

COMPLEX ORIGINS OF BREADFRUIT (*ARTOCARPUS ALTILIS*, MORACEAE): IMPLICATIONS FOR HUMAN MIGRATIONS IN OCEANIA¹

NYREE J. C. ZEREGA,^{2,4} DIANE RAGONE,³ AND TIMOTHY J. MOTLEY²

²The Lewis B. and Dorothy Cullman Program for Plant Molecular Systematic Studies, The New York Botanical Garden, Bronx, New York 10458 USA; and ³The National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, Hawaii 96741 USA

Breadfruit (*Artocarpus altilis*, Moraceae), a traditional starch crop in Oceania, has enjoyed legendary status ever since its role in the infamous mutiny aboard the *H.M.S. Bounty* in 1789, yet its origins remain unclear. Breadfruit's closest relatives are *A. camansi* and *A. mariannensis*. DNA fingerprinting data (AFLP, amplified fragment length polymorphisms) from over 200 breadfruit cultivars, 30 *A. camansi*, and 24 *A. mariannensis* individuals were used to investigate the relationships among these species. Multivariate analyses and the identification of species-specific AFLP markers indicate at least two origins of breadfruit. Most Melanesian and Polynesian cultivars appear to have arisen over generations of vegetative propagation and selection from *A. camansi*. In contrast, most Micronesian breadfruit cultivars appear to be the result of hybridization between *A. camansi*-derived breadfruit and *A. mariannensis*. Because breadfruit depends on humans for dispersal, the data were compared to theories on the human colonization of Oceania. The results agree with the well-supported theory that humans settled Polynesia via Melanesia. Additionally, a long-distance migration from eastern Melanesia into Micronesia is supported.

Key words: *Artocarpus altilis*; *Artocarpus camansi*; *Artocarpus mariannensis*; amplified fragment length polymorphisms; breadfruit; human migration; Oceania; origin of domesticated plants.

Breadfruit and its wild relatives—Breadfruit has long been a traditional starch crop throughout Oceania (Melanesia, Micronesia, and Polynesia) (Fig. 1). Over thousands of years of cultivation, humans have selected for hundreds of unique cultivars, many of which are seedless and are vegetatively propagated (Wilder, 1928; Ragone, 1997). The loss of fertility in breadfruit is due to triploidy ($2n = 3x = \sim 84$), or in the case of sterile diploids ($2n = 2x = 56$) it is the result of hybridization (Ragone, 2001). While seedless cultivars provide an important source of starch, some cultivars produce few to many edible seeds. Generally, the prominence of seedless cultivars increases as one travels from New Guinea eastward through Melanesia (where seeded cultivars are common) into western Polynesia (where few-seeded and seedless cultivars are prevalent) and into eastern Polynesia (where virtually all cultivars are seedless triploids with identical zymotypes) (Ragone, 1991). In Micronesia, seeded and seedless diploid, as well as seedless triploid cultivars occur (Jarrett, 1959b; Ragone, 1997, 2001). Since breadfruit's discovery by Europeans nearly 400 years ago (Markham, 1904), a small number of cultivars have been introduced to tropical regions throughout

the world, including the Caribbean (Powell, 1973; Leakey, 1977), Africa, and India (Ragone, 1997). However, the genetic diversity and importance of breadfruit remain greatest in the Pacific islands.

Breadfruit belongs to the genus *Artocarpus* (Moraceae), which consists of approximately 60 species native to the Indian subcontinent, Southeast Asia, and Australasia (Jarrett, 1959a, b; Kochummen, 2000). By the time the first written record of breadfruit was published, the domesticate was already distributed throughout the islands of Oceania, beyond the range of any wild *Artocarpus* species (Markham, 1904). This led to much speculation and numerous theories on the possible area of origin of breadfruit, which included Polynesia (Purseglove, 1968), Pacific and Tropical Asia (Rajendran, 1992), the Malayan archipelago (Popenoe, 1920), and the region embracing New Guinea, the Philippines and the Moluccas (Smith et al., 1992). Additionally, the identity of its wild progenitors remained problematic. Quisumbing (1940) suggested that breadfruit was “derived, by selection, from some species perhaps even approximating the *camansi*” (= *A. camansi* Blanco). Fosberg (1960) proposed that the “wild breadfruit” (= *A. camansi*) and *A. blancoi* (Elmer) Merr. hybridized in the Philippines and gave rise to the triploid seedless breadfruit common in Polynesia. He also suggested, based on characters of lamina shape and indumentum, that subsequent secondary hybridization and introgression between triploid breadfruit and *A. mariannensis* Trécul occurred in Micronesia. Jarrett (1959b) put forward the idea that two or more wild ancestors may have been involved in the origin of breadfruit but did not indicate which species.

Wild populations of *A. camansi* have been recorded from primary forests in New Guinea (Jarrett, 1959b). It remains unclear whether it is also native to the Moluccas and the Philippines or simply naturalized there, because it is usually only associated with secondary forest and human habitation (Jarrett, 1959b; Ragone, 1997). *Artocarpus camansi* has been intro-

¹ Manuscript received 14 August 2003; revision accepted 18 December 2003.

The authors are grateful for the field assistance of R. Kiapranis, M. Kostka, V. Novotny, L. Raulerson, W. Raynor, and A. Rinehart. We would also like to thank H. Cross, G. Petersen, K. Wurdack, and two anonymous reviewers for useful comments on the manuscript. Finally, we would like to thank the National Tropical Botanical Garden, National Research Institute of Papua New Guinea (PNG), Forest Research Institute (Lae, PNG), The Parataxonomist Training Center (Madang, PNG), and the Nature Conservancy in Pohnpei, Federated States of Micronesia. This research was funded by the Lewis B. and Dorothy Cullman Foundation, NSF grant DEB-0073161, The Garden Club of America Award in Tropical Botany, The Explorers Club, and the Margaret and Herman Sokol Travel and Research Award for Predoctoral Students in the Sciences.

⁴ Author for correspondence and reprint requests, current address: Department of Plant Biology, University of Minnesota, 1445 Gortner Avenue, St. Paul, MN 55108 USA.

duced as a seed crop to other tropical locations and is especially common in the Caribbean and South America. *Artocarpus blancoi* is endemic to the Philippines where it is used for its timber (Jarrett, 1959b). *Artocarpus mariannensis* is native to the Mariana Islands and Palau and has been introduced to a limited number of other islands in the Pacific (Micronesian atolls, Tuvalu, and Tokelau) for its edible fruits and seeds (Ragone, 1997, 2001). Phylogenetic analysis of 38 species of *Artocarpus* and 13 outgroup taxa based on morphological data and DNA sequences from the internal transcribed spacers (ITS) and the *trnL-F* region revealed that *A. altilis*, *A. camansi*, and *A. mariannensis* form a very highly supported monophyletic lineage, while *A. blancoi* is much more distantly related (Zerega, 2003). This suggests that *A. camansi* and *A. mariannensis* are breadfruit's closest wild relatives.

Human migrations in Oceania—Because breadfruit movement through the Pacific islands was human-mediated (cultivars are either seedless or have short-lived seeds that would not survive long ocean voyages), understanding breadfruit's origins is not only useful for agronomic and conservation purposes, but can also provide information about human migrations in the Pacific. Scientists continue to contemplate the migration patterns of Pacific Islanders' ancestors and the relationships among Melanesia, Polynesia, and Micronesia. The human settlement of the islands of Polynesia is dated to within the last 4000 years. It is generally agreed upon that they were settled from somewhere in Island Southeast Asia via Melanesia by the Lapita cultural complex, a group known for their distinctive pottery and excellent seafaring skills (Kirch and Hunt, 1988; Spriggs, 1989; Intoh, 1997; Lum and Cann, 1998, 2000; Kirch, 2000; Gibbons, 2001) (Fig. 1, pathway 1). However, the exact location from whence these Austronesian-speaking people originated and how extensively they integrated with Melanesians who had already been living in New Guinea and the Solomon Islands for upwards of 40000 years is debated (Diamond, 1988; Terrell, 1988; Richards et al., 1998; Lum and Cann, 1998; Kirch, 2000).

The human settlement of the culturally and linguistically heterogeneous Micronesian Islands is more complex. It was likely settled from several directions at different times, and based on evidence from linguistics, archaeology, and genetics, several nonexclusive hypotheses have been proposed. These include, but are not limited to, the following: (a) Palau and Yap experienced human migrations from New Guinea (Fig. 1, pathway 2) (Lum and Cann, 2000), (b) central-eastern Micronesia (Caroline Islands, Marshall Islands, and Kiribati) was settled from somewhere between the Bismarck archipelago and the southeast Solomons-Vanuatu region, either directly by long-distance voyaging (Fig. 1, pathway 3), or (c) indirectly with the Kiribati archipelago being used as a stepping-stone passageway (Fig. 1, pathway 4) into the high islands of central Micronesia (Petersen, 1995; Lebot and Lévesque, 1989; Kirch, 2000). Subsequent migrations also occurred within the islands of Micronesia (Kirch, 2000; Lum and Cann, 2000).

Because of the questions surrounding breadfruit origins and the role of humans in its dispersal, the objectives of this study were to (a) test the relationships among breadfruit and its closest relatives, *A. camansi* and *A. mariannensis*, using DNA fingerprinting data (amplified fragment length polymorphisms, AFLP) and (b) trace human-mediated breadfruit dispersal through Oceania.

MATERIALS AND METHODS

Plant materials—Fresh leaf samples from 30 *A. camansi*, 24 *A. mariannensis*, 183 *A. altilis* (34 from Melanesia, 15 from western Polynesia, 66 from eastern Polynesia, and 68 from Micronesia), and 19 putative Micronesian *A. altilis* × *A. mariannensis* hybrids were collected and stored on silica gel. Collections were made in Papua New Guinea, the Mariana Islands, Pohnpei of the Federated States of Micronesia, or from the National Tropical Botanical Garden (NTBG) in Hawaii (see Supplemental Data accompanying online version of this article). Individuals were considered to be putative hybrids if they possessed certain characters from both putative parents. Characters considered were leaf shape, leaf indumentum, and infructescence surface color and texture.

DNA extraction and amplified fragment length polymorphisms (AFLP)—Genomic DNA was extracted from approximately 1 cm² of dried leaf tissue using a CTAB (cetyltrimethylammonium bromide) method (Zerega et al., 2002). DNA concentrations were estimated by comparing genomic DNA to known quantities on an agarose gel.

AFLP involves the restriction of genomic DNA with two enzymes coupled with the ligation of known flanking sequences onto the restriction fragments, followed by two rounds of increasingly selective PCR (Vos et al., 1995). The AFLP technique was chosen for this study due to its ability to detect polymorphisms in very closely related species and cultivars in a wide range of plant species (Milbourne et al., 1997; Cervera et al., 1998; Paran et al., 1998; Yamamoto et al., 1998; Loh et al., 1999). Because AFLP uses the entire genome as a template for detecting polymorphisms, the likelihood of detecting polymorphisms in closely related individuals increases. Additionally, AFLPs have proven to be highly reproducible (Jones et al., 1997).

AFLP reactions were accomplished using the AFLP Plant Mapping kit (Applied Biosystems, Foster City, California, USA) and a modified protocol (Zerega et al., 2002). Briefly, genomic DNA (0.2–0.3 µg) was digested with *EcoRI* and *MseI* enzymes, known flanking sequences were ligated onto the restriction fragments, and pre-selective PCR reactions with a single selective nucleotide on the 3' end of the primers were run followed by selective PCR with three selective nucleotides on the 3' end of the primers. Sixty-four selective primer combinations were screened on six samples (two each of *A. altilis*, *A. camansi*, and *A. mariannensis*), and three were chosen based on having the highest number of bands and the highest percentage of polymorphic bands (*EcoRI-ACA/MseI-CTC*, *EcoRI-ACA/MseI-CAT*, and *EcoRI-AAG/MseI-CTG*). The selective amplification products were separated and visualized on a 5% Long Ranger (Cambrex, Rockland, Maine, USA) gel on an ABI 377 sequencer using Genescan 3.1 and a Genescan Rox standard in each lane (Applied Biosystems). The standard contained 16 fluorescent-labeled fragments ranging in size from 35 to 500 base pairs so that the size of the AFLP fragments could be determined.

Genotyper 2.1 (Applied Biosystems) was used to score AFLP data manually for the presence and absence of different sized fragments. Ambiguous size categories (those in which the intensity of the fragment varied so widely among samples that it was difficult to ascertain its presence or absence in some samples) were excluded. Fragments of the same size were considered homologous and were scored as either present or absent in each individual to create a binary data matrix. The assumption that equal length equals homology can be mistaken as has been shown in studies of fragment homology in RAPDs (Thormann et al., 1994; Stammers et al., 1995). However, those studies were looking at intergeneric species, and as genetic distances increase, the probability of equating fragment size with homology decreases (van de Zande and Bijlsma, 1995). In addition, the use of polyacrylamide gels to separate AFLP fragments rather than agarose gels provides more accurate resolution of fragment size.

Principal components analysis—AFLP data were analyzed using principal components analysis (PCA) on a square symmetric matrix of correlations in the software package JMP (SAS Institute, Cary, North Carolina, USA). Four subsets of the data were analyzed based on the geographical region from which the breadfruit cultivars originated. The four subset analyses consisted

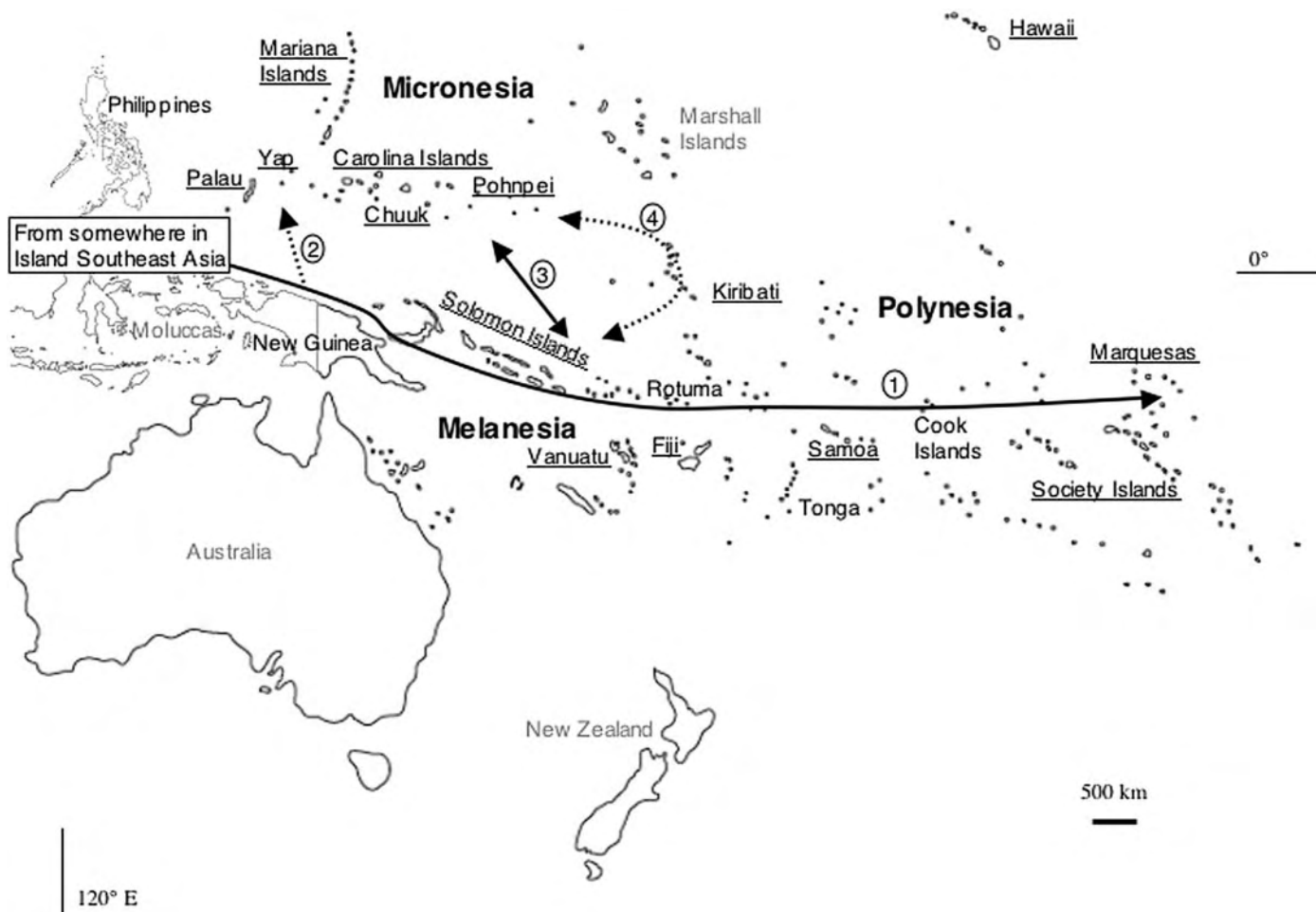


Fig. 1. Map of Oceania indicating the regions Melanesia, Micronesia, and Polynesia as well as generalized, previously proposed human migration routes. Pathway 1 indicates a simplified Lapita expansion from somewhere in Island Southeast Asia eastward along the coast of New Guinea through Melanesia and into Polynesia. Pathway 2 indicates a migration from New Guinea into Palau and Yap. Pathway 3 indicates a direct northerly Lapita expansion into Micronesia, whereas pathway 4 indicates an indirect route via the atolls of Kiribati. The pathways with solid lines are supported most strongly by the breadfruit data (see Discussion). Underlined locations indicate areas where both *Artocarpus mariannensis* and *A. camansi* fingerprints are found within individual breadfruit cultivars. Locations that are not underlined indicate areas with only *A. camansi* fingerprints present in breadfruit cultivars. Locations with gray text were not sampled.

of all *A. camansi* and *A. mariannensis* individuals with breadfruit cultivars from either Melanesia (34 individuals), western Polynesia (15 individuals), eastern Polynesia (66 individuals), or Micronesia (87 individuals including *A. altilis* and *A. altilis* × *mariannensis*). Melanesia includes New Guinea, Solomon Islands, Vanuatu, Rotuma, and Fiji. Western Polynesia includes Samoa and Tonga. Eastern Polynesia includes Cook Islands, Society Islands, Hawaii, and Marquesas. Micronesia includes Palau, Yap, Chuuk, Pohnpei, Mariana Islands, and Kiribati.

RESULTS

Three AFLP primer pair combinations were used to study 212 breadfruit cultivars and breadfruit's two closest wild relatives (30 *A. mariannensis* and 24 *A. camansi* individuals) and generated 175 markers (68 markers from *EcoRI*-ACA/*MseI*-CTC, 51 markers from *EcoRI*-ACA/*MseI*-CAT, and 56 markers from *EcoRI*-AAG/*MseI*-CTG), 149 of which were polymorphic. The AFLP data were subjected to four separate principal components analyses based on geographic regions, and two general patterns were revealed. In Melanesia and Polynesia, *A. altilis* cultivars cluster most closely with *A. camansi*,

while in Micronesia, *A. altilis* cultivars cluster between *A. camansi* and *A. mariannensis* individuals (Fig. 2).

AFLP markers unique to each wild species, *A. camansi* and *A. mariannensis*, were categorized as either constant (present in all individuals of one wild species and absent in all individuals of the other wild species) or nonconstant (present in at least one individual of one wild species and absent in all individuals of the other wild species) (Motley and Morden, 2001). Upon examination of all the AFLP markers, one constant and five nonconstant *A. camansi*-specific markers were identified, while three constant and two nonconstant *A. mariannensis*-specific markers were identified (Table 1). The distributions of both *A. camansi*- and *A. mariannensis*-specific markers were traced in all *A. altilis* cultivars. The majority of breadfruit cultivars in Melanesia (91%) and Polynesia (88% in western Polynesia and 89% in eastern Polynesia) have only *A. camansi*-specific markers and no *A. mariannensis*-specific markers present within an individual (Fig. 3). However, cultivars in Melanesia (only in the Solomons, Fiji, and Vanuatu), western Polynesia (only in Samoa), and eastern Polynesia

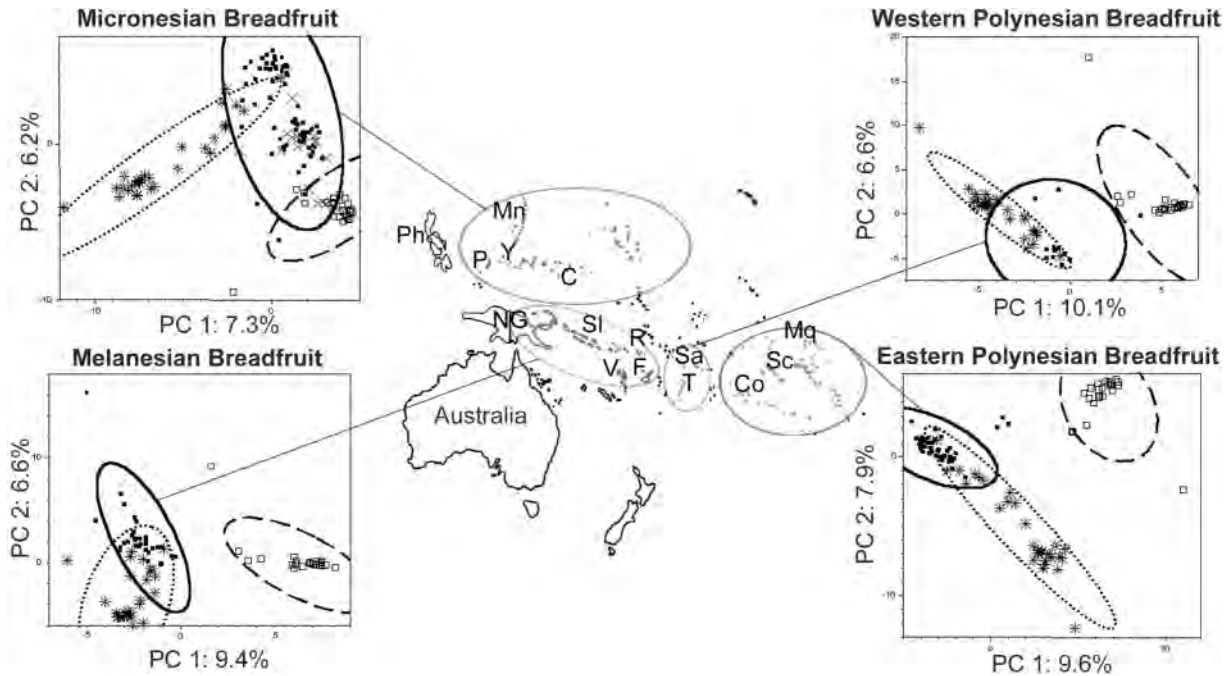


Fig. 2. Principal components analysis of breadfruit and its wild progenitors. The regions from which breadfruit cultivars were sampled in Melanesia, western Polynesia, eastern Polynesia, and Micronesia are circled on the map. Abbreviations for islands are as follows: C, Caroline Islands (including Pohnpei and Chuuk); F, Fiji; K, Kiribati; Mn, Mariana Islands; Mq, Marquesas; NG, New Guinea; P, Palau; Ph, Philippines; R, Rotuma; Sa, Samoa; Sc, Society Islands; SI, Solomon Islands; T, Tonga; V, Vanuatu; and Y, Yap. Symbols for the species are as follows: filled squares, *Artocarpus altilis*; stars, *A. camansi*; open squares, *A. mariannensis*; X, putative *A. altilis* × *A. mariannensis*. Bivariate normal ellipses with $P = 0.95$ are solid black for *A. altilis*, short-hatched for *A. camansi*, and long-hatched for *A. mariannensis*.

(only in the Society Islands, Marquesas, and Hawaii) occasionally have at least one each of *A. camansi*-specific and *A. mariannensis*-specific markers present in an individual (9, 12, and 11% of the samples, respectively) (Fig. 3). Among all the Micronesian breadfruit sampled, 78% of the cultivars contain at least one each of *A. mariannensis*- and *A. camansi*-specific markers per individual (although only 20% were previously identified as hybrids based on morphology), 20% have only *A. camansi*-specific markers, and 2% have only *A. mariannensis*-specific markers present (Fig. 3).

DISCUSSION

Breadfruit origins—Previous phylogenetic studies of the genus *Artocarpus* based on molecular and morphological data strongly support a close relationship among breadfruit, *A. ca-*

mansi, and *A. mariannensis* (Zerega, 2003). However, the role of each species in the origins of breadfruit remained untested. The data presented here suggest at least two stages in the origins of cultivated breadfruit, vegetative propagation of *A. camansi* and subsequent human selection in Melanesia and Polynesia, and hybridization between *A. camansi*-derived breadfruit and *A. mariannensis* in Micronesia. The distribution of *A. camansi*- and *A. mariannensis*-specific AFLP markers in breadfruit cultivars indicates that nearly all Melanesian and Polynesian cultivars have only *A. camansi*-specific markers present, while most Micronesian cultivars have both *A. camansi*- and *A. mariannensis*-specific markers present within individual cultivars (Fig. 3). Thus, most cultivars in Melanesia and Polynesia are derived from a single species, *A. camansi*. These cultivars include both diploids and triploids (Ragone,

TABLE 1. Distribution of AFLP markers specific to either *Artocarpus camansi* or *A. mariannensis* in the two species.

Taxa	Primers <i>EcoRI/MseI</i>	Fragment size (bp)	Percentage of <i>A. camansi</i> individuals with marker present	Percentage of <i>A. mariannensis</i> individuals with marker present
<i>A. camansi</i>	AAG/CTG	91	100	0
<i>A. camansi</i>	ACA/CAT	95	67	0
<i>A. camansi</i>	ACA/CAT	219	57	0
<i>A. camansi</i>	ACA/CTC	70	73	0
<i>A. camansi</i>	ACA/CTC	124	73	0
<i>A. camansi</i>	ACA/CTC	369	93	0
<i>A. mariannensis</i>	AAG/CTG	405	0	87
<i>A. mariannensis</i>	ACA/CTC	68	0	100
<i>A. mariannensis</i>	ACA/CTC	248	0	96
<i>A. mariannensis</i>	ACA/CTC	262	0	100
<i>A. mariannensis</i>	ACA/CTC	267	0	100

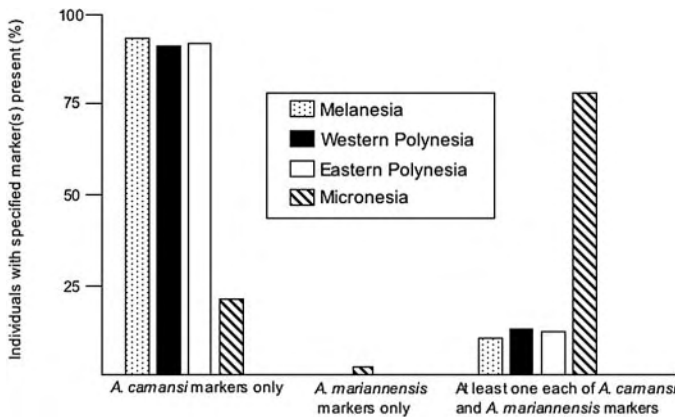


Fig. 3. Distribution of *Artocarpus camansi* and *A. mariannensis* markers in breadfruit cultivars by region.

2001). The presence of only *A. camansi* markers in most of these cultivars suggests that they are primarily autotriploids (Fig. 3). In contrast, most Micronesian cultivars are of hybrid origin, even those that were not previously recognized as hybrids based on morphological characters. More in-depth morphological studies that are currently in progress confirm the higher incidence of hybrids among Micronesian cultivars (Ragone, personal communication). Micronesian hybrids include both sterile and fertile diploids and triploids (Ragone, 2001). The presence of fertile diploid hybrids would allow for the possibility of introgression with *A. mariannensis* in Micronesia.

These findings support, in part, Fosberg's (1960), Quisumbing's (1940), and Jarrett's (1959b) ideas on breadfruit origins. However, Fosberg's inclusion of *A. blancoi* as a wild progenitor seems unlikely given its distant relationship to breadfruit (Zerega, 2003), and the notion that triploid breadfruit is introgressing with diploid *A. mariannensis* in Micronesia seems highly improbable. Quisumbing's hypothesis that only *A. camansi* was involved does not completely explain all of breadfruit's variation. Jarrett (1959b) did not specifically identify possible wild progenitors; however, she did suggest that "two or more taxonomic entities" may have been involved in "a complex hybridization."

Breadfruit and human migrations—Because breadfruit movement through the Pacific islands had to be human-mediated, it is reasonable to consider the data in the context of human migrations. The finding that most Melanesian and Polynesian breadfruit cultivars are derived from *A. camansi* complements the well-accepted theory of a west to east human migration of the Lapita people through Melanesia into Polynesia (Fig. 1, pathway 1) (Lum and Cann, 1998, 2000; Kirch, 2000; Gibbons, 2001). New Guinea, the Bismarck Archipelago, and the Solomon Islands are considered part of Near rather than Remote Oceania (Green, 1991), because they are all intervisible and were settled in the late Pleistocene (ca. 40 000 years ago) before the advent of the Austronesian-speaking Lapita people (ca. 4500 years ago) (Kirch, 2000). Thus, the seeds of *A. camansi* could have been transported from their native New Guinea by pre-Lapita, non-Austronesian speaking humans as far east as the Solomons. Such sexual reproduction of plants would explain the presence of primarily seeded cultivars in these islands. However, when the Lapita people ar-

rived and ventured on longer ocean voyages eastward into the unsettled distant islands of Melanesia and Polynesia in Remote Oceania, a shift to vegetative propagation would have been necessary. In fact, the Lapita people are known for their dependence on vegetatively propagated crops such as bananas, taro, yam, sugarcane, and kava (Barrau, 1963; Lebot, 1992; Kirch, 2000). This shift to vegetative propagation would have made long-distance transportation of breadfruit possible and increased the chances of few-seeded or seedless cultivars originating (due to accumulated somatic mutations and meiotic defects) and persisting (due to human selection). In regions where vegetative propagation and sexual reproduction both occurred, unreduced diploid gametes could have joined with normal haploid gametes to produce triploid seedless cultivars. Indeed, it is in the eastern Solomon Islands and Vanuatu where few-seeded cultivars begin to appear and in western Polynesia where few-seeded and seedless cultivars emerge (Ragone, 1997). Seedless cultivars were then preferentially propagated and dispersed eastward, effectively transforming breadfruit into a starch crop in Polynesia (Ragone, 2001). Isozyme studies of breadfruit (Ragone, 1991) also support this west to east migration route into Polynesia. Zymotypic diversity of cultivars decreases eastwards correlating with increasing clonal propagation and decreasing genetic stock that would have been carried with each successive move eastward.

Human migration through Melanesia eastward into Polynesia explains the prevalence of solely *A. camansi*-derived breadfruit cultivars in those regions, but the presence of *A. camansi*-specific markers in Micronesian cultivars and *A. mariannensis*-specific markers in a minority of Melanesian and Polynesian cultivars requires a second event. Three previously mentioned nonexclusive hypotheses on the human settlement of Micronesia will be considered in discussing the introduction of *A. camansi* markers into Micronesia and the introduction of *A. mariannensis* markers into Melanesia and Polynesia: (a) human migration (transporting diploid *A. camansi*) from New Guinea into Yap and Palau (Fig. 1, pathway 2), (b) northerly Lapita migration (transporting diploid *A. camansi*-derived breadfruit) from the southeast Solomons-Vanuatu region into central-eastern Micronesia directly (Fig. 1, pathway 3) (Shutler and Marck, 1975; Kirch, 2000; Lum and Cann, 2000), and (c) an indirect northerly Lapita migration with the Kiribati archipelago being used as a stepping-stone passageway (Fig. 1, pathway 4) (Petersen, 1995). None of these possibilities can be ruled out or confirmed conclusively with the breadfruit data, but the data presented here provide the greatest support for a direct northerly Lapita migration.

Regarding the first scenario, an introduction of *A. camansi* from New Guinea into Yap and Palau, *A. camansi* is not found in either of the latter two locations nor elsewhere in Micronesia, except for a few recent introductions (Ragone, 2001). Therefore, if *A. camansi* was introduced by early settlers into Micronesia from New Guinea, it grew there only long enough to hybridize with *A. mariannensis* and has since disappeared. If this indeed occurred, there is no evidence that the human movement was reciprocal, because no Micronesian (*A. mariannensis*) markers were found in New Guinea.

Regarding the latter two scenarios of a northerly Lapita migration into Micronesia, if *A. camansi*-derived breadfruit was introduced into central-eastern Micronesia (Caroline Islands, Kiribati, Marshall Islands), then subsequent human migrations within Micronesia (Kirch, 2000; Lum and Cann, 2000) could have brought the *A. camansi*-derived material into the range

of wild *A. mariannensis* (Mariana Islands and Palau), allowing the two species to hybridize. There has been debate whether a northerly Lapita migration into Micronesia occurred directly into the high islands of the Carolines (Fig. 1, pathway 3) or indirectly (Fig. 1, pathway 4) via island hopping through the atolls of the Kiribati archipelago (Petersen, 1995). Because breadfruit cultivars without *A. mariannensis* traits do not grow well in harsh atoll conditions (Ragone, 1988), a human migration successfully transporting breadfruit was most likely directly into the high islands of Micronesia as opposed to a pathway through the low atolls of Kiribati where purely *A. camansi*-derived cultivars would have fared poorly. Genetic and cultural evidence from kava, *Piper methysticum*, another cultivated Pacific plant, also suggests a direct migration (Lebot and Levesque, 1989; Petersen, 1995). Such a direct route from Melanesia into Micronesia may have been reciprocal because Micronesian *A. mariannensis*-specific markers are also present in some breadfruit cultivars in the Solomons, Vanuatu, and eastward into Polynesia (Fig. 3) Thus, a small percentage of breadfruit cultivars with *A. mariannensis*-specific markers could have subsequently been dispersed into Polynesia with the eastward Lapita migration.

Conclusions—At least two species (*A. camansi* and *A. mariannensis*) and at least two different events (vegetative propagation coupled with human selection in Melanesia and Polynesia, and introgressive hybridization in Micronesia) were involved in the origins of breadfruit. Furthermore, the data suggest that long-distance reciprocal voyages occurred between eastern Melanesia and Micronesia. Additional research into the direction of hybridization between *A. mariannensis* and *A. camansi*-derived breadfruit, and the extent to which *A. mariannensis* has introgressed in Micronesian breadfruit will lead to a better understanding of the evolution of domesticated breadfruit. It is important that both wild species are included in breadfruit germplasm collections. The National Tropical Botanical Garden is currently home to the world's largest breadfruit collection and includes over 200 trees representing over 173 accessions of breadfruit from 17 different island groups. As a result of this study, 60 *A. camansi* and nine *A. mariannensis* plants have been added to increase the genetic diversity, conservation, and research value of the collection.

Human settlement of Oceania represents a complex series of events. Studying plants, such as breadfruit, whose survival and dispersal are dependent upon humans can be a useful tool in recreating past human migration events. However, it can also be confounding, because people continue to use and move these plants, making it difficult to unambiguously differentiate past and present events. Considering evidence from several disciplines is a useful way to cross test hypotheses.

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