The Papaya in Hawai'i

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Abstract. Dioecious papayas were introduced shortly after Cook's 1778 discovery of Hawai'i but were supplanted for commercial uses by the gynodioecious solo papaya brought from the Caribbean in 1911. Growth of a local papaya industry based on hermaphrodite plants was enabled by research allowing prediction of seedling sex segregation and by development of cultivars with high quality, symmetrical fruits free of stamen carpelody, and carpel abortion. The industry expanded into export markets after 1940 by providing an alternative use for land and expertise abandoned by declining sugar plantations, adopting a cultivar capable of tolerating long-distance shipping, developing postharvest technology to overcome fruit fly quarantine restrictions, capitalizing on a growing tourism industry for marketing and air freight logistics, and forming an organization to support industry growth. In recent years, the industry has withstood pest and disease challenges by adopting innovative technologies that have allowed high-quality solo papayas to continue to participate in an increasingly competitive export market.

The papaya (*Carica papaya*) is a member of the Caricaceae, which consists of five New World genera and one African genus. In 2000, the genus *Carica* was split to better reflect molecular and morphological differences between a group of ≈21 predominantly South American species, now assigned to genus *Vasconcellea*, and the single remaining *Carica* species, *C. papaya*, which has a native range restricted to Central America (Badillo, 2000, 2001). Although there is at least one Peruvian archaeological ceramic pot from ≈300 CE (Common Era) that is said to resemble (not very convincingly) a papaya fruit (Wikimedia Commons, 2009), the homeland of the typical wild papaya is limited to the region extending from southern Mexico to perhaps as far south as northern Costa Rica (Manshardt and Zee, 1994). Wild papayas are dioecious, and the fruits borne on pistillate plants are small (less than 100 g) and seedy with very little edible flesh. Human selection for self-pollinating hermaphrodite mutations and larger fruit size has produced gynodioecious cultivars and genotypes that yield succulent fleshy fruits weighing as much as several kilograms. Fruit quality varies considerably within the species, and many genotypes have fruits with low total soluble solids (TSS) and/or objectionable flavor or texture. However, all papayas are predisposed to travel, because they are derived from opportunistic wild types that are pioneer species in disturbed habitats (Bartlett, 1937; Lundell, 1936). Characteristics that have facilitated the rapid movement of papaya around the tropical regions of the world include their

continuous bearing habit, the attractive and abundant fruits, and plentiful seeds of long viability.

EARLY HISTORY IN HAWAII

Arrival and characteristics. Papaya is a relatively recent introduction in Hawai'i. Its arrival is usually dated at ≈1820 and attributed to Don Francisco de Paula Marin, the Spanish adventurer turned horticulturist who was given land on O'ahu in payment for services rendered to Kamehameha I. However, many crop introductions connected with this legendary figure are poorly documented. For 250 years (1550–1800) before Don Marin's activities, the Spanish court had operated a lucrative trade route between Acapulco, Mexico, and Manila in the Philippines (Hayes, 2001). Although there is no record of contact with Hawai'i during that period, legends of visitors arriving in Hawai'i in large boats before Captain Cook (1778) suggest that there may have been opportunity for earlier introductions (Kāne, 1996). Regardless of which Spaniard made the initial introduction, the first papayas were probably large-fruited dioecious types from the west coast of Mexico. These are the types commonly illustrated in Hawaiian publications from the early 1900s, among which was the important bulletin entitled "The Papaya in Hawai'i," authored by J. Edgar Higgins and Valentine Holt, horticulturists at the Hawai'i Agricultural Experiment Station (HAES) in Honolulu in 1914. They noted that dioecious papayas were more common than gynodioecious and that there were no real papaya cultivars in Hawai'i in the sense that seed could not be depended on to yield plants with predictable characteristics.

The prevailing notion at that time in Hawai'i was that papaya fruits were fit only for hog feed (Crawford, 1937), but there existed sufficient demand for the fruit on the U.S. mainland to merit investigation of export potential. Higgins and Holt described successful shipping experiments of color-break fruit under refrigeration to Portland, Seattle, and Vancouver and indicated that the

long cylindrical shape of the hermaphrodite fruits was better for packing in single-tier wooden crates than the more spherical fruit shape of pistillate plants. Interestingly, even at this early stage of export development, shipments to California were restricted as a result of Mediterranean fruit fly quarantine! Fields planted with gynodioecious lines were also noted to be more productive than those planted with dioecious lines, because nearly every tree produced fruit as a result of the absence of male plants. Consequently, Higgins and Holt bent their efforts toward selecting improved gynodioecious lines, beginning a trend that eventually displaced dioecious papayas from commercial fields.

The solo papaya. Three years before Higgins and Holt published their papaya research, an event happened that would accelerate the trend toward gynodioecious cultivars and determine the future of the papaya industry in Hawai'i. In 1911, Gerrit P. Wilder, a scion of an old *kama'aina* family and an amateur horticulturist, who later was appointed botanist at the Bishop Museum in Honolulu (University of Hawai'i at Mānoa, Botany Department, 2012), collected seeds of a single small papaya from Barbados in the Caribbean and brought it back to Hawai'i (Storey, 1941). This was the introduction of the solo papaya, a small-fruited, high-quality gynodioecious line, the descendants of which, over the subsequent 25 years, accomplished Higgins and Holt's objective of replacing the dioecious types originally introduced into Hawai'i in the 1800s. Today, dioecious lines are rare under cultivation but still exist because feral populations escaped from agriculture in numerous locations in the islands such as Kualoa Beach Park on Kāne'ohe Bay, O'ahu, and in the region around Captain Cook above Kealahou Bay in the South Kona District of Hawai'i Island.

Solo is not the name of a specific cultivar; rather, it refers to the general class of export-quality, gynodioecious papayas having pear-shaped fruits weighing ≈450 to 675 g, yellow or red flesh color, TSS in the 12% to 15% range, and superior flavor characteristics. The name was given by J.E. Higgins (HAES, 1920) and was said to derive from HAES

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personnel of Puerto Rican descent, who differentiated the small-fruited papayas that could be consumed by a single person (solo) from the large “watermelon” types that could feed a group. Small fruit size was as important as the excellent flavor and texture traits in establishing the solo as the export standard, because it kept the cost of individual fruits, sold on a cost/lb basis, acceptable in mainland U.S. markets.

Genetics of sex determination. With the adoption of gynodioecious solo lines as the preferred commercial production model came several significant production problems. The occurrence of both pistillate and hermaphrodite sexes among seedling progenies of gynodioecious lines and the inability to distinguish these using purely vegetative characters led growers to question how to establish a field of seedlings with the maximum number of commercially desirable hermaphrodite plants.

The phenomenon of sex segregation in papaya had been noted by all early researchers, including Higgins and Holt (1914), Earley V. Wilcox (1916), and Willard Pope (1930), who published “Papaya Culture in Hawai’i”. However, it was William B. Storey who first provided experimental evidence to explain papaya sex segregation. Storey was born in Hawai’i and was educated at Cornell University. He returned to become a horticulturist at the University of Hawai’i (UH). Over a period of 10 years from 1936 to 1945, Storey (1938b) and J.D.J. Hofmeyr (1938), who worked independently on the same topic in South Africa, published a series of articles that showed that sex segregation was controlled by a single Mendelian locus with three alleles (Table 1). The male and hermaphrodite states are determined by different dominant alleles (M_m and M_h , respectively), and these sexes are genetically heterozygous, sharing the locus with the recessive allele (m) that in homozygous condition determines the female state. A sex-linked lethal gene prevents the formation of homozygous M_m/M_m or M_h/M_h , or M_m/M_h genotypes. With this genetic model, Storey worked out the expected segregation ratios for various matings of the different sexes. The theoretical sex segregation ratios allowed efficient and predictable establishment of commercial papaya

fields based on calculations of the minimum number of seedlings required per planting hole to achieve any desired probability of sex uniformity in the field (Jones and Story, 1941). The standard planting procedure now involves planting each hole with three seedlings from a self-pollinated hermaphrodite parent followed several months later at flowering time by roguing of females and extra hermaphrodites to yield a field with hermaphrodites in $\approx 96\%$ of the holes.

Fruit carpellody. A second production problem that accompanied the commercial exploitation of gynodioecious lines was the sensitivity of many hermaphrodite genotypes to fruit deformity caused by stamen carpellody. This is a genetic proclivity affecting floral development in hermaphrodites such that stamens become carpel-like and attach to the ovary in irregular or occasionally symmetrical lobes (Storey, 1938a, 1941), particularly during the cool, wet season. This causes distorted growth resulting in production of unattractive and unmarketable fruit. The opposite tendency toward abortion of carpels from the ovary in some hermaphrodite genotypes results in fruits with mango or banana shapes or total loss of the ovary leading to unproductive zones in the fruit column. Carpel abortion is usually most pronounced under warm, dry conditions. These environmental influences on fruit morphology are unique to hermaphrodites, but the tendencies are under genetic control, and it is possible to select effectively against these negative characteristics.

Early improvement objectives. An early description of papaya production in the United States, focusing primarily on Florida, listed six named cultivars there, including Hawaiian solo (Traub et al., 1942). Writing in Hawaii at the same time, Storey (1941) echoed the observations of Higgins and Holt 25 years earlier that there were no true-breeding cultivars in Hawai’i as a result of the tendency to outcross among types unless grown in isolation or intentionally self-pollinated. Named types were usually descriptive of economically important morphologies such as the small pyriform-fruited “solo” or large red-fleshed “watermelon” papayas or they were named after the farmer that produced them. Storey pointed out the desirability of a more uniform and predictable crop and set about developing such by stabilizing the genetics through inbreeding selected hermaphrodites with good fruit qualities and production characteristics. The objectives that he and subsequent breeders have generally identified for improvement included fruit weight of 450 to 675 g, high TSS in the range of 12% to 15%, good flavor and texture, minimal seasonal variation in fruit shape caused by stamen carpellody or carpel abortion, and early flowering leading to fruit production low on the trunk. Working primarily at the Waimānalo Experiment Station on windward O’ahu, he released Line 5 in 1948 and Line 8 in 1953. Line 8 is a yellow-fleshed cultivar with excellent flavor, but fruits are too soft for export. It was still grown to a limited extent on O’ahu until the early 1990s.

DEVELOPMENT OF EXPORT POTENTIAL

By the mid-1950s, papaya production reached 4.5 million kilograms annually and became the largest component of the diversified crops sector (crops other than sugar and pineapple) in terms of gross production, and it was third in value behind coffee and tomatoes (HAES, 1958). However, papaya was nearly exclusively marketed locally. The large growth in the industry over the subsequent 25 years was the result of development of export markets in North America and Japan. The shift in marketing was made possible by several advances, which overcame technical problems or allowed improvements in logistical capacity.

Fruit fly disinfestation. The initial barrier to papaya shipments to California was the quarantine restriction imposed in 1914 to exclude fruit flies. Although color-break papaya fruits are not a major host for fruit flies, compliance with quarantine regulations required a disinfestation procedure. An existing vapor heat treatment was modified for papaya by UH plant physiologists (Jones, 1940a), and subsequent experimental shipping and testing in mainland markets led to the first commercial shipments in 1940. That same year, methyl bromide was approved for fruit fly disinfestation (Jones, 1940b) followed by ethylene dibromide (EDB) in 1951. EDB treatment became the standard disinfestation method until 1984 as a result of its relative low cost and freedom from adverse effects on fruit quality.

‘Kapoho’ papaya. Another step in the evolution of the papaya industry toward export markets resulted from the confluence of several factors that effectively moved the major production areas from O’ahu to Hawai’i Island. Increasing urbanization and rising land values in the 1950s and 1960s, combined with repeated outbreaks of *Papaya ringspot virus* (PRSV), served to make papaya production increasingly problematic on O’ahu. The area of the state with cheap land available for agriculture was the Puna District in East Hawai’i. The chief agricultural employer of the area, Puna Sugar Company, was in decline through the 1970s and closed in 1982, gifting laid-off workers with 5-acre land parcels and creating a pool of new farmers looking for profitable crops (University of Hawai’i at Mānoa Library, Hawaiian Collection, 2006). This region became the new center of the papaya industry. Puna has abundant rainfall, well distributed throughout the year, but it is a volcanically active region with geologically young lava substrate and little soil development. It was not clear that papaya could be grown successfully under Puna conditions, but in fact a cultivar specifically adapted to Puna had been under selection in the region for several decades. Hanichi Masumoto was a farmer with land near Hilo, who requested seed from the Cooperative Extension Service to grow papayas. He was initially given “pig food” papaya seed, because the extension agent handling the request knew that Masumoto raised pigs, and he

Table 1. Single-locus model with multiple alleles for sex determination in papaya (Storey, 1941).

Scheme for sex determination in *Carica papaya*

M_1 = dominant factor for maleness

M_2 = dominant factor for hermaphroditism

m = recessive factor for femaleness

M_1m = the male or staminate tree; form D

M_2m = the hermaphrodite tree; forms B and C

mm = the female or pistillate tree; form A

1. $mm \times M_1m \rightarrow 1 mm : 1 M_1m$

2. $mm \times M_2m \rightarrow 1 mm : 1 M_2m$

3. M_1m selfed $\rightarrow 1 mm : 2 M_1m : (1 M_1M_1)$

4. M_2m selfed $\rightarrow 1 mm : 2 M_2m : (1 M_2M_2)$

5. $M_2m \times M_2m \rightarrow 1 mm : 2 M_2m : (1 M_2M_2)$

6. $M_2m \times M_1m \rightarrow 1 mm : 1 M_2m : 1 M_1m$
: (1 M_2M_1)

assumed that was the intended use for the fruit. Anecdotal information suggests that Masumoto, on discovering the poor quality of the fruits, made his displeasure abundantly clear and was quickly provided with solo papaya seed, from which he gradually refined his selection. It was initially known as 'Masumoto' solo but was renamed 'Kapoho' as it became more widely planted in the Puna District (Hamilton and Ito, 1986).

'Kapoho' has several characteristics that destined it for success as the standard export cultivar from Hawai'i. Fruit quality is excellent, and it is free of carpelody and carpel abortion. 'Kapoho' fruits remain firm after harvest, which makes them well suited for packing and shipment to distant export markets. Under the high rainfall conditions in Puna, the fruit size is the preferred 450 kg, but grown anywhere else, the combination of different soil and climatic factors tend to produce very tall trees and fruits that are too small for export. For this reason, Puna is the only area of the state that can benefit from the other desirable qualities of 'Kapoho'. The combination of land availability, unique environmental conditions, and a papaya cultivar adapted to those conditions conspired to favor the Puna District as the new home of the Hawai'i papaya industry after its decline on O'ahu during the decades of the 1950s and 1960s (Loudat et al., 1987).

Tourism connection. Another factor contributing to and enabling the growth of papaya as an export crop was the concurrent development of the tourism industry in Hawai'i. In the years after World War II, increasing numbers of visitors from the mainland and later from Japan traveled to Hawai'i for their first encounter with tropical environments. Exposure to papaya in restaurants and in produce sections of local groceries amounted to free advertising for the industry and resulted in a growing demand for the fruit in temperate regions when tourists returned to their homes. Moreover, tourists increasingly arrived in the Islands by air, so that starting in the 1960s, air freight provided an alternative to sea shipment with an accompanying improvement in quality at market destinations. The growth in papaya exports from 1960 to 1986 closely tracked the increase in air traffic from the mainland to Hawai'i (Fig. 1), and in 1969, the first air shipments to Japan commenced (Loudat et al., 1987).

Cultivar development. New cultivars were developed and introduced in the 1960s and 1970s by breeders at the UH College of Tropical Agriculture and Human Resources (CTAHR). All earlier commercial releases had produced yellow- or orange-fleshed fruits, including the industry standard cultivar Kapoho. In 1963, Richard A. Hamilton and Philip Ito selected the red-fleshed cultivar Sunrise derived from a cross between the red-fleshed Line 9 and a yellow-fleshed solo breeding line called 'Kariya' (Hamilton and Ito, 1968). 'Sunrise' is a high-quality papaya with fruit weights greater than 'Kapoho' under the same growing conditions. It is free of carpelody and usually has only a brief sterile period resulting

from carpel abortion in warm weather. 'Sunrise' flesh softens to a greater extent than that of 'Kapoho' and is not as well suited for export from Hawai'i, although it became the basis of Brazil's European export industry in the 1980s and seems to be adaptable to a broader range of environments than 'Kapoho' (Hamilton and Ito, 1986). Since its release, 'Sunrise' has been popular among breeders as a parental line in the development of papaya F1 hybrid cultivars, including 'Tainung No. 2' from Taiwan and 'Exotica' from Malaysia, because of its high TSS, excellent flavor, red flesh color, and lack of carpelody. A sib line of the same parental cross was released later under the name 'Sunset', but its characteristics are very similar to 'Sunrise' (Hamilton et al., 1993). 'Sunset' has been planted extensively in Brazil and to some extent has replaced 'Sunrise' there as the chief export cultivar.

About the same time, the experimental line X-77 was released by CTAHR horticulturist Henry Y. Nakasone as the papaya cultivar Waimanalo (Nakasone et al., 1972). This cultivar was derived from a cross made in 1948 between solo Line 5 and a dwarf line from Florida called 'Betty' with the intent to create a high-quality papaya with a precocious, low-bearing habit. 'Waimanalo' produces larger yellow-fleshed fruits weighing 675 to 900 g and of a more spherical shape than 'Kapoho' or 'Sunrise'/'Sunset', and it is modestly lower-bearing than either. It is notable for its relative resistance to the serious fungal pathogen *Phytophthora palmivora* and has served as a parent in breeding programs to improve *Phytophthora* resistance in other lines. On the negative side, it has a rather narrow adaptation to conditions on windward O'ahu and tends to be subject to fruit disfigurement as a result of stamen carpeloidy in other locations. A selection from 'Waimanalo' called 'Kamiya' was made by Ken Kamiya, a farmer on O'ahu's windward coast. It is very similar to the parent line and has been popular in Honolulu markets.

PROBLEMS IN PARADISE

Production and postharvest problems. Production and postharvest problems with fungal diseases received attention from UH and U.S. Department of Agriculture (USDA) researchers during the 1960s. Description and identification of the major postharvest pathogens affecting papayas in shipment to mainland and Japanese markets was the work of plant pathologists at UH at Mānoa, particularly Anne Alvarez and Wayne Nishijima (1987). Stricter controls on fungicide use imposed by the Food and Drug Administration in 1963 led to the initiation of hot water dipping as a control measure for postharvest fruit rots. The hot water treatment, developed by Ernest Akamine at UH during the 1950s (Akamine and Arisumi, 1953) and uniformly implemented in the industry by 1972, was effective in controlling postharvest infections and had the added benefit that it improved the efficacy of EDB treatment for fruit fly disinfestation (Loudat et al., 1987). In wet

windward production fields, *Phytophthora palmivora* and *Pythium aphanidermatum* extracted high tolls on papaya seedlings, particularly when fields were replanted repeatedly (Trujillo and Hine, 1965). This so-called "replant problem" was addressed by Wen-Ho Ko of the UH Plant Pathology Dept. Ko found that the competitive effect of the microbial flora in native soils obtained from non-agricultural areas provided effective protection in the root zone of young papaya seedlings during the critical early stages of development. His "virgin soil" technique involved placing several gallons of soil not previously used for papaya production at each planting site in the field and planting the seedlings in that (Ko, 1982). This approach was used successfully in areas without adequate land available for crop rotation. *Phytophthora* is also a serious problem on ripening fruits on the trunk, and it is controlled by frequent applications of dithiocarbamate fungicides, which were evaluated and cleared for use with papayas in the 1970s.

In the early 1980s, the Environmental Protection Agency gave notice that the use of EDB for fruit fly disinfestation would be curtailed, and this initiated a switch from chemical to physical postharvest treatments that evolved through multiple steps over several decades. The task of finding a replacement treatment to maintain exports of papaya fruit to the mainland originally fell mainly on the USDA Agricultural Research Service (ARS), Tropical Fruit and Vegetable Research Laboratory in Hilo, Hawai'i. By the federal deadline for ending EDB use in 1984, Mel Couey and coworkers had devised a "double-dip" hot water treatment that met quarantine requirements for fruit fly control. However, this procedure impaired fruit ripening, resulting in lumpy or "hard shell" fruits that failed to soften normally, particularly when harvested at less than the one-fourth-ripe maturity stage (Paull et al., 1997). Quick modifications of the double-dip procedure produced better results and a crisis was averted, but over the next decade, the double-dip procedure was replaced by a vapor heat treatment using modern equipment manufactured in Japan or by a high-temperature forced-air treatment developed by Jack Armstrong of the ARS Tropical Fruit and Vegetable Research Laboratory in Hilo and engineered by Michael Williamson at the UH Agricultural Engineering Department. Important contributions to understanding how all three heat treatments impacted fruit ripening were made by Robert Paull, Postharvest Physiologist, and Ms. Catharine Cavaletto, quality evaluation specialist, both of CTAHR (Paull et al., 1997). The vapor heat and high-temperature forced-air treatments were determined to have less negative effect on fruit quality and also heated the fruit uniformly to the central cavity rather than just the outer regions. This latter feature became crucial when it was discovered that a morphological abnormality called "blossom-end defect" made a small percentage of papaya fruits vulnerable to fruit fly oviposition directly into the central seed cavity, where

Source: Statistics of Hawaiian Agriculture 1984.

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Fig. 1. Growth in papaya export shipments by air was closely linked with development of tourism industry in Hawai'i (Loudat et al., 1987).

eggs and larvae were unaffected by the double-dip treatment. Mainland exports were interrupted several times in 1987 when live fruit fly larvae were discovered in papaya shipments by California quarantine inspectors, precipitating an urgent re-examination of the quarantine protocol. Francis Zee, curator of the newly opened USDA National Clonal Germplasm Repository in Hilo, made the observation that carpels at the style end of the ovary occasionally fail to fuse completely, allowing a route for ovipositing fruit flies to bypass the double-dip treatment (Zee et al., 1989). Papaya packing houses had to undertake careful monitoring to eliminate fruits with abnormal morphology in the years leading up to 1990 when the replacement high-temperature forced-air disinfestation protocols became available. During the interval, Zee produced a cross between 'Kapoho', which manifested the problem most often, and 'Sunrise', which had a more elliptical fruit shape with better carpel fusion, and offered these hybrids to the industry to reduce the probability of blossom-end defects. This marked the first use of a hybrid cultivar in Hawai'i, and the new hybrid and derived lines were used for some years by Diamond Head packing company. Vapor heat and forced-air dry-heat treatment chambers were unchallenged as disinfestation protocols during the decade of the 1990s, but in 2000, a particle beam irradiator was built in Hilo by a private group, Hawai'i Pride LLC, headed by local businessman Eric Weinert and mainland investor John Clark. Staunch local opposition in the 1980s and 1990s to irradiation based on radioactive isotopes had prevented development of a disinfestation facility for fresh export commodities, but concerns were finally overcome by using an X-ray machine employing an electron beam accelerator technology. The ability to turn off the beam when not in use mitigated most public concerns about the dangers of ionizing radiation that accompany radioactive sources.

Hawai'i Papaya Industry Association. The Hawai'i Papaya Industry Association

was organized in 1965 through the UH Cooperative Extension Service (CES) to provide a forum for industry communications among growers, packers, and state agencies, including the UH (Loudat et al., 1987). This goal was facilitated by annual meetings organized by UH CES and attended by growers, packers, marketers, agricultural suppliers, and researchers. The CES liaison for over 25 years was C.L. Chia, who organized meeting programs and edited the program proceedings for publication by the CES. The proceedings serve as a valuable historical record of the growth of the industry. A secondary goal was to provide a statewide papaya marketing cooperative to address erratic swings in production and pricing. This was achieved in 1971 by creation of the Papaya Administrative Committee (PAC), a federally authorized structure to enforce the marketing order. The PAC had the authority to levy an assessment on growers and packers, which was used to promote sales through generic marketing and occasionally to fund research on problems of high priority to the industry.

Papaya ringspot virus. Two other battles affecting the Hawai'i papaya industry were fought during the 1990s, one biological and the other political. In 1992, the perennial problem of PRSV arrived at the main production areas in Puna, ~30 years after it had destroyed most of the state's production, at that time, on O'ahu. The geographical isolation that had protected production fields in eastern Puna from PRSV introduced years earlier near the city of Hilo had been breached over this time period by the growth of intervening housing developments and their associated backyard papaya plants. The damage started slowly enough, but by 1998, papaya production in Puna had dropped by 50% from levels of the late 1980s and early 1990s (National Agricultural Statistics Service, 1999). Research to solve the PRSV problem had been ongoing since the 1970s and 1980s involving screening papaya germplasm for resistant lines, using cross-protective mild-symptom virus strains (Mau

et al., 1989; Yeh and Gonsalves, 1984), and investigating wide crosses with PRSV-resistant wild relatives (Manshardt and Wenslaff, 1989; Mekako and Nakasone, 1975). None of these approaches proved successful in delivering economical protection or a resistant cultivar. By the mid-1980s, genetic engineering technology had advanced to the point that it was possible to conceive a plan to provide Hawai'i's papaya cultivars with PRSV resistance by this approach. Beginning in 1987, a team of scientists under the leadership of a Cornell University virologist, Dennis Gonsalves, provided the needed skills to accomplish the task. Gonsalves, who was born in Hawai'i and was familiar with the PRSV problem, identified and isolated the resistance gene from the PRSV genome itself. Jerry Slightom of the Upjohn Company engineered the gene into a functional transformation vector. Maureen Fitch of the USDA's Sugarcane Research Laboratory in Aiea, O'ahu, developed the tissue cultures for transformation and regeneration of the genetically engineered plants as part of her doctoral research at UH at Mānoa. Confirmation of the efficacy of PRSV resistance under field conditions in Hawai'i was the contribution of Richard Manshardt and Stephen Ferreira of UH at Mānoa aided by cooperating growers Delan and Jenny Perry of Kapoho, Hawai'i (Ferreira et al., 2002). Ironically, 'SunUp', the first "transgenic" papaya with successful PRSV resistance (Fitch et al., 1992), was rejected by the papaya industry, because it was the wrong color. Marketing of Hawaiian papayas was based on the yellow flesh color of the standard Kapoho cultivar and 'SunUp', a genetically engineered version of the existing Sunset cultivar was pink-fleshed. This impediment was overcome by a conventional sexual cross between 'Kapoho' and 'SunUp' to yield the yellow-fleshed, PRSV-resistant F1 hybrid named 'Rainbow' (Manshardt, 1998). These names were suggested provisionally by UH Horticulture Department chair H.C. Bittenbender as symbolically hopeful for papaya growers after the PRSV "storm," and

they stuck, becoming the official cultivar appellations. In addition to its resistance to PRSV, the resulting hybrid was more highly productive and more widely adapted to microclimatic variation than its 'Kapoho' parent but also somewhat more susceptible to *Phytophthora* fruit rot, stem canker, and root rot. When released in 1998, 'Rainbow' and 'SunUp' became the world's first genetically engineered tree fruit cultivars to reach commercial production and the first transgenic cultivars to be released by public institutions in the United States (Gonsalves, 1998). 'Rainbow' was rapidly adopted by growers in the Puna District, and by 2009, plantings of 'Rainbow' accounted for $\approx 75\%$ of commercial papaya acreage in Hawai'i (National Agricultural Statistics Service, 2009) (Fig. 2). Several other PRSV-resistant papaya hybrids have been produced by conventional crosses with the transgenic cultivars after their 1998 release. The most important of these, released by USDA plant physiologist Maureen Fitch in 2002, is the cross of 'Kamiya' with a transgenic inbred derived from 'Rainbow'. The resulting hybrid, called 'Laie Gold', is a high-quality, yellow-fleshed fruit that is popular with growers along the windward eastern coast of O'ahu.

Control of the Papaya Administrative Committee. The other major battle in the Hawai'i papaya industry in the 1990s involved competition for control of the PAC between groups with differing points of view. Several contentious changes of management ensued, and turmoil centering on the burden of PAC assessments on growers during a period of falling fruit prices led growers in 2002 to vote out the papaya marketing order and abolish the PAC. These events resulted in an industry organization with fewer resources and a less cohesive membership.

FUTURE PROSPECTS

The industry today is leaner than in the last decades of the 20th century. Market share in the U.S. mainland was lost to international competitors in Central and South America during the drop in Hawaiian production caused by PRSV in the 1990s, and that loss was not regained after introduction of PRSV-resistant varieties (Figs. 3 and 4). Imports of the large Mexican 'Maradol' papayas into the United States have risen dramatically since 1990 but are less damaging competition for Hawai'i than other producers of solo papayas such as Belize and Brazil. Reductions also occurred in lucrative exports to Japan as a result of Japanese quarantine restrictions against shipments of transgenic papaya cultivars. Statistics from the late 1980s indicate that more than 300 papaya farms statewide harvested ≈ 975 ha of papaya, compared with 177 farms and 535 ha in 2009 (National Agricultural Statistics Service, 2009). In recent years, Hawai'i has produced ≈ 13.5 million kilograms of fruit annually for fresh consumption, approximately half the amount produced in the mid- to late 1980s, and annual crop value has averaged $\approx \$14$ million.

PAPAYA: Total Acreage, Varietal Distribution, State of Hawaii, 2000-2009

Fig. 2. 'Rainbow' was an immediate success when introduced in 1998 as a result of its resistance to *Papaya ringspot virus* (National Agricultural Statistics Service, 2009).

PAPAYA: Fresh Utilization and Price, State of Hawaii, 1955-2008

Fig. 3. Growth of papaya industry and recent decline resulting from foreign competition in traditional export markets (National Agricultural Statistics Service, 2009).

Origin & Magnitude of Papaya Imports into Mainland US (1990 - 2009)

Fig. 4. Hawai'i's market share on the U.S. mainland has declined as a result of *Papaya ringspot virus* (1994–99) and to increased competition from foreign producers of solo papayas (Belize and Brazil) (National Agricultural Statistics Service. Hawaii Papayas. U.S. Imports of fresh papaya, by country, 1990–2009.).

Papaya genome sequenced. Although competition has caused a contraction in the papaya industry, advances in technology in the present decade and the potential for acceptance of transgenic fruits in overseas markets provide some hope for a more positive outlook. In 2008, an international team of researchers based in Hawai'i published a draft sequence for the papaya genome of 327 million bps (Ming et al., 2008). Hawai'i

principals in this effort were Ray Ming, formerly of the Hawai'i Agriculture Research Center in Aiea, O'ahu, Maqsoodul Alam of the UH at the Mānoa genomics center, and Dennis Gonsalves, currently Director of the USDA Pacific Basin Agriculture Research Center in Hilo, along with an international group of collaborators including a number of faculty and graduate students at UH. This project is informing research in

papaya improvement that will favorably impact the industry in the future. The first genome sequence has already benefitted papaya breeding efforts by making available a broad assortment of DNA markers, potentially linked with important economic traits, for marker-assisted selection. In the near future, it may allow dissection of the genetic control of sex in papaya and enable development of homozygous hermaphrodite genotypes that will eliminate the current necessity of roguing females from segregating seed-propagated plantings. Like a book of deep knowledge that reveals its meaning in proportion to our ability to comprehend, the genome sequence will provide understanding in measure with our ability to reinterpret it in the light of new experience.

International acceptance of 'Rainbow'. In addition, a decade-long effort has recently succeeded in gaining approval in Japan for export of transgenic 'Rainbow', and the first fruits were shipped from Hawai'i in early 2012. The production of data and documents to satisfy the exacting requirements of Japanese regulatory agencies was the work of many researchers, whose efforts were tenaciously motivated and coordinated by Dennis Gonsalves. Gonsalves is also leading a similar project to open markets for 'Rainbow' in China.

In 1914, Higgins and Holt wrote: "Excepting the banana, there is no fruit grown in the Hawaiian Islands that means more to the people of this Territory than the papaya, if measured in terms of the comfort and enjoyment furnished to the people as a whole." A century later, their words apply more than ever. In Hawai'i, a combination of progressive growers and modern horticultural research moved papaya from "pig feed" status to iconic tropical delicacy. The prosperity of the Hawaiian papaya industry has been the result of its success in extending that appeal to other countries and peoples of the world. With new markets opening overseas for virus-resistant solo papayas, there is new hope that papaya will remain an important Hawaiian commodity.

Looking back over the century of papaya history that separates us from the time of Higgins and Holt, it seems true to say that the little fruit from the Caribbean has found a favored home in the middle of the Pacific Ocean.

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