

Breadfruit and Breadfruit Diseases in Hawai'i: History, Identification and Management

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INTRODUCTION

Breadfruit

<Fig. 1 about here> Breadfruit are one of the few staple crops grown on trees. Although a fruit, it is high in complex carbohydrates.

Breadfruit (*Artocarpus altilis* Fosberg), or 'ulu in Hawaiian, is a tropical tree in the fig family (Moraceae) that produces large starchy fruit akin to a potato or plantain depending on the state of maturity. Breadfruit has served as a staple crop for people in the Pacific for millennia, and during the past two centuries it has been spread to the global tropics and become a prominent local food in many areas. As a long-lived tree that produces a staple food, breadfruit has the potential to dramatically change agricultural practices in tropical regions. Breadfruit has been named a priority crop for addressing global hunger, rural livelihoods, and environmental degradation associated with agriculture (Lucas and Ragone, 2012; FAO, 2019). Recent advances in technology (e.g., commercial-scale propagation and value-added products) and efforts in promotion (e.g., public education and tree giveaways or distributions) have resulted in a substantial increase in awareness and interest in breadfruit, although the crop is still considered underutilized. Underutilized crops typically suffer from a lack of study (Ragone, 1997). One of the primary issues that growers face, which can be attributed to climate change and an increase in global trade, is the establishment and spread of plant pathogens that reduce the production and quality of breadfruit crops.

History in Pacific

Breadfruit likely originated in Papua New Guinea or the surrounding islands, where the wild ancestor—breadnut (*Artocarpus camansi* Blanco)—is widespread (Zerega et al., 2004, 2006). Cross-pollination with wild breadnut limited the evolution of the breadfruit until the crop was transported to nearby islands, such as Vanuatu, Fiji and Samoa. In the absence of breadnut, the diversity of breadfruit truly proliferated. Over millennia, Pacific Islanders have developed and named hundreds of cultivars distinguished based on fruiting season, fruit shape, color and texture of the flesh and skin, presence of seeds, flavor cooking qualities, leaf shape (particularly the degree of dissection), tree form, and horticultural needs (Wilder, 1928; Ragone, 1997). There are more than 2,000 cultivars names documented across the Pacific (Ragone and Wiseman, 2007)!

Cultivars change as one moves across the Pacific (MacMillan, 1908), with the genetic diversity decreasing from the west (Melanesia/southeast Asia) to the east (Polynesia) (Zerega et al., 2005).

Most notably, distance from New Guinea correlates strongly with the average number of seeds in each breadfruit cultivar (Xing et al., 2012). In the Society Islands in the far eastern Pacific, breadfruit cultivars with seeds are so exceptional that the name for the only known seed-producing cultivar is ‘Huero’ – literally, “with a seed” (Ragone, 2001). A related species of breadfruit—*A. mariannensis* Trécul, known as dokdok and chebiei—and interspecific hybrids (*A. altilis* × *A. mariannensis*) were traditionally restricted to Micronesia.

Breadfruit, cultivated throughout Oceania, grows well in a range of habitats and cropping systems, including marginal habitats (Mausio et al., 2020). Most often the trees were grown around house sites and in semi-wild “food forests”. On low lying atolls or old, steep volcanic islands, tree cultivation was among the primary agricultural opportunity available. Murai et al., (1958) shows that the distribution of productive breadfruit closely follows the pattern of salinity in the groundwater. Anecdotal observations and ethnography indicate that the hybrids are hardier, more salt-tolerant, and are prevalent on the low-lying Micronesian atolls.

History in Hawai‘i

<Picture of kalu‘ulu about here> Traditionally breadfruit was grown as part of diversified agroforestry, such as this restored section of the famous kalu‘ulu breadfruit belt in Kona, Hawai‘i Island.

A sterile, seedless cultivar of breadfruit was transported to Hawai‘i at least 800 years before present, with the earliest archaeological samples dating to the late 1200s (McCoy et al., 2010). Extensive investigation of archaeological charcoal in fire pits on O‘ahu shows an increase in the use of breadfruit over time, especially in and after the 15th century (Dye and Sholin, 2013). These and other studies suggest a gradual and relatively late development of breadfruit agroforests in Hawai‘i.

Like elsewhere in the Pacific, breadfruit made substantial contributions to food production, security, and resilience in Hawai‘i, along with other carbohydrate sources such as kalo (taro), ‘uala (sweet potato), uhi (yam) and mai‘a (banana/plantain). ‘Ulu was third in importance as a staple behind kalo and ‘uala (Winter et al., 2018). Breadfruit was seasonally abundant, but unlike elsewhere in the Pacific, fermentation and storage of breadfruit in underground pits appears to have been rare, while use as an animal feed appears to have been extensive (Meilleur et al., 2004).

Breadfruit cultivation in Hawai‘i took many forms, including individual trees around households and within the agricultural landscapes, as small groves of trees, as highly managed orchards, and as semi-wild food-forests (Handy et al., 1972; Meilleur et al., 2004). Breadfruit was cultivated most everywhere it was warm enough and wet enough (Mausio et al., 2020). In Hawai‘i, breadfruit is confined to below about 2500 ft (760 m) elevation, and if persisting on rainfall requires ~30 in/y (750 mm/y). Somewhat unique to Hawai‘i, were extensive breadfruit groves that were often named and associated with specific chiefs (Handy et al., 1972; Meilleur et al., 2004), suggesting they were

seen as political capital investments. On Hawai'i Island, explorers in the late 18th century noted the high productivity of tree crops, and the growth of understory crops, in a breadfruit belt termed the kalu'ulu (Kelly, 1983; Lincoln and Ladefoged, 2014).

Breadfruit is associated with prosperity and planning in Hawai'i. The development of tree resources, such as breadfruit, can be seen as investing into the land to develop resources for future prosperity. The seasonal surplus of breadfruit may have powered social dynamics and rituals, such as the emergence of the Makahiki - an extended period where work and certain religious ceremonies were suspended, corresponding to a time of increased recreation and tax collection (Handy et al., 1972; Kirch, 2012). During Makahiki, breadfruit served many ritualistic purposes (Handy et al., 1972) and the occurrence of the festival in October to January corresponds well with the breadfruit season, similar to other Pacific Islands where annual religious and ceremonial occurrences align with the productive periods of breadfruit, yams and other crops (Kirch, 1975). The abundance from 'ulu also has an important place in Hawaiian cosmology, associated primarily with the deity Kū who turned himself into an 'ulu tree to feed his starving wife and children (Handy et al., 1972). Many concepts of Hawaiian traditions and values are captured in a range of 'ōlelo nō'eau (Hawaiian proverbs, sayings or stories) that utilize 'ulu as a metaphor for wealth, success and planning. The reoccurring themes associate breadfruit with values of sharing and hospitality, warnings to be kind to travelers, and making sacrifices for the benefit of others (Beckwith, 1940; Pukui, 1983).

Global Spread

Breadfruit was first described in writing by Pedro Fernández de Quirós, following his expedition to the Marquesas Islands in 1595 (De Quiros, 1904; Hedrick, 1972). However, it was first coined as *breadfruit* by William Dampier in 1686, when he utilized the fruit in Guam and attributed it to saving the lives of his scurvy-ridden crew (Dampier, 1703). Starting in the late 1790's, several expeditions, such as those by Captain William Bligh and the French explorer La Pérouse prioritized transporting breadfruit from the Pacific to other European colonies, particularly in the Caribbean (Leakey, 1977; Leakey and Roberts-Nkrumah, 2016). Throughout the 1800s and 1900s breadfruit was widely distributed to many locations in Central and South America, and various parts of Asia, Australia, and Africa. Of note, the largest distributions of trees have been undertaken since 2009 as part of the Breadfruit Institute's Global Hunger Initiative (Lincoln et al., 2018).

Contemporary Breadfruit Industries in Hawai'i

Breadfruit has seen a dramatic rise in production, growing rapidly from fewer than 500 trees in commercial plantings 25 years ago, to over 8,000 trees today (Langston and Lincoln, 2018). Fresh fruit is typically available in season at farmers markets and some grocery stores. Numerous processed products are made from 'ulu, including baked goods, hummus, chocolate mousse, baby foods, chips, flour, and pickles. At the wholesale level, the fruit is sold as minimally processed (par-steamed and frozen). Although breadfruit is gaining in popularity, most people still only eat breadfruit less than three times per year, and most people access it through friends and family as opposed to commercial markets (Needham and Lincoln, 2019). A negligible amount of breadfruit is currently exported from the state as minimally processed or value-added products. Fresh fruit cannot be exported from Hawai'i to the U.S. mainland due to United State Department of Agriculture restrictions on the movement of fresh fruits, including breadfruit, to prevent introduction of quarantine pests, such as fruit flies. Certified treatment, inspection, and facilities are required for interstate movement (Federal Register Vol. 73, No. 88).

BREADFRUIT DISEASES

History

Traditionally, reports of breadfruit disease appear extremely rare in oral histories and stories. Management of disease in the past was primarily through destroying the tree and burning the area to purify it (Lawrence, 1964; McKenzie, 1964).

In the early 1960s, a disease in breadfruit was first reported and recorded on Pingelap atoll, later to be called the "Pingelap Disease." Ten years later it was widespread in Samoa, French Polynesia, Micronesia, the Marshall Islands, Fiji, and Guam. The disease carried a high mortality rate, and on some islands ~95% of all breadfruit trees died. The alarming losses of breadfruit trees in the Pacific basin spurred a three-year study of breadfruit disease and decline in the Pacific. Trujillo (1971) documented three pathogens: a fruit rot pathogen, a stem rot pathogen, and a leaf pathogen, but ultimately attributed the Pacific-wide decline in breadfruit, not to disease but to "a complex of environmental factors, coupled with minor root pathogens."

Other staggering losses have occurred since, indicating that the Pingelap disease is not an isolated occurrence. Between 1958 and 1987, a serious disease killed all but 46,000 of the estimated two million breadfruit trees in Jamaica (Coates-Beckford and Pereira, 1992). In Kiribati, in 2000, fruit rot from *Colletotrichum gloeosporioides* reduced yields of 'Bukiraro' by 70% (Redfern, 2007). More recently, another breadfruit disease epidemic occurred in the Northern Pacific between 1990 and 2000 causing various symptoms including trunk canker, dieback, fruit rot, and death of trees. Although fungal pathogens were isolated from diseased trees and fruits—including *C. gloeosporioides*, *Diplodia theobromae*, *Fusarium solani* and *Rhizopus* sp.—they were regarded

more as secondary pathogens (Ploetz, 2003). With increased globalization and mobility within breadfruit growing regions, an increasing number of severe diseases have been documented for breadfruit.

Based on previous and recent reports of breadfruit disease, it is clear that the underlying cause of frequent epidemics of breadfruit diseases is lack of management, which is exacerbated during unfavorable environmental conditions (Ploetz, 2003).

Types of Diseases

In general, diseases of breadfruit in Hawai‘i are not rampant and most trees are healthy. However, under the right conditions outbreak can and have occurred. Widespread *Phytophthora* in Waiahole Valley in 2017 killed several trees, caused significant die-back in others, and caused extensive fruit loss throughout the valley for a several year period. Within large plantings, low disease incidence is typical, suggesting the pathogens are present and can flare up should conditions become favorable. We consider breadfruit diseases in three major classes: leaf, fruit, and stem/root diseases. Leaf diseases are the most prevalent and can easily be found at any given time. While leaf diseases are not particularly impactful on tree vitality, we suggest they serve as useful indicators of how well fungal pathogens are controlled in an area. Fruit disease is the second most prevalent, with varying degrees of impact on the fruit quality and usability. Twig and root rot are the least common but also the most impactful, associated with dieback, drastic reductions in productivity, and tree mortality (Redfern, 2010; Lincoln et al., *in prep*). *Colletotrichum* and *Phytophthora* are the most prevalent pathogen on fruit, *Phoma* on leaves, and *Fusarium* and *Lasiodiplodia* in branches. *Phoma* and *Fusarium* are prevalent and demonstrated potential to cause significant impacts; however, *Phytophthora* is considered the most important pathogen.

It is important to note that the pathogenicity for many of the agents presented here have not been fully confirmed for breadfruit. In most cases, the pathogenicity is assumed if (1) a potential causal pathogen has been consistently isolated from the disease symptoms and (2) the potential pathogen is known to cause similar symptoms in other crops. For this publication, pathogens are considered “associated” with the symptoms unless otherwise stated.

Leaf Diseases

Leaf pathogens, considered quite common, contribute to an important group of diseases of breadfruit. We consider leaf diseases in four categories: leaf spots, leaf anthracnose, algal leaf spots, and leaf rust.

<Fig 3a, b, c about here> We categorize leaf diseases as (a) leaf spots, which are typically small, isolated lesions, (b) leaf anthracnose, in which patches of leaf decay can occur, and (c) algal spots and leaf rust, which are often raised protrusions on the leaf.

Leaf Spots

Multiple pathogens have been isolated from leaf spots that vary in size, shape, color, and density. *Corynespora cassiicola* has been shown to cause irregular spots on breadfruit leaves and, less often, stems, roots and flowers in the south Pacific (Dingley et al., 1981; Macfarlane, 1997). The lesions are up to 2 cm in diameter and often have an undulate border, which displays a zonate pattern that darkens with age. Shot holes and defoliation may occur. In Hawai'i, *Alternaria* sp. are associated with small dark-brown lesions with a chlorotic margin. *Fusarium* sp. are associated with larger, more amorphous dark brown spots. *Lasiodiploidia* and *Macrophoma* are both associated with small black spots. *Phoma* sp. have been isolated from very small, dispersed dark-brown spots with rust-colored margins. *Phyllosticta* sp. form small, dark-brown spots. Leaf spots are found on virtually all breadfruit trees in Hawai'i, with varying degrees of severity. However, losses in productivity from these leaf diseases do not appear to be significant.

Leaf Anthracnose

Leaf anthracnose, shown to be caused by *Colletotrichum gloeosporioides* in Hawai'i and elsewhere, may initially resembles other leaf spots but rapidly changes in appearance. This disease can significantly reduce the canopy when infection levels are high. Symptoms usually start as reddish-brown colored spots, that grow to dark-brown spots with reddish-brown margins that expand gradually, eventually forming a gray center with the margins remaining dark brown. The spots increase in number and size as the leaf expands, with larger leaves having more prominent leaf spots than younger leaves, and in bad cases spots can coalesce to cause blighting of young leaves (Trujillo, 1971). Concentric rings of acervuli (fungal growth) may be visible (Gerlach, 1988; Ploetz, 2003). This disease is more severe in areas with high rainfall and with shady conditions. Splashing raindrops effectively spread spores to young leaves and new infections are initiated. Shady conditions provide optimal growth conditions and softer leaves allow multiplication of *Colletotrichum*, resulting in severe infection in shaded fields in contrast to trees grown in full sun. Anthracnose causes premature defoliation, and when severe significantly reduces the canopy of the tree, which decreases fruit production. Leaf anthracnose is uncommon in Hawai'i.

Rust and Algae Spots

Rust and algal leaf spot are common leaf diseases. Rust is caused by *Uredo artocarp* and is characterized by prominent russeting formed by small, irregular leaf spots on both surfaces of the leaf. The spots are composed of uredinia (reddish, swollen plant tissue) and these may be discrete or merge to produce the conspicuous russeting. *Uredo artocarp* has been reported from Hawai'i Island and Puerto Rico (Gardener, 1997; Parrotta, 1994). Algal leaf spot is caused by *Cephaleuros virescens* with the algae forming orange, velvety spots on the upper surface of leaves. This semi-parasitic alga is extremely common in Hawai'i, and it is rare to see a tree in any habitat devoid of the orange spots. Overall, rust and algae, although very common, do not seem to impact the health of the trees and healthy trees show reduced incidence.

Fruit Diseases

Fruit diseases are the best documented category for breadfruit. We further categorize fruit diseases as: fruit spots, fruit anthracnose, soft rot and fruit rot.

<Fig. 4a, b, c, d about here> We categorize fruit as (a) fruit spots, which are typically small, isolated lesions, (b) fruit anthracnose, in which large occur, (c) soft rot, in which the flesh quality deteriorates, and (d) fruit rot, in which the skin and flesh of the fruit is degraded.

Fruit Spots

Various small fruit spots have been reported for breadfruit. Spotting can enlarge and merge to cover much of the fruit. High prevalence of fruit spots can be unsightly but is typically superficial and has no or minimal effect on fruit quality. In Hawai'i, *Fusarium* is most often isolated from fruit spots that are light brown. Spots start as small, isolated spots that can grow quickly to merge and cause solid brown discoloration. *Phoma* spp. are also commonly isolated from the fruit spots, forming darker brown, almost black spots that tend to remain separated from each other. Neither has been confirmed as the casual pathogen. Fruit spotting is generally not problematic, but excessive spotting is unsightly and heavy infestations can impact fruit quality.

Fruit Anthracnose

Fruit anthracnose known to be caused by *Colletotrichum gloeosporioides*, with the sexual stage or teleomorph, *Glomerella cingulata* (Ploetz, 2003). Symptoms of fruit anthracnose are large dark-brown spots that develop on the epidermal layer and expand gradually to form larger lesions. The flesh typically hardens around the lesion, often causing deformation of the fruit, although this hardening may be the result of secondary pathogens moving in. On immature breadfruit, anthracnose may develop in association with injuries that are caused by insects (Trujillo, 1971; Ploetz, 2003). In 2002, this disease caused approximately 70% reduction in yields in Kiribati (Redfern, 2007). This disease symptoms and isolation of *Colletotrichum* is common and widespread in Hawai'i. In most orchards, at any given time a fruit with anthracnose symptoms can typically be found, although the prevalence is variably expressed from year to year, ranging from sporadic to common. Although *Colletotrichum* is most visibly and commonly associated with fruit anthracnose, various species of *Colletotrichum* have also been associated with leaf spots, leaf anthracnose, and stem rot (Zakaria, 2021). It has been suggested that *C. acutatum* may cause premature fruit fall of breadfruit, but this is unconfirmed (McKenzie and Jackson, 1990). *Colletotrichum* is spread by water, rain and wind, and high relative humidity and temperature encourage disease development.

Soft Rot

In Hawai'i, *Rhizopus* is associated with a soft, watery rot of mature fruit. It can be severe on ripening fruit on the tree and is also considered a post-harvest disease that develops on wounds

during storage or shipment (Trujillo, 1971). *Geotrichum* is also associated with soft rot in Hawai'i. Symptoms often include small external lesions that soften and can cause rapid internal rot of the breadfruit flesh. *Lasiodiplodia* was isolated from internal soft rot that demonstrated little or no external symptoms and appeared to emanate from the fruit core. Other pathogens have been reported on necrotic, rotted fruit or premature fruits. These include a *Phomopsis* sp., which was recovered from necrotic epidermal fruit spines, a *Sclerotium* sp. from rotten fruit on the ground, and *G. acutata*, associated with premature fruit fall (Ploetz, 2003; Brooks, 2006). No pathogenicity studies have been conducted with these pathogens. Soft rot is not common in Hawai'i, but a handful of symptomatic fruit are invariably seen each year. Soft rot appears to most often originate from the core of the fruit.

Fruit Rot

Fruit rot is attributed to *Phytophthora palmivora* and *P. tropicalis* in studies from Hawai'i and elsewhere. Symptoms include the development of small lesions on the fruit which grow in size until the infection consumes the fruit. The advancing front of infection has a characteristic white band that forms a ring around the entire lesion. Symptoms are most often observed under wet and humid conditions as well as areas with poor soil drainage. Rotted fruit tissue falls to the soil where the infection cycle is renewed. Multiple pathogenicity tests confirm the virulence (Trujillo, 1970; Gerlach and Salevao, 1984; Redfern, 2010). The pathogen takes 2-3 days for the first visible symptoms to occur after infection. Fruits from varieties with rough skin were more susceptible than fruits from smooth-skinned varieties. 'Puou' was found as the most susceptible cultivar in the field, whereas 'Aveloloa', 'Ma'afala', 'Maopo' and 'Ulua' cultivars were more resistant. In a recent study in Hawai'i, the susceptibility of 'Puou' was confirmed, along with 'Fiti' while 'Otea' and 'Ma'afala' were more resistant. Maturity of fruits was found to affect susceptibility, with very young fruits being largely immune, intermediate fruits were slightly resistant, and mature green fruits were highly susceptible. *Phytophthora palmivora* has been documented to grow best at temperatures ranging from 28-32°C (Rao, 1970). Severe cases of *Phytophthora* fruit rot can lead to branch dieback, defoliation, and tree death.

Stem and Root Diseases

Stem and root diseases can cause severe damage and death to trees. We consider three categories: seedling dieback, crown and root rot, and stem rot.

<Fig. 5a, b, c about here> *Stem and root diseases are moderately common in Hawai'i, most often associated with (a) branch weakening, tapering or die back, (b) internal rot, and (c) overall decline in tree growth and health.*

Seedling Dieback

Seedling blight associated with *Sclerotium rolfsii* and loss of seedlings and young trees caused by *Rosellinia* sp. have been reported from Puerto Rico (Parrotta, 1994) and Trinidad (Morton, 1987); however, no symptomology or progression of these diseases were described. Dieback is generally characterized by wilting, yellowing, and necrosis of the leaves, premature defoliation and branch dieback (Trujillo, 1971). Such dieback has been witnessed in Hawai'i, usually associated with multiple, simultaneous stressors to the trees.

Crown and Root Rot

Brown root rot disease, one of the most serious breadfruit diseases in the Pacific and Southeast Asia, is caused by a basidiomycete fungus, *Phellinus noxius*, causing tree decline and death (McKenzie, 1996). The fungus is well known as a major disease of timber trees and its introduction to the Pacific region is believed to have been through infected timber that was imported to the islands (E. Trujillo, pers. comm.). The name brown root rot refers to a brown to black mycelial crust formed by the fungus on the surface of infected roots and stem bases (Chang and Yang, 1998). Trees were considered infected by *P. noxius* if two or more of the following signs were present. On most trees, thick mycelial crust enveloped infected roots and the base of the stem up to 2 m (Bolland, 1984; Hodges and Tenorio, 1984; Ivory, 1990). *Phellinus noxius* infects the base of the tree and moves to the root and may persist in roots and stumps of infected plants for more than 10 years after death of the host (Chang, 1996). As roots become infected, symptoms of wilting, yellowing and necrosis of leaves occur. Branch dieback and tree death will eventually result (Trujillo, 1971; Gerlach, 1988). Fine mats of mycelium present between infected bark and sapwood and underlying colonized heartwood eventually became white, spongy, dry, and honeycombed with reddish-brown or dark lines (Singh et al., 1980). The disease develops most rapidly during the hot, rainy season and is spread by root contact and not by basidiospores. This devastating disease has not yet been reported in Hawai'i.

Another causal agent reported to cause collar rot is *Lasiodiplodia theobromae* (*Botryodiplodia theobromae*) which has been reported from the islands of Wallis and Futuna (Kohler et al., 1997). The collar and trunk have dry rot symptoms which are associated with external white strands of the fungus. The wood beneath the bark has white patches with dark-brown margins. Pathogenicity tests are needed. Trunk canker is characterized by sunken, brown and dry rot areas on the bark with the infection expanding 2 - 3 cm deep into the wood.

Root pathogens recovered from diseased and dying trees include *Rhizoctonia solani*, which is consistently associated with feeder root dieback, and *Pythium* sp., associated with brown rot of lateral roots (Trujillo, 1971). *Fomes* sp. causes death of breadfruit trees and was reported from Ebon Island in the Southern Marshall Islands and Brazil (Trujillo, 1971; Parrotta, 1994). This pathogen rots larger roots and causes a soft heart rot of the tree (Trujillo, 1971). *Polyporus zonalis* is a pathogen identified in Brazil associated with heart rot (Parrotta, 1994).

Stem Rot

Small branches and stems may be infected, leading to dieback of branches. Such infections are often associated with *Fusarium* spp. In general, the *Fusarium* family invades the vascular system of its host and proceeds to disrupt the translocation of water and nutrients, leading to symptoms such as browning and the development of head blight. Internal twigs will have black or dark-brown streaks, and the twig surface may deform or crack. In Hawai'i, *Fusarium* was consistently isolated from a number of branches with declining health. *Phoma* sp. have also been isolated from twig rot, with light brown/reddish streaks. Anthracnose, severe twig disease and defoliation can develop on breadfruit, but causal agents are unknown (Abraham et al., 1988). Bacterial dieback, caused by *Erwinia carotovora*, has been recorded on chempedak (Agrolink, 1999), where it causes leaf yellowing and gummy exudate from stems and branches.

Disease Management

For most of the pathogens identified for breadfruit, it is not possible to entirely eradicate diseases, but using an integrated pathogen management approach, the impacts can be minimized. Once established, the disease agents continue to cycle through crops until the infection cycle is broken. Here we summarize a range of best-practices that can help to mitigate diseases in general, in addition to specific treatments for individual pathogens.

General Hygiene

Crops need to grow in areas with proper drainage. An abundance of moisture increases the risk of *Phytophthora* epidemics. Clean water sources are needed, while avoiding irrigation that wets the trunk or leaves. Any plants with severe disease should be destroyed and removed from the site or sterilized, typically through burning. Caution should be taken with plants which neighbor the sick plant, and preemptive measures taken. All material brought to the site should be as clean as possible, particular if bringing in organic material. In particular, importing foreign plant material may introduce new pathogens to a region, and all appropriate bio-security laws must be followed. Adhering to phytosanitary practices when visiting or having visitors can reduce local transmission of diseases. Sterilization of equipment and tools can help prevent the spread of disease. Treatments with flame heat, 70% alcohol, or freshly prepared 10% bleach are all effective at eliminating most pathogens (Rutala and Weber, 2008).

Trees should have good airflow and not be in excessively shaded areas. The area should be well drained without excessive moisture. Orchards should be regularly monitored for diseases with appropriate responses taken. Often, the lowest fruits on a tree are infected first and the topmost last, likely due to increased moisture and poor airflow in the lower canopy (Gerlach and Salevaio, 1984). At harvest, fruit should not come in contact with soil. Any adhering organic debris should be cleaned from fruit prior to packing. Skin damage and the use of dirty wash water should be avoided. Fruit should not be packed with organic materials such as plant leaves, coconut fibre or

wood shavings as these materials can damage the skin and allow infection to spread directly from the organic materials into fruit (R. Paull pers. comm.)

Cultivars

Cultivars have exhibited varying degrees of susceptibility for each disease, although few systematic studies have been conducted. Early documentation of *Phytophthora palmivora* in Western Samoa showed that only ‘Puou’ was susceptible (Gerlach and Saleva, 1984) and that, in general, fruits with rough skin are more susceptible than smooth-skinned cultivars (Trujillo, 1971). In Pohnpei, Federated States of Micronesia, rough-skinned cultivars were reportedly more susceptible than smooth-skinned types, however, one smooth-skinned cultivar became more susceptible as the season progressed (Frownes and Raynor, 1993). In Hawai’i, the smooth-skinned variety ‘Fiti’ and rougher ‘Puou’ were both highly susceptible, with ‘Otea’ and ‘Ma‘afala’ were more resistant. Dieback associated with the Pingelap disease showed that susceptible cultivars such as ‘Bukrol’ often died, while hybrid cultivars (*A. altilis* x *A. marianensis*) normally recovered (Trujillo, 1971).

<Fig. 6 about here> *Different breadfruit varieties, pictured here along with Artocarpus camansi and A. odoratissima, exhibit a range of skin textures that is associated with more or less susceptibility to Phytophthora and other diseases.*

Pruning and Removal of Infected Material

Pruning diseased parts to remove inoculum reduces the incidence and severity of a number of diseases including anthracnose and *Phytophthora*. Opening the canopy increases ventilation and reduces humidity, reducing the habitat for many fungal and bacterial pathogens. Painting pruning wounds with proprietary wound sealants, *Trichoderma* preparations or house paint may also reduce risk of infection, although opinions on this approach differ with many arborists suggesting painting is unnecessary or even potentially harmful. Removal and destruction of diseased fruit from trees and the ground reduces the risk and severity of outbreaks. Occasionally, trees can be cured if diseased parts are removed immediately after symptoms appear. Even for the brown root rot disease, tree-to-tree spread has been prevented by removing diseased trees and roots more than 1 inch (Kohler et al., 1997). Removal and burning of infected trees and other debris may also reduce disease spread and help to sterilize the soil (J. Friday, pers. comm.).

Groundcover

The use of vegetative ground cover, especially nitrogen-fixing species has been somewhat successful in reducing incidence of *Fusarium* by about 20% (Pattison et al., 2014). It was also suggested that the use of leaf litter mulch might have decreased the chances of *Phytophthora* infection, as it promoted parasitism of the pathogen as well as acting as a rain splash barrier

(Konam and Guest, 2002). Planting herbaceous crops with vigorous roots, such as grasses, will increase the breakdown of woody debris in the soil that may harbor the fungus.

Soil and Water Management

Maintaining healthy soil and water can reduce the incidence of many pathogens. Maintaining soil nutrition ensures that the trees are well fed and can more effectively fend off opportunistic diseases. A clean water source reduces introduction of potential pathogens. A healthy soil supports diverse microbial communities, including species that prey on plant pathogens. In particular, maintaining high soil organic matter can help to promote the physical and chemical environments of a healthy biome and reduce pathogen outbreaks (Larkin, 2015). Physical management of the soil, such as appropriate aeration and maintaining good drainage, can reduce prevalence of many fungal pathogens.

Physical Management

Few physical management practices for breadfruit have been employed. Other than pruning infected areas, some stem cankers are scraped to expose the lesions and dry them out. The exposed lesions could also be painted with a fungicide to prevent further spread of infection. Bagging of fruit is a practice of using bags to cover or protect fruits from pests and diseases, and is widely utilized in southeast Asia, including on breadfruit (R. Paull, pers. comm.). When multiple fruit are clustered together it is recommended that the other fruit should be removed to avoid fruit skin damage and allow less competition for nutrients. Fruit thinning is associated with reduced spread of some diseases (Ingels, 2001).

Biological Management

Bio-fertilizers including *Bacillus* or *Trichoderma* have been shown to reduce the incidence of *Fusarium* diseases. While researchers did not believe that *Bacillus* or *Trichoderma* were directly responsible for the reduction of disease, it was believed that the presence of one of these organisms stimulated a healthier soil microbiome (Xiong et al., 2017). The application of plant extracts on bananas tested with *Colletotrichum musae* has also shown progress in reducing disease symptoms as well as extending its shelf life (Bazie et al., 2014). Several plant extracts proved effective in pathogen inhibition, such as *Solanum torvum*, *Jatropha curcas*, and *Embllica officinalis*. Of these extracts, *S. torvum* was the most effective and was able to completely arrest the development of mycelial masses (Torres et al., 2016). In American Samoa, it is believed a member of the lily family, lau talo talo (*Crinum* sp.), planted next to a tree will protect it from *Phellinus noxius* (Brooks, 2001), but this has not been tested objectively. The application of neem cake fertilizer after the main harvest season is another practice that has been suggested to be effective (N. Dickinson, pers. comm.).

Chemical Management

Strategic sprays with mancozeb can reduce losses of anthracnose (Sirayoi, 1993). The application of copper fungicides or dithiocarbamates to flowers and young fruit have reduced losses from *Phytophthora* in jackfruit and breadfruit (Almeida and de Landim, 1980; Singh and Singh, 1989). The use of potassium phosphonate fungicide showed increased defense responses of crops against *P. palmivora* infection, and some farmers advocate for the application of phosphoric acid as a foliar spray. These heightened defenses fought against invasive sporangia (Daniel et al., 2005). The biopesticide *Tetramycin* was also shown to inhibit *P. capsici* invasion by reducing mycelial growth and sporulation (Ma et al., 2018). The use of *Trichoderma martiale* strain ALF 247 proved to be an effective biological control agent of *P. palmivora*. Cacao plants treated with this biological control showed a reduction in symptoms of blackpod disease (Hanada et al., 2009). For best results, ALF 247 was applied in combination with copper-based fungicides. *Colletotrichum gloeosporioides* was documented as being highly sensitive to the application of benomyl. However, caution should be exercised when using benomyl as other species of *Colletotrichum*, including *C. acutatum*, were only somewhat sensitive to this treatment (Freeman et al., 1998). This means that if benomyl was used when multiple *Colletotrichum* species were present, a shift to benomyl resistant species of *Colletotrichum* could occur (Uchida and Kadooka, 1997). It should be noted that it is important to monitor pathogen sensitivity to applications as the development of resistance is possible. It has been recommended that if growers do choose to use fungicides, they should be used solely as a preventative measure and not as a cure. In addition, the label is the law. Read and follow product labels for all pesticides.

Holistic approach

For general best practices, it is best to have a holistic approach to control or reduce fungal issues. A holistic approach would mean good management by improving moisture management, pruning and good spacing, good airflow through canopy, having ground cover, good hygiene, and good tree nutrition first and foremost, with application of more detailed methods if needed.

<picture of healthy orchard about here>

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REFERENCES

- Abraham, M., Padmakumary, G. and Nair, M.C. (1988). Twig blight (die-back) of *Artocarpus incisa*. Indian Phytopathology 41, 629–630.
- Agrolink (1999). Department of Agriculture Malaysia website:
http://agrolink.moa.my/doa/english/croptech/che_pes.html
- Almeida, R.T. and de Landim, C.M.U. (1980). *Rhizopus stolonifer* (Ehrenb. ex Fr.) Vuill., causal agent of soft rot of jackfruit (*Artocarpus heterophyllus* Lam.) and breadfruit (*Artocarpus altilis* Fosberg) in Ceara State. Fitossanidade 4, 23–24.
- Bazie, S., Ayalew, A. and Woldetsadik, K. (2014). Integrated management of postharvest banana anthracnose (*Colletotrichum musae*) through plant extracts and hot water treatment. Crop Protection 66: 14-18. ISSN 0261-2194, <https://doi.org/10.1016/j.cropro.2014.08.011>
- Beckwith, M.W. Hawaiian Mythology; University of Hawai'i Press: Honolulu. (1940). Sustainability 2018, 10, 3965
- Bolland, L. (1984). *Phellinus noxius*: cause of a significant root-rot in Queensland hoop pine plantations. Australian Forestry 47(1): 2-10.
- Brooks, F. (2006). List of Plant Diseases in American Samoa. Land Grant Technical Report No. 44, American Samoa Community College, Pago Pago.
- Chang, T. T. (1996). Survival of *Phellinus noxius* in soil and in the roots of dead host plants. Phytopathology 86: 272-276.
- Chang, T. T., and Yang, W. W. (1998). *Phellinus noxius* in Taiwan: distribution, host plants and the pH and texture of the rhizosphere soils of infected hosts. Mycological Research 102(9): 1085-1088.
- Coates-Beckford, P.L., and M.J. Pereira. (1992). Survey of root-inhabiting microorganisms on declining and non-declining breadfruit (*Artocarpus altilis*) in Jamaica. Nematropica 22(1):55–63.
- Dampier, W. (1703). A New Voyage Round the World. Vol. I, 5th ed., corr. Printed for James Knapton, London.
- Daniel, R., & Guest, D. (2005). Defence responses induced by potassium phosphonate in *Phytophthora palmivora*-challenged *Arabidopsis thaliana*. Physiological and Molecular Plant Pathology, 67(3-5), 194-201.
doi:10.1016/j.pmpp.2006.01.003
- De Quiros, P.F. (1904). The Voyages of Pedro Fernandez de Quiros, 1595 to 1606. Vol. I. (trans. and ed. Sir Clements Markham). Hakluyt Society, London.
- Dickinson, N. Personal communication. Mar 1, 2021.
- Dingley, J.M., Fullerton, R.A. and McKenzie, E.H.C. (1981). Records of Fungi, Bacteria, Algae, and Angiosperms Pathogenic on Plants in Cook Islands, Fiji, Kiribati, Niue, Tonga, Tuvalu, and Western Samoa. South Pacific Commission, Noumea, New Caledonia.
- Dye, T. S., and Sholin, C. E. (2013). Changing patterns of firewood use on the Waimānalo Plain. *Hawaiian Archaeology*, 13, 30-68.
- FAO. International Treaty on Plant Genetic Resources for Food and Agriculture. (2019). Available online: <http://www.fao.org/3/a-i0510e.pdf> (accessed on 12 June 2019).
- Interstate Movement of Fruit From Hawaii. (2008). 24852 Federal Register (73): 88. Rules and Regulations.
- Fownes, J.H., and W.C. Raynor. (1993). Seasonality and yield of breadfruit cultivars in the indigenous agroforestry system of Pohnpei, Federated States of Micronesia. Trop. Agric. (London then Trinidad) 70:103–103.
- Freeman, S., Katan, T., and Shabi, E. (1998). Characterization of *Colletotrichum* Species Responsible for Anthracnose Diseases of Various Fruits. Plant Disease, 82(6), 596–605. doi: 10.1094/pdis.1998.82.6.596
- Friday, J.B. Personal communication. Feb 4, 2021.
- Gardener, D.E. (1997). Additions to the rust fungi of Hawaii. Pacific Science 51:174-182.
- Gerlach, W.W.P. (1988), Plant Diseases of Western Samoa, Samoan German Crop Protection Project, Apia.

- Gerlach, W.W.P. and Salevao F. (1984). Fruti rot of breadfruit, *Artocarpus altilis*, caused by *Phytophthora palmivora* in Western Samoa. *Alafua Agricultural Bulletin* 9:21-27.
- Hanada, R. E., Pomella, A. W., Soberanis, W., Loguercio, L. L., and Pereira, J. O. (2009). Biocontrol potential of *Trichoderma martiale* against the black-pod disease (*Phytophthora palmivora*) of cacao. *Biological Control*, 50(2), 143-149. doi:10.1016/j.biocontrol.2009.04.005
- Handy, E.S.C., E.G. Handy, and M.K. Pukui. (1972). *Native Planters in Old Hawaii: Their Life, Lore, and Environment*. Bishop Museum Press, Honolulu, HI.
- Hedrick, U.P. (ed.). (1972). *Sturtevant's Edible Plants of the World*. Dover Pubs, Inc. New York.
- Hodges, C.S., and J.A. Tenorio. (1984). Root disease of *Delonix regia* and associated tree species in the Mariana Islands caused by *Phellinus noxius*. *Plant Dis.* 68(4):334–335.
- Ingels, C. (2001). *Fruit trees: Thinning Young Fruit*. University of California, Division of Agriculture and Natural Resources.
- Ivory, M. H. (1990). Brown root-rot of tropical forest trees in the South-West Pacific region. In C. Hutacharn, K. G. MacDicken, M. H. Ivory, and K. S. S. Nair (Eds.). *Proceedings of the IUFRO Workshop on Pests and Diseases of Forest Plantations*, pp. 100-106. Food and Agricultural Organization of the United Nations, Bangkok, Thailand.
- Kelly, M. (1983). *Na Mala o Kona: Gardens of Kona*. Department of Anthropology Report, 83-2. Bernice P. Bishop Museum, Honolulu.
- Kirch, P.V. (1975). *Cultural Adaptations and Ecology in Western Polynesia: An Ethnoarchaeological Study*. Doctoral Dissertation, Yale University, Department of Archaeology.
- Kirch, P.V. (2012). *A Shark Going Inland is My Chief: The Island Civilization of Ancient Hawaii*. Berkeley: University of California Press, <https://doi.org/10.1525/9780520953833>
- Kohler, F., Pellegrin, F., Jackson, G., and McKenzie, E. (1997). *Diseases of cultivated crops in Pacific Island Countries*. South Pacific Commission, Noumea, New Caledonia.
- Konam, J.K., and Guest, D.I. (2002). Leaf litter mulch reduces the survival of *Phytophthora palmivora* under cocoa trees in Papua New Guinea. *Australia Plant Pathology* 31: 381-383. <https://doi.org/10.1071/AP02043>
- Langston, B. J., and Lincoln, N. K. (2018). The role of breadfruit in biocultural restoration and sustainability in Hawai'i. *Sustainability*, 10(11), 3965.
- Larkin, R.P. (2015). *Soil Health Paradigms and Implications for Disease Management*. *Annual Review of Phytopathology* 52 (1): 199-221. 10.1146/annurev-phyto-080614-120357
- Lawrence, P. (1964). Breadfruit cultivation practices and beliefs in Ponape. p. 43–64. In: *Breadfruit Cultivation Practices and Beliefs in the Trust Territory of the Pacific Islands*. Anthropological Working Papers No. 7–8 (Revised). Trust Territory Pacific Islands, Saipan.
- Leakey, C.L.A. (1977). *Breadfruit reconnaissance study in the Caribbean region*. C.I.A.T./ Inter-American Development Bank.
- Leakey, C., and L. Roberts-Nkrumah. (2016). The introduction of the breadfruit (*Artocarpus altilis*) to the Caribbean – the role of Sir Joseph Banks. In: 49th Annual Meeting, 30 June–6 July 2013, St. Thomas, US Virgin Islands. No. 253501. Caribbean Food Crops Society, Mayagüez, Puerto Rico.
- Lincoln, N.K. and T.N. Ladefoged. (2014). Agroecology of pre-contact Hawaiian dryland farming: The spatial extent, yield and social impact of Hawaiian breadfruit groves in Kona, Hawai'i. *J. Archeological Sci.* 49:192–202.
- Lincoln, N.K., D. Ragone, N. Zerega, L.B. Roberts-Nkrumah, M. Merlin, and A.M. Jones. (2018). Grow us our daily bread: A review of breadfruit cultivation in traditional and contemporary systems. *Hort. Rev.* 46:299–384.
- Lincoln, N. and Uchida, J. (in prep). Fungal pathogen prevalence and expressed resistance in breadfruit (*Artocarpus altilis*) cultivars?
- Lucas, M.P. and D. Ragone. (2012). Will breadfruit solve the world hunger crisis? New developments in an innovative food crop. *ArcNews Summer*: 6–7.

- Ma, D., Zhu, J., He, L., Cui, K., Mu, W., and Liu, F. (2018). Baseline Sensitivity and Control Efficacy of Tetramycin Against *Phytophthora capsici* Isolates in China. *Plant Disease*, 102(5), 863-868. doi:10.1094/pdis-09-17-1396-re
- Macfarlane, R. (1997). *Corynespora cassiicola*. Global Plant Protection Information System, FAO, Rome.
- MacMillan, H.F. (1908). Breadfruits of the tropics. *Trop. Agric. (Ceylon)* 31:428-429.
- Mausio, K., Miura, T., and Lincoln, N. K. (2020). Cultivation potential projections of breadfruit (*Artocarpus altilis*) under climate change scenarios using an empirically validated suitability model calibrated in Hawai'i. *PloS one*, 15(5), e0228552.
- McCoy, M.D., M.W. Graves, and G. Murakami. (2010). Introduction of breadfruit (*Artocarpus altilis*) to the Hawai'ian Islands. *Econ. Bot.* 64:374-381.
- Mckenzie, J.B. (1964). Breadfruit cultivation practices and beliefs in the Trust Territory of the Pacific Islands. p. 43-64. In: B. MacKenzie, R.K. McKnight, and P. Lawrence (eds.), *Anthropological Working Papers 7-8* (revised). Saipan.
- McKenzie, E.H.C. (1996). Fungi, Bacteria and Pathogenic Algae on Plants in American Samoa. South Pacific Commission, Noumea, New Caledonia.
- McKenzie, E.H.C. and Jackson, G.V.H. (1990). The fungi, bacteria and pathogenic algae of the Federated States of Micronesia. SPC Technical Paper 199.
- Meilleur, B.A., Jones, R.R., Titchenal, C.A., and Huang, A.S. (2004). Hawaiian Breadfruit: Ethnobotany, Nutrition, and Human Ecology, CTAHR, University of Hawaii Press, Honolulu.
- Morton, J. (1987). Breadfruit. in *Fruits of Warm Climates*.
- Murai, M., Pen, F. and Miller, C.D. (1958). *Some Tropical South Pacific Island Foods: Description, History, Use, Composition and Nutritive Value*. University of Hawaii Press, Honolulu.
- Needham, A., and Lincoln, N. (2019). Interactions between People and Breadfruit in Hawai'i: Consumption, Preparation, and Sourcing Patterns. *Sustainability*, 11(18), 4983.
- Parrotta, J.A. (1994). *Artocarpus altilis* (S. Park.) Fosb.: Breadfruit, Breadnut. SO-ITF-SM-71. Department of Agriculture, Forest Service, Southern Forest Experimental Station, New Orleans, LA.
- Pattison, A., Wright, C. and Kukulies, T. (2014). Ground cover management alters development of Fusarium wilt symptoms in Ducasse bananas. *Australasian Plant Pathology* 43: 465-476. <https://doi.org/10.1007/s13313-014-0296-5>
- Paull, R.E. Personal communication. Feb. 26, 2021.
- Ploetz, R.C. (2003). *Diseases of tropical fruit crops*, CABI, Wallingford, Oxon, UK.
- Pukui, M.K. (1983). *'Olelo No'ēau: Hawaiian Proverbs and Poetical Sayings (71)*. Bishop Museum Press: Honolulu, HI, USA.
- Ragone, D. (1997). Promoting the conservation and use of underutilized and neglected crops. Breadfruit *Artocarpus altilis* (Parkinson) Fosberg. International Plant Genetic Resources Institute. Rome.
- Ragone, D. (2001). Chromosome numbers and pollen stainability of three species of Pacific Island breadfruit (*Artocarpus*, Moraceae). *Am. J. Bot.* 88(4):693-696.
- Ragone, D. and Wiseman, J. (2007). Developing and applying descriptors for breadfruit germplasm. *Acta Hort.* 757:71-80.
- Rao, V.G. (1970). Influence of temperature upon growth and sporulation in two species of *Phytophthora*. *Mycopathologia et Mycologia Applicata* 42: 39-48. <https://doi.org/10.1007/BF02051824>
- Redfern, T. (2007). Breadfruit improvement activities in Kiribati. *Acta Hort.* 757:93-100.
- Redfern, T. (2010). Etiological study of breadfruit diseases in Hawai'i. Master's thesis, Department of Plant and Environmental Protection Science, University of Hawaii at Manoa, Honolulu, HI.
- Rutala, W.A., and Weber, D.J. (2008). Guideline for Disinfection and Sterilization in Healthcare Facilities. <https://www.cdc.gov/infectioncontrol/guidelines/disinfection/>
- Singh S., Bola I., and Kumar J. (1980). Diseases of plantation trees in Fiji Islands: 1. Brown root rot of mahogany (*Swietenia macrophylla* King). *Indian Forester*: 526-533.

- Singh, N.I. and Singh, K.U. (1989). Efficacy of certain fungicides against Rhizopus rot of jackfruit. *Indian Phytopathology* 42, 465–466.
- Sirayoi, A. (1993). *Diseases of Fruit Crops, Spices and Control*. Takansak Foundation, Kasetsart University.
- Torres, G. A., Sarria, G. A., Martinez, G., Varon, F., Drenth, A., and Guest, D. I. (2016). Bud Rot Caused by *Phytophthora palmivora*: A Destructive Emerging Disease of Oil Palm. *Phytopathology*, 106(4), 320-329. doi:10.1094/phyto-09-15-0243-rvw
- Trujillo, E.E. (1971). *The breadfruit diseases of the Pacific basin*. South Pacific Commission, Noumea.
- Trujillo, E.E. Personal communication. Oct 22, 2010.
- Uchida, J. Y., and Kadooka, C. Y. (1997). *Colletotrichum Leaf Spot of Red Sealing Wax Palm*. CTAHR, 1-4. Retrieved July 29, 2020.
- Wilder, G.P. (1928). *The Breadfruit of Tahiti*. Bulletin 50. Bernice P. Bishop Museum, Honolulu.
- Winter, K. B., Lincoln, N. K., and Berkes, F. (2018). The Social-Ecological Keystone Concept: A quantifiable metaphor for understanding the structure, function, and resilience of a biocultural system. *Sustainability*, 10(9), 3294.
- Xing, X., A.M. Koch, A.M.P. Jones, D. Ragone, S. Murch, and M.M. Hart. (2012). Mutualism breakdown in breadfruit domestication. *Proc. R. Soc. Lond. B. Biol. Sci.* 279(1731):1122–1130.
- Xiong, W., Guo, S., Jousset, A., Zhao, Q., Wu, H., Li, R., ... Shen, Q. (2017). Bio-fertilizer application induces soil suppressiveness against *Fusarium* wilt disease by reshaping the soil microbiome. *Soil Biology and Biochemistry*, 114, 238–247. doi: 10.1016/j.soilbio.2017.07.016
- Zakaria, L. (2021). Diveristy of *Colletotrichum* Species Associated with Anthracnose Disease in Tropical Fruit Crops – A Review. *Agriculture* 11(4), 297; <https://doi.org/10.3390/agriculture11040297>
- Zerega, N.J.C., D. Ragone, and T.J. Motley. (2004). Complex origins of breadfruit (*Artocarpus altilis*, Moraceae): implications for human migrations in Oceania. *Am. J. Bot.* 91:760–766.
- Zerega, N.J.C., Ragone, D. and Motley, T.J. (2005). Systematics and species limits of breadfruit (*Artocarpus*, Moraceae). *Systematic Botany* 30:603-606.
- Zerega, N., D. Ragone, and T.J. Motley. (2006). Breadfruit origins, diversity and human facilitated distribution. p. 213–238. In: T.J. Motley, N. Zerega, and H. Cross, (eds.), *Darwin’s Harvest: New Approaches to the Origins, Evolution, and Conservation of Crops*. Columbia University Press, New York.