):21-22, 33.
- _____. 1958b. *Subsistence Agriculture in Melanesia*. Bernice Pauahi Bishop Museum. Bulletin 219. Honolulu.
- _____. 1959a. Investigation to extend season of breadfruit yields. *South Pacific Bulletin* 9(2):41,43.

- Barrau, Jacques. 1959b. *South Pacific Commission Research Council Tenth Meeting Report*.
Appendix I. Noumea, New Caledonia.
- _____. 1961. *Subsistence Agriculture in Polynesian and Micronesia*. Bernice Pauahi
Bishop Museum. Bulletin 223. Honolulu.
- Barrau, Jacques. 1965. Witnesses of the past: notes on some food plants of Oceania.
Ethnology 4:282-294.
- _____. 1976. Breadfruit and relatives. 201-202. In: N.W. Simmonds (ed.). *Evolution of
Crop Plants*. Longman. London.
- Bascom, W.H. 1946. *Ponape: A Pacific Economy in Transition*. Vol. 8. U.S. Commercial
Co. Economic Survey of Micronesia. Honolulu.
- Beggerley, Patricia Price. 1976. Hawaiian settlement patterns. 53-139. In: *Micronesian and
Polynesian Voyaging: Three readings*. Pacific Island Studies Program.
Miscellaneous Working Papers Series. University of Hawaii, Honolulu.
- Bellwood, Peter 1979. *Man's Conquest of the Pacific. The Prehistory of Southeast Asia and
Oceania*. Oxford University Press. New York.
- _____. 1987. *The Polynesians. Prehistory of an Island People*. Thames and Hudson.
New York.
- Bennett, F.D. and C. Nozzollilo. 1988. How many seeds in a seeded breadfruit,
Artocarpus altilis (Moraceae). *Economic Botany* 41(3):370-374.
- Bennett, G. 1860. *Gatherings of a Naturalist*. cited in P. J. Wester, 1924. The seedless
breadfruits of the Pacific archipelagoes. *Philippine Agriculture Review* 17(1):24-
39.
- Bligh, William. 1792. *A Voyage to the South Sea. For the Purpose of Conveying the
Breadfruit Tree to the West Indies in H.M.S. Bounty*. George Nicol. London.
- _____. 1976. *The Log of H.M.S. Providence. 1791-1793*. Genesis Publications. Surrey,
England.

- Blumenstock, D.I., F.R. Fosberg and C.G. Johnson. 1961. The resurvey of typhoon effects of Jaluit Atoll in the Marshall Islands. *Atoll Research Bulletin* 75:1-105.
- Bousquet, J., W.M. Cheliak, and M. Lalonde. 1987. Allozyme variability in natural populations of green alder (*Alnus crispa*) in Quebec. *Genome* 29:345-352.
- Bower, Bruce. 1987. Prehistoric Polynesian puzzle. *Science News* 132:232-233.
- Brantjes, N.B.M. 1981. Nectar and pollination of breadfruit, *Artocarpus altilis* (Moraceae). *Acta Botanica Neerlandica* 30(5/6):345-352.
- Buck, Peter H. 1927. *The Material Culture of the Cook Islands (Aitutaki)*. Memoirs of the Board of Maori Ethnological Research. Vol. 1. New Plymouth, New Zealand.
- _____. 1930. *Samoan Material Culture*. Bernice Pauahi Bishop Museum. Bulletin 75. Honolulu.
- _____. 1938. *Ethnology of Mangareva*. Bernice Pauahi Bishop Museum. Bulletin 157. Honolulu.
- Bulmer, R.N.H. 1964. Edible seeds and prehistoric stone mortars in the Highlands of East New Guinea. *Man* 182/183:147-150.
- Burkill, I.H. 1935. *A Dictionary of the Economic Products of the Malay Peninsula*. Vol. 1. Crown Agents for the Colonies. London.
- Burrows, E.G. 1936. *Ethnology of Futuna*. Bernice Pauahi Bishop Museum. Bulletin 138. Honolulu.
- Burrows, Edwin G. and Melford E. Spiro. 1957. *An Atoll Culture*. Human Relations Area Files Press. New Haven.
- Byrne, David H. and Thomas G. Littleton. 1988. Electrophoretic characterization of diploid plums of the southeastern United States. *Journal American Society of Horticultural Science* 113(6):918-924.
- _____. 1989. Characterization of isozyme variability in apricots. *Journal American Society of Horticultural Science* 114(4):674-678.

- Catala, R.L.A. 1957. Report on the Gilbert Islands. Some aspects of human ecology. *Atoll Research Bulletin* 59:1-186.
- Cerezo, M. Socias i Company, R. and P. Arós. 1989. Identification of almond cultivars by pollen isoenzymes. *Journal American Society of Horticultural Science* 114(1):164-169.
- Cheeseman, Thomas F. 1903. *The Flora of Rarotonga*. Transactions Linnean Society 2d Series. 6:262-313. London.
- Christian, F.W. 1897. Notes from the Caroline Islands. *Journal Polynesian Society* 6:187-200.
- _____. 1899. *The Caroline Islands*. Methuen and Co. London.
- _____. 1910. *Eastern Pacific Lands, Tahiti and the Marquesas Islands*. Robert Scott. London.
- Christophersen, E. 1935. *Flowering Plants of Samoa*. Bernice Pauahi Bishop Museum. Bulletin 128. Honolulu.
- Clunie, N.M.U. 1978. The Vegetation. 1-11. In: John S. Womersley (ed.). *Handbook of the Flora of Papua New Guinea*. Melbourne University Press. Carlton, Victoria.
- Coenan, Jan and Jacques Barrau. 1961. The breadfruit tree in Micronesia. *South Pacific Bulletin* 11(4):37-39, 65-67.
- Conroy, W.L. and L.A. Bridgeland. 1950. Native agriculture in New Guinea. 82-91. In: E.H. Hipsley and F.W. Clements (eds.). *Report of the New Guinea Nutrition Survey Expedition 1947*. Government Printer. Sydney.
- Cox, Paul Alan. 1980. Two Samoan technologies for breadfruit and banana preservation. *Economic Botany* 34(2):181-185.
- Craib, John L. 1983. Micronesian prehistory: an archaeological overview. *Science* 219:922-927.
- Croft, J.R. 1987. The other products from the forest. *Klinki* 3(3):35-53.

- Dampier, William. 1729. *A New Voyage Round the World*. James and John Knapton. London.
- Darlington, C.D. and A.P. Wylie. 1955. *Chromosome Atlas of Flowering Plants*. George Allen and Unwin. London.
- Davidson, Janet. 1967. Archaeology on coral atolls. 363-376. In: G.A. Highland et al. (eds.). *Polynesian Cultural History: Essays in Honor of Kenneth P. Emory*. Bernice Pauahi Bishop Museum. Special Publication No. 56. Honolulu.
- de Candolle, Alphonse. 1908. *Origin of Cultivated Plants*. D. Appleton and Co. New York.
- DeWald, Maria G., Gloria A. Moore and Wayne B. Sherman. 1988. Identification of pineapple cultivars by isozyme genotypes. *Journal American Society of Horticultural Science* 113(6):935-938.
- Duncan, Thomas and Bernard R. Baum. 1981. Numerical phenetics: its use in botanical systematics. *Annual Review Ecological Systematics* 12:387-404.
- Dyer, A.F. 1979. *Investigating Chromosomes*. John Wiley and Sons. New York.
- Elbert, S.H. 1947. *Trukese-English and English-Trukese Dictionary*. U.S. Naval Military Government. Pearl Harbor. Honolulu.
- Elbert, S.H. 1972. *Puluwat Dictionary*. Pacific Linguistics Series C. No. 24. Department of Linguistics. Research School of Pacific Studies. Australian National University. Canberra.
- Ellis, John. 1775. *A Description of the Mangosteen and the Breadfruit*. 35-87. In: William Bligh. 1796. *The Log of H.M.S. Providence. 1791-1793*. Genesis Publications. Surrey. England.
- Ellis, William. 1967. *Polynesian Researches*. Facsimile of 1829 original edition in 2 Vol. Dawsons of Pall Mall. London.
- Fiji Department of Agriculture. 1956-1958, 1959, 1960, 1961. *Plant Introduction Lists*. Naduruloulou. Fiji.

- Fischer, John L. and Ann M. Fischer. 1970. *The Eastern Carolines*. Human Relations Area Files Press. New Haven.
- Fosberg, F.R. 1941. Names in *Amaranthus*, *Artocarpus* and *Inocarpus*. *Journal Washington Academy Science* 31(3):93-96.
- _____. 1960. Introgression in *Artocarpus* in Micronesia. *Brittonia* 12:101-113.
- Fosberg, F.R., M.-H. Sachet and K. Oliver. 1979. A geographical checklist of the Micronesian Dicotyledonae. *Micronesica* 15:41-295.
- Fox, Charles E. 1974. *Lau Dictionary*. Department of Linguistics. Research School of Pacific Studies. Australian National University. Canberra.
- Gerlach, Wolfgang P. and Fatu Salevao. 1984. Fruit rot of breadfruit, *Artocarpus altilis*, caused by *Phytophthora palmivora* in Western Samoa. *Alafua Agricultural Bulletin* 9(2):21-22.
- Glassman, S.F. 1952. *The Flora of Ponape*. Bernice Pauahi Bishop Museum. Bulletin 209. Honolulu.
- Gottlieb, L.D. 1971. Gel electrophoresis: new approach to the study of evolution.
- _____. 1977. Electrophoretic evidence and plant systematics. *Annals Missouri Botanical Garden* 64:161-180.
- _____. 1982. Conservation and duplication of isozymes in plants. *Science* 216:373-380.
- Graham, H.D. and E.N. Bravo. 1981. Composition of the breadfruit. *Journal Food Science* 46(2):535-539.
- Hall, Edward T. and Karl J. Peltzer. 1946. *The Economy of the Truk Islands - An Anthropological and Economic Survey*. Vol. 7. U.S. Commercial Co. Economic Survey of Micronesia. Honolulu.
- Hamilton, R.A., R.A. Criley and C.L. Chia. 1982. Rooting of stem cuttings of breadfruit under intermittent mist. *Proceedings International Plant Propagators Society* 32:347-350.

- Hancock, James F. 1982. Alcohol dehydrogenase isozymes in *Gossypium hirsutum* and its putative diploid progenitors: the biochemical consequences of enzyme multiplicity. *Plant Systematics and Evolution* 140:141-149.
- Handy, E.S. Craighill. 1923. *Native Culture in the Marquesas*. Bernice Pauahi Bishop Museum. Bulletin 9. Honolulu.
- Hans, A.S. 1972. Cytomorphology of arborescent Moraceae. *Journal Arnold Arboretum* 53(2):215-226.
- Harlan, Jack R. and J.M.J. DeWet. 1975. On ô. Winge and a prayer: The origins of polyploidy. *The Botanical Review* 41(4):361-390.
- Harrison, S.P. and S. Albert. 1977. *Mokilese-English Dictionary*. University of Hawaii Press. Honolulu.
- Hatheway, W.H. 1953. Land vegetation of Arno Atoll, Marshall Islands. *Atoll Research Bulletin* 16:1-68.
- _____. 1957. Agricultural notes on the southern Marshall Islands. *Atoll Research Bulletin* 55:1-9.
- Hawaii Agricultural Experiment Station. 1921, 1924, 1926, 1927, 1929, 1931. *Annual Report*. Honolulu.
- Hazelman, M.P. 1981. Plant genetic resources in Western Samoa. 110-112. In: J.T. Williams and J.L. Creech (eds.). *Crop Genetic Resources of the Far East and the Pacific*. International Board for Plant Genetic Resources. FAO. Rome.
- Henry, Teuira. 1928. *Ancient Tahiti*. Bernice Pauahi Bishop Museum. Bulletin 48. Honolulu.
- Herbst, Derral. 1973. Report from the Gilbert and Ellice Islands. *Pacific Tropical Botanical Garden Bulletin* 3(1):2-6.
- Hezel, Francis X. 1983. *The First Taint of Civilization. A History of the Caroline and Marshall Islands in Pre-colonial Days*. Pacific Islands Monograph Series. No. 1. University of Hawaii Press. Honolulu.

- Hooper, Anthony and Judith Huntsman. 1973. A demographic study of the Tokelau Islands. *Journal Polynesian Society* 82(4):366-411.
- Huguenin, Paul. 1902. *Ratatea la Sacree*. P. Attinger. Neuchatel.
- Jackson, G.V.H. 1982. Visit of the plant pathologist to Temotu Province, June 3-30. 2-26. In: *Solomon Islands Department of Agriculture Annual Report*. Honiara.
- Jacobs, Hubert. 1980. Father Francisco Miedes discovers the Caroline Islands before they are discovered. *Archivum Historicum Societatis Iesu*. Extractum e Vol XLIX:393-417.
- Jardin, Edälestant. 1862. *Essai sur l'histoire Naturelle de l'archipel des Marquises*. Bailliere. Paris.
- Jarret, R.L. and R.E. Litz. 1986a. Enzyme polymorphism in *Musa acuminata* Colla. *Journal of Heredity* 77:183-188.
- _____. 1986b. Isozymes as genetic markers in bananas and plantains. *Euphytica* 35:539-549.
- Jarrett, Frances M. 1959a. Studies in *Artocarpus* and allied genera. I. General considerations. *Journal Arnold Arboretum* 40(1):1-29.
- _____. 1959b. Studies in *Artocarpus* and allied genera. III. A revision of *Artocarpus* subgenus *Artocarpus*. *Journal Arnold Arboretum* 40(2):113-155; 40(3):298-326.
- _____. 1976. The syncarp of *Artocarpus* - a unique biological phenomenon. *Gardener's Bulletin Singapore* 29:35-39.
- Jensen, J.T. 1977. *Yapese-English Dictionary*. University of Hawaii Press. Honolulu.
- Kanehira, R. 1931. A desultory talk on the South Seas. I. Breadfruit. *Forestry (Sanrin)* 588:118-124.
- Keegan, William F. and Jared M. Diamond. 1987. Colonization of islands by humans: a biogeographical perspective. 49-92. In: Michael B. Schiffer (ed.). *Advances in Archaeological Method and Theory*. Vol. 10. Academic Press. London and New York.

- Kephart, Susan R. 1990. Starch gel electrophoresis of plant isozymes: a comparative analysis of techniques. *American Journal Botany* 77(5):693-712.
- Kerr, I.S. 1976. *Tropical Storms and Hurricanes in the Southwest Pacific*. New Zealand Meteorological Service. Miscellaneous Publication No. 148. Wellington.
- Kiang, L.T. and M.B. Gorman. 1985. Inheritance of NADP-active isocitrate dehydrogenase isozymes in soybeans. *Journal of Heredity* 76:279-284.
- Kirch, Patrick. 1984. The Polynesian outliers. *Journal Pacific History* 19(4):224-238.
- _____. 1985. *Feathered Gods and Fishhooks: An Introduction to Hawaiian Archaeology and Prehistory*. University of Hawaii Press. Honolulu.
- _____. 1986. Rethinking East Polynesian prehistory. *Journal Polynesian Society* 95(1):9-40.
- _____. 1987. Lapita and Oceanic cultural origins: excavations in the Mussau Islands, Bismarck Archipelago. *Journal Field Archaeology* 14(2):163-180.
- _____. 1988. The Talepakemalai Lapita site and Oceanic prehistory. *National Geographic Research* 4:328-342.
- _____. 1989. Second Millennium Arboriculture in Melanesia: archaeological evidence from the Mussau Islands. *Economic Botany* 43(2):225-240.
- _____. 1990. La colonisation du Pacifique. *La Recherche* 225 (21):1227-1232, 1235.
- Koroveibau, D. 1966. *Some Fiji Breadfruit Varieties*. Fiji Department of Agriculture. Bulletin 46. Suva.
- Lam, H.J. 1945. *Fragmenta Papuana (Observations of a Naturalist in Netherlands New Guinea)*. Trans. from the Dutch by L.M. Perry. Arnold Arboretum, Jamaica Plain, Massachusetts.
- Lambert, M. 1974. *Present Status and Conditions for Improving Agriculture in the Tokelau Islands*. South Pacific Commission. Noumea, New Caledonia.

- Lawrence, Pencile. 1964. Breadfruit cultivation practices and beliefs in Ponape. 43-64. In: *Breadfruit Cultivation Practices and Beliefs in the Trust Territory of the Pacific Islands*. Anthropological Working Papers No. 7-8 (Revised). Trust Territory Pacific Islands. Saipan.
- Leakey, C.L.A. 1977. *Breadfruit Reconnaissance Study in the Caribbean Region*. CIAT/ InterAmerican Development Bank.
- LeBar, Frank M. 1964. *The Material Culture of Truk*. Department of Anthropology, Yale University. New Haven.
- Lebot, Vincent, Mallikarjuna K. Aradhya and Richard M. Manshardt. 1991. Geographic survey of genetic variation in kava (*Piper methysticum* Forst. f. and *P. wichmannii* C. DC.). *Pacific Science* 45(2):169-185.
- Lebot, Vincent and J. Levesque. 1989. The origin and distribution of kava (*Piper methysticum* Forst. f., Piperaceae): A phytochemical approach. *Allertonia* 5(2):223-280.
- Lee, Kee-dong. 1976. *Kusaiean-English Dictionary*. University of Hawaii Press. Honolulu.
- Lopez, C.R. 1975. A method to obtain relatively uniform breadfruit trees from a stockplant. *Journal Agriculture University of Puerto Rico*. 59:77-78.
- Luomala, Katharine. 1953. *Ethnobotany of the Gilbert Islands*. Bernice Pauahi Bishop Museum. Bulletin 213. Honolulu.
- MacGregor, Gordon. 1937. *The Ethnology of Tokelau*. Bernice Pauahi Bishop Museum. Honolulu.
- MacKenzie, J. Boyd. 1964. Breadfruit cultivation practices and beliefs in the Marshall Islands. 1-15. In: *Breadfruit Cultivation Practices and Beliefs in the Trust Territory of the Pacific Islands*. Anthropological Working Papers No. 7-8 (Revised). Trust Territory Pacific Islands. Saipan.
- Markham, Clements Sir. 1904. *The Voyages of Pedro Fernandez de Quiros, 1595-1606*. Vol. I. Hakluyt Society. London.

- Massal, Emile and Jacques Barrau. 1954. Pacific subsistence crops: breadfruit. *South Pacific Bulletin* 4(4):24-26.
- Masse, W.B. 1990. Radiocarbon dating, sea-level change and the peopling of Belau. *Micronesica. Recent Advances in Micronesian Archaeology*. Supplement 2:213-230.
- Mason, L.E. 1947. *The Economic Organization of the Marshall Islands*. Vol. 9. U.S. Commercial Co. Economic Survey of Micronesia. Honolulu.
- McEwen, J.M. 1970. *Niue Dictionary*. Department of Maori and Island Affairs. Wellington.
- McKnight, Robert K. 1964. Breadfruit cultivation practices and beliefs in Palau. 17-41. In: *Breadfruit Cultivation Practices and Beliefs in the Trust Territory of the Pacific Islands*. Anthropological Working Papers No. 7-8 (Revised). Trust Territory Pacific Islands. Saipan.
- Mehra, P.N. and B.S. Gill. 1974. Cytological studies in Ulmaceae, Moraceae, and Urticaceae. *Journal Arnold Arboretum* 55:663-677.
- Menancio, D.I. and T. Hymowitz. 1989. Isozyme variation between diploid and tetraploid cytotypes of *Glycine tabacina* (Labill.) Benth. *Euphytica* 42:79-87.
- Merrill, E.D. 1912. *A Flora of Manila*. Bureau of Printing. Manila.
- _____. 1914. Plants of Guam *Philippine Journal Science. C. Botany*. 9:1-155.
- _____. 1918. *Species Blancoanae: a critical revision of Philippine species of plants described by Blanco and by Llanos*. Bureau of Printing. Manila.
- Miller, C. D., H. Denning and A. Bauer. 1948-1950. Food values of native foods from the Pacific Islands. 106-107. *Hawaii Agriculture Experiment Station Biennial Report*. Honolulu.
- Miracle, Marvin P. 1967. *Agriculture in the Congo Basin*. University of Wisconsin Press. Madison.
- Moncur, M.W. 1985. Floral ontogeny of the jackfruit. *Australian Journal Botany* 33:585-593.

- Moore, D.M. 1976. *Plant Cytogenetics*. John Wiley and Sons. New York.
- Moreuil, C. 1971. Brief notes on some fruit species on the east coast of Madagascar. *Fruits d'Outre Mer* 36:53-65.
- Moti, D.L. and O.P. Chaturveill. 1976. Propagating some subtropical and tropical fruits by budding. *Punjab Horticultural Journal* 16(1/2):33-38.
- Mowrey, Bruce D. and Dennis J. Werner. 1990. Developmental specific isozyme expression in peach. *Hortscience* 25(2):219-222.
- Murai, M., F. Pen and C.D. Miller. 1958. *Some Tropical South Pacific Island Foods. Description, history, use, composition and nutritional value*. University of Hawaii Press. Honolulu.
- Murray, C. 1894. Varieties of breadfruit, New Hebrides. *Journal Polynesian Society* 3:36.
- Muzik, T.J. 1948. Effect of hormones on root formation of *Artocarpus communis*. *Science* 107:225.
- Nalo, Caroline. 1967. *The Food Plants of Tango, South Santo, New Hebrides*. South Pacific Commission. Noumea, New Caledonia.
- National Tropical Botanical Garden 1990. Living collections. *The Bulletin* 20(1):15.
- Negron de Bravo, Edna, Horace D. Graham and Miquel Padovani. 1983. Composition of the breadnut (seeded breadfruit). *Caribbean Journal Science* 19:(3-4):27-32.
- Nishiyama, I. and N. Kondo. 1942. Chromosome studies in tropical plants. *Setken Jiho*. 1:26-28.
- Oomen, H.A.P.C. and S.H. Malcolm. 1958. *Nutrition and the Papuan Child*. South Pacific Commission. Technical Paper 118. Noumea, New Caledonia.
- Otanes, R.T. and T.P. Ruiz. 1956. Propagation of rimas by root cuttings. *Araneta Journal Agriculture* 3:56-66.
- Pacific Tropical Botanical Garden. 1973. A gift for Kahanu Gardens. *The Bulletin* 3(4):61.
- _____. 1978. Garden notes. *The Bulletin* 8(1):20.

- Pacific Tropical Botanical Garden. 1979. Garden notes. *The Bulletin* 9(1):5.
- _____. 1981. Directors report. *The Bulletin* 11(3):72.
- Paijmans, K. 1976. Vegetation. 23-105. Part II. In: K. Paijmans (ed.). *New Guinea Vegetation*. Elsevier. Amsterdam.
- Parham, B.E.V. 1959. Plant introductions in Western Samoa. *South Pacific Bulletin* 9(4):44-47.
- _____. 1967. Plant introduction and quarantine station, Fiji. *Fiji Agriculture Journal* 24(1/2):18-29.
- Parham, J.W. 1966. *Coconut and Breadfruit Surveys in the South Pacific*. South Pacific Commission. Technical Information Paper 1. Noumea, New Caledonia.
- Parkinson, Susan. 1984. *The Preservation and Preparation of Rootcrops and some Other Traditional Foods in the South Pacific Islands*. FAO RAS 83/001, Field Document 1. Suva, Fiji.
- Pawley, Andrew and Roger C. Green. 1984. The Proto-oceanic language community. *Journal Pacific History* 19(3):123-146.
- Pawley, Andrew and M. Ross. 1990. *The Prehistory of Oceanic Languages: A current view*. Paper presented at the "Comparative Austronesian Project Conference." Research School of Pacific Studies. Australian National University. Canberra.
- Perlman, Steve. 1977. Collecting breadfruit in the Society Islands. *Pacific Tropical Botanical Garden Bulletin* 7(4):81-84.
- Petard, P. 1986. *Plantes Utiles de Polynesie Raaui Tahiti*. Haere Po No Tahiti. Papeete.
- Petersen, Glenn. 1991. *The Complexity of Power, the Subtlety of Kava: Pohnpet's Sakau*. Paper presented at the "XVII Pacific Science Congress." Honolulu.
- Pollock, Nancy. 1970. *Breadfruit and Breadwinning on Namu Atoll*. Marshall Islands. Ph.D Dissertation. University of Hawaii. Honolulu.

- Pope, Willis T. nd. *Useful Fruits of the Hawaiian Islands and Other Tropical and Semi-tropical Lands*. University Microfilms. Ann Arbor, Michigan.
- _____. 1926. *A Study of Certain Economic Fruit Plants of the Hawaiian Islands*. Vol. III. Section 2:1-25. Doctor Science Thesis. University of Hawaii, Honolulu.
- _____. 1929. Propagation of plants by cuttings in Hawaii. *Hawaii Agricultural Experiment Station*. Circular No. 9. Honolulu.
- Powell, J.M. 1976. Ethnobotany. 106-184. Part III. In: K. Pajmans (ed.). *New Guinea Vegetation*. Elsevier. Amsterdam.
- Primack, R.B. 1985. Comparative studies of fruit in wild and cultivated trees of champedak (*Artocarpus integer*) and terap (*A. odoratissimus*) in Sarawak East Malaysia with additional information on the reproductive structure of Moraceae in Southeast Asia. *Malayan Nature Journal* 39:1-40.
- Purseglove, J.W. 1968. *Tropical Crops*. Dicotyledons. Longman. London.
- Quijano, Jairo and Gabriel J. Arango. 1979. The breadfruit from Colombia - a detailed chemical analysis. *Economic Botany* 33(2):199-202.
- Quisumbing, Eduardo. 1940. The validity of *Artocarpus camansi* Blanco. *Philippine Journal Science* 72(2):331-337.
- _____. 1951. *Medicinal Plants of the Philippines*. Bureau of Printing. Manila.
- Ragone, Diane. 1987. Collecting breadfruit in the central Pacific. *Pacific Tropical Botanical Garden Bulletin* 17(2):37-41.
- _____. 1988. *Breadfruit Varieties in the Pacific Atolls*. UNDP Integrated Atoll Development Project. Suva, Fiji.
- _____. 1989. Our breadfruit collection grows. *Pacific Tropical Botanical Garden Bulletin* 19(3):86-89.
- _____. In press. The Ethnobotany of Breadfruit in Polynesia. In: P.A. Cox (ed.). *Plants and Man in Polynesia*. Dioscorides Press. Portland.

- Raynor, William C. 1989. *Structure, Production of Seasonality in an Indigenous Pacific Island Agroforestry System: A Case Example on Pohnpet Island*. F.S.M. Master of Science Thesis. University of Hawaii, Honolulu.
- Reeve, R.M. 1974. Histological structure and commercial dehydration potential of the breadfruit. *Economic Botany* 28(1):82-96.
- Rowe-Dutton, P. 1976. Breadfruit. 248-268. In: R.J. Garner and S.A. Chaudhri (eds.). *Propagation of Tropical Fruits*. Horticultural Review No. 4. Commonwealth Bureau of Horticulture and Plantation Crops. CAO/FAO.
- Russell, O.S. 1953. Progress report on research in tropical and subtropical fruits at the Government Experiment Station, Nassau. *Proceedings Florida State Horticulture Society* 66:187-188.
- Sabatier, E. 1971. *Gilbertese-English Dictionary*. Bridge Printery. Sydney.
- Safert, E. 1983. Kosrae. In: G. Thilenius (ed.). *Results of the 1908-1910 South Seas Expedition. II. Ethnography. Vol. 4. 1919-1920*. Friederichsen and Co. Hamburg. Trans. by E.A. Murphy. German SÅdsee Translation Project. Pacific Island Studies Program, University of Hawaii. Honolulu.
- Safford, W.E. 1905. *The Useful Plants of the Island of Guam*. Contributions from the U.S. National Herbarium. Vol. 9. Smithsonian Institution. Washington, D.C.
- Sanford, J.C. 1983. Ploidy manipulations. 100-123. In: J.N. Moore and J. Janick (eds.). *Methods in Fruit Breeding*. Purdue University Press. West Lafayette, Indiana.
- Sasuke, Nakao. 1953. Breadfruit, yams and taros of Ponape Island. *Proceedings of the 7th. Pacific Science Association Congress* 6:159-170.
- Savage, Stephen 1962. *A Dictionary of the Maori Language of Rarotonga*. Department of Island Territories. Wellington.

- Schattenburg, Patricia. 1976. Food and cultivar preservation in Micronesian voyaging. 29-51. In: *Micronesian and Polynesian Voyaging: Three readings*. Pacific Island Studies Program. Miscellaneous Working Papers Series. University of Hawaii, Honolulu.
- Schwartz, F. 1966. *The Origin of Cultivated Plants*. Harvard University Press. Cambridge.
- Seeman, Berthold C. 1865-1873. *Flora Vitiensis: A Description of the Plants of Viti or Fiji Islands*. Reeve and Co. London.
- Setchell, W.A. 1924. *American Samoa. Part I. Vegetation of Tutuila Island*. Department Marine Biology. Carnegie Institute. Washington D.C.
- Sharma, M.R. 1965a. Morphological and anatomical investigations on *Artocarpus* Forst. III. The flower. *Phytomorphology* 15(2):185-201.
- _____. 1965b. Morphological and anatomical investigations on *Artocarpus* Forst. IV. The fruit. *Proceedings Indian Academy Science* 60:380-393.
- Shutler, Richard and Jeffrey C. Marck. 1975. On the dispersal of the Austronesian horticulturists. *Archaeology and Physical Anthropology in Oceania* 10(2):81-113.
- Simmonds, N.W. 1979. *Principles of Crop Improvement*. Longman. London.
- Singh, S., S. Krishnamurthi and S.L. Katyal. 1967. Breadfruit. 276-280. In: *Fruit Culture in India*. Indian Council Agricultural Research. New Delhi.
- Small, C.A. 1972. *Atoll Agriculture in the Gilbert and Ellice Islands*. Department of Agriculture. Tarawa.
- Solomon Islands Department of Agriculture. 1982. Annual Report. Honiara.
- Soltis, D., C. Haufler, D. Darrow and G. Gastony. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers and staining schedules. *American Fern Journal* 73:9-26.
- Sonnerat, Pierre. 1776. *Voyage de la Nouvelle Guinee*. Ruault. Paris.

- Sorenson, E.R. and D.C. Gajdusek. 1969. Nutrition in the Kuru region. I. Gardening, food handling and diet of the Fore people. *Acta Tropica* 26(4):281-330.
- Soucie, E.A. 1978. Types of Breadfruit in Ponape. In *Tropical Horticulture for Secondary Schools*. Appendix II. Department of Education. Trust Territory Pacific Islands. Saipan.
- South Pacific Commission. 1983. *Food Composition Tables for Use in the Pacific Islands*. Noumea, New Caledonia.
- Spriggs, Matthew. 1984. The Lapita cultural complex: origins, distributions, contemporaries and successors. *Journal Pacific History* 19(4):202-221.
- Standley, P.C. and J.A. Steyermark. 1946. The flora of Guatemala. *Fieldiana. Botany* 24(4):1-493.
- Stebbins, G.L. 1971. *Chromosome Evolution in Higher Plants*. Edward Arnold. London.
- Stone, B.C. 1970. The flora of Guam. *Micronesica* 6:248-249.
- Terrell, John. 1986. *Prehistory in the Pacific Islands*. Cambridge University Press. Cambridge.
- Thaman, Randy R. 1983. Food for urbanising Polynesian peoples. *Proceedings of the Nutrition Society of New Zealand* 8:25-37.
- Theobald, William L. 1976. Ethnobotany of the breadfruit. *Pacific Tropical Botanical Garden Bulletin* 6(1):1-3.
- Thomas, S. and M. Corden. 1977. *Metric Tables of Composition of Australian Foods*. Commonwealth Department of Health. Government Printing Service. Canberra.
- Thompson, L. 1940. *Southern Lau, Fiji: An Ethnography*. Bernice Pauahi Bishop Museum. Bulletin 162. Honolulu.
- Torres, A.M. 1983. Fruit trees. 401-421. In: S.D. Tanksley and T.J. Orton (eds.). *Isozymes in Plant Genetics and Breeding*. Part B. Elsevier, Amsterdam.
- Tri Sunarto, A. 1981. Fertility test of *Artocarpus altilis* pollen. *Berita Biologia* 2(6):118.

- Trujillo, E. 1971. *Breadfruit Diseases of the Pacific Basin*. South Pacific Commission. Information Document 27. Noumea, New Caledonia.
- Tryon, D.T. 1984. The peopling of the Pacific: a linguistic appraisal. *Journal Pacific History* 19(3):147-159.
- Tuvalu Ministry of Commerce and Natural Resources. 1982. Department of Agriculture Annual Report. Funafuti.
- Useem, J. 1946. *Report on Yap and Palau*. Vol. 6. U.S. Commercial Co. Economic Survey of Micronesia. Honolulu.
- Visher, S.S. 1925. *Tropical Cyclones of the Pacific*. Bernice Pauahi Bishop Museum. Bulletin 20. Honolulu.
- Walter, Annie. 1989. Notes sur les cultivars d'arbre de pain dans le Nord de Vanuatu. *Journal de la Societe des Oceanistes* 1/2:3-18.
- Weeden, N.J. and R.C. Lamb. 1985. Identification of apple cultivars by isozyme phenotypes. *Journal American society Horticultural Science* 110(4):509-515.
- Werth, Charles R. 1985. Implementing an isozyme laboratory at a field station. *Virginia Journal Science* 36(1):53-76.
- Wester, P.J. 1920. The breadfruit. *Philippine Agriculture Journal* 13(3):223-229.
- _____. 1924. The seedless breadfruits of the Pacific archipelagoes. *Philippine Agriculture Review* 17(1):24-39.
- Western Samoa Department of Agriculture. 1956, 1959-1962, 1964, 1968, 1972. *Annual Report*. Apia.
- Wiens, H.J. 1957. Field notes on atolls visited in the Marshall Islands. 1956. *Atoll Research Bulletin* 54:1-24.
- _____. 1962. *Atoll Environment and Ecology*. Yale University Press. New Haven.
- Wilder, Gerrit Parmille. 1928. *Breadfruit of Tahiti*. Bernice Pauahi Bishop Museum. Bulletin 50. Honolulu.

- Wilder, Gerrit Parmille. 1931. *Flora of Rarotonga*. Bernice Pauahi Bishop Museum. Bulletin 86. Honolulu.
- Wilkes, Charles. 1845. *Narrative of the United States Exploring Expedition During the Years 1838-1842*. Lea and Blanchard. Philadelphia.
- Wooten, M. and F. Tumalii. 1984. Breadfruit production, utilisation and composition. A review. *Food Technology in Australia* 36(10):464-465.
- Yen, D.E. 1973a. Agriculture in Anutan Subsistence. 113-149. In: D.E. Yen and J. Gordon (eds.). *Anuta: A Polynesian Outlier in the Solomon Islands*. Pacific Anthropological Records No. 21. Department of Anthropology. Bernice Pauahi Bishop Museum. Honolulu.
- _____. 1973b. Ethnobotany from the voyages of Mendana and Quiros in the Pacific. *World Archaeology* 5:32-43.
- _____. 1974. Arboriculture in the subsistence of Santa Cruz, Solomon Islands. *Economic Botany* 28(3):247-284.
- _____. 1987. *Polynesian Cultigens and Cultivars: The Questions of Origin*. Paper presented at the "Plants and Man in Polynesia Ethnobotany Symposium." Laie, Hawaii.
- Yndgaard, F. and A. Hoskuldsson. 1985. Electrophoresis: a tool for genebanks. *FAO/IBPGR Plant Genetic Resources Newsletter* 63:34-40.
- Yuncker, T.G. 1943. *The Flora of Niue Island*. Bernice Pauahi Bishop Museum. Bulletin 178. Honolulu.
- _____. 1959. *Plants of Tonga*. Bernice Pauahi Bishop Museum. Bulletin 220. Honolulu.
- Zaiger, D. and G.A. Zentmeyer 1966. A new lethal disease of breadfruit in the Pacific Islands. *Plant Disease Reporter* 50(12):892-896.