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RESEARCH ARTICLE OPEN ACCESS

ORIGIN, DISTRIBUTION, TAXONOMY, BOTANICAL DESCRIPTION, GENETICS AND CYTOGENETICS, GENETIC DIVERSITY AND BREEDING OF BREADFRUIT (*Artocarpus altilis* (Parkinson) Fosberg)

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ABSTRACT

This Breadfruit belongs to the family Moraceae, genus *Artocarpus* and species *Artocarpus altilis.*In English it is known as breadnut (seeded varieties) and dugdug. The common names are breadfruit, sukun, suku, kulur, kKelor Breadfruit, Sukun, Suku, Kulur, Kelor. The names in different countries are in Cambodia: sakee, khnaor samloo; English: Breadfruit; French: Arbre ¨¤ pain; Indonesia: sukun (seedless); kelur, timbul (seeded); Malaysia: sukun (seedless), kelor (seeded); Papua New Guinea: kapiak (Pidgin); Philippines: rimas (seedless), kamansi (seeded); Thailand: sa-ke (seedless), khanun-sampalor (central); Vietnam: sake. Vernacular names of *A. altilis* are: breadfruit (English), *arbre à pain* (French), *árbol del pan* (Spanish), *Brotfruchtbaum* (German), *rimas* (Philippines), *sukun/ timbul* (Indonesia), *kulur/ kuror* (Malaysia), *kapiak* (New Guinea), *uto/ kulu* (Fiji), *bia/ nimbalu* (Solomon Islands), *beta* (Vanuatu), *ulu* (Hawaii, Samoa), *uru* (Tahiti and Society Islands), *kuru* (Cook Islands), *mei/ mai* (Micronesia, Tonga, Marquesas), *lemai* (Mariana Islands) and *mos* (Kosrae). Common Names in different countries are *beta* (Vanuatu); *bia, bulo, nimbalu* (Solomon Islands); breadfruit (English); *kapiak* (Papua New Guinea); *kuru* (Cook Islands); *meduu* (Palau); *mei* (*mai*) (Federated States of Micronesia, Kiribati, Marshalls, Marquesas, Tonga, Tuvalu);*mos* (Kosrae); ‘*ulu* (Hawai‘i, Samoa, Rotuma, Tuvalu); ‘*uru* (Society Islands); *uto, buco* (Fiji). Common names in different countries are Bislama (beta); Creole (vèritab,laba pen); English (breadfruit, breadnut); Fijian (uto,kulu); Filipino (kamansi,rimas); French (arbre à pain,âme veritable,veritable); German (brotfruchtbaum); Hawaian (ulu); Indonesian (sukun,kelur,timbul); Khmer (sakéé,khnaôr sâmloo); Malay (sukun,kuror,kulur); Mandinka (tubab tio); Pidgin English (kapiak); Portuguese (rimas); Samoan (ulu); Spanish (castaña,albopán,arbol del pan,pana de pepitas,panapén); Swahili (mshelisheli); Tamil(seema pila); Thai (khanun-sampalor,sa-ke); Tongan (mei,mai); Vietnamese (saké). The term *breadfruit* was first used in the 17th century to describe the bread-like texture of the fruit when baked. Breadfruit has hundreds of varieties and numerous common names varying by its geographic distribution. The leaves and fruits of breadfruit are found to have diversity of shapes, sizes, and shades of color. Breadfruits with seeds, few seeds and seedless breadfruit was observed. Variation in breadfruit fruit shape was observed. Variastion in skin texture was obsereved. Entire, moderately dissected, and deeply dissected leaves were observed. Variation in fruit shape of breadfruit - A. Spherical; B. Broad ovoid; C. Oval; D. Oblong; E. Ellipsoid; F. Heart-shape was observed. Breadfruit leaf morphological variations among cultivars - (A) ‘Timor’; (B) ‘Kashee Bread’; (C) ‘Cassava’; (D) ‘Meitehid’; (E) ‘Puou’ and (F) ‘Yellow’ was observed. Breadfruit morphological variations among cultivars-Smooth-skinned cultivars {(A) ‘Yellow’; (B) ‘Afara’; (C) ‘Timor’} and Rough skinned cultivars {(D) ‘Kashee Bread’; (E) ‘Toneno’ and (F) ‘Piipiia’} was observed. Representative leaves, whole fruit, and halved fruit was observed. In this review article on Origin, Distribution, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding, Cultivation of Breadfruit are discussed.

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INTRODUCTION

Breadfruit belongs to the family Moraceae, genus *Artocarpus* and species *Artocarpus altilis* (Nayeem *et al.* 2013; Sikarwar *et al*., 2014; RojasSandoval and Acevedo-Rodríguez, 2021; Wikipedia, 2024). In English it is known as breadnut (seeded varieties) and dugdug. The common names are breadfruit, sukun, suku, kulur, Kelor breadfruit, Sukun, Suku, Kulur, Kelor.

The names in different countries are in Cambodia: sakee, khnaor samloo; English: Breadfruit; French: Arbre ¨¤ pain; Indonesia: sukun (seedless); kelur, timbul (seeded); Malaysia: sukun (seedless), kelor (seeded); Papua New Guinea: kapiak (Pidgin); Philippines: rimas (seedless), kamansi (seeded); Thailand: sa-ke (seedless), khanun-sampalor (central); Vietnam: sake **(**Asianplant, 1941). Vernacular names of *A. altilis* are: breadfruit (English), *arbre à pain* (French), *árboldel pan* (Spanish), *Brotfruchtbaum* (German), *rimas* (Philippines), *sukun/ timbul* (Indonesia), *kulur/ kuror* (Malaysia),

kapiak (New Guinea), *uto/ kulu* (Fiji), *bia/ nimbalu* (Solomon Islands), *beta* (Vanuatu), *ulu* (Hawaii, Samoa), *uru* (Tahiti and Society Islands), *kuru* (Cook Islands), *mei/ mai* (Micronesia, Tonga, Marquesas), *lemai* (Mariana Islands) and *mos* (Kosrae) (Ragone, 1997). Common Names in different countries are *beta* (Vanuatu); *bia, bulo, nimbalu* (Solomon Islands); breadfruit (English); *kapiak* (Papua New Guinea); *kuru* (Cook Islands); *meduu* (Palau); *mei* (*mai*) (Federated States of Micronesia, Kiribati, Marshalls, Marquesas, Tonga, Tuvalu); *mos* (Kosrae); '*ulu* (Hawai'i, Samoa, Rotuma, Tuvalu); '*uru* (Society Islands); *uto, buco* (Fiji) (Manner et al., 2006). Common names in different countries are Bislama (beta); Creole (vèritab,laba pen); English (breadfruit, breadnut); Fijian (uto,kulu); Filipino (kamansi,rimas); French (arbre à pain,âme veritable,veritable); German (brotfruchtbaum); Hawaian (ulu); Indonesian (sukun,kelur,timbul); Khmer (sakéé,khnaôr sâmloo); Malay (sukun,kuror,kulur); Mandinka (tubab tio); Pidgin English (kapiak); Portuguese (rimas); Samoan (ulu); Spanish (castaña,albopán,arbol del pan,pana de pepitas,panapén); Swahili (mshelisheli); Tamil(seema pila); Thai (khanun-sampalor, sake); Tongan (mei, mai); Vietnamese (saké) (Agroforestry, 2024). The term *breadfruit* was first used in the 17th century to describe the bread-like texture of the fruit when baked. Breadfruit has hundreds of varieties and numerous common names varying by its geographic distribution (Wikipedia, 2024).

Hundreds of traditional cultivars have been selected which are adapted to various climates and soils and accommodate a wide range of horticultural needs. These traditional cultivars need to be conserved and evaluated to maximize their potential use (Ragone, 1997). Breadfruit has long been a traditional starch crop throughout Oceania (Melanesia, Micronesia, and Polynesia). Over thousands of years of cultivation, humans have selected for hundreds of unique cultivars, many of which are seedless and are vegetatively propagated (Zerega *et al*., 2004). 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. While seedless cultivars provide an important source of starch, some cultivars produce few to many edible seeds (Zerega *et al.,* 2004). 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) (Zerega *et al.,* 2004). In Micronesia, seeded and seedless diploid, as well as seedless triploid cultivars occur. Since breadfruit's discovery by Europeans nearly 400 years ago, a small number of cultivars have been introduced to tropical regions throughout the world, including the Caribbean, Africa, and India. However, the genetic diversity and importance of breadfruit remain greatest in the Pacific islands (Zerega *et al*., 2004). 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) (Zerega *et al.,* 2004).

Breadfruit has long been an important staple crop and a primary component of traditional agroforestry systems in Oceania, where numerous varieties are grown. The fruitcan be cooked and eaten at all stages of maturity, is high in carbohydrates, and is a good source of minerals and vita mins. In addition to producing abundant, nutritious, tasty fruits, this multipurpose tree provides medicine, construction materials, and animal feed. The attractive, evergreen trees grow to heights of 15 to 21 m or more and the trunks may be as large as 2 m in diameter at the base. The trees begin bearing in 3–5 years and are productive for many decades. They are easy to propagate, require little attention and input of labor or materials, and can be grown under a wide range of ecological conditions. Most breadfruit is produced for subsistence purposes and small quantities are available for sale in town markets as fresh fruit or chips. There is interest in establishing small- scale orchards to provide fresh fruits and chips for export from Pacific islands to New Zealand, the United States, and Canada (Manner *et al*., 2006). The breadfruit is a tropical fruit tree, originated in the Indo-Malayan Archipelago which serves as an important staple crop for several countries. The tree is native to Polynesia and promptly realizing its nutritive values, the British introduced it into their colonies in west indices from south sea Islands (Sreekumar *et al*., 2007). The tree is also an important tree fruit vegetable grown in the homesteads of southern part of India. Its intro- duction from the native home to India may have taken place through the efforts of early Dutch voyagers. In India, its cultivation is confined to southern parts especially on the west coast. Recent molecular study on breadfruit and its relatives shows that the two species *(A. camansi* Blanco and *A. mariannensis* Trécul) at least two different events such as vegetative propagation coupled with human selection in Melanesia and Polynesia, and introgressive hybridization in Micronesia were involved in the origins of bread-fruit (Sreekumar *et al*., 2007). The plant populations may show morphologicalvariation as adaptation to different selection pressure. The adaptation may result from phenotypic plasticity or genetic differentiation due to natural selection and other evolutionary forces. A combination of both molecular and morphological variation will be useful for determining the roles of phenotypic plasticity and genetic differentiation on population variation and adaptation. Of the different DNA based markers, the amplified fragment length polymorphism technique is considered a highly informative fingerprinting tool and widely used for genetic differentiation of different tropical tree species. The purpose of the present studyis to examine the level of genetic variation within and among populations of breadfruit using AFLP markers and morphological characters (Sreekumar *et al*., 2007). In this review article on Origin, Dstribution, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding, Cultivation of Breadfruit are discussed.

ORIGIN AND DISTRIBUTION

The exact origin of breadfruit is uncertain. The centre of genetic diversity extends from Indonesia to Papua New Guinea. In a broad sense, it is a native of the Pacific and tropical Asia. It has long been an important staple food in Polynesia. Breadfruit is now widely distributed throughout the humid tropics **(**Asianplant, 1941). Most of the cultivars (seeded and seedless) of breadfruit in Micronesia east of the Mariana Islands exhibit characteristics of both *A. altilis* and *A. mariannensis*. *Artocarpus mariannensis* grows wild on the uplifted rock islands of Belau and on the limestone ridges of Guam and the Northern Mariana Islands. Native fruit bats have contributed to its dispersal. It is cultivated throughout the islands of Micronesia and south into Kiribati, Tuvalu and Tokelau (Ragone, 1997). The ability to grow on coral soils may have been a crucial factor in the now-widespread distribution of hybrids throughout the low-lying Micronesian atolls. *Artocarpus mariannensis* has not been distributed beyond the northern Pacific Islands with the exception of a possible introduction to the Philippines in the 1600s by the Spanish. Ray's *Historia Plantarum,* published in 1704, describes 'dugdug marianorum' a tree introduced from Guam and different from the seedless breadfruit, 'rimas marianorum', introduced at the same time (Ragone, 1997). Seeded breadfruit appears to occur wild only in New Guinea where, along with breadnut, it is a dominant member of secondary forests in lowland areas. Seeded breadfruit trees grow widely scattered in primary forest due, in part, to their dispersalby birds, fruit bats and other arboreal mammals which feed on the flesh and drop the large seeds. Wild breadfruit is an important component of the subsistence economy in lowland areas. Both thefruit pulp and the seeds are eaten in some varieties, while in others only the seeds are edible, since the flesh is tough and stringy. While seedless breadfruit typical of Polynesia is grown in village areas of New Guinea, it did not originate inthese islands. In fact, seedless cultivars were introduced from Fiji and Samoa by missionaries in the 19th century (Ragone, 1997). Breadfruit seeds quickly lose their viability and seedlings would be difficult totransport and keep alive during longer voyages.

The use of vegetative propagative material allowed successful long-distance transfer of this cultigen. 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 in western Melanesia to primarily a starchy fruit crop eastwards (Ragone, 1997). The greatest diversity of seedless cultivars occurs in the eastern Polynesian islands (Society Islands and Marquesas) and Pohnpei and Chuuk in Micronesia. Breadfruit cultivars with one to a few seeds are so unusual in eastern Polynesia that the presence of a sporadic seed is denoted in the cultivar name: *huero* in the Society Islands and *mei kakano* in the Marquesas, both meaning "with a seed". It is important to note that many of the seedless cultivars in Micronesia are hybrids between *A. altilis* and *A. mariannensis* and are unique to those islands, unlike the ' Polynesian' seedless breadfruit which has been distributed all over the globe (Ragone, 1997).

The dissemination of seedless breadfruit beyond Oceania is well documented and involves only a handful of cultivars, primarily Tahitian. Breadfruit has been an evocative symbol of Oceania since Europeans first ventured into the region in the late 1600s. After the long, often arduous, sailing voyage from Europe to the islands, ship-worn sailors were amazed and delighted by a tree that produced prolific fruits that, when roasted, resembled fresh bread. They were especially impressed by the ease with which this abundant food was produced. Numerous accounts were published about this wonder fruit, beginning with Quiros who sailed with Mendana on voyages during 1595-1606. He described seedless breadfruit in the Marquesas and seeded breadfruit in the Solomon Islands. The Spanish may have introduced seedless breadfruit to Guam from elsewhere in the Pacific in the 1600s to help provision their new colony. They did introduce seedless breadfruit to the Philippines in the 17th century (Ragone, 1997). Breadfruit was also widely distributed to Central and South America, including Colombia, Guatemala, Costa Rica and elsewhere. Seedless breadfruit was introduced to Brazil from Cayenne in 1811, although the Portuguese may have made a direct introduction of seedless cultivars to Brazil from other sources, possibly the Maldives (Ragone, 1997). Breadfruit was introduced and established in Sri Lanka before 1796, possibly from the Bligh collections. Only one seedless type is found in the extensive Malay Archipelago and its origin is unknown. It is interesting to speculate that the Tongan cultivar *kele kele* may be the original source of seedless breadfruit in Java and from there was dispersed to other islands in that archipelago. One visitor there surmised in 1820 that the Javanese had only recently obtained breadfruit, possibly from the Moluccas while trading for spices. Another wave of breadfruit introductions occurred at the end of the 19th century (Ragone, 1997).

Previous phylogenetic studies of the genus *Artocarpus* based on molecular and morphological data strongly support a close relationship among breadfruit, *A. camansi*, and *A. mariannensis.* 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 (Zerega *et al*., 2004). Thus, most cultivars in Melanesia and Polynesia are derived from a single species, *A. camansi*. These cultivars include both diploids and triploids. The presence of only *A. camansi* markers in most of these cultivars suggests that they are primarily autotriploids (Zerega *et al.,* 2004). 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. Micronesian hybrids include both sterile and fertile diploids and triploids. The presence of fertile diploid hybrids would allow for the possibility of introgression with *A. mariannensis* in Micronesia (Zerega *et al*., 2004). 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 (Zerega *et al.,* 2004). Breadfruit, 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 (Zerega *et al*., 2004).

Breadfruit belongs to the genus *Artocarpus* (Moraceae), which consists of approximately 60 species native to the Indian subcontinent, Southeast Asia, and Australasia. 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. This led to much speculation and numerous theories on the possible area of origin of breadfruit, which included Polynesia, Pacific and Tropical Asia , the Malayan archipelago, and the region embracing New Guinea, the Philippines and the Moluccas (Zerega *et al.,* 2004). The wild, seeded, ancestral form of breadfruit or breadnut, is native to New Guinea, and possibly the Moluccas (Indonesia) and Philippines. Bread-fruit, both seeded and seedless forms, does not naturally occur in the Pacific islands, although long-abandoned plantings are sometimes mistaken for wild trees. It was first domesticated in the western Pacific and spread by humans throughout the region beginning 3000 years ago (Manner *et al.,* 2006). Breadfruit is cultivated on most Pacific islands, with the exception of New Zealand and Easter Island. It is now pantropical in distribution. In the late 1700s several seed-less varieties were introduced to Jamaica and St. Vincent from Tahiti, and a Tongan variety was introduced to Martinique and Cayenne via Mauritius. These Polynesian varieties were then spread throughout the Caribbean and to Central and South America, Africa, India, Southeast Asia, Madagascar, the Maldives, the Seychelles, Indonesia, Sri Lanka, and northern Australia. Breadfruit is also found in south Florida (Manner *et al.*, 2006). Breadfruit was first domesticated in the western Pacific and spread by humans throughout the region over the past 3,000–4,000 years. From Melanesia to Micronesia to Polynesia, many islanders grow and use breadfruit as part of their daily diet (Elevitch *et al*., 2014). This species originated in the South Pacific and was spread throughout Oceania by intrepid islanders settling the numerous islands of Melanesia, Micronesia, and Polynesia. Hundreds of varieties have been cultivated and more than 2,000 names have been documented.

The tree is grown on most Pacific Islands, with the exception of New Zealand and Easter Island. It is now cultivated throughout the tropics. Due to the efforts of Captain Bligh and French voyagers, a few seedless varieties from Polynesia were introduced to the Caribbean in the late 1700s. These Polynesian varieties were then spread throughout the Caribbean and to Central and South America, Africa, India, Southeast Asia, Madagascar, the Maldives, the Seychelles, Indonesia, Sri Lanka, northern Australia, and south Florida. Breadfruit is now grown in close to 90 countries. Breadfruit is a versatile crop and the fruit can be cooked and eaten at all stages of maturity. The seeds are also edible when cooked (Breadfruit, 2019). The species is native to the Pacific and tropical Asia and is now widely planted throughout the humid tropics.

Breadfruit likely originated and was first domesticated in New Guinea and associated islands, such as the Bismarck Archipelago. Two closely related species that possibly contributed to breadfruit are breadnut *A. camansi* Blanco from New Guinea, the Indo-Malay region and possibly the Philippines; and dugdug *A. mariannensis* Trécul from western Micronesia. Breadnut is a wild ancestor of the breadfruit indigenous to the lowlands of New Guinea, where it grows in flooded riverbanks, secondary and primary growth forest, and freshwater swamps, and in cultivation. It may also be indigenous to the Moluccas and possibly the Philippines. Dugdug is morphologically very distinct from *A. altilis* and grows wild in Palau, Guam and the Northern Mariana Islands. Introgression between the two species has occurred in Micronesia and there are a number of hybrid varieties (Rojas-Sandoval and Acevedo-Rodríguez, 2021). The exact origin of *A. altilis* is uncertain, but it is believed to be native to Papua New Guinea, the Moluccas (Indonesia), and the Philippines. This species has long been an important staple food crop in Polynesia and is widely cultivated throughout the tropics. *A. altilis* is now widely distributed throughout the humid tropics, including in Oceania, Asia, Africa, North, Central and South America and the West Indies (Rojas-Sandoval and Acevedo-Rodríguez, 2021).

Breadfruit is a species of flowering tree in the mulberry and jackfruit family (Moraceae) believed to be a domesticated descendant of *Artocarpus camansi* originating in New Guinea, the Maluku Islands, and the Philippines. It was initially spread to Oceania via the Austronesian expansion. It was further spread to other tropical regions of the world during the Colonial Era. British and French navigators introduced a few Polynesian seedless varieties to Caribbean islands during the late 18th century. Today it is grown in some 90 countries throughout South and Southeast Asia, the Pacific Ocean, the Caribbean, Central America and Africa. Its name is derived from the texture of the moderately ripe fruit when cooked, similar to freshly baked bread and having a potato-like flavour (Wikipedia, 2024). Extent of the Austronesian expansion that carried crops like breadfruit, bananas, and coconuts throughout the Indo-Pacific islands. Breadfruit is an equatorial lowland species. It has been spread from its Pacific source to many tropical regions. In 1769, Joseph Banks was stationed in Tahiti as part of the *Endeavour* expedition commanded by Captain James Cook. The late-18th-century quest for cheap, high-energy food sources for slaves in British colonies prompted colonial administrator and plantation owners to call for breadfruit to be brought to the Caribbean. As president of the Royal Society, Banks provided a cash bounty and gold medal for success in this endeavour and successfully lobbied for a British Naval expedition. After an unsuccessful voyage to the South Pacific to collect the plants as commander of HMS *Bounty*, in 1791, William Bligh commanded a second expedition with *Providence* and *Assistant*, which collected seedless breadfruit plants in Tahiti and transported these to St. Helena in the Atlantic and St. Vincent and Jamaica in the West Indies (Wikipedia, 2024).

The breadfruit has been cultivated in the Malay Archipelago (where the species is held to be indigenous) since remote antiquity. From this region it spread throughout the tropical South Pacific region in prehistoric times. Its introduction into the New World was connected with the memorable voyage of Capt. William Bligh in HMS *Bounty*, a voyage recommended by Capt. James Cook, who had seen the breadfruit in the Pacific islands and considered that it would prove highly useful as a foodstuff for slaves in the West Indies (Petruzzello, 2024). Breadfruit is probably native to an area extending from New Guinea to Micronesia. It has spread widely over time in tropical areas around the globe not only in the Pacific Ocean but also to Southeast Asia, India, the Caribbean Sea, Central America, northern South America and parts of Africa. It is believed that breadfruit initially came to Hawaii in canoes from Polynesia (MGB, 2024). It is Distributed in Antigua and Barbuda, Australia, Bahamas, Barbados, Brazil, Byelarus, Colombia, Cook Islands, Costa Rica, Cuba, Dominica, Dominican Republic, Fiji, French Guiana, French Polynesia, Gambia, Grenada, Guadeloupe, Guatemala, Guinea, Guyana, Haiti, India, Indonesia, Jamaica, Kiribati, Madagascar, Maldives, Marshall Islands, Martinique, Mauritius, Mexico, Montserrat, Netherlands Antilles, New Caledonia, New Zealand, Norfolk Island, Puerto Rico, Samoa, Seychelles, Solomon Islands, Sri Lanka, St Kitts and Nevis, St Lucia, St Vincent and the Grenadines, Taiwan, Provinceof China, Tonga, Trinidad and Tobago, US, Vanuatu, Virgin Islands (US) (Agroforestry, 2024).

TAXONOMY

Breadfruit belongs to the family Moraceae, genus *Artocarpus* and species *Artocarpus altilis* (Nayeem *et al.* 2013; Sikarwar *et al*., 2014; RojasSandoval and Acevedo-Rodríguez, 2021; Wikipedia, 2024). Preferred scientific name is *Artocarpus altilis* (Parkinson) Fosberg (Manner *et al*., 2006). The generic name comes from the Greek words 'artos' (bread) and 'karpos' (fruit).The fruit is eaten and is commonly called breadfruit. Specific epithet means fat or stout in reference to the fruit (MGB, 2024). The breadfruit is a widely grown and nutritious tree fruit. It is a member of the genus *Artocarpus* (Moraceae) which contains about 50 species of treesthat grow in the hot, moist regions of the Southeast Asian tropics and the Pacific Islands. The generally accepted name for breadfruit is *Artocarpus altilis* (Parkinson) Fosberg which has taxonomic priority and replaced *Artocarpus incisus* (Thunb.) L. (*A. incisa* variant spelling), and *Artocarpus communis* Forst. These names for breadfruit are based solely on specimens or descriptions of seedless Tahitian breadfruit collected during Captain Cook's voyages there in 1768-1771 (Ragone, 1997). Breadfruit belongs to the genus *Artocarpus* (Moraceae), which consists of approximately 60 species native to the Indian subcontinent, Southeast Asia, and Australasia. 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 (Zerega *et al*., 2004). This led to much speculation and numerous theories on the possible area of origin of breadfruit, which included Polynesia. Pacific and Tropical Asia, the Malayan archipelago and the region embracing New Guinea, the Philippines and the Moluccas. Additionally, the identity of its wild progenitors remained problematic (Zerega *et al.,* 2004).

Three related species—*Artocarpus altilis* (Parkinson) Fosberg, *Artocarpus camansi* Blanco, and *Artocarpus mariannensis* Trécul—make up what is known as the "breadfruit complex." They are members of the Moraceae family. The nutritious fruit and seeds of all three species are edible. The multipurpose trees are easy to grow, beneficial to the environment, and produce an abundance of nutritious, tasty fruit. They also provide construction materials, medicine, fabric, glue, insect repellent, animal feed, and more. The trees begin bearing in 3 to 5 years and are productive for many decades. This 'tree of bread' has the potential to play a significant role in alleviating hunger in the tropics (Breadfruit, 2019). Breadfruit has been a major staple crop for millennia in the islands of Oceania, where hundreds of cultivars have been developed and named. The first accepted botanical description of breadfruit dates back to 1773 by Sydney Parkinson, one of the artists who accompanied Joseph Banks on the voyage of the *Endeavour*. Since then a proliferation of names for breadfruit and its close relatives have been published, leading to much confusion in the literature about the correct scientific name for and the delimitation of the domesticated breadfruit. Recent examination of both morphological and molecular characters of

hundreds of samples of breadfruit from throughout Oceania as well as related species has lead to a better understanding. The domesticated breadfruit is *Artocarpus altilis* (Parkinson) Fosberg (the most commonly seen synonyms include *A. communis* (Forster) and *A. incise* (Thun.) L.f.) (Zerega, 2020). The Moraceae are monoecious or dioecious trees, shrubs, and rarely herbs comprising about 39 genera and 1125 species distributed mostly in tropical to warm temperate regions. Nearly all species within this family contain milky latex and have alternate or opposite leaves and small, unisexual, and minute flowers. The genus *Artocarpus* includes 61 species native to the Indian subcontinent, Southeast Asia, and Australasia. The generic name *Artocarpus* comes from the Greek words '*artos*' (bread) and '*karpos*' (fruit) and many species and varieties produce fruits which are eaten by humans (Rojas-Sandoval and Acevedo-Rodríguez, 2021). Presently, what is known as breadfruit consist of *Artocarpus altilis* and the less common *Artocarpus altilis* × *Artocarpus mariannensis* hybrids which were produced from interspecific hybridization, originating in Micronesia. The original *A. altilis* comes in various forms, either producing no seeds, two or a few seeds. Whilst the initial generation hybrids take after the *A. mariannensis* parent, the later generation hybrids take after the *A. altilis* and are seedless. Breadfruit's taxonomy has been a challenge to classify, resulting in erratic binomial nomenclatures. This can be attributed to a lack of standardized methodology for data collection, coupled with morphological similarities between breadfruit hybrids and its close relatives, such as Breadnut (*Artocarpus camansi*) and *Artocarpus mariannensis* (Mehta et al., 2023). According to DNA fingerprinting studies, the wild seeded ancestor of breadfruit is the breadnut (*Artocarpus camansi*) which is native to New Guinea, the Maluku Islands, and the Philippines. It was one of the canoe plants spread by Austronesian voyagers around 3,000 years ago into Micronesia, Melanesia, and Polynesia, where it was not native (Wikipedia, 2024). *A. camansi* was domesticated and selectively bred in Polynesia, giving rise to the mostly seedless *Artocarpus altilis*. Micronesian breadfruit also show evidence of hybridization with the native *Artocarpus mariannensis*, while most Polynesian and Melanesian cultivars do not. This indicates that Micronesia was initially colonized separately from Polynesia and Melanesia through two different migration events which later came into contact with each other in eastern Micronesia (Wikipedia, 2024).

Synonyms

Synonyms (Asianplant, 1941)
Artocarpus altilis var. *non-seminiferus* (Duss) Fournet
Artocarpus altilis var. *seminiferus* (Duss) Fournet
Artocarpus camansi Blanco
Artocarpus communis J.R.Forst. & G.Forst.
Artocarpus incisifolius Stokes [Illegitimate]
Artocarpus incisus (Thunb.) L.f.
Artocarpus incisus var. *non-seminiferus* Duss
Artocarpus incisus var. *seminiferus* Duss
Artocarpus laevis Hassk.
Artocarpus papuanus Diels [Illegitimate]
Artocarpus rima Blanco
Radermachia incisa Thunb. [Unplaced]
Saccus laevis Kuntze
Sitodium altile Parkinson ex F.A.Zorn

Synonyms (Zerega, 2020)
Artocarpus altilis (Parkinson) Fosberg, 1941
Artocarpus altilis
Artocarpus communis J.R.Forst. & G.Forst.
Artocarpus communis

Other Scientific Names (Rojas-Sandoval and Acevedo-Rodríguez, 2021).
Artocarpus altilis var. *non-seminiferus* (Duss) Fournet
Artocarpus altilis var. *seminiferus* (Duss) Fournet
Artocarpus camansi Blanco
Artocarpus communis J. R. Forst. & G. Forst.
Artocarpus incisus (Thunb.) L. f.
Artocarpus incisus var. *non-seminiferus* Duss
Artocarpus incisus var. *seminiferus* Duss
Artocarpus laevis Hassk.
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Artocarpus incisus var. non-seminiferus Duss
Artocarpus incisus var. seminiferus Duss
Artocarpus laevis Hassk.
Artocarpus papuanus Diels [Illegitimate]
Artocarpus rima Blanco
Radermachia incisa Thunb. [Unplaced]
Saccus laevis Kuntze
Sitodium altile Parkinson ex F.A.Zorn

Species

1. Artocarpus altilis: Leaves broadly obovate to broadly ovate, almost entire with only slight lobing to deeply pinnately lobed with sinuses from 2/3 to 4/5 of the distance from margin to midrib, or deeper; blade generally smooth with few to many pale toreddish hairs, especially on the midrib and veins. Fruits globose to oblong, skin light green, yellowish-green or yellow, flesh creamy white or pale yellow; surface smooth to slightly bumpy or spiny with individual disks ranging from areolate to slightly raised and flattened, to widely conical up to 3 mm high and 5 mm across at the base, to narrowly conical upto 5 mm long. Seedless, with some forms seeded (Ragone, 1997).

2. Artocarpus camansi: Leaves pinnately lobed with sinuses cut halfway to the midrib; densely pubescent on upper and lower surfaces, midribs and veins. Fruits oblong, light green with white flesh; spiny with flexible, elongated sections 5-12 mm long. Seeded (Ragone, 1997).

3. Artocarpus mariannensis: Leaves broadly obovate to broadly elliptic; entire or a few lobes mostly in the distal third or half of the leaf; sinuses cut less than half way to the midrib; blade smooth; midrib and veins on the underside covered with dense,appressed reddish hairs. Fruits cylindrical or asymmetrical, skin dark green, flesh dark yellow; perianth disks conical when immature, flattened on top when mature. Seeded (Ragone, 1997).

1. Breadfruit: *Artocarpus altilis* (Parkinson) Fosberg

An evergreen tree (12-15 m up to 21 m), breadfruit tends to have a denser, more spreading canopy than *Artocarpus camansi*. Leaves (15-60 cm or longer) are almost entire to deeply dissected with 1-6 pairs of lobes. Fruit (10-30 cm long × 9-20 cm wide) vary in shape, size, and skin texture. They are usually round, oval or oblong weighing 0.25-6 kg. Skin texture ranges from smooth to rough to spiny. The color is light green, yellowish-green or yellow when mature, although one unusual variety ('Afara' from French Polynesia) has pinkish or orange-brown skin. The flesh is creamy white to pale yellow. Fruit are typically mature and ready to cook and eat as a starchy staple in 15-20 weeks. Ripe fruit have yellow or yellow-brown skin and soft, sweet, creamy flesh that can be eaten raw or cooked. Fruit contain no to many seeds depending upon the variety. Seeds have a pale to dark brown seed coat. Seeds germinate immediately and cannot be dried or stored (Breadfruit, 2019).

2. Breadnut: *Artocarpus camansi* Blanco

Breadnut is native to New Guinea, and possibly the Moluccas (Indonesia) and the Philippines. This species is propagated by seed. In New Guinea, it is widely scattered in alluvial forests in lowland areas and naturally spread by birds and fruit bats that feed on the fruit and

drop the large seeds. It is also cultivated in home gardens. It only occurs in cultivation in the Philippines where it is typically grown as a backyard tree. Breadnut is often considered to be a form of seeded breadfruit. However, it is a separate species and the ancestor of seeded and seedless breadfruit (Breadfruit, 2019). Breadnut is infrequently grown in the Pacific outside of its native range. A few trees are now found in New Caledonia, Pohnpei, FSM, the Marquesas, Tahiti, Palau, and Hawaii, introduced by immigrants from the Philippines in recent years. While breadnut is uncommon in Oceania, it has long been grown and used in other tropical regions. Beginning in the late 1700s, the French spread breadnut throughout the tropics and it is now widespread in the Caribbean, Central and South America, Southeast Asia, and West Africa (Breadfruit, 2019). The tree grows up to 20 m tall. It typically forms buttresses at the base of the trunk and has a more open canopy than *Artocarpus altilis* or *A. mariannensis*. Leaves are large (40-60 cm long) and moderately dissected with 4-6 pairs of lobes. The oblong, spiky fruit is dull green to greenish-brown when ripe. As evident by the name, this species is mostly grown for the numerous large, nutritious seeds or "nuts." The immature fruit and seeds are often consumed as a vegetable in soups, stews, or salads after the entire fruit is thinly sliced, then boiled. The seeds can be boiled or roasted and resemble chestnuts in texture and flavour (Breadfruit, 2019).

3. Dugdug or Chebiei: *Artocarpus mariannensis* Trécul:

This wild seeded breadfruit relative is native to Palau and the Mariana Islands where it grows in limestone and ravine forests from the coast to lower mountain slopes. It is distributed through its natural range by fruit bats. Wild populations are seriously declining due to typhoon damage, predation by feral deer, and the disappearance of fruit bats. It has naturally hybridized with *A. altilis* and the numerous interspecific hybrid varieties are considered to be 'breadfruit', whether they are seeded or seedless (Breadfruit, 2019). *Artocarpus mariannensis* and hybrid varieties are a major staple food tree and widely cultivated throughout Palau, Mariana Islands, Federated States of Micronesia, Kiribati, Republic of the Marshall Islands, Tokelau, Tuvalu, Nauru, and Banaba Island. They are not grown elsewhere in the Pacific or other tropical regions except for a few trees in Hawaii and Rabi Island in Fiji, the latter introduced in the 1940s from Banaba. Hybrid varieties may be well suited for other atoll countries and coastal areas in the tropics because they are better adapted to sandy soils and saline conditions than most seedless *A. altilis* breadfruit varieties (Breadfruit, 2019). Trees of *Artocarpus mariannensis* and hybrid varieties can reach heights of 20 m or more. They tend to be more massive than breadfruit and breadnut, with large trunks 2 m wide at the base, extensive buttresses, and full, rounded canopies. They also tolerate salinity better. Leaves are typically entire or shallowly dissected with 1-3 lobes on the upper third of blade. The fruit is small, weighing 0.25-0.5 kg with dark green skin— even when ripe—with a pebbly texture. The flesh is deep yellow when ripe, with a sweet aroma and flavor. The fruit is not as solid or dense as breadfruit and contains few to many rounded dark brown, shiny seeds. This species is seed propagated (Breadfruit, 2019). The numerous hybrid varieties in Micronesia exhibit great variability in fruit and leaf form and can be seeded or seedless. The fruit are typically rough-skinned or pebbly, with light to dark green glossy skin, and creamy white to yellow flesh. The flesh is not as solid or dense as seedless Polynesian breadfruit varieties. Seeded varieties typically have lumpy, asymmetrical fruit 12-30 cm long. Some unusual forms have narrow, elongated fruit up to 45 cm long. Most seeded hybrid varieties are unique to a particular area since they are local seedling selections. Some varieties, such as seedless 'Meinpadahk', are widely distributed and grow on high islands and coral atolls (Breadfruit, 2019).

BOTANICAL DESCRIPTION

Propagation: Breadfruit trees are generally propagated vegetatively. They are traditionally propagated from root cuttings or shoots. The roots grow on or slightly below the surface of the ground and will often produce a shoot, especially if it is cut or damaged. Pacific islanders and others will intentionally wound roots to induce shoot production. When the shoot is 0.5-0.75 m high and has developed its own root system, it is removed by cutting the root 10-15 cm on either side of the shoot (Ragone, 1997). Air-layering or marcottage is one method which has shown good results and is widely practiced in Tokelau. Branches (5-15 cm,and occasionally up to 30cm, in diameter) are prepared for air-layering by removinga strip of bark 2.5-5 cm wide around the circumference of the branch. Compost, mulch or other organic material is wrapped around this area and held in place with a tightly tied copra bag. After 2-6 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. Air layers are most frequently made on branches that have previously borne fruit as the air layer will bear fruit as soon as 1-2 years after planting (Ragone, 1997). Root suckers can be successfully air-layered . Shoots are air layeredwhen 2cm or more in diameter. If two or more nodes are left below the surface, newshoots will arise from these nodes after the air layers are removed. Several air layers can thus be made over a period of time from one original root sucker. They root quickly and can be separated in 2-3 months (Ragone, 1997). Another method which promised to facilitate propagation of breadfruit is the use of stem cuttings under intermittent mist. Withthis method, leafless stem cuttings were treated with rooting hormone and placed under intermittent mist. After 10weeks, 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 (Ragone, 1997). Seeds are extracted from ripe fruits and immediately planted since they lose viability within a few weeks. Seeds are planted about 5 cm apart and 1 cm deep and germinate about 2 weeks after sowing. The germinating bed should be kept moist; seedlings can be transplanted into individual containers as soon as they sprout. They grow quickly and are ready for planting in the field whenthey are about 1 year old. Breadnut trees tend to grow slowly and may start fruiting in 6-10 years (Ragone, 1997). Asexually propagated breadfruit trees start fruiting in 3-6 years. Regardless of the method used to propagate trees, young plants do best under shade,but trees require full sun once established (Ragone, 1997). Breadfruit is easy to propagate from root shoots or root cuttings, by air-layering branches, or from seeds. Breadfruit can also be grafted using various techniques. Stem cuttings are not used. Seeds are rarely grown because they do not develop true to type. Vegetative propagation is a must for seedless varieties, and root shoots or root cuttings are the preferred methods for both seeded and seedless va rieties (Manner *et al*., 2006). In general, breadfruit is vegetatively propagated using root shoots or root cuttings. Other methods include seed propagation, grafting, air layering (marcotting), and in vitro (tissue culture) propagation. Breadfruit grown from seed will fruit in 5 to 10 years. Seedless varieties must be vegetatively propagated and this method is also preferred for seeded types as the trees are clones of the mother plant (NTBG, 2024).

Seeds: One of the oldest methods used to propagate breadfruit trees is to grow them from seeds. Remove seeds from soft, ripe fruits and wash to remove any pulp. Plant immediately because the seeds lose viability–ability to sprout and grow–within a few weeks. Seeds cannot be stored and are damaged by chilling or drying. Plant in loose, well-drained soil and keep moist, but not wet. Seeds germinate within 10-14 days. Seedlings grow quickly and are ready to plant into the field in about one year. Propagation by seed has become more difficult in modern times because many of the most desirable varieties have evolved to become seedless, causing a greater need to develop and perfect new and traditional methods to grow new trees (NTBG, 2024).

Root Shoots: Root shoots are new breadfruit trees that grow from the root system of the mother. Roots typically grow on or slightly below the surface of the ground and often produce a shoot, especially when wounded or injured. When the shoot is at least 0.3 m tall, detach it from the mother plant by severing the root 10 to 15 cm on either side of the shoot. Be careful not to damage the tender roots at the base of the shoot. Trim off the large leaves and plant in a pot with well-

drained soil until the plant is larger. If directly transplanted into the field, place in a hole amended with organic material, and provide shade and keep moist until established. Root shoots should be removed from the mother tree to maintain tree health, as they drain resources such as water and nutrients, and prevent air flow and light penetration as they grow larger (NTBG, 2024).

Root Cuttings: Sections of roots can also be used as propagating material. It is best to collect roots after the fruiting season is over and when the tree is in an active vegetative stage, producing new leaves. This generally coincides with the end of the dry season and root cuttings should be collected as the rainy season begins. This is when carbohydrate stores in the roots are highest, increasing the success rate of the cuttings. Select healthy roots growing slightly below the soil that are 1.5 to 6 cm in diameter (3-4 cm is best). Cut into 12 to 30 cm long sections. Roots should be scrubbed clean and kept moist. Plant directly into the ground in loose, organic soil or in a pot with well-drained soil. Roots can be oriented horizontally below the surface of the soil or diagonally with the upper few centimeters exposed to air (NTBG, 2024).

Air Layering: Air layering (or marcotting) involves cutting part way into a stem or branch and packing the area with a moist medium to stimulate root formation, so that the stem or branch can be removed and grown as an independent plant. It is best to air layer branches at the beginning of the rainy season when the tree is in an active vegetative stage, meaning the period of growth between germination and flowering. Select newly developed shoots (2-4 cm diameter) and do not use the ends of branches that have previously flowered or fruited. Carefully remove a 3 to 5 cm strip of the outer bark around the circumference of the branch leaving a narrow, vertical connecting strip. Wrap moistened sphagnum moss, compost, or other organic material around the area. Rooting hormone can be added, but is not required. Tie a piece of burlap, plastic, etc., around the organic material to hold it in place. After 2 to 6 months, new roots will develop and grow through the media. Remove the air layer by cutting the branch directly below the roots. Place in a pot with well-drained soil until the plant is larger and has an established root system (about one year). Transplant into the ground. Depending on the size of the original branch, air-layered branches can fruit in 3 to 4 years (NTBG, 2024).

Grafting: Grafting involves uniting (joining) a bud or shoot of one plant (scion) to another plant (stock). Several methods have been successful with breadfruit, including cleft, slice, and approach grafts. Thin cuts, 5 to 7 cm long, are made in equal-sized branches of the scion and stock. The two branches are carefully brought together at the wounded area and tightly wrapped. It is essential that the cambial layer (actively growing part of the branch) of scion and stock plant are in contact. Once the graft has fused together the scion can be separated from its parent plant. Grafting different varieties of trees together can reduce the time to first production of fruit and flowers, and can allow one tree to extend its growing season by producing fruit of more than one variety (NTBG, 2024).

Tissue Culture (*In vitro*) Propagation: Each individual plant cell has the potential to become a whole plant in the right conditions. In vitro (tissue culture) propagation is a recently developed method to propagate breadfruit trees. Buds, shoots, or other small vegetative parts of the plant are thoroughly, washed and disinfested to reduce pathogens, such as fungus and bacteria, cut into small pieces, and placed in a growing medium. The growing medium provides the necessary vitamins, nutrients, and growth regulators to grow a plant identical to the original source plant. The best composition of the medium is different for each variety, and can take several years to optimize. The resulting young plant is not genetically modified (GMO), rather it is a copy, or clone, of the parent plant (NTBG, 2024). Breadfruit is propagated mainly by seeds, though seedless breadfruit can be propagated by transplanting suckers that grow off the surface roots of the tree. The roots can be purposefully injured to induce the growth of suckers, which are then separated from the root and planted in a pot or directly transplanted into the ground. Pruning also induces sucker growth. Sucker cuttings are placed in plastic bags containing a mixture of soil, peat and sand, and kept in the shade while moistened with liquid fertilizer. When roots are developed, the transplant is put in full sun until time for planting in the orchard. For large-scale propagation, root cuttings are preferred, using segments about 10 centimetres thick and 20 centimetres long. Rooting may take up to 5 months to develop, with the young trees ready for planting when they are 60 centimetres high (Wikipedia, 2024).

Botanical Description

Monoecious tree, up to 30 m tall, evergreen in the humid tropics, semi-deciduous in monsoon climates. Trunk straight, 5-8 m tall, 0.6-1.8 m in diameter, often buttressed; trunk of clonally propagated trees branched low; twigs spreading, very thick, with pronounced leaf and stipule scars and lenticels; buds 10-20 cm long, covered with big conical keeled stipules. Leaves alternate, ovate to elliptical in outline, 20-60(-90) cm x 20-40(-50) cm, undivided when young, older ones entire or deeply pinnately cut into 5-11-pointed lobes, thick, leathery, dark green and shiny above, pale green and rough below, petiole 3-5 cm long. Inflorescences axillary, peduncles 4-8 cm long; male ones drooping, club-shaped, 15-25 cm x 3-4 cm, spongy, yellow, flowers minute with single stamen; female ones stiffly upright, globose or cylindrical, 8-10 cm x 5-7 cm, green, flowers numerous, embedded in receptacle, calyx tubular, ovary 2-celled, style narrow, stigma 2-lobed. Fruit a syncarp formed from the entire inflorescence, cylindrical to globose, 10-30 cm in diameter, rind yellow-green, reticulately marked with 4-6-sided faces, sometimes bearing short spines; a large central core is surrounded by numerous abortive flowers which form a pale yellow juicy pulp, the edible portion of the fruit. Most cultivated breadfruits are seedless, seeded ones are known as breadnuts. Breadnuts bear fleshy prickles, the edible pulp is largely replaced by the seeds, which are brownish, rounded or flattened, 2.5 cm long. All parts of the tree are rich in white gummy latex (Asianplant, 1941). In general, breadfruit trees are large, attractive and evergreen, reaching heights of 15 to 20 meters. The tree has smooth, light-colored bark, and the trunk may be as large as 1.2 m in diameter, occasionally growing to a height of 4 m before branching. The wood is an attractive golden color, turning darker upon exposure to air. Latex is present in all parts of the tree. Two large stipules enclose the terminal bud. They are up to 30 cm long at maturity, yellowing and falling with the unfolding of leaves or emergence of inflorescences. The thick leaves are leathery with a dark-green upper side which is often glossy. The underside is dull with an elevated midrib and main veins. 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 usually larger, more dissected and more hirsute.

Leaf dissection in breadfruit ranges from almost entire with only slight lobing to deeply pinnately lobed with sinuses from 2/ 3 to 4/ 5 of the distance from margin to midrib, or deeper. Leaves are sometimes smooth but are often covered with a few to many pale to reddish hairs, especially on the midrib and veins. The leaves of breadnut 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 *dugdug* are generally smaller, broadly obovate to broadly elliptic in outline. The 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 smooth. The midrib and veins on the underside are covered with dense reddish-coloured hairs that lie flat against the veins and give them a velvety appearance (Ragone, 1997). The fruit is a highly specialized structure, a syncarp, composed of 1500-2000 flowers attached to the fruit axis or core. The core contains numerous latex tubes and large vascular bundles which discolour rapidly upon cutting, due to oxidative enzyme activity. The bulk of the fruit is formed from the persistent perianth of each flower. The perianths are fused together except at the base. As the fruit develops, this area grows vigorously and becomes fleshy at maturity, forming the edible portion of the fruit. The tough rind of the fruit is composed of five- to seven-

sided disks, each the surface of an individual flower. Two to three strap-shaped, reflexed stigmas protrude from the centre of the disk and often leavea small distinctive scar when they blacken and wither. The rind is usually stained with latex exudations at maturity. The fruits of breadfruit are globose to oblong, ranging from 12 to 20cm wide and12 cm long. The rind is light green, yellowish-green or yellow when mature and the flesh is creamy white or pale yellow. The fruit surface varies from smooth to slightly bumpy or spiny with individual disks ranging from areolate to slightly raised and flattened, to widely conical up to 3mm high and 5mm across at the base, to narrowly conical up 5 mm long. The fruits of breadnut *(A. camansi)* are oblong and spiny with flexible, elongated sections 5-12 mm long that narrow to a point (Ragone, 1997).

Fruits of *dugdug* (*A. mariannensis*) are cylindrical or asymmetrically shaped with a deep-yellow flesh. They are generally smaller than breadfruit, averaging 8-10cm wide and 10-14cm long. The perianth disks of the dark green rind are conical when immature, becoming flattened on top when mature. Adjacent flowers fuse at the middle region of the perianths, leaving the lower and upper parts free from each other. The fruits of this species, unlike any other breadfruit, can be eaten raw. Hybrids between *A. altilis* and *A. mariannensis* exhibit characteristics of both species. *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, pyramidal or flattened perianth disks to the fruit, yellow flesh and reddish hairs on the lower veins. Hybrid cultivars show the full range of variability from seedless to having only a few seeds or numerous seeds (Ragone, 1997). Breadfruit/ breadnut seeds are thin-walled, subglobose or obovoid, irregularly compressed, 1-2cm thick, embedded in the pulp. Seeds have little or no endosperm,no period of dormancy and germinate immediately. They are not able to withstanddesiccation (Ragone, 1997; Ragone, 2003).

Trees can reach heights of 21 m or more at maturity,more commonly around 12–15 m. The trunk may be large as 2 m in diameter, occasionally growing toa height of 4 m or more before branching. A white milky latex is present in all parts of the tree. Single-trunked tree with spreading, evergreen canopy. Monoecious with male and female flowers on the same tree and the male inflorescence appearing first. Male flowers are club-shaped, up to 5 cm in diameter and 45 cm long. Thousands of tiny flowers with two anthers are attached to a central, spongy core. Female inflorescences consist of 1500–2000 reduced flowers attached to a spongy core. The flowers fuse together and develop into the fleshy, edible portion of the fruit. It is cross-pollinated, but pollination is not required for the fruit to form (Manner *et al*., 2006). Leaves are alternate, broadly obovate to broadly ovate, almost entire, with only slight lobing to deeply pinnately lobed, with sinuses up to 2/3 or more of the distance from margin to midrib, with up to six pairs of lobes and a large apical tip. Blade is generally smooth, glossy, dark green with green or yellow-green veins, and few to many white to reddish-white hairs on the midrib and veins. Leaves on new shoots and root suckers are generally larger and more hirsute than leaves on mature branches. Size is variable depending on the variety, ranging from 15–60 cm long (Manner *et al.,* 2006). Fruits are variable in shape, size, and surface texture. They are usually round, oval, or oblong ranging from 9 to 20 cm wide and more than 30 cm long, weighing 0.25–6 kg. The tough skin is composed of five- to seven-sided flower. Two strap-shaped, reflexed stigmas protrude from center of the disk and often leave a small distinctive scar when they blacken and wither. The skin texture varies from smoothly to slightly bumpy or spiny. The color is light green, yellowish-green, or yellow when mature, although one unusual variety ('Afara' from the Society Islands) has pinkish or orange-brown skin. The skin is usually stained with dried latex exudations at maturity. The flesh is creamy white or pale yellow and contains none to many seeds, depending upon the variety. Fruits are typically mature and ready to harvest and eat as a starchy staple in 15–19 weeks.Ripe fruits have a yellow or yellow-brown skin and soft, sweet, creamy flesh that can be eaten raw but rarely is in the Pacific (Manner *et al*., 2006). Seeds are thin-walled, subglobose or obovoid, irregularly compressed, 1–2 cm thick, and embedded in the pulp. The outer seed coat is usually shiny dark brown with a light brown inner seed coat. Seeds have little or no endosperm and no period of dormancy; they germinate im mediately and are unable to withstand desiccation. Seeds are distributed by flying foxes, where they occur. Seeds are rarely used for propagation (Manner *et al*., 2006).

In general, breadfruit trees are very large, evergreen which can reach to heights of 15 to 20 meters. The tree comprises smooth, light-colored bark, and the trunk is large in 1.2 m in diameter, occasionally growing to a height of 4 m before branching. The wood is gold in colour, but when contact with air, turns to a darker colour. Latex can be seen in all parts of the tree which are milky in nature. The leaves are thick and leathery with a dark-green colour on the dorsal side, which often appears to be glossy. The underside is dull with an elevated midrib and main veins. The leaves varies in size and shape even on the same tree. At the end ofthe branches, the leaves are seen as clusters. The crown is conical in shape when the trees are young or grown under shaded condition and they become rounded and irregular when it turns older. Blade is generally smooth, glossy dark green with green or yellow-green veins and many white to reddish-white hairs on the midrib and vein (Sikarwar *et al*., 2014). Breadfruit tree bears a multitude of tiny flowers. The breadfruit is monoecious which means the female and male flowers grows on the same plant. Club shaped spikes which are 5 cm in diameter and 45 cm in long are found in Male flowers whereas the female flowers are elliptical, green, pricky head measuring about 6.35 cm long. Flowers undergo cross pollination with small powdery pollen grain spread by both the wind and insects. Once both the male and female flowers are fused together, it develops into a fleshy and edible fruit. Although the reproduction of flowers involves cross pollination, but pollination does not require the fruit to form (Sikarwar *et al*., 2014). Fruits of *Artocarpus altilis* are of a very specific structure. In fruit, the central part contains many latex tubes and large vascular bundles. These vascular bundles can rapidly discolour upon cutting because of the oxidative enzyme activity.

The fruits are variable in size, shape and surface texture. Mostly they are round, oval and oblong in shape ranging from 9-20 cm, more than 30 cm in long and usually weighing around 0.25-6 kg. Aggregate fruit (syncarp) is formed by the enlargement of the entire female head. The ripe fruits of these female flowers are roundish in shape and are 4 to 8 inches in diameter. The ripe fruits have yellow or yellow-brown skin and the fruits are soft and sweet at the same time. The colour of the breadfruits are usually light green, yellowish green or yellow in colour when mature and the fruit (Afara) found in Society Island is pinkish or orange-brown in colour. The flesh of the fruit is usually creamy, soft with a pleasant fragrant (Sikarwar *et al*., 2014). Breadfruits are available with seeds and also without seeds. The seeded types of breadfruit are available in south western Pacific, whereas seedless types of breadfruit are common in Micronesia and Eastern islands of Polynesia. All the breadfruit varieties elsewhere especially in topic region are of seedless type. Seeds are brown in colour, shiny, round or ovoid in shape and irregularly compressed. Moreover, the seeds have little or no endosperm, no period of dormancy and they can germinate immediately. Since they can germinate immediately, they are not able to be dried or stored. Trees that grow with the help of seeds can produce their fruits in a timeline of 6-10 years or sooner. On the contrary, asexually propagated trees can start to produce their fruits in 3-6 years of time (Sikarwar *et al*., 2014). Monoecious tree, up to 30 m tall, evergreen in the humid tropics, semi-deciduous in monsoon climates. Trunk straight, 5-8 m tall, 0.6-1.8 m in diameter, often buttressed; trunk of clonally propagated trees branched low; twigs spreading, very thick, with pronounced leaf and stipule scars and lenticels; buds 10-20 cm long, covered with big conical keeled stipules. Leaves alternate, ovate to elliptical in outline, 20-60(-90) x 20-40(-50) cm, undivided when young, older ones entire or deeply pinnately cut into 5-11-pointed lobes, thick, leathery, dark green and shiny above, pale green and rough below, petiole 3-5 cm long. Inflorescences axillary, peduncles 4-8 cm long; male ones drooping, club-shaped, 15-25 x 3-4 cm,

spongy, yellow, flowers minute with single stamen; female ones stiffly upright, globose or cylindrical, 8-10 x 5-7 cm, green, flowers numerous, embedded in receptacle, calyx tubular, ovary 2-celled, style narrow, stigma 2-lobed. Fruit a syncarp formed from the entire inflorescence, cylindrical to globose, 10-30 cm in diameter, rind yellow-green, reticulately marked with 4-6-sided faces, sometimes bearing short spines; a large central core is surrounded by numerous abortive flowers which form a pale yellow juicy pulp, the edible portion of the fruit (Rojas-Sandoval and Acevedo-Rodríguez, 2021). Most cultivated breadfruits are seedless, seeded ones are known as breadnuts. Breadnuts bear fleshy prickles, the edible pulp is largely replaced by the seeds, which are brownish, rounded or flattened, 2.5 cm long. All parts of the tree are rich in white gummy latex (Rojas-Sandoval and Acevedo-Rodríguez, 2021).

Breadfruit trees grow to a height of 26 metres. The large and thick leaves are deeply cut into pinnate lobes. All parts of the tree yield latex, which is useful for boat caulking. The trees are monoecious, with male and female flowers growing on the same tree. The male flowers emerge first, followed shortly afterward by the female flowers. The latter grow into capitula, which are capable of pollination just three days later. Pollination occurs mainly by fruit bats, but cultivated varieties produce fruit without pollination. The compound, false fruit develops from the swollen perianth, and originates from 1,500 to 2,000 flowers visible on the skin of the fruit as hexagon-like disks. Breadfruit is one of the highest-yielding food plants, with a single tree producing up to 200 or more grapefruit-sized fruits per season, requiring limited care. In the South Pacific, the trees yield 50 to 150 fruits per year, usually round, oval or oblong weighing 0.25 to 6 kilograms. Productivity varies between wet and dry areas. Studies in Barbados indicate a reasonable potential of 15 to 30 tonnes per hectare. The ovoid fruit has a rough surface, and each fruit is divided into many achenes, each achene surrounded by a fleshy perianth and growing on a fleshy receptacle. Most selectively bred cultivars have seedless fruit, whereas seeded varieties are grown mainly for their edible seeds. Breadfruit is usually propagated using root cuttings (Wikipedia, 2024). The breadfruit tree grows 12 to 18 metres (40 to 60 feet) high and has large, oval, glossy green leaves, three- to nine-lobed toward the apex. Male and female flowers are borne in separate groups on the same tree: the staminate (male) flowers appear in dense club-shaped catkins; the numerous female, or pistillate, flowers are grouped and form a large prickly head upon a spongy receptacle. The ripe fruits, or matured ovaries, of these pistillate flowers are roundish, 10 to 20 centimetres (4 to 8 inches) in diameter, and greenish to brownish green and have a white, somewhat fibrous pulp (Petruzzello, 2024).

It is a monoecious tree that can grow up to 40 m. *Artocarpus altilis* is an evergreen tree in humid tropics but semi-deciduous in monsoon climate. Its, 5 – 8 m tall, trunk can reach a diameter of 0.6 – 1.8 m. Alternate, ovate to elliptical, leaves. Inflorence; axillary, male flower drooping, shaped like a club and the female flower stiffly upright, globose or cylindrical. Propagated from seed, the seed must be planted when fairly fresh as they will lose viability within a few weeks and it cannot be stored in refrigerator. Before planting breadfruit trees in a well-enriched hole, 40 cm deep and 90 cm wide, the hole must be sterilise by burning trash in them and mixed the soil with insecticide to protect roots and shoots from grubs, thick wormlike larva. However, well-drained clay loams under partial shade are the optimum condition for it to grow. Fruits, immature or ripe, and seeds are boiled, baked, roasted or fried before consuming. Before making it into a biscuit, the ripe fruits are cooked before drying it in sun or oven. Fruits can be made into a nutritious cheese-like paste, by letting it ferments, and made into cakes and baked. Blended with the fibre of paper mulberry, the male flower spikes can be used to produce loincloths. When diluted with rain water, the latex, from the trunk, can be used to treat diarrhoea. As the wood is light yet firm and nicely grained, it is used to make canoes, surfboards, toys, boxes and crates (Florafaunaweb, 2024). Each tree features leathery, pinnately-lobed, dark green leaves (to 10-36" long and to 10-20" wide), each of which features 5-11 deeply cut lobes. Monoecious flowers (male and female flowers on the same tree) bloom somewhat continuously year round in the Pacific Islands, but often with more sporadic periods of bloom occurring in other geographic areas. Flowers grow on short stems from the trunks and large branches (cauliflorus). Male flowers appear in pendant spikes to 10" long and female flowers in oval-rounded heads to 2 1/2" long. Female flowers give way to large, rounded, smooth to spiny, green to yellowish-green, compound, rounded fruits (massive spherical syncarps) which typically mature to 5-12" in diameter with a weight of 7-10 pounds. Each fruit has white to pale yellow flesh. Fruit flesh is quite edible if cooked (boiled or baked), with the cooked fruit reportedly having a potato-like flavor. Baked fruit has the aroma and texture of fresh baked bread, hence the common name. Eating raw uncooked fruit flesh will cause nausea. A single tree can produce as many as 200 grapefruit-sized fruits per year (MGB, 2024).

Artocarpus altilis is a large, attractive, evergreen tree, reaching heights of 15-20 m; bark smooth, light colored; trunk up to 1.2 m in diameter, may reach a height of 4 m before branching; 2 large stipules enclosing the terminal bud, up to 30 cm long at maturity, yellowing and falling when leaves fold or inflorescence emerges. Leaves thick, leathery; top dark green, often glossy; underside dull with an elevated midrib and main veins; striking variation in leaf outline and dissection; leaves broadly obovate to broadly ovate, varying in size and shape; juvenile leaves on young trees and new shoots of mature trees usually larger, more dissected and more hirsute; leaves sometimes smooth but often with few to many pale to reddish hairs, especially on the midrib and veins (Agroforestry, 2024). Fruit a highly specialized structure, a syncarp, composed of 1500-2000 flowers attached to the fruit axis or core; bulk of fruit formed from the persistent perianth of each flower; perianths are fused together except at base. As the fruit develops, this area grows vigorously and becomes fleshy at maturity, forming the edible portion of the fruit; tough rind composed of 5- to 7-sided disks, each the surface of an individual flower; 2-3 strap-shaped, reflexed stigmas protrude from the centre of the disk and often leave a small distinctive scar when they blacken and wither; rind at maturity usually stained with latex exudations (Agroforestry, 2024). Fruit globose to oblong,12-20 cm x12 cm; rind light green, yellowish-green or yellow when mature, flesh creamy white or pale yellow; surface varies from smooth to slightly bumpy or spiny, with individual disks ranging from areolate to slightly raised and flattened, to widely conical, up to 3 mm high and 5 mm across at the base, to narrowly conical up to 5 mm long; seedless, some forms seeded. Seeds have a thin, dark-brown outer skin about 0.5 mm thick and an inner, fragile, paper like membrane that surrounds the fleshy, white edible portion of the seed (Agroforestry, 2024). Vegetative Propagation and Botanical Description is given in Fig. 1.

Floral Biology

Inflorescences are axillary and monoecious, with the male inflorescence originatingfirst. Male inflorescences are club-shaped, up to 5 cm in diameter and 45 cm long. The thick, spongy axis is covered by numerousminute flowers. Each flower consistsof a reduced tubular perianth enclosing a single stamen with a two-lobed anther ona thick filament. In young flowers, the perianth has a narrow opening, but at anthesisits lobes are widely separated and the anther is exserted above the perianth. Abnormal inflorescences with both male and female flowers have been observed (Ragone, 1997). The pollination mechanisms of breadfruit are not fully understood, with questions raised as to whether this is mediated by wind or insects. Breadfruit treesare monoecious with male and female flowers occurring separately on the same tree.Male inflorescences originate first, followed by female inflorescences. Pollen is shed10 to 15 days after the emergence of the male inflorescence for a period of about4 days. Female flowers are receptive 3 days after the emergence of the female inflorescence from the bracts and open in successive stages with basal flowers opening first. As with other members of this genus, breadfruit is cross- pollinated (Ragone, 1997). Seedless cultivars generally produce little viable pollen compared with fertile, seeded and few-seeded cultivars.

Seeds

Germinating seed

Root sucker

Root sucker

Air layering

Air layers

Graft

Flower, foliage, fruit

Flowers

Leaves

Female inflorescence showing a spongy core of 1500-2000 tiny flowers;

Club shaped spike male inflorescence (ranges from 5 to 12 inches long)

Mature fruit

Ripe fruit

Plant

Plant

Plantation

Branches

Whole, sliced lengthwise, and n cross-cross-section of fruit

Fig. 1 : Vegetative Propagation and Botanical Description

In fertile cultivars, the anthers of hundreds of flowers will protrude and dehisce, releasing thousands of pollen grains, so much so that a dusting of pollen can be seen on leaves under the inflorescence. Only a few flowers in male inflorescences of seedless breadfruit produce and release pollen (Ragone, 1997). *A. altilis* trees are monoecious -- male and female flowers occur separately on the same tree. Male inflorescence emerges before the female. Pollen is shed 10-15 days after the emergence of the male inflorescence, for a period of about 4days. Female flowers are receptive 3 days after the emergence of the female inflorescence from the bracts and open in successive stages, with basal flowers opening 1st. As with other members of its genus, *A. altilis* is cross-pollinated (Agroforestry, 2024). Honeybees have been observed actively working the male inflorescence and collecting pollen, especially from fertile, seeded accessions. Other insects such as earwigs have also been observed on the male inflorescence. Only a few flowers in the male inflorescence of seedless *A. altilis* produce and release pollen. Pollen grains from fertile cultivars are uniformly shaped and stain well, while triploid cultivars have the lowest pollen sustainability, averaging 6-16%. Pollen grains are typically malformed, clumped and poorly stained (Agroforestry, 2024). Breadfruit is monoecious with male and female flowers developing on the same tree at the end of branches. The male inflorescence (flower) typically appears first. It is club shaped, ranging from 10 cm to 45 cm long. The inflorescence consists of thousands of tiny, creamy yellow individual flowers attached to a spongy core. The inflorescence fades to dark brown with age. Pollen is shed 10 to 15 days after the emergence of the male inflorescence for a period of about four days. Honeybees are attracted to the abundant pollen produced by some varieties. Each female inflorescence consists of 1500–2000 reduced flowers attached to a spongy core. The flowers fuse together and develop into the fleshy, edible portion of the fruit. Each breadfruit is a compound or multiple fruit called a syncarp. The female inflorescence, appearing after the male, consists of 1500-2000 minute flowers attached to a spongy core. The flowers fuse together and develop into the fleshy, edible portion of the fruit. No pollination is required for a fruit to form. The skin is light to dark green, yellow-green, or yellow when mature, although one unusual variety has pinkish or orange-brown fruit. The thin skin is patterned with pentagonal or hexagonal markings and can be smooth, bumpy, or spiny. Fruit are typically mature and ready to harvest, cook, and eat in 15-20 weeks. The skin of ripe fruit can be green, but is more typically yellow or yellow-brown. The soft, sweet, creamy flesh can be eaten raw or cooked (Fig. 2) (NTBG, 2024a).

Fig. 2. Femasle and Male flower

Genetics and Cytogenetics: Breadfruit, a staple food in tropical regions, presents a unique model for studying plant development due to its distinct growth stages and versatile culinary applications. Understanding the genetic and developmental changes in breadfruit not only enhances our comprehension of plant biology but also opens new avenues for agricultural innovation. Breadfruit exhibits both male and female inflorescences, the latter being what we commonly refer to as the fruit. The development of breadfruit can be categorized into several key stages, each with its own culinary uses and challenges (Agroforesteriasa, 2024):

Flowering (0 weeks): The initial stage involves the emergence of female inflorescences. Although these are technically flowers, they are edible and widely consumed at this stage. The very young fruit has a texture and taste akin to artichokes, making it a unique vegetable option in various dishes.

Immature Stage (0–16 weeks): As the fruit develops, it transitions through a deep green phase where it remains firm and rubbery. This stage is ideal for using the fruit as a vegetable, similar to how one might use squash or eggplant in cooking.

Full Size Green Stage (12–16 weeks): At this point, the fruit is physically mature but still immature in terms of its starch content. It possesses a longer shelf life but is generally less favored by consumers unless used in specific vegetable-based dishes.

Mature Stage (16–20 weeks): This is the stage where breadfruit's starches are fully developed, transforming it into a starchy staple. The early part of this phase (16–18 weeks) offers fruits with smooth texture and excellent flavor, ideal for stews, curries, and fried dishes. Fruit harvested during the later part (18–20 weeks) maintains excellent eating qualities but has a shorter shelf life.

Post-Maturity: As the fruit over-ripens, it transitions into a sweet, dessert-like stage where the starches convert to sugars. Initially, the half-ripe fruit resembles sweet potatoes in texture and sweetness, suitable for similar culinary uses. Eventually, the fruit becomes very soft, emitting a sweet fragrance and is perfect for raw consumption in desserts or cooked in various sweet dishes. Each stage of breadfruit development is controlled by complex genetic mechanisms that dictate the transformation of textures and flavors. By decoding these genetic pathways, researchers can potentially manipulate growth patterns and improve both the yield and nutritional value of the fruit. For instance, enhancing the starch content in earlier stages could make the fruit more versatile, while extending the shelf life at later stages could improve its marketability. Moreover, understanding the genetic basis of breadfruit's development can aid in breeding programs aimed at producing varieties that are resilient to climate change and diseases, thereby supporting sustainable agricultural practices in tropical regions (Agroforesteriasa, 2024). *Artocarpus altilis*is diploid ($2n = 56$) and triploid ($2n = 84$) (Ragone, 1997**;** Agroforestry, 2024). The chromosome number for *A.mariannensis* and for *A.camansi* is $2n = 56$ (Ragone, 1997). Chromosome numbers were determined for 48 accessions of breadfruit (*Artocarpus altilis*, *A. mariannensis*, and *A. camansi* [Moraceae]) from 16 Pacific Island groups, Indonesia, and the Philippines. *Artocarpus camansi* and *A. mariannensis* exhibit counts of 2n = 56; 2n = 56 (diploidy) and 2n = 84 (triploidy) were observed for *A. altilis*. Most diploid cultivars of *A. altilis* were seeded, but two cultivars with reduced seed number were observed. Micronesian accessions included putative interspecific hybrids between *A. altilis* and *A. mariannensis*. The majority of these accessions were seedless diploids, but triploid putative hybrids were also observed. Pollen stainablility was shown to correlate with the degree of seediness (Ragone, 2001).

GENETIC DIVERSITY

While *A. altilis* (and synonyms) has appropriately been applied to the seedless breadfruit typical of Polynesia — a type that is now widely distributed throughoutthe tropical world — the nomenclature for other forms of breadfruit is not as straightforward. Throughout the Pacific, breadfruit exhibits great morphological variability, ranging from true seedless fruits to fruits with numerous, minute, aborted seeds, to fruits with one to few viable seeds, to fruits with numerous seeds. Many authors have taken the broad view and encompass all of this variability within one species. However, there is another valid species of breadfruit in the Pacific Islands. *Artocarpus mariannensis*Trécul is a wild, seededbreadfruit, known as *dugdug* and *chebiei,* endemic to the high islands of the western north Pacific. It

was described from a specimen collected in the Mariana Islands in 1819. This species is morphologically very distinct from *A. altilis* and involved in introgression with this species in Micronesia where numerous cultivars with characters of both species are found. The real question to be resolved concerns a spiny, seeded type of breadfruit (breadnut, kamansi, pakok) described from the Philippines and naturally found in New Guinea and possibly the Moluccas (Ragone, 1997). Breadfruit, 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. ariannensis* 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 (Zerega *et al*., 2004). The genetic diversity and importance of breadfruit remain greatest in the Pacific islands (Zerega *et al*., 2004).

Throughout the Pacific, breadfruit exhibits great morpho logical variability, ranging from true seedless varieties to those with several small aborted seeds, or one to a few viable seeds, to varieties with numerous viable seeds. Seeded types are most common in the southwestern Pacific. Seed less varieties are most common in Micronesia and the eastern islands of Polynesia. All of the breadfruit varieties elsewhere in the tropics are seedless (Manner *et al.,* 2006). Breadfruit is genetically diverse, especially the seeded forms in the western Pacific and hybrids (with *Artocarpus mariannensis*) in Micronesia. Numerous Polynesian triploid varieties are genetically identical but morphologically distinct. These Polynesian triploids tend to not thrive under atoll conditions, while both seeded and seedless hybrid varieties are best adapted to these conditions (Manner *et al*., 2006). *Artocarpus altilis* (Park.) Fosberg is an important fruit vegetable tree grown in the homesteads of southern part of India. To provide reasoned scientific management practices and conservation measures, the pattern of morphological and genetic variation were investigated for six populations using Amplified Fragment Length Polymorphism (AFLP) markers and 15 morphological traits. The use of five selective primer combinations on 60 samples resulted a total of 414 bands in which 85% were polymorphic. The values of Nei's genetic distance varied from 0.0044 (Palai– Palghat) to 0.3376 (Palghat–Mangalore). Analysis of molecular variance revealed most of the variation within populations (57.45%) than (42.55%) among populations. The genetic variation by AFLP data is not reflected in quantitative morphological variables. However, the genetic and geographical distances were positively correlated which were further well sup- ported by the PCO analysis and Dollo-parsimony tree, both show the tendency of the individuals to group according to the geographical localities (Sreekumar *et al*., 2007).

Fruits are variable in shape, size and surface texture, region and in Trinidad, fruiting occurs throughout the often they are round, oval, or oblong ranging from 9 to 20 year, where as in Hawaii, breadfruit production is cm 10- 20 wide and more than 30 cm long, seasonal, typically occurs between June and August weighing 0.25-6 kg. The rind is greenish-yellow with a pattern of hexagonal markings and the markings may be smooth, spiny, or spiky surface. Flesh is usually soft, creamy white or pale yellow with pleasant fragrant adaptability to ecological conditions. It grows best in and depending on the varieties it may contain none or equatorial lowlands below 600-650 m. Fruits may contain no seeds, less seeds, or many seeds (Fig. 3) (Subramanian and Bhore, 2010).

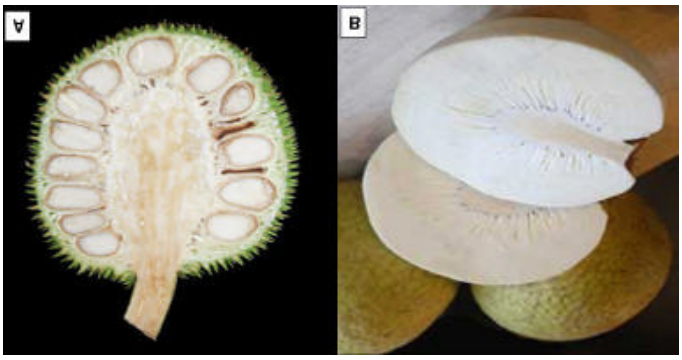

Fig. 3. Artocarpus altilis Fosb. fruit (breadfruit); (A) breadfruit with seeds; and (B) seedless breadfruit

Over millennia of breadfruit cultivation, hundreds of named cultivars have been developed that display a high degree of morphological diversity. Thecurrent study was undertaken to evaluate morphological diversity within the National Tropical Botanical Garden's breadfruit germplasm collection, the largest and most diverse breadfruit collection in the world. A set of 57 standardized morphological descriptors including 29 leaf, 22 fruit, four seed, and two male inflorescence characteristics were used to describe and contrast 221 accessions of breadfruit including accessions of *Artocarpus camansi* Blanco, *A. altilis* (Parkinson) Fosberg, *A. mariannensis* Trécul, early generation *A. altilis* x *A. mariannensis* hybrids, and domesticated *A. altilis* x *A. mariannensis* hybrids. A morphological transition from heavily seeded fruit covered with flexible spines to fewer seeded, smoother skinned fruit of similar size was observed in the domestication of *A. altilis* from *A. camansi.* The National Tropical Botanical Garden (NTBG) breadfruit germplasm collection includes 281 individual accessioned trees of breadfruit (*Artocarpus altilis* (Parkinson) Fosberg and *A. altilis* x *A. mariannensis* Trécul hybrids), breadnut (*A. camansi* Blanco), and dugdug (*A. mariannensis*) (Jones et al., 2013).

This study examines important germplasm collections of breadfruit and its closest wild relatives and aims to (1) characterize genetic diversity, including identification of unknown and duplicate accessions, (2) evaluate genetic structure and hybridization within the breadfruit complex, and (3) compare utility of microsatellite markers to previously reported amplified fragment length polymorphism (AFLP) and isozyme markers in differentiating among cultivars. Data for 19 microsatellite loci were collected for 349 individuals (representing 255 accessions) including breadfruit (*A. altilis*), two wild relatives (*Artocarpus camansi* and *Artocarpus mariannensis*), and putative hybrids (*A. altilis* × *A. mariannensis*). Accessions were of mixed ploidy and regional origin, but predominantly from Oceania. Microsatellite loci collectively had a polymorphic information content (PIC) of 0.627 and distinguished 197 unique genotypes sorted into 129 different lineages, but a single genotype accounts for 49 % of all triploid breadfruit examined. Triploid hybrids and diploid *A. altilis* exhibited the highest levels of diversity as measured by allele number and gene diversity. Most accessions (75 %) of unknown origin matched either a known genotype or lineage group in the collection. Putative hybrids all had genetic contributions from *A. mariannensis* but ranged in the level of genetic contribution from *A. altilis*. Microsatellite markers were found to be more informative than isozyme markers and slightly less informative, with regard to accession discrimination, than AFLP markers. This set of microsatellite markers and the dataset presented here will be valuable for breadfruit germplasm management and conservation (Zerega *et al*., 2015).

Breadfruit has significant molecular genetic diversity. One effort to improve the quality of breadfruit plants is a breeding program to engineer high productivity through molecular characterization. This study examines the diversity of breadfruit tree DNA (*Artocarpus altilis* P.) in different regions based on marker RAPD (*Random Amplified Polymorphic* DNA). Nine samples of breadfruit plants were

taken from several areas in Yogyakarta, Indonesia. Genetic markers were determined using RAPD analysis of 6 primers selected from 20 screened primers (OPC5, OPD2, OPD3, OPD8, OPD11, and OPD19). The results showed diversity at the genetic distance of 0.31–0.95. Dendrograms are divided into 3 groups, including individual GK1, individual GK2 and large groups consisting of GK3, B1, B2, B3, S1, S2, and S3 (Ifah *et al*., 2018). The most extensive research by far has been conducted and examined 221 accessions in a germplasm collection at the National Tropical Botanical Garden in Hawai'i using 57 morphological characteristics. Variation in fruit shape, skin texture and leaf dissection are shown in (Lincoln *et al*., 2018).

One of the ways to preserve species germplasm is by identifying the genetic distance and intraspecific diversity. The aims of this study was to study the distribution and cultivation status, genetic distance, and diversity of breadfruit plants, in Bawean Island, Gresik, Indonesia based on morphological characters. The study made 30 accessions of breadfruit plants spread throughout Bawean Island, which were found to be neither cultivated intensively nor used optimally by the inhabitants. The genetic distance showed that breadfruit in Bawean Island was clustered into 6 groups with similarity coefficient of around 0.9984 to 0.9999. The diversity index value of 1.48 indicated medium diversity of breadfruit on this island (Rahmah and Waluyo, 2019). Breadfruits in Bawean Island had glossy to dull, green and dark green leaves with moderately dissected and deeply dissected leaves. (Rahmah and Waluyo, 2019). The breadfruit shape characters observed were spherical, broadly ovoid, oval, oblong, ellipsoid and heart-shape (Rahmah and Waluyo, 2019). This study focuses on the morphological characterization of 27 breadfruit accessions, which either have existed in the Caribbean since the 18th century or were introduced in the 1990s. All accessions were established in a field collection at the University of the West Indies, Trinidad and Tobago. Results of the current study showed that breadfruit accessions were highly variable and that for several morphological characteristics, including fruit characters that are of economic importance, the recently introduced accessions have expanded the range for selection. Fruit characters such as skin texture, skin colour, shape and pulp colour were also the most useful for distinguishing among accessions. Descriptors related to leaf lobing were also important for distinguishing a few accessions. The results confirmed the usefulness of morphological traits for breadfruit germplasm characterization and also for combining with other methods of diversity analysis (Daley et al., 2020). The greatest diversity of seeded and few-seeded cultivars is found in the eastern Solomon Islands and Vanuatu, while the greatest diversity of seedless cultivars occurs in eastern Polynesia (Society Islands and Marquesas) and Pohnpei and Chuuk in Micronesia (Rojas-Sandoval and Acevedo-Rodríguez, 2021). Breadfruit is recognized as a tropical fruit tree crop with great potential to contribute to food and nutrition security in the Caribbean and other tropical regions. However, the genetic diversity and germplasm identification in the Caribbean and elsewhere are poorly understood and documented. This hampers the effective conservation and use of the genetic resources of this tree crop for commercial activities. This study assessed the genetic identity, diversity, ancestry, and phylogeny of breadfruit germplasm existing in the Caribbean and several newly introduced accessions using 117 SNPs from 10 SSR amplicon sequences.

The results showed that there was high and comparable genetic diversity in the breadfruit germplasm in the Caribbean, and the newly introduced breadfruit accessions were based on nucleotide diversity (πT) 0.197 vs. 0.209, respectively, and nucleotide polymorphism (θW) 0.312 vs. 0.297, respectively. Furthermore, the existing Caribbean breadfruit accessions and the newly introduced breadfruit accessions were statistically genetically undifferentiated from each other ($p < 0.05$). Ancestry and phylogeny analysis corroborated the genetic relatedness of these two groups, with accessions of these groups being present in both main germplasm clusters. This suggests that the existing Caribbean breadfruit germplasm harbors a higher level of genetic diversity than expected. Ninety-five of the initial 153 samples collected were selected for sequencing. This included one breadnut (*A. camansi*), 91 *A. altilis*, and three *A. altilis* × *A. mariannensis* hybrids. This selection was based on the quality of amplicons produced over all ten primer pairs and a deliberate attempt to represent as many cultivar names as possible, leaf and fruit morphological variations and collection sites. This resulted in multiple samples for some cultivars and single samples for other cultivars (Daley et al., 2024).

BREEDING

Genetic Resources: Numerous collections of breadfruit have been assembled for conservation and study. The FAO — World Information and Early Warning System on Plant Genetic Resources lists 14 institutions holding 112 germplasm accessions of breadfruit. Following are the countries reported in this database as holding breadfruit accessions and the number and type of holdings (if stated): Brazil (10 landraces or primitive cultivars), Colombia (2), Costa Rica (3), Fiji (70 old cultivars), France (2 local cultivars), Honduras (2), Indonesia (3 old cultivars), Jamaica (5 advanced cultivars), Papua New Guinea (6 old cultivars), Philippines (1 advanced cultivar), Taiwan (1), Tanzania (1) and Vietnam (4 landraces). This information is inaccurate for holdings in the Pacific Islands and out of date. For example, the Koronivia Research Station in Fiji does not maintain a collection of 70 old cultivars (Ragone, 1997). The genetic diversity of breadfruit throughout the world — with the exception of some of the Pacific Islands — rests on a very narrow base. Globally, this now widespread, important crop has derived from only a few Polynesian cultivars. These in turn represent a narrowing of the genetic diversity of breadfruit in the Pacific Islands from west to east with little genetic variation in eastern Polynesia. Even though numerous cultivars exist in eastern Polynesia, they are primarily clones selected from a few original introductions many centuries ago (Ragone, 1997). The National Tropical Botanical Garden can provide selected varieties from an extensive breadfruit germplasm collection. The USDA Clonal Germplasm Repository, Waiakea, Hawaii, can provide selected breadfruit varieties (Manner *et al*., 2006). Seeds display recalcitrant storage behavior. The short-lived seeds should not be allowed to dry out and should be kept moist at 20 deg. C. Seeds germinate immediately and are unable to withstand desiccation, hence loose viability within a few weeks and cannot be stored. Wherever seeds occur they are distributed by flying foxes (Agroforestry, 2024).

Breeding

There has been little deliberate breeding of breadfruit. Indigenous farmers have selected seedling populations or somatic variants for desirable and observable traits over millennia. Beginning 3000-4000 years ago, islanders began venturing eastwards into the vast expanse of the Pacific Ocean. Breadfruit and other crops were carried in colonizing canoes to ensure a supply of food in new lands. Repeated vegetative propagation of breadfruit trees that survived would have multiplied the limited resource. In addition, seeds from seeded cultivars probably were planted to further increase the number of trees. Selected seedlings then would have been vegetatively propagated along with seedless types (Ragone, 1997). 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 useful traits would be preserved and perpetuated. The need to carefully conserve 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. Hundreds of cultivars of breadfruit are now grown in the Pacific Islands (Ragone, 1997). Since many cultivars of breadfruit are seedless it has been inferred that fruit development is due to parthenocarpy. Seedlessness in breadfruit generally has been attributed to sterility due to triploidy, but failure of breadfruit to set seed can also be due to other genetic factors. A preliminary cytological study of breadfruit suggests that triploidy is the cause of sterility for those cultivars with a somatic number of $2n = 84$. 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 very unusual (Ragone, 1997). The origin of seedless breadfruit was particularly significant for utilization of this crop. Triploid seedless breadfruit probably arose in western Polynesia (Fiji, Tonga, Samoa) where seeded, few-seeded and seedless cultivars are all found (Ragone, 1997). Micronesian breadfruit cultivars are diverse for zymotypic, morphological and cytological characters. Seeded or seedless diploids, as well as seedless triploid cultivars, which are all interspecific hybrids between *A. altilis* and *A. mariannensis*, are found in Micronesia. There are also seedless Polynesian triploid cultivars. Cluster analysis of isozyme zymotypes shows that hybridization and introgression between the two species occurred in more than one island group, and that the Polynesian triploid was involved in some islands. Additional cytological studiescombined with isozyme analyses of breadfruit are needed to understand the origin of interspecific hybrids in Micronesia (Ragone, 1997). Improvement of breadfruit will depend on systematic evaluation and characterization of traditional Pacific Island cultivars, selection of superiour clones, and their introduction to other areas to expand the existing cultivar base. This is particularly relevant for the Caribbean and other areas where breadfruit is an important staple but limited to only one or a few cultivars. Caribbean cultivars should also be systematically evaluated and compared with their Polynesian progenitors. Improvement and selection of breadfruit should focus on identificationof (Ragone, 1997):

- A suite of cultivars that when grown together will supply a consistent supply of fruit year-round
- High-yielding cultivars
- Cultivars with good texture and flavour
- Cultivars with improved keeping qualities
- Cultivars suitable for processing into flour, chips and other products.

Fruit Maturity Indicators: Every variety of breadfruit has its own indicators for fruit maturity. Although the following maturity indicators are not universal for all varieties, they apply to many varieties present in Hawai‘i. Not all indicators are always present in mature fruit. Some indicators can be deceptive. For example, sap drip may be caused by wind damage to an immature fruit. Therefore several indicators should be present to have reasonable certainty about fruit maturity.

Draining sap: Every part of the breadfruit tree, including the fruit, contains a white, sticky sap (also called latex). In the fruit the sap is concentrated in the skin and around the core. This sticky sap can adhere to kitchenware during the cutting and cooking process, and is often the cause of complaints by people who are new to breadfruit. Harvesting fully mature fruit and allowing the sap to drain from the fruit immediately after harvest can greatly reduce or eliminate the presence of sap in the kitchen. A recommended method for draining the sap is to cut the stem close to the base and then setting the fruit on the stem end on a clean surface for about an hour. Resting the fruit on the cut stem reduces the amount of sap that adheres on the fruit surface during the draining process.

Harvesting safety: Although tempting to many, climbing breadfruit trees for harvesting is not recommended due to the inherent dangers of loose footing, breaking branches, falling fruit. Climbing should only be attempted in healthy trees by those with certified safety training and equipment (harness, ropes). Climbing becomes unnecessary for trees that are regularly pruned to a height of 4.5–5.5 m. When harvesting from taller trees, a sturdy platform (such as a truck bed or agricultural lift) or an orchard ladder can be used to extend reach. Hard hat and eye protection are essential gear for harvesters. Fruit, dead branches, and other debris can inadvertently fall, presenting danger of injury to those below. Head and eye protection are simple and convenient precautions well worth taking. Some harvesters attempt to have one person cut the fruit stem while another person stands underneath the tree to catch the fruit.

Harvest: Even though breadfruit is edible at any stage of development, it is essential to understand and recognize the different stages of fruit development and maturity, and harvest fruit at the optimal stage for the desired market or use. Fruit that are picked too green and still immature have a longer shelf life than fruit harvested at the full mature stage, which explains why immature fruit is often sold in supermarkets and at farmers markets. However, immature fruit is undesirable for most dishes. Such fruit has a rubbery texture and characterless flavor unsuitable for most dishes where a creamy texture and rich flavor are desired. Immature fruit will become soft over time, but does not ripen, making it unacceptable for dishes requiring ripe fruit. For many chefs and consumers, immature breadfruit is their first introduction to this food, and the negative experience often discourages them buying or eating it again.

Varieties (Elevitch *et al*., 2014).

Table 1. Breadfruit varieties introduced into Hawai‘i since the late 1800s

Variety	Region of origin	Botanical name
Ma‘afala	Samoa	*Artocarpus altilis*
Puou	Samoa/Tonga	*A. altilis*
Maopo	Samoa/Tonga	*A. altilis*
Puero	Tahiti	*A. altilis*
Dugdug	N. Marianas	*A. mariannensis*
Breadnut	Philippines	*A. camansi*
Meinpadahk, Mejenwe	Micronesia	*A. altilis* × *A. mariannensis*

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