Breeding Tropical Vegetable Corns

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Abstract.
Breeding of tropical corn (or 'maize', *Zea mays* L.) as a vegetable assumes many genotypes and products. In temperate agriculture the familiar types are 'sweet and supersweet corns' involving genes *sugary-1*, *shunken-2* and *sugary extender*. Most familiar in the tropics are field corns and *waxy-1* corns, harvested immature (or 'green'), and corns for 'baby corn', milk and ice cream. The sweets and supersweets are limited to a few market areas. Temperate sweet and sueprsweet corns fail almost universally in the tropics. This is shown to be due largely to their susceptibility to a wide range of diseases, pests and ecological factors, notably short day-lengths. The genotypes chosen by tropical breeders uniquely include genes *brittle1* and *waxy1*. Their advantages include stress tolerance facilitating year-round production. Vegetable corns play a significant role in the tropics as a source of energy, not primarily as a carnival item. Genetic improvements have been made primarily in the tropical and sub-tropical ecosystems represented by the authors and contributor Taweesak Pulam—Hawaii, Queensland, and Thailand. Breeding began in Hawaii with Mangelsfdorf's 'Hawaiian Sugar', released in 1947 and now underlying almost all tropical sweets.

Tropical breeding was initially focused on open-pollinated varieties that could be grown by small tropical farmers without excessive seed costs. Dominating among these was 'Hawaiian Supersweet #9' (*brittle-1* gene) and waxies like 'Kao Neo'. Conversions to the sweeter *shrunken-2* gene and inbreeding for hybrid production closely followed. Diseases and pests and their diverse and constantly-evolving races abound on corn in the tropics. Most significant is the family of fusarium diseases basically found in every corn plant in the tropics. It can cause germination failure, seedling death, stalk rot, and ear and kernel rots. Similar challenges involve many diseases like the blights, with multiple races. The breeder in the tropics also deals with short days, limited incident light, high temperatures, and a wide variety of pests (largely insects). Present adoption of tropical vegetable corns is largely limited to hybrids, both public and private. Large-scale production for canneries occurs in Thailand, with outputs equaling or exceeding those of the United States. Tropical production and processing presents some unique challenges, including ear type and unusual products that include sweet corn milk, sweet corn ice cream, and waxy ('mochi') food products. Access to markets is often limited, and seasonal variations can greatly limit year-round fresh corn production. The earliest hybrid development depended on open-pedigree inbreds. As the industry develops, however, commercial production may come to rely heavily on closed-pedigree parents as it does in temperate regions, thus limiting hybrids to wealthy tropical estates. With a billion people in the tropics who go to bed hungry and often suffer from Vitamin A deficiency, this must not happen. Easily grown and attractive as food world-round, the continued development of improved tropical corn as a vegetable must have public support and that of the major international research centers.

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ABBREVIATIONS: BLB (Bacterial leaf blight; BLS (Bacterial leaf streak); CSD (Corn stunt Disease;, CIMMYT (International Center for Improvement of Maize and Wheat), DAP (Days after pollination); DTS (Days to silk); FAO (Food and Agriculture Organization of the United Nations; IITA (International Institute of Tropical Agriculture); MCMV (Maize chloroic mosaic virus; MMV (Maize mosaic virus); MRDV (Maize rough dwarf virus); MSV (Maize streak virus); NCLB (Northern corn leaf blight); OP (Open pollinated); QPM (Quality protein maize); QTL (quantitative trait locus); RFLP (Restriction fragment length polymorphisms); SX (single cross hybrid).

I. TROPICAL vs. TEMPERATE VEGETABLE CORNS

A. Introduction.
Temperate sweet and field corns (*Zea mays* L.) are of essentially no value per se in the tropics, only as gene sources in conversion (Pulam, 1997, 2003) Similarly, tropical field and vegetable corns (often referred to as 'exotic') are unadapted in temperate regions and require extended conversions of adapted inbreds that in fact can be quite rewarding (Nelson and Goodman 2008; Hallauer and Carena 2014). Corn (maize) evolved in the tropics, where most of the >200 races are daylength sensitive and fail to flower seasonally under 14 to 16 hr. days (Logroño 1990). In contrast temperate *sugary-1* sweet corns evolved from a narrow gene base in the northeastern U.S.A. flint corns, and are marked by earliness, high tillering and long flag leaves due to homozygosity for *grassy tiller* gene (Brewbaker and Josue 2007). Corn belt dents have a similarly narrow genetic base in races 'Southern Dent' and 'Northern Flint'. None of America's fine vegetable corns have even a partial array of tolerances to typical maize diseases in the tropics, and have to be seed-treated and sprayed for production there (Brewbaker 1979).

Dominating among tropical corn diseases are species of the genus *Fusarium* that cause rotting of kernels, ears, stalks and seedlings. The fusariums occur in all wet lowland tropics and become unusually problematic with thin-pericarped corns grown year-round. Among the indigenous races of maize, about half are highland flouries generally susceptible to the fusariums and half are lowland flints and popcorns that are more tolerant (e.g., Wellhausen et al. 1952, Grobman et al. 1961). The disease is rarely of consequence in temperate regions or in cool tropical highlands, where costly seed-pesticide coatings are employed. Breeding vegetable and floury corns like the improved-protein *opaque-2* varieties known as QPM (CIMMYT, pers. corresp.) enforces selection for the generally polygenic tolerance to fusarium and related pathogens.

Breeding the supersweet vegetable corns has been thoroughly and elegantly reviewed by W. F. Tracy (1997). Essentially focused on temperate maize, little reference could be made to tropical hybrids based on the supersweet genes. Stressed throughout the following review is the fact that temperate and tropical corns are wisely dealt with as subspecies. Bringing fine temperate sweet inbreds like P39 and P51 (marvelous parents of Golden Cross Bantam) into the tropics is much like bringing a Chihuahua into a wolf's den. Our early 1950's attempts to bring temperate sweet corns into the Philippines (J. L. Brewbaker and H. K. Hayes, unpubl.) made this very clear. Previous publications on genetic improvement of tropical vegetable corns include Brewbaker (1979, 1982, 1992) and Brewbaker et al. (2007).

Corn as a vegetable is defined simply in this review as any type of *Zea mays L.* eaten immature. In temperate agriculture it is best known from mutants that reduce endosperm starch and increase its sugar, including the gene *sugary-1* and the 'high-sucrose' or 'supersweet' genes, *shrunken-2* and *brittle-1*. The supersweet term is used here as in Tracy's thorough 1997 review, where however it applies only to the *shrunken-2* genotype. In their native Latin America and throughout the tropics field corns are also harvested immature or at 'sweet-corn-stage' and roasted or boiled. Roasted, they are referred to as 'elote' (Mexico) or 'kcancha' (Peru), and boiled as 'choclo'. Races with floury and often colorful kernels are favored, such as Harinoso de Ocho in Mexico. There have been a few sweet mutants (gene *sugary-1*) in highland races like the Andean 'Maiz Dulce' and 'Chullpi' that are roasted as food. Many historic vegetable corns in the U.S.A. were harvested immature and roasted over a fire, a common practice before ceramics had been introduced (ca. 900 AD. The glutinous mutant (gene *waxy-1*) is a type of field corn that is commonly harvested immature and cooked in Asia. Waxy has a long and undocumented history of food use in temperate and subtropical regions of Asia since corn was first introduced there in the 1600's, but is essentially unknown this way in temperate America. "Baby corn" is the young cob commonly used in Asian cooking. Preferred are male-sterile single crosses of either field or vegetable corns.

Many of the data summarized in this review came from four primary research stations that have the following characteristics (yearly average values for temperature and rainfall):

	Latitude	Elevation	Temp.	Rainfall
Waimanalo, Hawaii	22°N	6 m	25.4 C	1400 mm
Mealani, Hawaii	21°N	830 m	18.5 C	1400 mm
Kairi, Qld., Australia	17°S	715 m	27.8 C	1270 mm
Prabuthabat, Thailand	14°N	87 m	31.4 C	1200 mm

Contributing significantly to this manuscript are Thai data from the highly successful corn breeding programs of Dr. Taweesak Pulam, based in Prabuthabat, Thailand. His center is among the four listed stations and all have facilities for irrigation in dry seasons. This ensures the year-round presence of corn and continuous epibiotics of many diseases and insects. All stations are near areas with sugarcane, Johnsongrass, and other grasses that host many of the pests and diseases of maize. As a result the spectrum of diseases and stresses at these sites represents a wide sample of those encountered in the tropics. Supplemental trials at different locations, often with farmers, have been used as necessary to estimate yields and evaluate tolerance notably to diseases having diverse pathogenic

strains. Commercial experience of growers in Thailand,   Queensland, and Hawaii provided us much data evaluating the successes and failures of tropical vegetable corn improvement.

B. Temperate Vegetable Corns

Temperate corns referred to as 'sweet' are sometimes referred to as *Zea mays saccharita*. These sweet corns evolved largely from *sugary-1* mutants of northeastern-U.S.A. Iroquis-Indian flint corns (Gerdes and Tracy 1994; Tracy 1997). An indication of the narrow germplasm base of these corns is the universal presence of gene *grassy-tiller* (Figure 1) with long flag leaves on the husks and varying numbers of tillers (Josue and Brewbaker 2007). Three *sugary-1* open-pollinated (OP) sub-populations laid the foundation of most modern inbreds. These were the white 'Stowell's Evergreen' (1848) and 'Country Gentleman' (1891), and the first yellow-endosperm variety, 'Golden Bantam', that appeared in 1902 (Gerdes and Tracy 1994). Upon this yellow foundation many *sugary-1* hybrids appeared, being led by the Stewarts-wilt resistant 'Golden Cross Bantam' (1931, from P39 x P51). Later marketed hybrids included 'Iochief' (1951, from Ia453 x Ia5125) and the superior quality white-endosperm 'Silver Queen' (1955). The percent similarity among these best known publicly available inbreds is relatively high (~85%) based on RFLPs (Gerdes and Tracy 1994), and similar to that of corn belt corns on the somewhat wider gene base in two temperate races, Northern Flint and Southern Dent. Genetic similarity based on phenotypes (Gerdes and Tracy 1994) were much lower (~35%). Tropical vegetable corns have much more diverse parentage in tropical maize and thus have extremely low genetic similarities (Nourse 2002). Correlations of similarity data with heterosis values are low and of debatable value in tropical studies.

The first "supersweet" or high-sucrose hybrid named 'Ilini Chief' was based on conversions by Dr. John Laugnan, then graduate student, of 'Iochief' to the *shrunken-2* gene (Tracy 1997). Germination problems with this supersweet single-cross led to later release of the 3-way 'Illini Xtra Sweet', (Ia453sh2 x P39sh2) x Ia5125sh2. Three-way hybrids became standard. A more sub-temperate 'Florida Sweet' was bred from blight- resistant conversions of Ia453sh2 and Ia5125sh2, and it was succeeded also by a 3-way 'Florida Staysweet'. Essentially no use in tropical breeding has been found for the extraordinary inbreds P39, P51, Ia453, Ia2132 and Ia5125 of the past, despite our early efforts in Hawaii to market hybrids with them as parents (Brewbaker et al. 1966). The basic problem was simply keeping the temperate inbreds alive. Private industry assumed leadership in breeding supersweets for the increasingly lucrative American market but their closed pedigrees obviated use in tropical breeding. Many new mutant genes modifying starch synthesis have appeared and now play a role in breeding, notably the mutant *se1* (*sugary-extender*) from inbred Illinois101T (Gerdes and Tracy 1994). For about a century white-endosperm corns were considered 'people-corns', while corn with yellow endosperm was reserved for animals. This tradition continues in 2014 in most of the tropics, and is troubling for its health consequences. Glutinous corn is a significant vegetable in south east Asia and is based on the gene *waxy-1*.The mutant was probably selected for food soon after introduction of corn in 1600's. First introduced into U.S.A. from China in 1909, the historic varieties were evidently developed over a wide range of ecosystems, temperate to tropical. Strangely they never came into food use of immature ears in temperate regions, although this became the dominating use in Asia. Major genetic variation of waxies occurs in south east Asia and temperate regions of China, Vietnam and Korea (Brewbaker et al. 2007). Endosperm color is universally white ($y1/y1$), but aleurones are often purple (C R Pr) and rarely red (C R pr). Breeding of tropical glutinous varieties may have originated from small-eared corns like Tien and Khao Neo in Thailand and Macapuno in the Philippines. Our attempts in the 1950's to include these cultivars into composites like Phil wx Comp 1 failed to combine quality with tropical tolerances (J. L. Brewbaker, unpubl.). Evaluations of these and other waxy entries in Thailand in 1967-8 revealed several with high tolerance of local diseases (T. Pulam, 2003), and extensive breeding has occurred in Korea and China for temperate waxies (M.H. Lee, unpubl.). As with sweets the tropical waxy strains are usually of little interest to temperate breeders, where the market is solely for dry corn as a starch use (e.g., tapioca).

C. Tropical Vegetable Corns

All corns can be eaten as a vegetable when immature.   Often this is best around 20 to 30 days after pollination, at a stage of approximately half their ultimate dry weight. Most field corns, however, have qualities like thick pericarp that make them much better for cows and goats than people (Ito and Brewbaker 1991; Wang and Brewbaker 2001). Throughout the historic Latin American region of corn's origin, however, are some races of maize favored as vegetables with unusually thin pericarps. A survey in Hawaii of pericarp thicknesses in 181 of the native races of corn (~80% of all races) revealed more than 35 with very thin pericarp (<55 microns), figures comparable to modern commercial sweet corns with high tenderness (Brewbaker et al. 1996). Overall the races averaged 71 microns in thickness. Pericarps of modern corn belt field and pop corns, in contrast, averaged >130 microns and proved very unwise to use as parents for sweet corn breeding (Davis et al. 1988; Ito and Brewbaker 1991; Wang and Brewbaker 2001). In Latin America these immature field corns are usually roasted over a fire and referred to as 'elote', a Nahuatl name for corn on the cob, e.g., Mexico's races Cacahuacintle, Harinoso de Ocho and Conico (Wellhausen et al. 1952). In South America immature floury corns are commonly cooked and known as 'kcancha' (toasted) or 'choclo' (boiled), and they are also used to make 'chicha', a rather strange kind of beer fermented from germinating kernels (Grobman et al. 1961). In modern markets boiled young field corn ears are often served smothered in butter, cheese, mayonnaise, lime juice, and chili pepper that generally disguise any corn flavor.

Glutinous corn is a mutant version of field corn based on the gene *waxy-1*. It is a significant vegetable in S. E. Asia, harvested at about the same maturity and boiled much as the field corns. Unlike field corn (that has largely amylose starch), the waxy has largely the highly branched amylopectin starch. As in waxy (or "mochi") rice, this glutinous texture is attractive and is associated with more sweetness. The Chromosome 9S:64 mutant was probably selected for food soon after introduction of corn to Asia in 1600's. First introduced into U.S.A. from China in 1909, the historic varieties were evidently developed over a wide range of ecosystems, temperate to tropical. Strangely the vegetable use became dominating in Asia but never came into food use of immature ears in temperate regions, Major genetic variation of waxies occurs in south east Asia and temperate regions of China, Vietnam and Korea (Brewbaker et al. 2007). Endosperm color is universally white ($y1/y1$), but aleurones are often purple (C R Pr) and rarely red (C R pr). Breeding of tropical glutinous varieties may have originated from small-eared corns like Tien and Khao Neo in Thailand and Macapuno in the Philippines. Our attempts in the 1950's to include these cultivars into composites like Phil wx Comp 1 failed to combine quality with tropical tolerances (J. L. Brewbaker, unpubl.). Evaluations of these and other waxy entries in Thailand in 1967-8 revealed several with high tolerance of local diseases (T. Pulam, 2003). Extensive breeding has occurred in Korea and China for temperate waxy hybrids (B. H. Choe and M.H. Lee, unpubl.). As with sweets the tropical waxy strains are usually of little interest to temperate breeders, where the market is solely for dry corn as a starch use (e.g., tapioca).

'Baby corn' is based on immature ears harvested soon after silk emergence and preferably on unpollinated ears. They are widely used as a vegetable worldwide, and literally can be harvested from any type of corn. They are an important canned product in Thailand, valued c. $30 million in 2014 and derived from >40,000 ha annually (T. Pulam, pers. corres.). Both field and sweet corns can be used. Single-crosses of male-sterile field corns dominate the market. The nutritional quality is similar to many vegetables, with average moisture content of 90%, protein level of ~2g/100g, and carbohydrate ~8g/100g. (Chamnan Chutkaew, unpubl.).

Tropical *sugary-1* (*su1*) mutants were identified in ancient Peruvian races of maize, notably the large-kernelled 'Chullpi' or 'Chuspillo') of the Andes (Grobman et al. 1961). Historic *sugary-1* tropical varieties 'Maiz Dulce' of Mexico, 'Pajimaca' of Cuba and 'Country Gentleman' of southern U.S.A. appear to trace to these highland Andean races, with their ovoid ears, irregular kernel rows and high susceptibility to kernel and seedling rots (Grobman et al. 1961; Shaver 2005). These were largely highland races with poor performance in the lowlands and in quality, and were eliminated from Hawaii's breeding (Brewbaker 1965). Modern mutations affecting the *sugary-1* locus are common and lead to a wide range of quality and starchiness among the alleles. Many similar products around the world involve immature field corn in cooked preparations. African corns of this type are commonly white floury or dent corns derived from historic long-eared varieties with flexible cobs like 'Hickory King' from southeast U.S.A.

and 'Piricinco' in Peru. Like the white sweet corns   preferred until the time of 'Golden Bantam' (1902), the consumption of white corns is closely associated with macular degeneration of eyes due to lack of significant carotenoids. This continues to a very serious problem in some tropical regions where white corns are favored as human food, leading to the blindness of African children, estimated in 2014 by F.A.O. to be at a level of ~500,000 per year. There appears to be no published literature on the genetic improvement or selection of field corns more appropriate for use harvested green.

Modern tropical hybrids are primarily of high-sucrose genotypes *sh2* and *bt1*, with sugar contents that often exceed 40% at sweet-corn stage. The most extensive development of commercial tropical hybrids of this type has occurred under leadership of the authors and of T. Pulam (unpubl.) in Hawaii, Australia and Thailand. Thailand presently ranks fourth internationally in sales of processed vegetable corn. Our breeding and genetic studies have revealed and exploited genes that undergird many of these traits and that should facilitate genetic advance in the future. Very limited interest in corn as a vegetable has occurred in international research centers.

D. Failure of Temperate Vegetable Corns in the Tropics

Incident light is a major factor in the failure of temperate sweet and field corns in the tropics. The photo in Figure 2 was taken in Hawaii in a typical winter nursery with sunlight limited to 4 to 6 hours. Under these environmental conditions the yields of tropical field corn hybrids are 60-75% of normal, while temperate hybrids (foreground) are not harvestable (Jong et al. 1982). Temperate sweets and related Northern flints evolved under long days (16 to 18-hour) with high light intensities that approximately double those of the tropics. G. Edmeades (1984, unpubl.) summarized data that averaged 37 cal cm^2 per degree-day in temperate New Zealand vs. an average of 25 cal cm^2 per degree-day in tropical Ghana. Summarizing four years of monthly field corn trials in Hawaii, Jong et al. (1982) and Brewbaker (1985) reported a linear regression of yield on incident light, with field corns averaging 10 t/ha under a typical high-light temperate day at 500 cal cm^2 per degree-day but averaging only 5 t/ha under a typical tropical day at 250 cal cm^2 per degree-day. Short-day winters (<11 hours, cloudy) in the tropics lead to impressive yield losses and dwarfing of temperate sweet corns, e.g. to <150 cm with ears <35 cm as in Figure 2.

Daylength sensitivity characterizes most tropical varieties. Long daylengths (e.g., >14 hrs) delay flowering for up to one month, while temperate sweet corns have little or no sensitivity to the long days. Logroño (1990) conducted studies in Waimanalo in fields with 150W lighting applied in the evenings. He reported that 90 tropically-adapted field corn inbreds averaged 64.5 days to silk under 12-hour 'short' days, but 86.9 days to silk under 16-hour long-days. Nourse (1992) showed that the sensitivity involved two or more QTLs, and conversions either way were straightforward for both sweet and field corns. This sensitivity has historically reduced interest of temperate breeders in tropical germplasm, despite the wealth of genes that could easily be transferred (Nelson and Goodman 2008; Hallauer and Carena, 2014). Tropical x temperate ('trop-temp') hybrids usually are intermediate in sensitivity but high in performance. They also provide a wider range of adaptability favored in much tropical breeding for grain and silage.

Temperate corns generally have few husks, long flag leaves, and poor ear-tip cover that attract insects, fungi, birds and rats. Temperate sweets and supersweets carry the unusual *grassy-tiller* gene, *gt1* (Brewbaker and Josue 2007) that creates a many-tillered plant with long husk or 'flag' leaves (Figure 1). The *gt1* allele is almost never found in tropical corns, which rarely tiller or have long flag leaves, although common in related species like *Zea diploperennis* (Srinivasan and Brewbaker 1999). Lush tillers and flags exacerbate damage from insects that include aphids, thrips and leahoppers. Temperate sweet corns have few and fragile The flag leaves do facilitate commercial husking, as does the lower number of relatively fragile husks (Brewbaker and Kim 1979). Customarily they have 16 kernel rows that end abruptly, leading to an open ear-tip cover that correlates closely with damage from tropical ear- and army-worms and following molds and diseases. The failure is most dramatic when it involves year-round production systems (Brewbaker 2003), with temperate hybrids that are dwarfed and flower prematurely, yield poorly, and succumb to diseases and insects (Brewbaker 1965).

Introductions of historically important *sugary-1* cultivars like 'Golden Bantam' and 'Country Gentleman' were early failures in the Philippines and Thailand, where they were soon replaced by Dr. A. J. Manglesdorf's 'Hawaiian Sugar' originating from hybrids of Puerto Rican USDA34 and Golden Bantam (Brewbaker 1965). Breeders who tried to convert temperate sweet corns based on a few QTLs to make them tropical have generally failed, reflecting the very great genetic differences. Early sweet corn breeders attempted also to convert corn belt stiff-stalk varieties to genes for sweet corn and failed, largely due to the remarkably thick pericarps of stiff-stalk corns (Ito and Brewbaker 1991; Wang and Brewbaker 2001). *Sugary-1* populations like NE-HY were bred to incorporate temperate field corn genes for high yield and tolerance to common rust but they proved to be very poor in tenderness and quality (Davis et al. 1988). Stiff-stalk field corns bred for mechanical harvest in general were shown by Wang and Brewbaker (2001) to have thick, chewy pericarps. These are evidently linked traits that deserve further study (J. L. Brewbaker, unpubl.). A question to be researched is whether the poor standability and weak stems of most sweet corns come from this correlation with thin pericarps, both maternal tissues.

Diseases and pests constitute the primary restrictions on use in the tropics of temperate field and sweet corns. In a series of 40 performance trials of 120 field corn inbreds at 28 locations in 11 countries in the 1980's (Kim et al. 1988a; Brewbaker et al. 1989), temperate corns customarily lacked resistance to diseases limited to the tropics or to racial variations uncommon in temperate climates. These pests and diseases included fusarium rots, tropical rusts, blights, downy mildews, earworms, borers and other insects. Resistance was especially rare in temperate corns to many tropical viruses, which are virtually unknown in temperate regions. These included MMV (maize mosaic virus), MCMV (maize chlorotic mottle virus), SCMV (sugarcane mosaic viruses), MSV (maize streak virus) and their virus-transmitting leafhoppers, thrips and aphids (Brewbaker 1982, 1983, 1992). Corn in the tropics must also have high tolerance of pests and environmental stresses. These include tropical earworms and fall armyworms whose injury correlates with husk numbers (Brewbaker and Kim 1979). Short days, drought, low inputs and excessive heat are problematic for sweet corn throughout the tropics, as demand for water is elevated by typically high tropical evaporation rates (>500 mm per crop; Brewbaker 2003). Despite more than a century of breeding fine temperate hybrids of sweet and waxy corn, largely in the private sector, few can be grown profitably under these limitations. Initial evaluations of 70 temperate hybrids at seven research stations in Hawaii (Brewbaker et al. 1966) showed none to be commercially acceptable, data confirmed (J. L. Brewbaker, unpubl.) by our trials in Thailand (1967-8), Colombia (1978) and Nigeria (1989). A few temperate hybrids like 'Silver Queen' and 'Florida StaySweet' have been profitably grown in the dry and long-day summers in parts of India, Australia and Hawaii. Genetic studies have increasingly revealed and exploited genes that undergird many of these traits and that should facilitate genetic advance in the future. Unfortunately, very limited support for improvement of tropical sweet and waxy corns has occurred in international research centers and in public institutions of the USA.

II. GENETICS OF VEGETABLE CORNS

A. Mutant Genes of Vegetable Corns.
"Vegetable corn" is a term applied in this review to corn of all types that are harvested immature, including field corn, waxy, sweet, supersweet, synergistic, baby, etc. 'Sweet corn' (or 'sweet maize') is a common term worldwide for corn eaten as a fresh vegetable. Historically most important are the *sugary-1* sweets, now largely replaced by high-sucrose 'supersweets' (Gerdes and Tracy 1994; Tracy 1997). However, all corns can be eaten as a vegetable when immature (18 to 24 days after pollination). Most field corns have very thick pericarps and endosperms that make them much better for cows and goats than people (Ito and Brewbaker 1991; Brewbaker et al. 1996; Wang and Brewbaker 2001). About half of the corn eaten immature as a vegetable worldwide is not technically sweet, but is starchy and is simply immature field corn or glutinous (*waxy* gene) corn. However, many mutant genes that affect starch synthesis have been used in sweet corn improvement. These often lead to great increases in sugar levels at harvest (reviewed by Boyer and Shannon 1984) and include the following loci with chromosomal locations from the summary of Ed Coe (2005).

ae1 (amylose-extender)   chromosome 5L-   96.0
bt1 (brittle-1)   chromosome 5L-93.0
bt2 (brittle-2)   chromosome 4S-70.9
se1 (sugary-enhancer)   chromosome 2 (Bin 2.09)
sh2 (shrunken-2)   chromosome 3L-141.9
su1 (sugary-1)   chromosome 4S-66.3
wx1 (waxy-1)   chromosome 9S-63.7

Other genes that have been used in sweet and waxy lines include other carbohydrate loci (*dull-1, sugary-2*), the flouries (*opaque-2* and f*loury-2*), and the many genes affecting kernel colors.

B. Sugary Vegetable Corns.

The *sugary-1* gene is of historic significance in temperate agriculture, dominating production for almost two centuries. The commercial allele evidently arose as a mutant in northeastern temperate flint corns (Gerdes and Tracy 1994). This gene reduces starch synthesis and results in a highly branched product called phytoglycogen or WSP (water-soluble polysaccharide). Levels of sugars are slightly elevated (~15%). WSP is, however, at a high level (~28%) and dissolves readily to sugars upon cooking to confer a highly-favored creamy texture. This sweetness is lost rapidly after harvest, and sugar is commonly added during processing. All American *su1* corns and supersweets derived from them are tillering and have leaves on the tips of husks as a result of the presence of gene *grassy tiller (*Brewbaker and Josue 2007). As noted earlier, the *su1* mutant has also occurred in highland Andean races like 'Chullpi' where it is used as a roasting corn, a common practice worldwide to bring out caramelized flavors. Pericarp colors vary widely in 'Chullpi', related races, and in some contemporary *sugary-1* hybrids, reflecting the lack of close linkages to loci like A1, A2, and C. Different alleles at the *sugary-1* locus have differing effects on sugar and WSP levels, and some are very pseudo-starchy (Tracy 1997). The history and breeding of *sugary-1* corns is thoroughly reviewed by Boyer and Shannon (1984).

C. Supersweet Corns.

The two most common 'supersweet' genes are *brittle-1* (*bt1*) and *shrunken-2 (sh2)*, each of which raises total sugar levels to about 40% at harvest stage and confers a crispy texture. Most widely used in temperate hybrids is the gene *sh2*, thoroughly reviewed by Tracy (1997), that is linked very closely (0.3 nm) on Chromosome 3 to an *a1* allele that inhibits plant or kernel colors. As a result *sh2* corns generally lack anthocyanins and flavonoids in plant, in pericarp, and in endosperm and aleurone. The gene *bt1* (Brewbaker 1971. 1974, 1977) has been most widely used in Hawaii and can be found in tropicals internationally. It is also linked to a color-inhibiting allele *a2* but at a distance of 8 μm. Mutant allele *bt1A* (Hannah and Basset 1977) has the common *A2* allele that permits development of colored kernels and plants. The high sugars and crisp textures of these supersweets are retained well during storage, freezing and processing. The supersweets were shown by Zan and Brewbaker (1999) to germinate poorly, as seen here in the average germinations of a set of six isogenic hybrids under cold-soil stress:

Wild-type +/+   91%
Sugary-1 *su1/su1*   73%
Brittle-1 supersweet *bt1/bt1*   53%
Shrunken-2 supersweet *sh2/sh2* 30%

These germination values were shown by Zan and Brewbaker (1999) to correlate highly with levels of reducing sugars and conductivity values in milliSiemens m^2 of electrolytes leaking from soaked seedlings. Under stressed conditions all supersweets germinate and emerge weakly. They suffer more from fusasrium damage than do sugary, waxy, or wild-type corns, with *bt1* normally much better than *sh2*. Sugar levels reviewed by Tracy (1997) were highest in *sh2* (~22%), lower in *bt1* (19%) and in *bt2* (18%), although these were not isogenic NILs.

Th*e bt2* gene was used by Banafunzi (1974) and marketed as 'Hawaiian Supersweet #6' (Brewbaker and Banafunzi 1975). The *bt2* gene acts in the same way as *sh2* does to obstruct production of ADPG-

pyrophosphorylase and greatly reduce starch. The   function of gene *bt1* is quite different from *bt2* and *sh2*, restricting membrane transport of sugars in the endosperm. Although *bt2* is basically a duplicate of *sh2,* it is not linked to *a1* (or *a2*, as is *bt1*), thus can be combined with colors (aleurone, pericarirp). Banafunzi (1974) created a series of composites with this gene and others like *opaque 2*, concluding that *bt2* was superior to other supersweets in length of the period of maximal quality (from 18 to 28 days). It became the source of a series of food products like raisins, milk, ice cream, all great for graduate students. Frozen and freeze-dried supersweet ears and kernels retain their textural quality, unlike *su1* ears or kernels (Brewbaker and Banafunzi 1975), and are common in Japanese dried noodle soups (probably *sh2*). Both *bt1* and *sh2* have weak seed quality and slow emergence. 'Hawaiian Supersweet #6' generally matched *sh2* in all traits like % sugar (46%) and weak emergence, but it was set aside in favor of *sh2* widely used in temperate breeding. However the composite was grown in some Asian markets and continues to be found and easily identified by red cobs, etc. The colors afforded by alleles *bt1A* or *bt2* offer tropical breeders some interesting options for the future. The collapsed, low-starch dry kernels of supersweet corns weigh less than half those of near-isogenic field corns, with single-cross hybrid seeds averaging ~ 9000 kg^{-1}.

D. Sugary-Enhancer.

The gene *se1* (*sugary-enhancer*) is among the more challenging genes for the breeder, and largely unused in the tropics. It was identified as improving quality of double mutants with *sugary-1*, acting quantitatively to improve chewy texture and increase levels of sugar (perhaps also maltose) and phytoglycogen (Tracy 1997). It also reduces yellow pigmentation and has poor storage ability. The *se1* alleles are thought also to modify quality of *sh2* stocks and referred to as "synergistic". The *se1* locus was originally placed on Chromosome 4, but is now believed to be in bin 2.09 on Chromosome 2 (Juvik, pers. corresp.). It originated in IL677a, a progeny of crosses at U. Illinois involving *su1* inbreds IL442a and IL442b (Tracy 1997). Both IL442a and IL677a conferred high tenderness and quality as parents of some early Hawaiian *sugary-1* hybrids like Hi68. Inbred 442a was later converted to *bt1* but in crosses the *bt se* kernels were slow to drydown and highly infected with fusarium. IL677a provided a unique source, not used, of monogenic resistance to common rust (Kim and Brewbaker 1987a). In Hawaii it was typical to observe segregation of *se* as 3:1 ratios of normal to fusarium-infected kernels at maturity, eliminating options for normal grain harvest. Delayed drydown of *se* seeds has limited interest for tropical breeders, and none of the available temperate stocks are well adapted to the tropics.

E. Synergistic Combinations.

Many genes and unique alleles of common loci probably act as QTLs to modify sugar and starch syntheses in grass endosperms. Many combinations of *su, se, sh2, bt* and *wx* have been attempted by breeders to improve sweetness or quality, and are referred to as "synergistic". An early series of combinations involved *su* with *wx* and also with *ae wx* (Boyer and Shannon 1984). It is relatively easy to create hybrids that segregate for one or more of these recessive genes. An early commercial patent was for *su1* hybrid ears segregating 1/4 *sh2* kernels (from crosses of *su* females x *su sh2* males). However, the double mutants of *su* with *sh2* or *bt* usually have very small, collapsed kernels that are very difficult to harvest and germinate in the tropics. They often can be retained only by keeping much thicker pericarps in the double mutant. Many temperate hybrids are being marketed that segregate *su, se* and *sh2*, with the double mutant *se sh2* of reputedly high quality. Commercial hybrid 'Mirai' of superior quality may be of this genotype. Some Asian breeders (S.K. Kim, pers. corresp.) are producing hybrids that segregate *sh2* or *bt* on *wx* ears (e.g., by crossing *wx* female x *sh2 wx* male). These provide a major challenge of choosing harvest dates that provide best quality for sh2 (early, 18 DAP) vs. for wx (late, 24 DAP).

Creating tropically adapted synergistic sweet corns that yield well and resist diseases and stresses presents a formidable challenge to tropical breeders and seed producers. They require harvest of immature grain shortly after physiological maturity (e.g., ~35 DAP, ~35% kernel moisture) followed by slow, careful drying and expensive seed treatments and storage conditions. In the U.S.A this is done largely in dry regions of Idaho. All of these

recessive genes have been used in breeding research at   the University of Hawaii, and populations were released carrying each of the loci (Brewbaker 1977, 1998). However, no synergistic varieties of hybrids were feasible to produce commercially.

F. Waxy Corn

Waxy corn is commonly harvested green as a fresh product in the tropics, Korea and southern China. As noted above, it is unknown in this manner in the U.S.A. and other temperate regions. The *waxy* gene causes a major conversion of starch in the endosperm of cereals like maize and rice to a glutinous texture. The gene suppresses the formation of amylose and leads to dominant production of amylopectin, the latter a highly branched starch while the former is a long-chain starch. The differences relate to the *ai*1-4 and *ai*1-6 bonds between glucose molecules in starch, the waxy having both and amylose having only *ai*1-4. Known as "mochi" in rice, the high amylopectin grains of waxy corn or rice provide a product on prolonged cooking that is much favored in Asia. Harvested between 20 and 25 DAP, waxy corn cooks up with a pleasant glutinous texture and some sweetness. The cooked product can be freeze-stored for future use, as can the supersweets, but not *sugary-1* (Brewbaker and Banafunzi 1974). *Waxy* locus was introduced to American geneticists by Collins in 1909 from a source in China. Double and triple mutants involving *waxy* were evaluated extensively in the 1970s (Boyer and Shannon 1984; Tracy 1997). Many of these involved the *ae* (*amylose extender*) locus that reduces synthesis of amylopectin. Since *wx* reduces synthesis of amylose, the *ae wx* double mutant greatly reduces overall starch synthesis and increases storage sugars. In Hawaii an OP variety of this type was bred with some tropical adaptability (J. L. Brewbaker, unpubl.) but was rejected despite its high sugar content. The *aewx* corn was difficult to breed and the tiny kernels emerged poorly due to fusarium rots. Other double mutants tested by temperate breeders included *su* with *wx* or with *ae wx*. Some conversions of sweet corns to the high-protein gene *opaque-2* known as QPM (quality protein maize) are also being investigated. As noted previously, field corns with normal amylose starch are often harvested green in the tropics and roasted or boiled. They are customarily of a floury type with much soft starch.

III. BREEDING POPULATIONS AND HYBRIDS

A. Tropical Open-pollinated Cultivars.

'Hawaiian Sugar' is an open-pollinated sweet corn (*su1*) variety that appears in the ancestry of essentially all tropical sweets. It was bred by Dr. Albert J. Mangelsdorf (Figure 3), then of the Hawaii Sugar Planter's Association, and its history is fully detailed in website www.ctahr.hawaii.edu/hfs/HawaiianSugar. Mangelsdorf came from a seed-producing family in Kansas, took his BS there, and became a PhD student of E. M. East at Harvard University, its focus on self-incompatibility. In 1926 he came to Hawaii and became a world expert on breeding of sugarcane, with an honorary PhD at U. Hawaii (1957). He was asked to add both field corn and sweet corn to his sugarcane breeding during World War II in reaction to possible food shortages in the Islands of Hawaii. The source of gene *sugary-1* was from mutants in the variety USDA 34 from Puerto Rico (pedigree unclear). These were crossed with 'Golden Bantam' and 'Ioana' to create a synthetic around 1942. Much recurrent mass selection was evidently conducted before Mangelsdorf's commercial release at U. Hawaii in 1947. It had to be focused on ear rot tolerance and resistance to a stunting virus now known as Maize mosaic virus (Brewbaker and Aquilizan 1965; Ming et al. 1997) Studies during the 1950's of 'Hawaiian Sugar' included several in the Philippines by Dr. H. K. Hayes who had graduated with Mangelsdorf at Harvard University in 1926. Its clear superiority over temperate varieties and hybrids for tolerance to tropical stress conditions was verified abundantly in subsequent research (Brewbaker and Aquilizan 1965; Brewbaker et al. 1966). This variety became wide-spread tropically. A collection of regional selections evaluated in the 1960's in Hawaii revealed significant effects of local adaptation. These include an improved low-ear version said to be from India grown by J. L. Brewbaker in Thailand and by I. Martin in Australia in the 1960s. All had high resistance to fusarium kernel and seedling rots and to the MMV and MDMV viruses that became serious as tropical corn production increased year-round. The 2014 population of 'Hawaiian

Sugar' represents over 20 cycles of recurrent mass and   S1 selection (www.ctahr.hawaii.edu/hfs). Its most significant inbred, AA8, in its current *bt1* version, is Hi80 that enters most commercial hybrids of U. Hawaii (Brewbaker 2010).

Breeding of composites and later of inbred-based synthetics (Table 1) began in 1961 in Hawaii (Brewbaker et al. 1966). All originated in part from *sugary-1* 'Hawaiian Sugar', whose average-to-poor market quality and standability led to its improvement and conversion to these composites. Major 'varietal' trials were conducted on all islands and first displayed at the Oct. 1964 "Sweet Corn Field Day", organized by J. L. Brewbaker and featuring Al Magelsdorf (Figure 3). Publications and conference papers (Brewbaker and Hamill 1967) attracted the 'winter' seed industry to Hawaii, becoming Hawaii Crop Improvement Association and by 2014 the largest agricultural enterprise in the state. Sweet corn research in these large private corporations, however, excludes tropical sweet evaluation or breeding. Three major trials were conducted in 1967-8 by J. L. Brewbaker (unpubl/) at Pak Chong, Thailand, with Rockefeller $_{Foundation}$ support. An autumn trial included 310 of the UH *sugary-1* composites and hybrids and 70 from US mainland. Severity of diseases was great, and on a 1-5 scale included (1) turcicum blight, (2) maydis blight, (3) curvularia leaf spot and (4) southern rust. A trial planted in October of 200 lines (mainland and Hawaiian) was completely wiped out by a combination of downy mildew, turcicum and maydis blights, bacterial leaf blight and southern rust. However a third trial of 400 sweets in early January, 1968 (dry season, irrigated) was successful and identified several outstanding composites and inbreds. Yielding well (i.e., surviving disease) were 'Hawaiian Sugar', new UH composites and UH hybrid H68 that was later marketed widely in Hawaii. Recurrent-selection generations were initiated of Composites HSXComp1 and 2 and HS SYN1 that were seed-increased and helped lay the foundation for sweet corn breeding in Thailand.

Breeding of tropical high-sucrose composites and inbreds proceeded rapidly after the introduction and success of John Laughnan's *shrunken-2* 'Ilini Supersweet' (Tracy 1997). Twenty of these populations are listed in Table 1 are include eight *su1*, three *sh2,* eight *bt1* and one *bt2* (Brewbaker 1998). Six of these were synthetics based on inbreds usually after six cycles of selection, notably for tolerance to fusarium and the blights (details on website www.ctahr.hawaii.edu/hfs). Composites represent OP cutivars often combining widely divergent parents, temperate and tropical. The names have 'Hi' and 'COMP' or 'SYN, a population number, and a letter a, b, or c that represents numbers of selection cycles (Table 1). The most widely grown and used in breeding of these populations have been HibtCOMP3m ('Hawaiian Supersweet #9'; Brewbaker 1977), and its conversion to *y/y* as HibtCOMP9aa ('Hawaiian Supersweet Silver').

The *bt1* gene was chosen as the primary basis for Hawaii's OP variety and hybrid breeding program in the 70's, and the first major release was 'Hawaiian Supersweet #9' (Brewbaker 1977). This variety involved 18 cycles of hybridization and recurrent mass selection at ~10% and based on three sets of crosses of *bt1* composites with *su1* lines and populations. The currently-marketed variety has an additional 12 cycles of recurrent mass selection in both yellow and white endosperm. An added conversion, 'Kalakoa' (Brewbaker 2011) has yellow endoperm with genes *A1 B1 Pl1* for purple stalk and husks. Also typifying their development, 'Hawaiian Supersweet #6' (Banafunzi 1974) involved introduction of allele *bt2* (clearly a duplicate of *sh2*) into tropical inbred Hi27 (Brewbaker 2013), backcrossed three times into 'Hawaiian Sugar', selfed once, then converted by crossing to *brittle-2* inbred Hi38, sib-increased through six cycles of recurrent selection and released (Brewbaker and Banafunzi 1975). Continued in subsequent years were 15 more cycles of recurrent mass selection, creating a uniquely colored (red cob) type of sweet corn, since *bt*2 is not closely linked to basic color loci. Genetic conversions were initiated to brown-midrib, high-lysine, C *Rf4* cytosterility, and to waxy and vestigial-glume genes before turning these into *bt1* populations having better fusarium and disease resistance.

The choice of the *bt1* gene was validated by germination studies of near-isogenic lines by Zan and Brewbaker (1999). In this and related studies, the *sh2* genotype is more closely associated with high electrolyte leakage and related seedling damage by fusarium (Tracy and Juvik 1998). Under accelerated aging, *bt1* kernels survived twice as well as *sh2* (Zan and Brewbaker 1999). Although intensive recurrent selection increased germination of

Hawaii's *sh2* populations significantly, inbreds were   very difficult to maintain in soils with high fusarium spore loads created by continuous year-round planting.

Colleagues in the National Sweet Corn Breeder's Ass'n. (Scully et al. 2001) also released three additional sub-tropical and more or less 'near-isogenic' populations designated NE-EDR (Table 1). The first was *sugary-1* that had a very broad genetic base in 11 outstanding temperate varieties and hybrids crossed with 11 of the best *sugary-1* populations from Hawaii. Conversions followed to *shrunken-2* (Scully et al. 2001) and to *brittle-1* (Brewbaker and Scully 2002). An average of 20 backcross and sibbed generations characterized each NE-EDR variety, and they were bred with high resistance to fusarium rots, tropical blights and rusts. An index of the rapidity of breeding advance largely with mass selection (~10%) in the tropics with three selection cycles per year is that more than 330 breeding populations have been grown for selection in these three populations alone (Brewbaker and Scully 2002). No treatments of seeds or plants with fungicide or insecticide were applied, nor have they been in 50 years of breeding in Hawaii.

Hawaii's composites and synthetics continue to be evaluated and advanced by recurrent selection, currently representing >250 cycles of recurrent mass and S1 selection. In origin they represent about one-quarter 'Hawaiian Sugar' and equal amounts of tropical flints and temperate sweets. They have proved to be useful resources or resistance to fungal and viral diseases, insects, and other problems. Many Asian inbreds trace also to *bt1* 'Hawaiian Supersweet #9' (Brewbaker 1977) and *sh2* 'Hawaiian Supersweet #2'. In Thailand the classic open-pollinated variety is 'Thai Super Sweet Composite #1 DMR' (TSSC#1DMR) (Pulam 2002). This composite was released in 1979 based on crosses of 'Hawaiian Supersweet #2' with Thai field corns resistant to downy mildew (DMR). It was improved through mass selection for DMR tolerance and large 16-row ears and released as 'Super Agro'. Lines from this composite were selected and combined into populations SHBQa (long ears) and SHLQa (large ears) in 1991 by Pulam (2002). Continuing and testcross selection led to choice of population A as superior male and F as superior female in 2000. Temperate *shrunken-2* hybrids and synthetics were used as males in conversions to improve quality. Pulam (1997, 2002) established the Sweet Seeds Co. in 1991 and developed inbreds based on these two heterotic populations. Among these inbreds were two as the basis of Sugar73, the first DMR hybrid in the market. Emphasis in Thailand then focused on line development for hybrids with improved quality and resistance to SCMVirus, rusts, blights and downy mildew. Several public institutions in Thailand are alse involved in corn improvement, including the Universities of Khon Kaen, Kasetsart and Chieng Mai.

In Australia Martin (Martin et al. 1993) initiated tropical-adapted sweet corn improvement in 1969 that focused initially on populations resistant to common rust (*Puccinia sorghi*). The synthetic SHPOP1 was *sh2* based on *su1* lines from Hawaii. A counterpart *sh2* population, SHPOP2, was derived by conversion of a group of *su1* Hawaiian synthetics and Mangelsdorf's 'Hawaiian Sugar' (Figure 2). The two were maintained under reciprocal recurrent selection, maximizing heterosis between them. Early years of selection focused on quality and resistance to common rust, blight, Heliothis earworms, MDMV viruses and quality.

In Africa S. K. Kim (2003) released an African-adapted variety named 'TZsupersweet SR' with resistance to MSV virus and other diseases. This variety was based on 1978 hybrids between the *bt2* population 'Hawaiian Supersweet #6" and "other OP varieties" with the MSV streak-resistant field corn population 'TZSR-Y'. Following cycles of S1 and half-sib selection, it was released in 1981. It is reported to have excellent tolerance of MSV virus and polysora rust with good ear position and resistance to root and stalk lodging. Further cycles of selection have sought to improve market quality, notably tenderness.

A rich assortment of endosperm colors can be found in *sugary-1* corns, in *brittle-2*, and in *waxy-1* and field maize. Such colors cannot occur in the supersweets without breaking the extremely tight linkage of *sh2* with *a1* and the linkage of *bt1* with *a2*. At the *brittle-1* locus, crosses involving mutant allele *bt1A* suggest it is linked to normal allele *A2*, allowing colored endosperms to exist as options for further breeding (T. Pulam and J. L. Brewbaker unpubl.). OP cultivar, 'Kalakoa' has the pericarp/cob genes A B and Pl (purple stem, husks, cob; Brewbaker 2011) and similar Peruvian-derived pericarp and cob color alleles "black" and "red" are being bred.

Breeding methods tend to be as variable as breeders themselves, especially with the very diverse types of germplasm and environment they face with tropical sweet corn. As emphasized throughout the review, our original populations are composites usually from a very wide base. Useable inbreds would be require about 15 to 30 generations. In contrast temperate genetic advance (Gerdes and Tracy 1997; Bernardo 2002) has been possible with inbreds from long-established sweet varieties (e.g., Golden Bantam) or often historic synthetics (e.g., BSSS). The pedigree techniques employed often reflect the limitations of two cycles per year and the focus on high-input production in a limited set of ecosysstems. Recurrent mass selection dominated early population improvement in Hawaii (Brewbaker 1998), only rarely using pedigree selection (e.g., the S2 selection used to create the significant Thai flint Suwan 1). Such populations were most used to provide potentially marketable OP cultivars and baseline varieties for inbreeding. A method developed by Dr. Mangelsdorf (Figure 2) for sugarcane was followed. Cane is a high polyploid where breeding had to be initiated with widely different species and clones. Mangelsdorf started clonal development with a composite of ~two million OP seedlings, expecting no more than 1% selection the first year. One or two annual selection cycles involved composites, and later cycles were built on clonal material. Hawaii's composite breeding followed a similar approach with simple mass selection in OP populations of 5000 or more plants (0.1 ha.). The selected 250-500 ears were bulked for at least two follow-up cycles of a similar nature and replicated at different locations and times of year. Hand sib-pollination normally began in cycle four or five, initially with similarly bulked populations from superior plants. A major participant in this phase was the Hawaii Sugar Planters' Ass'n. working with Mangelsdorf's breeder Chifumi Nagai. She planted many selection cycles at their station on hot dry lateritic soils of low pH and limiting phosphate (Pulam 2002), typical of sugarcane lands throughout the tropics. The G x E evidence from these and similar trials figured significantly in line development, as it was for Pulam in Thailand and Martin in Australia.

Inbreds created directly from composites usually failed due to high frequencies of deleterious alleles and epistatic combinations. As a result all tropical breeders have moved to synthetics based on sets of selfs and sibs, normally no earlier than S3 or S4. Combining the best 10-20 inbreds into a synthetic for future inbreeding and/or use as OP cultivars has become a standard for sweet corn improvement (Brewbaker 1998) and for Hawaii's eight field corn synthetics (Brewbaker et al. 1989). This continues in part as a reflection of the unique value of OP cultivars to small farmers of the tropics. In Australia and Thailand the breeding of improved populations often started with selected Hawaiian composites and focused early on the development of at least two major heterotic groups as basis for inbreeding.

B. Inbreds and Hybrids.

As noted, modern tropical vegetable hybrids are largely supersweet and based on the *sh2* and *bt1* genes. The challenges of both loci are thoroughly reviewed by Tracy (1997). Sugar contents often exceed 40% dry matter at sweet-corn stage. The most extensive development of the tropical inbreds has occurred under leadership of the authors in Hawaii, Queensland and Thailand. They represent a rich assortment of germplasm, temperate and tropical. In Figure 4 their genetic similarities based on SSRs were compared with widely-used temperate inbred Ia453, using the *sh2* version found in 'Florida Staysweet' (Nourse 2002). Large genetic distances generally characterized the two sets of Thai inbreds from different breeders (e.g, bA11 and bF47, Kbt13 and Kbt32) from those bred in Hawaii (Figure 4). A comparative value for genetic similarity is that of ~85% for RFLPs in 71 temperate sweets (Gerdes and Tracy 1994). Unlike temperate inbreds, most tropical inbreds must have major tolerance of diseases such as fusarium rots, southern rust, several viruses (MMV, MCMV, SCMV), turicum blight, and insects like earworms and aphids. They uniquely mimic tropical field corns in stature, absence of tillers and husk leaves, tolerance of low incident light and stress-tolerance to tropical heat and drought. Genetic studies have revealed some commonly polygenic systems and QTLs for some of these traits, undergirding genetic advance in the future.

Inbreeding in Hawaii began with 'Hawaiian Sugar' (Brewbaker 1965) that is now in the history of all tropical sweets, and from composites based on hybrids of 'Hawaiian Sugar' with mainland hybrids (Brewbaker 1965;

Brewbaker et al. 1966). As noted in the discussion of   varietal development, most early inbreds and hybrids tested in Thailand in 1967 failed due to disease. A few emerged from a third set of trials in 1968, with hybrid H68 (AA8 x 442a) soon marketed in Hawaii. Early inbreds showed their Caribbean ancestry with rich kernel color, poor form and standability, and occasional useful polygenic tolerance of diseases, insects and stresses. Twenty outstanding inbreds were chosen in 1968 from inbreeding within several versions of 'Hawaiian Sugar' (Brewbaker 1965). Supersweet inbreeding began in earnest in the 1970's with *su1* inbreds converted to *sh2* and later to the favored *bt1* locus in the first widely distributed composite 'Hawaiian Supersweet #9' (Brewbaker 1971, 1974). Initial marketed *su1* hybrids like H38 and H68 involved a favored inbred AA8 that was later converted to *bt1* as Hi38A and subsequently as Hi80 (Table 2; Brewbaker 2010). It and its white-endosperm conversion (Hi80y) occur in most of Hawaii's important commercial hybrids. Table 2 summarizes the pedigree of Hi80 over its 75 cycles of breeding during six major stages of backcrossing and selfing. Typifying most Hawaii inbreds, Hi80 (as Hi38 in Figure 4) is 22/32 AA8, 7/32 'HSX (*sh2*) Composite 2', 3/32 temperate inbreds like Il442a and with alleles like *Ht1* and *Rp-d* introduced from field corn sources. Early crosses involved the introduction of C cytoplasm male sterility that was subsequently dropped. Similar to that of many of our best tropical inbreds, we wish it could have thinner pericarps. Two new inbreds, Hi78 and Hi79 (Brewbaker 2010), represent an attempt to add thin pericarp, but with the usual problems of germination and emergence in tropical soils.

Table 2. Historical development of inbred Hi80				
Stage	Cycles	Year	Inbred	Approach and Major Emphases
1	16	1966	AA8	Inbreeding from 'Hawaiian Sugar' (*sugary-1*), Yield
2	14	1979	Hi38A	Conversion to *brittle-1*; Resistance to fusarium
3	12	1989	Hi38B	Rust resistance' C *rf4* conversion; Market quality
5	17	1996	Hi38C	Green silk; Brace roots; Erect habit; Yield
6	16	2013	Hi80	Tolerance of MCMV and Southern rust; Staygreen

'Hawaiian Supersweet #10' is a 3-way *bt1* hybrid of (Hi36 x Hi37) x Hi38 released in 1981 that continues to dominate Hawaii's commercial (fresh-market) production. Ears are tapered with 10 husks and tight tip cover, with no lack 'flag' leaves on the husks (Figure 5). An improved version '#10d Improved' = (Hi78 x Hi79) x Hi80 was released in 2013. Modified single-crosses 'Sweet Sarah' (yellow) and 'Sweet Jenny' (bicolor) currently excel in quality and uniformity, and appeal to some growers. These are generally based on the formula (A1 x A2) x B, so that growers plant vigorous seeds harvested on a sister-single-cross hybrid. Hawaii's program is based largely on six open-pedigree inbreds (Brewbaker 2010) that have no simple heterotic grouping (Figure 4: Nourse 2002). Continued advances often represent the occurrence of new races or diseases such as MCMV in 2010 (Nelson et al. 2011). Performance trials of hybrids in Hawaii routinely involve at least one in winter and one in summer. There were 77 such trials involving *bt1* hybrids based on Hi80 at Waimanalo between 1980 and 2000, and many more by I. Martin in Australia and T. Pulam in Thailand.

In Thailand the widely-grown hybrids Wan54 sh2 and Wan88 bt1 have helped Thailand rise to 1st or 2nd place in the world as exporter of sweet corn (Pulam 2014, pers. commun.). Figure 6 shows the Wan54 hybrid (to left) and local Chinese hybrid (to right) with Drs. T. Pulam, J. L. Brewbaker, and S. K. Kim. Breeding in Thailand has involved inbreds and hybrids both based on *shrunken-2* and *brittle-1* genes, the former focused on fresh market and the latter focused on processing. Pulam (1997) released in 1987 the first *sh2* processing hybrid with a background of inbreeding in hybrids of 'Hawaiian Supersweet #2' and local variety TSSC1DMR. This was followed in 2000 by inbreds from two heterotic groups, A for male and F for female. Hybrids based on *shrunken-2* inbreds from the A and F populations came to dominate the fresh market. Exceptional table quality characterized hybrids ATS5 ('Sugar 75') and Sugar 73. Pulam also expanded inbred development to include *brittle-1* lines generally with better seed quality and germination. Two major inbreds, bA11 as male and bF47 as female (Figure 4), became parents of

early commercial hybrids. Later generations provided improved inbreds developed with extensive testcross performance. Inbred bA11 was converted to the *bt1* gene and MMV resistance in Hawaii and renamed Hi79 (Brewbaker 2010). Typical of male parental lines, it is supersweet with tender pericarp but not as good in seed quality, fusarium tolerance, and field germination. Released *bt1* hybrids ATS-1 and ATS-2 came to dominate production for processing on 60,000 ha annually. Emphasis in Thailand continues on resistance to SCMV virus, rusts, blights and downy mildew. Several universities and seed companies are breeding for the Thai and Australian markets, and hold cooperative yield trials.

Hybrid breeding for the Queensland regions of tropical Australia (15° to 20° S latitude) was led by Ian Martin and colleagues McCarthy, Persley and McMahon (Martin et al., 1993). These were on *sh2* populations described above, with increasing focus on tropical pests and diseases. Two major populations (SHPOP1 and SHPOP2) were extracted by Martin on the Atherton Tableland on the basis of their heterosis and common rust resistance using reciprocal recurrent selection during inbred development. One inbred from each population, SHA3 and SHB5, forms the basis of the widely-grown, tropically-adapted single-cross hybrid, 'Hi-Brix 5'. Female SHL3 was reliable in field germination, pale yellow (probably gene *y11*), and 16-rowed, while male SHL5 was long-eared, also pale colored, difficult to self or sib and probably containing a *Ga1* allele. Breeding continued for improved quality, enriched kernel color and disease resistance. Ian Martin (unpubl.) also bred a series of *brittle-1* inbreds based on OP Hawaiian populations. Again this represented a focus on uniform single-crosses based on inbreds derived after reciprocal recurrent selection from heterotic parent populations. Some Hawaii inbreds were well adapted in Queensland and incorporated into breeding of white kernel inbreds. Limited molecular studies of genetic diversity among ten international inbreds (Nourse 2002) confirmed the breadth of the genetic base in tropical sweet corn breeding compared to temperate inbreds like Ia453 (Figure 4).

Inbreeding in the tropics inevitably involves many different selection targets, notably diseases and pests, and multiple generations of pedigreed lines are essential. However, inbred development is relatively quick with year-round nurseries. These factors make it unlikely that dihaploid inbred production will soon replace conventional kernel to kernel inbreeding. The focus on single-crosses vs. sister-single (or "modified") crosses will continue, with SX hybrids excelling in uniformity and sister-singles excelling in germination and emergence. Valuable transgenes like BT11 and Liberty Ready, now found in temperate sweets, will be incorporated into tropical inbreds as the patents expire, both for insect and weed control.

IV. BREEDING OBJECTIVES

A. Disease Resistance.

Plant diseases provide tropical sweet and field corn breeders their most difficult but enticing challenges especially in regions where production is year-round. The costly seed treatments common for temperate hybrids have been generally avoided to allow safe handling worldwide by seedsmen and small farmers. Pratt and Gordon (2006) thoroughly reviewed disease-resistant breeding of 13 diseases under the three categories of fungal, viral and bacterial. Tracy (1997) also carefully reviewed breeding for tolerance of a host of temperate diseases and pests, but that are often of little importance in the tropics. Brewbaker (1979) listed 42 tropical diseases of possible concern in the 9th century collapse of the Maya civilization. The review compared severity in tropical low-, mid-, and high-lands of 14 foliar diseases. 9 stalk rots, 7 ear rots, 5 viruses, 4 smuts and 3 downy mildews. Maize mosaic virus (MMV) was concluded persuasively to have led to the 9th century downfall of the remarkable maize-based civilization of the Maya. Similar collapses (Olmec, Teotihuacan, Zapotec, Anasazi, Inca) will likely succumb in time to the realization that evolving diseases and pests of corn can lead to a downfall through loss of the primary energy source in primitive diets. Early maize races were based on very narrow racial germplasm, often with a single race predominating (Wellhausen et al. 1952).

In Table 3 we list major tropical diseases of maize in the order discussed below—kernel and stalk rots, foliar, viral and bacterial diseases. The diseases are rated for severity in three general ecosystems,--wet lowlands, dry lowlands

and highlands. The simple scale ranges from 0 (none) to 3 (severe), summarizing our experiences with tropical sweet corns in a fashion similar to that of Brewbaker (1979). The scores relate obviously to susceptible maize grown in regions where the disease is known. Most of corn's fungal and viral diseases thrive where corn and related susceptible grasses occur year-round, thus distinguishing them for severity only in the tropics (Table 3). Local management conditions can greatly impact on these severity values; i.e., overhead irrigation and high weed cover favors almost all of the diseases otherwise rare in the dry tropics. Taxonomic nomenclature of pathogens has become challenging due to the return to a single name for fungi, bacteria, and viruses of identical DNA but different morphology (Shurtleff et al. 2014). It is common also to find many species of pathogens, noted here as spp., causing the same disease. Pathogens often incite diseases referred to with simple acronyms such as MMV and BLB. Many of them cause diseases in a large array of related grasses. In their extensive review of breeding resistance to foliar pathogens, Pratt and Gordon (2006) emphasize that the world movement of pathogens and their mutability provides a constant challenge to breeders and producers.

Where improved disease resistance has occurred in temperate regions, it is often monogenic and affect a single race of a disease like common rust and Northern blight (Pratt and Gordon 2006). In contrast such pathogens survive year-round in the tropics and rapidly evolve racial variants. S. K. Kim showed how common this is with *Puccinia sorghi* (Kim and Brewbaker 1977, 1987), with its sexual stage on year-round weedy Oxalis. Improvement for disease tolerance in the tropics also cannot rely on greenhouse screening for monogenic immunity of seedlings. The tropical breeder automatically must focus on the adequacy of genetic tolerance throughout the life of the plant as with the rust diseases (Kim and Brewbaker 1976a, 1976b; Brewbaker 2012) a tolerance that is commonly polygenic. An effective mature-plant tolerance that does not impair yields is usually the primary target of breeding, not the absence of disease symptoms. All of the authors here have created or nurtured reliable field epiphytotics to facilitate selection progress. Experimental trials throughout the year are desirable, since seasonal variations are often surprisingly great. The monsoonal tropics has wet summers and dry winters while Hawaii has dry summers and wet winters. In either environment there is no ideal month to plant for disease resistance breeding. Great differences thus occur in severity that can be related to elevation or season (Table 3). Were all this not so delightfully challenging, our successes could not continue to bring us such rich rewards.

1. Kernel and Stalk Rots.

Fusarium: Fusarium rots of kernels, ears, and stalks are a major challenge to tropical corn breeders (Figure 7, Table 3). They are historically associated with floury corns and sweet corns and resistance is only common in lowland flinty races (Grobman et al. 1961). A major family of rots is caused by *F. moniliforme* J. Sheld., while a related group of stalk and ear rots is based on *F. subglutinans* (Wollenweb. & Reinking) P.E. Nelson et al. (formerly *F. verticillioides* Sheldon). These species are asexual with their sexual phase represented by the genus *Gibberella*. Fusarium levels stay high in tropical soils used year-round and survive on a wide range of susceptible hosts, but are rarely of concern in temperate supersweet breeding, partly because all commercial corns are seed-treated (Tracy 1997). High-sucrose and synergistic temperate hybrids of superior quality like those of Japan's Matsunaga succumb dramatically to ear and kernel rots and insects in the tropics (Figure 8). Symptoms include failure of emergence, weak seedling vigor, yellowish or virescent seedlings that grow poorly, stalk rots, ear rots and kernel rots, and reduced yield. Infected kernels often show cottony mycelia or white pericarp streaks, and the infections can be lead to accumulation of fumonisin, a serious mycotoxin (Munkvold 2003). The sexual stage ('telomorph') of *F. moniliforme* is *Gibberella fujikori* (Sawada) Ito, and other Gibberellas have fusarium 'anamorphs' (asexual stages) that can also be pathogenic. Tropical corn is often grown year-round and the fungus persists on trash. Every corn plant in >800 historic breeding nurseries in Hawaii was believed to carry fusarium (J. Ooka, pers. commun). Among several hundred temperate field and sweet corn inbreds grown in these soils, about 20% failed to emerge without application of seed fungicides.

Germination and emergence of high-sucrose corn genotypes are very slow compared to field corns, exacerbating the fusarium problem (Styer and Cantliffe, 1994). This reflects the levels of sugar and rapidity of electrolyte

leakage from kernels (Zan and Brewbaker 1999).   Untreated seed of temperate high-sucrose corns often do not emerge at all when planted in the winter in Hawaii's cool wet soils. Trials under Regional Project NE124 in January 1990 were illustrative. The trials involved 12 seed treatments on 3 temperate hybrids. Emergence of untreated seed was only 1.5% and the 12 different seed treatments averaged only 8.6%. In contrast the untreated Hawaii check hybrids emerged 85%. In a duplicate June planting the untreated temperate seed emerged 57% and the treated seeds averaged 69% while the untreated local hybrid germinated 93%. On soils not previously used for corn, results similar to the June trial were common in plantings of other varieties at other locations. Seedling disease is directly reflected in emergence vigor, and this is closely correlated to later kernel and ear damage (e.g., in a study of 70 supersweet inbreds, r = 0.65. All major inbreds in Hawaii's breeding programs have been continuously evaluated for fusarium, with inbred sublines selected for tolerance. Data for 38 sublines of the thin-pericarped Hi36 in a 1986 winter nursery were normally distributed around a mean of 5.6 (1-9 scale) with none showing no injury and 12 discarded. This inbred now has a 50-generation pedigree and only rarely shows ear or kernel rotting (Brewbaker 2007).

Mutants that slow kernel dry-down are especially prone to fusarium rots (Figure 8). It is common to observe 3:1 segregations (healthy: infected) on selfed ears that segregate genes like *sugary-enhancer* or the high-lysine and soft-floury *opaque-2* and *floury-2*. Kernel and ear rots by fusarium are greatly enhanced in ears having open tip cover and few soft husks, a characteristic of many temperate sweet corns. Tropical flint inbred Hi27 has never shown such injury but many of its >150 near-isogenic lines have high levels of kernel rot (Brewbaker and Josue 2007; Brewbaker 2013) These are largely sweet or floury endosperm types and include *aewx, bt, h, fl, fl2, o2, o, os, su* and *sh2*. These mutants also tend to germinate poorly and show seedling injury. Four near-isogenic mutants on the short arm of chromosome 3 have unusually high fusarium seedling mortality, suggesting linkage to a major gene for susceptibility (Brewbaker and Josue 2007).

The production of supersweet seeds with high viability requires early harvest followed by gradual drydown. Among the factors increasing severity of fusarium are infections by earworms, armyworms, pineapple beetles and other insects. Breeding for ears with higher husk number and longer husk extension above the tip is essential in the tropics to reduce damage by insects and thus by fusarium and aspergillus, as noted by J. Duvick (2001) and Brewbaker and Kim (1979). Reduction of weed cover and other management practices can also have a significant effect in reducing fusarium infection (Munkvold 2003).

Fusarium can have a major influence on senescence and staygreen, the capability of corn plants to retain full color after physiological maturity. Examples in Hawaii data include a series of 72 closely related sublines of inbred Hi38 (*brittle-1*) converted to *Rf4* for C-cytoplasm restoration. The inbreds differed significantly in germination rates and staygreen scores in Hawaii (M. Logroño 1988, unpubl.). Four inbreds were chosen as parents for three GMA (generation mean analysis) progenies. Two parents averaged 69% germination with a high staygreen score of 2.35 on the 1 to 9 scale (good to bad). Two others averaged 39% germination with staygreen score of 5.90. High heritability values of 38%, 59% and 72% characterized the staygreen data and led to Castle-Wright gene number estimates of 0.89, 1.47 and 0.65 (averaging 1.01). Epistasis for staygreen was significant in only one of the three progenies. While germination rates for the near-isogenic parents were 69% and 39%, they were 75% for F1 and 83% for F2, and 81% for BC to P1 and 70% for BC to P2. These data confirm our general observation that the large and vigorously-germinating seeds of hybrids show high fusarium tolerance as expressed at emergence. Correlations of germinability and staygreen were high for the inbreds, but less ($R^2 = 29\%$) considering all 16 families (P1, F1, F2 and BC). Hybrids thus routinely exceed inbreds in tolerance of fusarium during germination and emergence, but may later succumb to early senescence from the fusarium infection. Early senescence and loss of staygreen was also documented for many mutants of maize in studies of Hi27 and its NILs, known for high resistance to southern rust (Brewbaker et al., 2011). Among 137 NILs grown under a rust epiphytotic, 24 were prematurely infected and failed to show the staygreen typical of this tropical flint inbred. The data were interpreted as indicating a pleiotropic effect of mutants that reduced plant vigor and photosynthesis, enhancing damage by fusarium and reducing staygreen.

Stalk rots induced by fusarium are rare in Hawaii but   much more common in the wet hot tropics. The stalk rots always correlate closely with kernel and ear rots. One Hawaii trial in August 1987 under unusually high temperature and humidity (>33ºC, >90% humidity) led to 100% stalk lodging of eight temperate sweet hybrids but with little damage to Hawaii hybrids. Toxins induced by fusarium are associated with many acute and chronic metabolic effects in animals and humans (Murphy et al. 2007). The toxins are fumonisin and deoxynivalenol that develop late during endosperm maturation and dry-down. They probably do not influence consumers of sweet corn, nor of field or waxy corn. The sexual stage *Gibberella zeae* Schwein) Petch of a related fusarium (*F. graminearum* Schwabe) appears to be common only in cool wet highland areas of the tropics. It can cause an ear rot with white mycelium growing down from the ear tip, and resistance has been little studied but appears to be uncommon in Hawaii's sweets.

All tropical sweet corn breeding programs have required cycles of selection for improved emergence and reduced kernel damage from fusarium. Selection is most effective under conditions that lead to high incidence of disease including high moisture, trash left in the field, and the avoidance of fungicide treatments of seeds or plants. As a result the tolerance of tropically-bred supersweet populations to seedling, ear, kernel and stalk rots is generally quite high (Brewbaker 1998; Brewbaker and Scully 2002).

Aspergillus. *Aspergillus flavus* and *A. parasiticus* are mold diseases of corn producing aflatoxin that can cause severe biological effects in many types of animals (Diener et al. 1983). *A. flavus* creates a strikingly greenish mold on corn ears on susceptible genotypes under hot and wet field conditions, and thus has only rarely been seen at Waimanalo. The pathogen thrives during kernel drydown (between 20 and 15% kernel moisture). As a result the toxins do not occur in vegetable corns consumed at sweet-corn stage (70 to 80% moisture) or harvested at physiological maturity (36%) as common in the seed industry. Temperate dents and sweets are often highly susceptible to aspergillus pathogens, but high tolerance occurs in many tropical sweets and flints tested in Hawaii (Zuber et al. 1982). Intensive breeding continues on grain and silage corns in the southeastern U.S.A., where these pathogens can be most aggressive and reduce marketability.

2. Foliar Diseases. Fungal diseases are very common in tropical maize. Fourteen were reviewed in the Maya study of Brewbaker (1979) and 24 are listed in Carlos De Leon's useful guide to field identification (De Leon 1984). Many of these are also significant temperate problems (Tracy 1997), including more temperate fungi like anthracnose (*Colletotricum graminicola)*. A number of these are summarized at the end of this section under the heading 'stalk rots'. Most challenging for tropical sweet corn breeders are the rusts and blights, with added attention to smuts, mildews and brown spot. Temperate sweet corns are often the standard susceptible checks in tropical disease nurseries. This is largely an indication of their common susceptibility to multi-racial pathogens and of the challenge of converting them for year-round production (Pataky et al. 1998). A large variety of pathogens and stalk borers cause stalk rots

Southern Rust. The dominant rust of warm tropics is southern rust (*P. polysora* Underw.), a pathogen without a sexual stage but with extensive racial variation in the tropics. The disease has become increasingly common throughout the lowland tropics, reflecting increased year-round production of maize (the primary host). A few grasses are believed to serve as alternate hosts, including species of *Erianthus, Euchlaena* and *Tripsacum*. Absolutely no general resistance could be verified in any temperate sweet or field corns (Brewbaker et al. 2011). Included in these evaluations were hundreds of temperate lines studied both in Hawaii and Illinois (Pataky et al. 2001). Several dominant monogenes (e.g., *Rpp1, Rpp9, RppQ*) conferred racially-specific immunity but none were sustainably effective in the tropics. Most tropical varieties and inbreds created by the authors in the presence of southern rust have a stable, polygenic general tolerance expressed as 'slow-rusting' or 'mature-plant tolerance' (Barker 1969; Pulam 1996; Brewbaker, 1998; Brewbaker et al. 2011). Martin et al. (1993) rejected use of monogenes in Australia as they became ineffective through racial evolution, including *Rpp1* (hypersensitive fleck

resistance), *Rpp2* (limited spore production) and *Rpp9*.   They converted two reciprocal sweet corn populations to tolerance using recurrent S2 selection. In the 1960s southern rust arrived in Hawaii, with tolerance high in only a few tropical varieties. Several decades of research and breeding for resistance in Hawaii involved GMAs, NILs, RILs, and backcross conversions using different sources of resistance (Brewbaker et al, 2011). The authors concluded that rust tolerance minimizing yield loss at sweet-corn stage was governed by two major QTLs acting without dominance, while field corn resistance involved more but similar loci. Field corns required a much higher degree of tolerance than did sweets, as rust damage could increase greatly from 18 to 36 days after pollination (typical dates for sweet and field corn maturity). Polygenic tolerance now dominates all Hawaii sweet and field corns and is common among tropical field corns bred in Australia, Colombia, Thailand and Nigeria, countries in which the disease has been dominating since WWII. In Australian trials the temperate hybrid Goldensweet registered 8 on scale of 1 to 9, representing 80% leaf damage. In contrast, I. Martin's marketed tropical hybrid HiBrix5 had a rating of 3 on this scale and advanced experimental hybrids scored a rating of 1.

   Common Rust. Common rust (*Puccinia sorghi*) typifies temperate regions but is rarely serious in subtropics and tropical highlands. Historically problematic for temperate sweet corns, common rust did not become widespread until the breeding and use of inbreds under H. E. Brewbaker (Stakman et al. 1928). Through hybridization the authors achieved high general tolerance to the wide range of physiologic races then known by pathologists. In sweet corn breeding a single race came to dominate northern corn production, for which alleles of the *Rp1* locus on Chrom. 10 provided useful immunity (Pataky et al. 2001). In the tropics the rust undergoes a sexual stage on common year-round weeds like *Oxalis spp.* to give the fungus genetic diversity and greatly reduce yields in cool wet seasons (Kim and Brewbaker 1976b). A. L. Hooker (1967) sent Hawaii 30 sources of monogenic immunity of which six provided temporary protection (Kim and Brewbaker 1976a). Dominant alleles *Rp1-d* and *Rp1-j* were then backcrossed into all of our sweet and supersweet corns and proved effective for about four years. Subsequent racial evolution made these ineffective (Brewbaker 1983, Kim and Brewbaker 1977). International studies also verified the ineffectiveness of these *Rp1* monogenes (Brewbaker et al. 1989). The *Rp-d* allele had been used successfully by temperate sweet corn breeders for 15 years before a new virulent race ended its usefulness (Pataky et al. 2001). These dominant monogenes now clearly segregate in some of our tropical sweet populations but are wisely avoided in breeding.
   General or racially-nonspecific resistance has been used in all subsequent breeding of tropical sweet corns. QTLs for rust tolerance appeared to be common among highland tropical field corns. This resistance minimizes mature-plant injury without providing an immune genetic barrier to the pathogen. The *sugary-1* variety 'Hawaiian Sugar' provided early resistance for sweet corn breeding (Kim and Brewbaker 1977). Kim et al. (1988b) assessed tolerance in Hawaii of 98 temperate American sweet corn hybrids and could report only eleven with a low level of tolerance (<4 on a 1 to 9 scale). Hawaii's entries all showed tolerance that led to the breeding and release of 16 sweet corn composites and synthetics (Brewbaker, 1998) more than half of which were considered adequately resistant for commercial production. Another excellent later source of tolerance was composite NE-EDR in three genotypes—*bt1, sh2* and *su* (Scully et al. 2001; Brewbaker and Scully 2002). Common rust is of less importance than southern rust in Queensland. In 2004 trials, Ian Martin (unpubl.) reported scores of 0.5 for HyBrix5 vs. 5.3 for highly susceptible temperate hybrids Temp x trop hybrids were intermediate. No correlation has been shown between tolerances to common and southern rust (Brewbaker et al. 2011). Genetic advance in common rust through selection has been high in studies relying simply on natural epiphytotics (Kim et al. 1977), inferring the action of few QTLs for tolerance.

   Northern Leaf Blight (NCLB). Northern and southern corn leaf blights are among the most serious pathogens of corn worldwide. Northern blight is largely temperate or highland tropical and is caused by *Setosphaeria turcica* (formerly *Exserohilum turcicum* and before that *Helminthosporium turcicum*). Breeders simply call it NCLB or 'turcicum blight' (Figure 9). NCLB has been the subject of an incredible number of

research studies, and is a major subject of corn breeding   in Australia, Hawaii and Thailand. Emphasis is primarily on field corns where high levels of tolerance are essential to avoid yield loss. Most tropical-bred supersweet populations segregate adequate tolerance to harvest stage, but high tolerance is rare among temperate sweet corns (Pataky et al. 1998). NCLB is an uncommon disease at low elevations in Hawaii, even with controlled inoculation. However it is consistently severe at Hawaii's highland Mealani Research Station (830 m) where turcicum returns every summer and annual evaluations and breeding for tolerance are effective without inoculation. Dominant monogenes *Ht1, Ht2, Htn* can provide racially-specific resistance (Welz and Geiger 2000), but as with the rusts these monogenes soon became ineffective in Hawaii and many tropical regions due to racial evolution (Kim et al. 1988a; Brewbaker et al. 1989). In the 1970s the dominant, immune-type, *Ht1* resistance was bred quite simply into a series of our sweet corn inbreds in Waimanalo, but all failed within three years. One set of 125 RILs from the field corn hybrid of B68Ht1 x Thai Ki14 segregated 1:1 for *Ht1* resistance to the single race at Texcoco, Mexico, in 1997. However the same RILs in Hawaii showed that *Ht1* was ineffective (Figure 9). Tolerance segregated quantitatively under the mixture of races in Hawaii, with the suggestion of a major co-dominant QTL (provisionally named 'Etu') for tolerance from Thailand's flinty Ki14. Six international sets of NCLB data on 165 corn inbreds grown in Nigeria, Kenya and Hawaii were collected by our collaborators (Kim et al. 1988a; Brewbaker et al. 1989). The wide range of tolerance is evident from summaries of the data in percent of their mean; 22% highly resistant, 36% somewhat tolerant, 23% not tolerant and 13% susceptible. Inadequate tolerance characterized >80% of temperate inbreds. Only a few tropical sweet populations have been improved in Hawaii for this tolerance, often because their value is largely restricted to highlands. Hawaii's six major *bt1* inbreds and most of their hybrids have proved to be adequately tolerant (Brewbaker 2010). Australia's commercial tropical sweet hybrid HiBrix5 was ranked as highly tolerant to NCLB while commercial temperate hybrids failed. While a wide range of tolerance to NCLB has segregated in Hawaii's field corn RILs and GMAs, we would confirm the general conclusion (Welz and Geiger 2000) that high tolerance involves a combination of racially-specific monogenes and co-dominant QTLs. As with resistance to many of corn's pathogens, NCLB data remind us of the amphidiploid origin of maize and the evidence for duplicated chromosome segments throughout the genome.

Southern Corn Leaf Blight (SCLB). This disease is caused by *Cochliobolus heterostrophus,* better known as *Bipolaris maydis* and earlier known as *Helminthosporium maydis*. It is referred to simply as 'maydis blight' or SCLB The pathogen causes elliptical leaf lesions and is sub-tropical or -temperate. It has not been problematic in Hawaii or in most of the lowland tropics. Maydis gained international notoriety in 1969 for the severe susceptibility conferred by the T cytoplasm, making the disease strikingly widespread throughout U.S.A. Replacement of the T with the S and C cytoplasms solved the problem. Our international evaluations of maize inbreds at eight locations provided satisfactory epibiotics at only three—South Korea, highlands of Mexico and highlands of Nigeria (Kim et al. 1988a; Brewbaker et al. 1989). Resistance was most notable among inbreds from Earl Horner's program in Florida and inbreds from Thailand and Nigeria. In Florida several sweet corn hybrids have been bred with adequate resistance, presumed often to be a single recessive gene *rhm* or a pair of genes that became the subject of intensive biotech investigations (Chang and Peterson 1995; Simmons et al. 2001). This type of simple inheritance appears to segregate in the broad-based 'NE-EDR' composites of Scully et al. (2001) and in commercial composites and hybrids (Pataky et al. 1998). However monogenes of this type appear to be wisely avoided by tropical breeders. S. K. Kim bred a resistant African supersweet variety 'TZsupersweetSR', and resistance was selected for most of the IITA field corn inbreds adapted to mid elevations (Kim 2003). Their evidence suggests that tolerance can be treated by breeders as a quantitative trait based on few co-dominant loci. Southern leaf blight is less serious than NCLB in tropical Australia, but can reduce yield in periods of warm, humid weather.

Yellow Leaf Blight is a disease caused by *Ascochyta ischaemi*, also known by its former name 'Phyllosticta leaf spot' (pathogen then named *Phyllosticta maydis*). It leads to narrow necrotic lesions in young leaves that

extend in mature leaves to large blighted areas. It can be   found on plants under the same wet highland conditions as turcicum blight (long dew periods, cool nights and warm days). In our four decades of study in Hawaii it was only seen twice (1974, 2002) on a few plants in breeding nurseries at the highland Mealani station (900 m). It was never seen in the lowlands. Phyllosticta was earlier associated with the T-cytoplasm via its sexual stage, *Mycosphaerella zeae-maydis*. This became a serious disease in late 1960's in northern U.S.A., and susceptibility was ascribed to the T cytoplasm as it was for SCLB. Little is known of resistance breeding.

Purple sheath rot is a condition related to fungal organisms colonizing detritus inside the leaf sheaths, and tends to be common in plants with very short internodes under the ear. It can lead to poor ear development, even in sweet corns. Studies in Queensland by Ian Martin (unpubl., 2013) revealed high tolerance of tropical hybrid HiBrix5 with other hybrids ranging as high as 45% infection.

Smut Diseases. Common smut is caused by *Ustilago zeae* and is common in humid temperate regions but of less importance in the warm tropics. Smut swellings can be scattered over ears or cut tissues, and are often irregular in appearance or "smutty" (Figure 10). Well-formed smut heads developed from infected kernels are harvested as a preferred mushroom in Latin America as "huitlacoche". Genetic tolerance appears to be widespread. The unrelated 'head smut' is caused by the fungus, *Sphacelotheca reiliana* and can lead to severe damage in temperate regions (Oregon, California, S. Africa) and in dry temperate regions of the tropics. However, resistance appears to be common in tropical field and sweet corns (Brewbaker et al. 1989). Some resistance QTLs were mapped by Lu and Brewbaker (1999). The genus *Claviceps* is a source of the toxin, ergot, that can be very serious for humans and animals on infected grasses like rye and wheat. It was listed as known on corn in tropical highlands by Brewbaker (1979) but could not be confirmed.

Downy Mildews: The downy mildews represent a large family of related genera and species that can seriously reduce yields of corn and other grasses. In Asia these are predominantly in a group of Asian downy mildews (*Peronosclerospora spp*., formerly in genus *Sclerospora*). Resistance was identified by D. L. Umali (1952, pers. corresp.) among historic southern Philippine white flints (Cebu White, Tiniguib White, Aroman White Flint) commonly eaten in preference to rice. This resistance is quantitative and largely additive genetically (Kim 2003; Pulam 2003) and has been incorporated into several tropical field corns, especially by Thai and Philippine breeders. Seed treatments originally provided protection but have proven increasingly ineffective in curbing the pathogen, and resistance remains a challenge for sweet corns (Pulam 2003). A sub-temperate family of downy mildews includes 'crazy top downy mildew' (*Sclerophthora macrospora*) that appears not to occur in the tropics.

Brown Spot. Brown spot is caused by *Physoderma zeae-maydis* (also known as *P. maydis*), an obligate parasite of maize and teosinte. The pathogen can lead to leaf and stalk lesions, which seem to display a daily light-related cycle in Hawaii. The disease characterizes warm, wet locations notably of southeast U.S.A. (Thompson 1969). It is rare in the tropics and only seen under high humidity, e.g. under overhead irrigation (but rarely with drip) in Hawaii. Spores of brown spot are carried over the winter in corn trash, but do not survive well in plowed, hot soils and infect only under high humidity. In the summer of 1972 at Waimanalo (spray irrigation) our survey of 95 tropical and temperate inbreds revealed 9 to be highly resistant, 16 resistant, 51 intermediate and 19 susceptible (J. L. Brewbaker and students, unpubl). Resistance was equally common among temperate and tropical inbreds. Our supersweet inbreds rated very well, as did Hi27 and its NILs. One assessment of segregations from near-isogenic crosses of Hi38 (*bt1*) hybrids later revealed a common pattern of single gene dominance for resistance. In broader surveys of germplasm in E. USA genetic control was concluded to be quantitative but largely additive (Thompson 1969). Little breeding advance has been reported for tropical supersweets.

Other Foliar Diseases. Many pathogens of the grass family also 'visit' maize, occasionally with significant damage in specific ecosystems. Some are only found in the tropical highlands, regions of less importance in

tropical maize production. *Cochliobolus lunatus* (formerly *Curvularia lunata*) is a leaf spot member of a huge genus (~80 species) formerly identified as in genera like *Drechslera* and *Curvularia*. The fungus, like many, is now known to cause human diseases, and represents a genus of which many cause allergies. Although considered prominent in the subtropics, it has only rarely been associated with significant disease in corn, perhaps reflecting widespread resistance. It did become prominent in our winter nursery in 1967 in Thailand as a leaf spot (J. L. Brewbaker, unpubl.). *Cochliobolus carbonum* is a rare leaf blight of this genus, whose sexual stage has the more familiar name, *Helminthosporium carbonum*. It is prominent in temperate regions and rare in highland tropics. We found it problematic one late summer at our highland station (900 m) in Hawaii (J. L. Brewbaker unpubl). It has been known to be seed-transmitted. *Cercosora zeae-maydis* is a blight known as 'grey leaf spot' (or GLS) that is primarily problematic in temperate regions. It has been especially serious in southeastern USA, but can be found internationally and represents a huge genus affecting many crops. Spores require ~13 hours for germination, and only survive well in organic soils such as those managed with minimum tillage. Breeding resistance has been challenging. *Physopella zeae* causes rusty leafspots similar to those of common rust, but severity never matches that of the lowland Southern rust. It is a rust primarily of Latin American and Caribbean wet lowlands. Resistance must be fairly common, one study showing that it was polygenic (probably digenic), and largely additive genetically, like most the foliar diseases discussed here.

   Other Stalk Rots; Many of the pathogens listed above and bacteria listed later can cause a rotting stage of corn stalks, for which much 'stiff-stalk' breeding has had to be directed. These rots seem especially common in temperate regions with long periods of high humidity and high temperatures during early growth, often resulting from spores on leftover trash in cold soils. Many of these are rarely seen in the warm tropics, in part due to the rapid composting of trash in hot soils. Some may be seen in the cooler highlands, but none appear to have been reported as problematic on tropical sweet corn. Included in this list is the serious rot and blight due to anthracnose, *Colletotricm graminicola*. Others commonly cited in websites from universities in the USA include diplodia (*D. maydis*), pythium (*P. aphanidermatum*), nigrospora stalk rot (*N. orzyae*), and the furarium and physoderma pathogens reviewed above.

3. Viral Diseases. Viral diseases present sweet corn breeders a primary challenge in most of the tropics (Table 3). They and their transmitting insects are often confined to tropical or sub-temperate regions where over-wintering occurs. Thus, resistance is generally absent in all vegetable corns evolved in temperate climates (Brewbaker et al. 1991). Ten of the 13 viral and bacterial diseases listed by de Leon (1984) represent virus diseases that dominate the attention of tropical maize breeders. Many were the focus of our studies of 20 major tropical diseases that could have led to the collapses of early Latin American civilizations, e.g., Maya, Teotihuacan, Oaxaca and Anasazi (Brewbaker 1979). Maize mosaic virus (MMV) was concluded to be the cause of the 9th century collapse of the Maya civilization of Guatemala and southern Mexico.

Maize Mosaic Virus (MMV). No temperate sweet corns (Figure 11) and only a few temperate field corns have resistance to MMV (Brewbaker 1981; Brewbaker et al. 1991; Ming et al. 1997). This virus is found only on *Zea spp.* and is transmitted by a tropical leafhopper (*Peregrinus maidis*) that is restricted largely to maize. Thus the disease has only become serious where maize is grown year-round as it often is with sweet corn. The disease is thus rare in tropical regions with prolonged dry seasons. A similar if not identical virus is addressed as 'maize stripe virus" in Australia. A major gene *Mv* conferring sustainable tolerance but not immunity to MMV was identified in the variety 'Hawaiian Sugar' by Brewbaker and Aquilizan (1965). The gene was confirmed to exist only in maize races of the Caribbean islands (Brewbaker, 1979). The resistant gene was thus unexpectedly brought from Puerto Rico by A.J. Mangelsdorf (Figure 3) while breeding 'Hawaiian Sugar' (*sugary-1*) and its counterpart field corn 'Hawaiian Yellow'. It was subsequently transferred to all varieties and inbreds in the Hawaii program (Brewbaker 1998) and mapped by Ming et al. *(*1997) to chromosome 3L-78. The virus persists in leafhoppers, once

attained, and there is evidence that MMV resistance may   be related to this persistence (Higashi et al., 2013). High resistance requires homozygosity of co-dominant *Mv* locus (Moon et al.1999; Figure 6 in Moon et al.). With year-round production becoming increasingly popular in the tropics, MMV is expected to become common throughout the tropics in the future. As noted above, compelling evidence was presented (Brewbaker 1979) that the Maya collapse in the 800's involved MMV due to a newly introduced leafhopper, undoubtedly *P. maidis*, from the Caribbean. The Maya grew only a single highly-susceptible variety Nal-Tel, a situation typical of most civilizations prior to 1000 AD.

Maize dwarf mosaic virus (MDMV) and *Sugarcane mosaic Virus (SCMV)*. These viruses belong to the Potyvirideae, the most destructive family of plant viruses (Pratt and Gordon 2006). Many strains of MDMV and SCMV exist on corn in this family, some transferable by Johnsongrass (*Sorghum halapense*). They constitute the major aphid-transmitted family of corn viruses. Resistance is uncommon in temperate sweet corns but evidently common in tropical supersweets and southern U.S.A. field corns (Brewbaker et al. 1989; Brewbaker et al. 1991). In tropical regions like Australia and Thailand resistance is essential to the aphid-borne Johnsongrass strains like A and C. Martin and colleagues showed that monogenic co-dominant resistance occurred in their *su* and *sh2* composites (Persley et al. 1981; Martin et al. 1993). Five cycles of recurrent selection under virus epibiotics advanced tolerance from 20% to 90% in populations SH POP1 and SH POP2. Simply-inherited resistance to both MDMV and SCMV proved to be common in all basic Hawaiian populations (Brewbaker et al. 1991). MDMV/SCMV has not been encountered at Waimanalo, Hawaii, in the past two decades, although aphid infestations occur periodically. The potyviruses of the MDM family show great biochemical differences that also lead to variations in symptom severity following inoculations of seedlings vs. mature plants. Resistances appear to involve few loci, but with a major QTL labeled *Mdm1* located on Chromosome 6 (Pratt and Gordon 2006). MDMV has become of greater interest as a 'partner' virus with MCMV causing a lethal reaction known as MLN (maize lethal necrosis), common in highland Africa.

Maize Streak Virus (MSV). All temperate and many tropical sweet corns are susceptible to maize streak virus, also known as corn streak virus (Kim et al. 1987b; Brewbaker et al. 1991). Historically it has been one of the most important disease problems for corn in Africa. This geminivirus is transmitted largely by *Cicadulina spp.* leafhoppers and causes leaf streaking and dwarfing of plants. Corn is the preferred host but the virus also occurs widely among tropical grasses. Extensive breeding research at IITA in Nigeria by S. K. Kim and associates (Kim et al. 1987b, 1989a, 2003) led to the release of many well-adapted and highly tolerant field corns. One supersweet OP variety 'TZsuper-sweetSR' was also released in 1981 with MSV tolerance that was later reinforced through 10 cycles of selection (Kim et al. 1987b). Major and modifier genes conferring tolerance have been identified from many sources and are thoroughly reviewed by Pratt and Gordon (2006). However, the disease remains a persistent challenge. Strain variations of MSV are common and perhaps account for the difficulty in breeding resistance. Several types of polygenic genetic control have been supported by research data, but universal is the co-dominant gene identified by Kyetere et al. (1995, 1999). It was derived from Kim's inbred TZi4 (Kim et al. 1987b) and segregated in a set of RILs as a single co-dominant gene (Moon et al., 1999; Fig. 2h). Lu et al. (1999) mapped this gene on the short arm of Chromosome 1 near umc167, an area of several other disease resistance loci (e.g., *sw1* for Stewarts' wilt). If and when sweet corns become popular in Africa, resistance will be important.

Maize Chlorotic Mottle Virus. MCMV has become much more serious internationally as it can interact with potyviruses (MDMV, SCMV) to cause plant death or "maize lethal necrosis' (MLN), to be reviewed below. However, MCMV alone can seriously injure susceptible lines, and occurs on many different grasses. It is of no or little concern in temperate regions and was not included in the review of Pratt and Gordon (2006). The virus is transmitted in Hawaii mainly by thrips (Nelson et al. 2011). A survey of 103 field and sweet inbreds revealed 47 to be highly resistant, 32 to be tolerant, and 24 to have little or no tolerance, with temperate inbreds dominating the

susceptibles and tropicals dominating the highly   resistant lines (J. L. Brewbaker, unpubl.). Supersweet *brittle-1* inbreds and near-isogenic lines were largely susceptible, inferring a linked locus on Chromosome 5. Natural epibiotics have been maintained easily at Waimanalo since MCMV first was observed in 2010. High tolerance was bred into most of Hawaii's OP cultivars and inbreds of sweet and supersweet corn through several generations of recurrent or backcross selection. Heritability data imply a digenic form of tolerance, with one locus linked to *bt1*.

Maize Lethal Necrosis ("Corn lethal necrosis") is a disease of increasing concern in the tropics that represents the interaction of two viruses, MCMV and strains of MDMV or of wheat streak mosaic virus (Nelson et al. 2011). It first occurred in the Republican Valley of Nebraska 30 years ago and was known as CLN. Due to high genetic tolerance of the two interacting viruses, MLN has not been observed at Waimanalo in Hawaii with MDMV-resistant germplasm. It has led to major crop losses in highland East Africa since 2010, but appears to be uncommon in the hot lowlands.

 Maize Rough Dwarf Virus (MRDV) is in a family of related viruses found on many subtemperate grasses. It can be leafhopper transmitted to corn, causing leaf irregularities like tissue overgrowth and stunting. The virus has been most serious in sub-tropical and temperate regions like Korea (where it has been referred to as Black Streak Dwarf Virus) and in Mediterranean countries. A related subtemperate disease of grasses in Argentina is caused by Maize Rio Cuarto Virus (MRCV). These viruses are evidently uncommon in the tropics and little is known of the genetic basis for tolerance (Pratt and Gordon 2006).

Other Minor Viruses. Maize Chlorotic Dwarf Virus (MCDV) creates a rather unpredictable disease in sub-temperate regions, and tends to mimic MDMV. It is transmitted by leafhoppers in the genus *Graminella* and largely in sub-temperate regions where johnsongrass overwinters. Resistance is common among Caribbean tropicals (Pratt and Gordon 2006), but the disease is virtually unknown in the tropics. *Cereal Chlorotic Mottle Virus (CCMV)* is a minor disease of sweet corn in Australia that causes fine striations on leaves. It occurs on several common perennial grasses and can be spread to corn by leafhoppers. Resistance appears to be common in corn (L. Persely, pers. commun). *Maize Sterile Stunt (MSSV)* is a rare disease on corn in Australia that causes severe stunting with leaf discoloration. Tassels and ears can be reduced or eliminated. Transmission is by leafhoppers from common perennial grasses, and little is known of tolerance in corn to the virus. *Maize Rayado Fino Virus (MRFV)* is known only from the tropical Americas and is transmitted by leafhoppers of the genus *Dalbulus*. It causes fine leaf striping ("rayado fino") and chlorotic mottling, but rarely causes plant dwarfing. Resistance seems widespread in tropical races and breeding lines, and little is known of its inheritance. It has not been reported on Hawaiian supersweet varieties grown in Central America.

4. Bacterial Diseases.

Corn stunt disease (*CSD*). CSD has also been called 'Maize Bushy Stunt Disease' (MBSD) and has proved to be one of a dozen bacterial pathogens that can be found on corn in tropical and sub-temperate climates (Nault 1980; de Leon 1984; Shurtleff et al. 2014). CSD has been seen in the southern U.S.A. and can be serious in Central and South America. It is caused by an unusual type of spiral bacterium lacking cell wall, *Spiroplasma kunkelii* Whitcomb et al. Transmitted by leafhoppers (e.g., genus *Dalbulus*) it also can infect insects and some animals. It seems to be unknown in Hawaii and in Asia. First described on maize, CSD apparently can infect all related *Zea* species. The disease is marked by broad yellow chlorotic stripes (later turning reddish), stunting of plant, and abortive effects on tassel and ears (Nault 1980). It was earlier thought to be a strain ("Rio Grande") of the corn stunt virus known as 'achaparramiento' in Latin America, but has proved clearly to be bacterial. Temperate sweet corns appear to be susceptible (Nault 1980). 'Hawaiian Supersweet #9' has been planted many times in Colombia, Mexico, Costa Rica and other Latin American countries without reporting this disease (J. L. Brewbaker, unpubl.)

Bacterial Stalk Rot (BSR). The BSR family of diseases occurs under hot (28° to 30°C) and wet (90-100% RH) conditions in the tropics. These diseases cause late stalk rots with a foul smell that easily distinguishes them. Their taxonomy is very challenging and changing with newer DNA sequencing methods, as is happening to all bacteria (including the ~500 species in human bodies). The common BSR diseases have causal organisms in the genera *Erwinia* and *Xanthomonas* with the most common in S.E. Asia being *Pectobacterium chrysanthemi* pv. zeae Burk., McFad., and Dim. (formerly *Erwinia chrysanthemi* pv. Zeae). This BSR disease is ranked by Subekti and Salazar (2007) together with downy mildew and turcicum blight as one of three most serious tropical corn diseases. In contrast it has never been serious and only rarely suspected in the Hawaii research. The rotting bacteria are worldwide on literally hundreds of hosts and easily transferred on trash, manure, and living tissues. Stalk rot verified as *E. chrysanthemi* appeared in one of Hawaii's research fields (A. Alverez, pers. commun.) after farm staff accepted and spread loads of discarded soil suggested to be pineapple trash. Some genetic variation occurred among the hundred or so genotypes in the nursery, with Antigua inbred Hi34 quite tolerant. However the disease was short-lived and was not seen later. Painstaking hand-inoculation resulted in severe damage to all genotypes in a 6-entry field corn diallel of Subekti and Salazar (2007) in the Philippines. Tolerances of inbreds were highly correlated with those of hybrid array means, and a polygenic tolerance system with high additive variance was implied. No or little work has been done on tropical sweets. A similar BSR disease assumed to be *E. carotovora* subsp. *carotovora* (Jones) Bergey et al. was once observed inducing stalk lodging at Waimanalo under hot wet conditions of late August.

Bacterial Leaf Blight (BLB). This is a rare but worldwide disease caused by *Pseudomonas avenae* ssp. *avenae* Manns, an organism also having a wide host range notably on grasses. Leaf lesions originate as tiny spots that can coalesce and form extensive necrotic blotches and be followed by stalk rot above the ear. Early epiphytotics in SE U.S.A. showed most field corns to be resistant, but temperate sweet corns were often susceptible. BLB has occurred on rare occasions in Hawaii over the past two decades but confined to a few highly susceptible inbreds. Among these are Hi51 (formerly Fla2BT73) and Hi55 (formerly ICAL224br2) that became subject of intensive genetic study by Moon (1995) and Moon et al. (1999). During several generations of their conversion to the *Mv* allele for MMV resistance, these inbreds often segregated susceptible plants. H. G. Moon bred a series of 100 RILs based on the hybrid of Hi51 (susceptible) with Korea's DB544 (resistant) that were scored for BLB following manual infection by J. Pataky in U. Illinois and under natural infection at Waimanalo. The data ranged widely on the quantitative scale (1 to 9), especially in Hawaii, but fit closely a monogenic model, with co-dominance (Moon et al. 1999). Goodness of fit values were excellent (76.5** in Hawaii and 69.8** in Illinois) when applying the Brewbaker (2003) approach to RIL interpretation that is based on expected values derived from RIL parent means and variances. BLB did not appear among any tropical sweet corns in UH breeding programs during this time.

Bacterial Leaf Stripe (BLS) is caused by *Pseudomonas andropogonis* and occurs on many grassy hosts, is widespread and rarely of significance in corn. The disease is most obvious in highly susceptible inbred lines as fine, parallel, chlorotic leaf stripes that can coalesce. It is a disease of warm wet conditions, spread by weedy grasses and known to be seedborne. BLS has only rarely been confirmed in Hawaii and genetic resistance appeared to typify our sweet and field corns.

Stewart's Disease is a bacterial wilt diseasse caused by *Erwinia stewartii t*hat is extremely rare in the tropics but is among the best known bacterial diseases of corn. It is commonly transmitted by beetles (e.g., *Chaetocnema pulicaria*), can be seedborne, and historically was quite severe on sweet corns in temperate regions. Many early publications concluded tolerance to be polygenic with high additive effects. Moon et al. (1999) reported a 1:1 segregation in Kentucky of a single co-dominant allelic pair among 71 RILs of Hi58 (resistant and based on Ki14) and Hi31 (susceptible and based on B68). Hybrids were intermediate in tolerance indicating co-dominance at this

locus. Ming et al. (1999) designated the locus *sw1* and   mapped it with RFLPs near umc167 on the short arm of Chrom. 1. A similar modifying locus was mapped to Chrom. 9. The Chrom. 1 gene *sw1* occurred among a cluster of resistance loci also linked to umc167 including gene *msv* for maize streak virus (Lu et al. 1999).

B.   Insects and Other Pests.

Among the problems cited by growers of year-round tropical sweet corn are earworms, armyworms, rootworms, aphids, leafhoppers, spider mites, thrips, rose beetles, seed weevils, parasitic Striga plants, birds, rats, mice, pigs and people. Temperate sweet corn growers probably are concerned only about raccoons (and perhaps people), since growing a one-season crop and icy winters eliminate most other problems.

Earworms and Armyworms. Vegetable corn breeders in the tropics are inevitably concerned with pantropical earworms (*Helicoverpa zea*) and fall armyworms (*Spodoptera frugiperda*). Less has been reported on tropical rootworms that are common on corn and other grasses in temperate regions. Nematodes appear also to be of no significance. The earworm is a pest of hundreds of plant species, including many important crops (cotton, tomato, lettuce, sunflower). Husk numbers and husk tightness correlate highly with damage (Brewbaker and Kim 1979). Temperate sweet corns have few and soft husks (6-9) that often do not close tightly over the 12- or 16-row ears and even open out at tip of the ear. At night the earworm moth lays hundreds of eggs focused around the (warm) tip of ears, and only very tight husks reduce insect injury. Typical examples include temperate sweet inbred P39 (5.5 husks) and field inbred B73 (7.7 husks), vs. Caribbean-based sweet Hi38 (12.0 husks) and field inbred Hi29 (14.4 husks).

Early studies of earworm tolerance found no variation due to husk numbers, but were based on temperate sweet corns with very few husks. However, tropical corns have many husks (figure 12) that are coriaceous and tightly wrapped around tapered 14- or 18-rowed ears. Illustrated in the figure are husks typical of lowland tropical corns, with 15 in the photo that range from partial tip cover (~2 cm) to extended cover (~7 cm). Brewbaker and Kim (1979) showed that injury to corn ears by earworms in Hawaii and fall armyworms in Colombia were both correlated linearly with husk numbers up to 20, with r values of -0.40 for earworms and -0.68 for armyworms. Genetic analyses revealed a high ratio of GCA to SCA (5.3) but low narrow-sense heritability (24%) largely due to high environmental variability. No evidence was found for monogenes or dominating QTLs for tolerance. Similar results are reported by Martin (pers. corresp.) in breeding for reduced damage in Queesland. Most tropical sweet corn breeding has been on lines with more than ten husks that are often very long and provide excellent tip cover. A tightly wrapped ear tip ensures that the cannibalistic earworms will have fed largely on each other, and ears with row numbers of 10 or 14 or 18 excel in tolerance because of spiraling at eartip and the related tight husk cover. Among the highest husk numbers are races like 'Zapalote chico', the source also of silk flavonoids like maysin related to the *P* locus (pericarp and cob color) and rather toxic to earworms (Scully et al. 2001). Some experimental breeding for high maysin (I. Martin and J. L. Brewbaker, unpubl.) was discouraged by its association with reddish silks that blacken on drying or cooking. Although low numbers of fragile husks are greatly preferred by processors of temperate sweet corns, pretreatment of the tropical hybrids with hot steam facilitates husk removal in Thailand (T. Pulam, unpubl.). Improved control of earworms and armyworms can also lead to reduced infection by fungi (fusarium, aspergillus) and reduced fusaritoxins. The introduction of BT11 and other transgenes for control of chewing insects has been attractive in field corn and other corns for control of stem borers and earworms. Temperate BT sweet hybrids have been grown in Hawaii's summers with minimal earworm damage, but they are otherwise ill-adapted. Patent expiration will ultimately release the BT transgenes for public breeders' use, but concerns might remain for evolution of resistance in the pest that of course has a huge number of hosts.

Stalk Borers. The Asian Corn Borer, *Ostrinia furnacalis* (Guenee), known as 'ACB', is the most serious pest on maize in S. E. Asia (Nafus and Schreiner 1991). Several closely related species are considered present and potentially damaging throughout this region, but the famous European corn borer (*Ostrinia nubilalis*) is not among

them. The Asian borer's moths have an immense   number of host plants including sugarcane, sorghum, ginger, millets, cotton, Johnson grass and other weeds. They can cause damage on almost any of corn's organs from stalk to ear to tassel. Complete crop loss has been reported on sweet corns in Guam and the Philippines. The principle value of the BT transgene in Asia is for reduction of borer damage. This has been very effective in the Philippines but has not yet come into use in 2014 in other countries nor in tropical sweet corns. Some biocontrol measures can reduce damage, notably using the parasitic wasp *Trichogramma ostrinieae*. Some genetic tolerance to the European corn borer also occurs in tropical maize to reduce stalk damage, e.g. Hawaii's flint inbred Hi34 from Antigua. This rarity of genetic tolerance combines with the short season of sweet corns and reduced concern about mature stalk breakage has discouraged efforts in breeding tolerance in vegetable corns.

Thrips and Mites. Injury by thrips (*Frankliniella spp.*) on corn seedlings has been a persistent problem for Hawaii's seed industry based on temperate corn inbreds and hybrids. In contrast injury from the omnipresent thrips has never been noticeable in the Hawaii sweet-corn program, suggesting tolerance. Thrips are among the major transmitters for the maize chlorotic mottle virus (MCMV). Punctures by thrips may also exacerbate damage from fungi. MCMV resistance is common among tropical corns, but evidence for exclusive resistance to the thrips is wanting. Many types of spider mites can also be found on corn around the world. However, they are customarily associated with maturing leaves well after sweet-corn harvest.

Maize Seed Weevils. The maize weevils (*Sitophilus zeamais*) cause major losses to dry corn grain throughout the tropics. They can be most severe on floury or soft endosperm kernels, as the noted QPM or high-lysine (*opaque2*) varieties. Vegetable corn seeds show no unique resistance to weevils, and a common routine for tropical seedsmen is to freeze seeds briefly or treat with insecticides. A useful addition to bagged seed is diatomaceous earth. Genetic analyses have revealed QTLs associated with increased tolerance that involves cell-wall bound phenolics in pericarps, thus of interest for all types of corn seeds (Garcia-Lara et al. 2010).

Aphids and Leafhoppers. The corn-leaf aphid (*Rhopalosiphum maidis*) and other aphids are largely tropical and can cause severe damage to vegetable corns through infection of tassels and ears. Complete crop failures have been observed. Infestation often reduces greatly the value of fresh-marketed ears, as aphids hide under the husks. Tolerance is uncommon in tropical materials and largely absent in temperate (Carena and Glogoza 2004). Aphids also transmit viruses like MDMV and SCMV, to which most tropical sweets are resistant. Aphid resistance was observed in Hawaii among sub-lines of *bt1* inbred Hi38 by Brewbaker and Chang (1974). Genetic studies of this resistance were conducted by So (2003) using insects in clever cages attached to lower corn leaves. This research extended to a set of GMA progenies from the resistant inbred Hi38-71 with susceptible flint Hi27. Segregations revealed a single recessive gene named *aph* (*aphid resistance*) that greatly reduces insect attractiveness and damage (So 2003). Hawaii's aphids were more easily raised on leaves of wheat than of maize. Hawaii's aphids could also be of a single genotype, as the insect is self-fertile. The *aph* resistance would wisely be used with associated molecular markers, were they available. Although the use of insecticides can be effective (Carena and Glogoza 2004), application is costly and must be repeated. One key to minimizing aphid damage in Hawaii has been to eliminate insecticides, thus allowing rapid development of naturally-occurring predatory beetles and other parasitic insects. Leafhoppers are of concern through transmission of viruses. In Hawaii we are primarily concerned with *Peregrinus maidis* leafhoppers that transmit MMV virus, while hoppers in the genus *Dalbulus* are associataed with transfer of other viruses of grasses. Direct damage from the leafhoppers is rare in Hawaii and never seen on our field and sweet corns, despite high natural populations.

Rose beetles. These beetles (*Adoretus sinicus*) commonly eat holes in corn leaves that can attract great attention. They have many other hosts but variations in attractiveness occur in corn, with thin-leaved popcorns unusually susceptible. However, damage is marginal and not normally significant in sweet corn fields, and no attempt has

been made to breed for resistance. In one study, we   found tolerance to be associated with silicates in very erect field corn leaves.

Parasitic Plants. *Striga hermothica* and *S. asiatica* are members of a genus of parasitic plants in Africa of corn and other grasses. Infestations can dramatically reduce yields (S. K. Kim, unpubl). Resistance breeding has been concentrated in Central Africa and led by researchers at IITA (Kim 2003). Although little attention has been given to sweet corns, it may be assumed that most are highly susceptible.

Common Animal Pests. Sweet corn appears only to attract a few animals uniquely more than field corns. The soft and slowly germinating seeds of supersweets make them especially attractive to smart pigeons and cardinals, who quickly distinguish sweet from field corn rows in nurseries. Parrots can be devastating on sweet corns at sweet-stage, notably in Australia where the cockatoo can literally clean out a field (I. Martin unpubl.). Rats and mice are pantropical pests that can also be serious prior to harvest and during storage of sweets. Wild dogs even eliminated one of our first trials in Negros, Philippines (J. L. Brewbaker 1954, unpubl.). The omnipresent raccoons of temperate corns are thankfully absent in most of the tropics, since their preference for supersweets is legendary. Feral pig populations are out of control in many places around the world, and they commonly prefer corn at sweetcorn stage. Nurseries in Hawaii must often be protected by solar-powered wire fences. Unique pests of the tropics can include everything from feral goats to elephants, few of them controllable. Native races of tropical lowlands have high husk numbers (Brewbaker and Kim 1979) and often high ear position that can reduce damage, but only the former has been maintained by tropical sweet breeders. There is virtually no evidence that sweet or field corn can be bred against any of these animal pests, or transgenes can be moved in to kill such pests as goats and cockatoos.

C. Agronomic Traits and Yield.

Modern tropical vegetable corns mimic their field corn ancestors in most agronomic traits (Brewbaker 2010), but are easily distinguished from temperate sweets (Figures 1 and 4). However they are often heterozygous or segregating for genes derived from temperate stocks. Typifying tropical sweets for agronomic traits and yield is often challenging. Illustrative data are best found in studies of tropical field corns as those of Hawaii Foundation Seeds (Kim et al. 1988a, Brewbaker et al. 1989). This involved international trials of 120 of the outstanding tropically-adapted inbreds in the HFS collection. The 46 trials were conducted in 28 locations in 11 countries, including four states in U.S.A. The sites were often chosen to evaluate response to some local stress of environment including disease and drought. Fifteen different agronomic data and seven passport data were summarized by Brewbaker et al. (1989). Similar critical evaluation remains to be made of tropical supersweets involving hybrid evaluation similar to those of Pataky et al. (1998) in Illinois.

Breeding methods for sweet and waxy corns differ significantly, however, in many ways from those for grain or silage maize. The differences are amplified when one considers tropical trials that can literally be made weekly through the year. An attempt is made here to encapsulate these many options in three major areas—breeding for stress tolerance, breeding for yield, and breeding for quality. They differ as much as the breeders and environments themselves. Stress due to pests and diseases are addressed principally by creating and working with superb epidemics that permit genetic advance.

Daylength Sensitivity and Illumination Values. Daylength sensitivity characterizes most tropical varieties of corn and other grasses. Long days (e.g., >14 hrs) delay corn's flowering for up to one month. In contrast temperate varieties have evolved under long days with illumination light values that are about twice those of the tropics during grain fill (M. Logroño unpubl.). Jong et al. (1982) followed corn growth of a diallel of 15 hybrids through 44 successive monthly plantings in Hawaii. The light and grain yield values both varied about 100% and were highly correlated. Three of the 6 parents were temperate, three tropical. Negative responses followed the level of

temperate parentage, i.e. greatest for the three temperate x temperate hybrids (Jong 1980). Breeding for high tolerance of low light values is essential in the tropics, and clearly is a polygenic trait. Logroño (1990) conducted studies in Waimanalo in fields with 150W lighting applied in the evenings to create 16-hour long days. The 90 tropically-adapted field corn inbreds averaged 64.5 days to silk under 12-hour days and 86.9 days to silk under 16-hour days. An attempt was made to breed the tropical OP variety 'Hawaiian Supersweet #9' with little or no daylength sensitivity (Brewbaker 1977). Genetic advance from three cycles of simple mass selection reduced sensitivity from almost 50% to less than 20%. Nourse (1992) showed that the sensitivity involved two or more QTLs, and conversions either way were straightforward for both sweet and field corns. Conversion research by Gerrish (pers. commun. 2014) and Goodman's team in N. Carolina (Nelson and Goodman, 2008) have identified superior tropical ('exotic') inbreds to diversify the basis for yield heterosis in temperate maize, based as it is largely on the Southern Dent x Northern Flint type of heterosis. Hallauer and Carena (2014) also converted a large series of tropical field corn inbreds to day-neutrality in northern USA through stratified mass selection. They confirmed our evidence for control by few major QTLs and emphasize the ease and minimal costs of such conversion to permit introgression into established temperate lines. Some use has been made by W. F. Tracy and colleagues (pers. corresp. 2012) in the development of digenic lines with *bt1* and *su1*. Tropical x temperate hybrids appear intermediate in daylength sensitivity and provide a wide range of adaptability that could be favored in much of the tropics, where illumination and temperature values can change within miles (as in tradewind-affected Hawaii).

Maturity. Harvest maturity (days after pollination, DAP) is a most important breeding challenge, as quality is poor if too early and poorer if too late. This kernel maturation is rapid in the tropics and linear with time. Grain filling rates (i.e., dry matter accumulation) of tropical field corn inbreds ranged between 6.9 and 10.2 mg kernel day[1] in year-round studies of M. Logroño (unpubl). In Hawaii we distinguish between 'haole maturity' (about 18 DAP) and 'Pilipino maturity' (about 22 DAP) for sweet corn, with Americans ('haoles') favoring the soft, juicy, low dry weight kernels, ca. 75% moisture. Waxy corns are harvested about one week later than sweets. Recording of flowering dates is thus a demand in all breeding nurseries. Tropical sweet corns flower in about a month, followed by a month of grand growth before silking and a month more until physiological maturity (Brewbaker et al. 1989). Most tropicals are not intrinsically late in flowering, but daylength sensitivity makes them late when grown under long days. Typical sweet corn harvests thus range between 60 and 80 days to silk (DTS). These values decrease linearly as temperatures increase. In northern Thailand and in cool highlands of Hawaii (mean annual temp 18°C) DTS increases to about 70 days and market maturity to >100 days (T. Pulam, unpubl). Significant increases occur in filled ear length and yield with cooler temperatures as in field corns. There is normally no compelling reason to select for earliness in the tropics. Extreme earliness is closely correlated with yield loss. Growers do welcome similar hybrids that can be planted concurrently but that are 5 to 10 days different in harvest dates. When planted in warm tropical soils (avg. 25°C) temperate sweets flower early, e.g. 'Golden Bantam' with 45 DTS, B73 with 55 DTS, and 'Gaspé Flint' as early as 35 DTS. Unusually late lines are to be avoided as they often reflect high ear positions, poor standability, increased challenges for hybrid seed production ('splits'), and no or little added yield advantage. Dates to anthesis and silking are highly correlated (r>0.80) with numbers of leaves and nodes below the harvested ear (Brewbaker 1981; Logroño 1990). In unadapted corns the interval (ASI) between silking and anthesis can be highly correlated with yield (r<.90), so high ASI values must be avoided in breeding. They are often useful data as they reflect responses to environmental stresses including diseases, insects and short daylengths.

Heights. Tropical sweet corn inbreds also mimic field corn relatives in plant and ear heights (Figure 1, Table 1). However, improved temperate corns have a ratio of about 1:2 stalk length below and above the uppermost ear, while tropicals tend to average the reverse, e.g. 2:1 (J. L. Brewbaker and S. Jinyahon, 1968, unpubl.). Wild maize races can be very tall. Thus, primitive sweet and field corns were often too tall and ladging susceptible. An unsuccessful attempt was made in Colombia and later in Hawaii to use the dwarfing *brachytic 2* gene (Djisbar and

Brewbaker 1987). Reduced yields have made any   monogenic dwarfs little used in maize, unlike in other cereals (sorghum, wheat, barley). The Hawaii populations (Table 1) and Thai hybrids (T. Pulam, pers. corres.) averaged 76 cm ear height (basal node of uppermost ear) and 195 cm plant height (top of tassel). Typical modern sweet hybrids average 60 cm to basal node of upper ear primarily to facilitate harvesting. Few studies of tropical sweets provide data confirming the linear correlation of ear height and number of basal internodes and thus of earlier anthesis, but this is to be expected. Excessive heights and plant biomass have no apparent yield advantage. Experiences of all vegetable corn breeders is that height variations are polygenic and largely additive, allowing successful reduction simply during recurrent mass selection.

Stalk and Root Lodging. Strong root systems and stiff-stalked plants are essential for high grain yield of field-corn hybrids. This is exacerbated by the demands of mechanical harvesting, high plant densities, and extended time in the field to <15% moisture. Stalk and root lodging are of less importance to sweet corn producers. There is evidence that selecting for erect, highly lignified stalks is correlated with thicker pericarps and loss of sweet corn quality (Wang and Brewbaker 2001; J. L. Brewbaker, unpubl.). Pericarp is a maternal (2n) tissue, of course. An intimation of this correlation is the fact that few current marketed tropical sweet corns resemble the stiff-stalked and heavily brace-rooted ideotype of modern temperate field corns. These have thick pericarps often exceeding 150 μm (Brewbaker et al. 1996). Tropical sweet corn growers often seek to maximize ear size by keeping low plant densities (<60,000/ha). Extremely erect leaves (as in *liguleless-1*) may in fact become a disadvantage. Sweet corns in warm tropical soils often root rapidly and emerge weakly, features related to the low energy value of supersweet corn kernels. Coupled with this is the poor root and brace-root (stem) development of many tall-plant tropical races, notable also in 'Hawaiian Sugar'. In one study the *sugary* gene from Caribbean germplasm was linked to a gene similar to *rootless* (*rrt*) that suppressed lateral seedling roots (J. L. Brewbaker unpubl.). Breeding in Thailand has led to relatively erect-leaved hybrids with strong brace roots, of importance especially in regions prone to tropical storms (T. Pulam, unpubl.). Inheritance is believed to be polygenic and selection progress implies need for multiple generations of recurrent selection. Aggressive root systems like those in hybrids with *Zea diploperennis* (Swaminathan and Brewbaker 1999) are probably to be avoided, although offering attractive genetic conversions. However, under severe winds the increased brace-rooting of many field corns would be desirable, if not linked to quality.

  Tassel Type. A major trend in temperate corn breeding has been to reduce tassel size and branch number (Duvick and Cassman 1999). The implication is that large tassels obstruct light penetration and reduce grain yields or compete directly with the ear for photosynthate. Contemporary temperate inbreds thus average less than ten tassel branches. In contrast tropical corns usually have larger tassels with >15 branches, and there is no evidence that this reduces grain yield through shading or diversion of photosynthate. The inheritance of tassel branching is reviewed thoroughly by Brewbaker (2015) and indicates polygenic control in the absence of dominance and epistasis. Problems with tassels of tropical sweets often include their high fragility and wind breakage, and their drooping or 'floppy' appearance. A single gene *flta (floppy tassel*) leads to the common type of tassel with drooping branches, and it is closely linked to *waxy-1* on Chromosome 9 (Brewbaker and Yu 2009). Most waxies thus have this floppy tassel. A common monogene *brta (branched tassel)* also in tropical corn double the numbers of tassel branches and can lead to lax branch habit, from 30º to >50º branch angle (Brewbaker 2015). For single cross production breeders tend to look for small tassels on females and large and long-lasting on male parents (T. Pulam, unpubl.).

Husk Number. As reviewed in III B (earworms and armyworms), temperate inbreds and hybrids have few soft husks with flag leaves that are appealing to canners (Tracy 1997) but dispose them to greater damage by earworms and armyworms in the tropics. Tropical breeders wisely choose to favor higher husk numbers (e.g 10-13) with increased extension beyond ear tip and reduced insect damage. Illustrated in Figure 12 are typical husks of lowland

tropical corns, with 15 in the photo that range from   partial (~2 cm) to extended tip cover (~7 cm). Brewbaker and Kim (1979) reported the correlations of husk numbers and injuries by earworms in Hawaii and armyworms in Colombia to be high (r^2 = 60%) and to involve relatively high broad-sense heritability (60%). Husk removal in tropical canneries is facilitated by sprays of hot water as ears enter the husking machine (Pulam 1997, 2002). The very high numbers of husks (>20) of some tropical races like 'Zapalote' are wisely avoided, although they clearly reduce insect injury. There is evidence (B. T. Scully, pers. commun.) that Zapalote has a high level of maysin further inhibiting earworms. Husk numbers are best counted before table maturity (Figure 12) by cutting off base of the ear. Genetic progress is tedious and with probable polygenic base.

Tillers and Husk Leaves. As noted in Section 1 D temperate sweet corns are marked by the presence of gene *gt* (*grassy tiller*) that leads to tillering (Figure 1) and husk (or 'flag') leaves, the leafy extension of husks (Brewbaker and Josue 2007). Flag leaves and tillers provide attractive reservoirs for aphids, thrips, and other field insects, and they are not significantly related to improved yield in tropical maize. Tillering increases as plant populations are reduced. Their rarity in tropical maize and apparently simple inheritance makes breeding no problem.

Ear Traits. Data on filled ear length, cob length, ear diameter and numbers of kernel rows must be recorded routinely in tropical sweet corn trials. Variations of about 50% occur among the typical seasons of production, making any 'reference values' highly suspicious. Typically however Hawaiian sweets have short filled ears (e.g., 15 cm) with thin ear diameters (e.g., 4 cm) and 14-rowed ears. In Thailand typical data have been 20 cm ear length, 5 cm ear diameter, 16-rowed ears with ear weight 390 gm. Waxy corns of 12 rows are preferred for consumption, and breeding seeks very long ears (~25 cm). Filled ear lengths are most valued data as they correlate closely with yield (Jong et al. 1982). Ears filled to the tip with edible kernels almost never occur in the tropics. This correlates significantly with incident light that is customarily limiting (8-10 hours daily). A completely filled ear (Figure 8) is however typical of best temperate hybrids in 16-hour days. Kernel rows occur in pairs (formula 2k) and when k is an odd number, rows spiral slightly to the left leading to a more tapered ear that can minimize earworm damage. It has become the favorite in Hawaii's breeding for ears with tight husk covers directed to a fresh market. In processing the Thai sweet corns, like their temperate counterpoints, have k= 8 or 10. While such ears are more columnar and more easily shelled in processing, they are often more prone to earworm and fungal damage. There appears to be no advantage to large cobs except for 16 to 20-row processing hybrids. Waxy corns are preferred, however, with large kernels that can easily be plucked off at the typical late maturity. Ears with 12 or even 10 rows are thus common. There is little advantage to plants with more than one edible ear, as lower ears are later and smaller, but some prolificacy is valued to ensure that the plant produces at least one good ear under stress. "Multiple-ear" types, with shank bearing two or more ears, occur as a genetic variant and must be discarded. Long shanks and drooping ears occur on some temperate hybrids, but are of no obvious value in sweet corn. Most of these ear traits are the same as in temperate lines and succumb to breeder selection, and few have monogenic inheritance.

Stress Tolerance--Light: As we stress throughout this review, levels of incident light constitute a primary stress for corn in tropical growing regions. At the Waimanalo station in Hawaii and the Kairi station in Queensland, about the same latitudes N vs. S and with similar rainfalls, incident light values range almost 100% from low to high during a typical year. And even the best season data average about half that of a summer crop in Minnesota or Tasmania! A major effect is to reduce the kernel-filled length of ears. Field corn hybrids in Hawaii also range from <5 t/ha of grain in winter to >10 t/ha in summer as a result of low winter light (Jong et al. 1982; Brewbaker 2003). Sweet corn breeding in the tropics thus has to focus on efficient use of this limited light, whose effect on temperate corns is always dramatic (Figures 2, 6, and 8). Adequate near-isogenic data appear not to be available to document breeders' progress, but all the authors would argue that genetic advance in tolerance of low incident light has been good with repeated cycles of selection.

Heat and Drought Stress: Most temperate maize will suffer heat stress (reduced pollen shed and fertilization) in the hottest tropics. Some tolerance has been introgressed into our supersweet populations largely from Caribbean flint corns. Heat-tolerant sweets can be essential in the hot summers of monsoon tropics. Little advance has been made in breeding vegetable corns for drought tolerance, but sweet corns often escape damage due to their early harvest. Current interest in transgenic drought tolerance will probably not extend to the short-lived sweet corns. Irrigation is best with drip systems, as overhead sprays greatly increase disease incidence. Seedling or greenhouse tests provide no substitute for breeding with year-round trials.

Yield. The primary focus in breeding tropical vegetqable corns has necessarily been on quality, as most of the early varieties and hybrids were very poor in tenderness and sweetness (Brewbaker et al. 1966). As quality improves the focus returns to quantity under elevated plant densities and inputs. Days after anthesis data are critical for comparable yield evaluations. Weight of husks must be considered, as marketing is usually by weight, although it may be deceptive. In earliest stages of breeding the visual selection suffices for quality and weight assessments. Later assessments of single plots requires DTS data (days to silk), to allow harvest at very similar days after pollination (DAP). Plant densities affect ear size more than total yield, and range from 50,000 plants per ha for processing in Thailand to 75.000 plants per ha for fresh market in Hawaii (N rates >150 kg/ha). Careful assessment of recovered kernel weight in US canneries has encouraged application of marker-assisted selection for kernel yield, but under protected patents.

Yield breeding methods largely relate primarily to the marketing of highly uniform SX or 3-way hybrids. It is typical to harvest and weigh ten unhusked ears in a 3 to 5m single-row plot. On well-established sites replication can be avoided if testing a large number of hybrids, usually with repetition of favorite hybrids as 'running checks'. Breeders usually have favorite A and B lines for combining ability, as inbreds bF47 (female) and bA11 (male) of early successful Thai hybrid ATS2 (Pulam 1997, 2002). Yields in the Thai program (Pulam pers. commun.) have inceased from 9.4 t ha[1] in 1990 (ATS2) to 15.6 t ha[1] in 2001 (ATS5) to 25 t ha[1] in 2011 (Wan54). Although reciprocal recurrent selection may improve heterosis between inbreds from an A population to those from B, there appear to be as many combining ability groups as there are breeders in the tropics. Even near-isogenic lines provide surprisingly high yield heterosis (Brewbaker and Josue 2007).

D. Quality and Appearance.

Tenderness. Quality can be a much more challenging target for breeders than quantity. Achieving vigorous germination and emergence with supersweets often requires that they be more starchy and with thicker pericarps. Tender pericarp has been the most challenging target for early genetic improvement of tropical sweet and waxy corns, and notably the supersweets. Tenderness reflects primarily the thickness of pericarp and its differential from germinal to abgerminal side of kernel (Ito and Brewbaker 1981). Superior temperate sweet corns tend to average less than 50 microns. These very thin pericarps predispose them to germination failure in hot tropical soils. This is associated with extreme wrinkling of the kernel, particularly for the *sh2* and *se* genes that have high rates of electrolyte leakage during germination (Tracy and Juvik 1998) and high infection by fusarium (Zan and Brewbaker 1999). A survey of pericarp thickness in most of the ancient races of maize (Brewbaker et al. 1996) revealed that they ranged widely from 40 to 140 microns in thickness and averaged 75 microns. In contrast, temperate field corns evolved under selection for large denty seeds having very thick pericarps. These ranged from 100 to 180 microns, averaging 140, and could never be useable as fresh corn (Ito and Brewbaker 1981). Generation mean analysis of temperate x tropical sweet corns segregated 2 to 3 major loci (Ito and Brewbaker 1991), while recombinant inbred lines of temperate x tropical field corns segregated an additional 2 to 3 major QTLs (Wang and Brewbaker 2001). Heritability values were fairly high, e.g. 50-80%, and genetic progress was best when both bite-tests and pericarp measurements were used (Brewbaker 1982).

Temperate sweet corn breeders made attempts to convert field corns like the corn belt stiff-stalk varieties to sweet corn genes to provide tolerance to mechanical harvesting. Failure was due largely to the thick pericarps of thse field corns (Ito and Brewbaker 1991; Brewbaker et al. 1996). *Sugary-1* populations like NE-HY were bred to incorporate temperate field corn genes for high yield (HY) and rust tolerance, but they proved to be very poor in tenderness and quality (Davis et al. 1988). Wang and Brewbaker (2001) provided evidence that the stiff stalk of modern field corn hybrids, bred for mechanical harvest, is correlated with very thick, chewy pericarp. Both are maternal 2n tissues with many cellular similarities. Thick pericarps probably provide better germination in cold wet temperate soils. Quantifying tenderness can be the most annoying expense of breeders. At one extreme good early genetic advance has been reported (Banafunzi 1974; Brewbaker and Banafunzi 1975) in variable populations, e.g., by taking area samples of 200 plants, rouging to 100, choosing 50 ears to husk, tasting 25 and saving 10. Careful drydown then provides kernels with adequate germination for next-cycle tests. Plot evaluations of advanced hybrids also find that bite-tests of fresh ears in the field correlate well with lab tests of cooked ears in both tenderness and sweetness (Ito and Brewbaker 1981). To novices like schoolchildren the field taste-test is a surprisingly delicious treat. The same is not true at all for waxy green corn that must be cooked to assess qualities of tenderness, sweetness and 'stickiness'.

Sweetness and Flavor. Breeding for sweetness and tenderness presents similar challenges and approaches (Letrat and Pulam 2007). High-sucrose types are very appealing for sweetness and panelists always rate supersweets higher than *sugary-1* sweets. The correlation of taste-panel ratings with brix values was r = 0.897 in Hawaii organoleptic trials (C. Cavaletto, pers. commun.). Data were based on empirical scores of 1 (excellent) to 5 (poor), with an average score of 3.0 representing a brix value of ~14.5% total sugars. However, the sweetness data of advanced breeding lines rarely showed significant differences, not enough to justify the investment of time in brix evaluations. Field taste tests must be a routine at both early and late stages of breeding. Market acceptance can only be fully estimated by extension and evaluations by diverse types of people.

Periodic field days with field taste tests are a routine requirement for supplementary information on quality acceptance. Illustrated in Figure 13 is a typical Hawaiian field day, at which every participant is expected to husk and taste-sample the fresh ears. Incidentally, fresh ears are often preferred to cooked ears. In fact the use of cooked supersweet ears is largely bypassed in the Hawaii studies, since the fresh uncooked ears give excellent data on tenderness and sweetness. In general, sweetness is more a problem of maturity than of genetics, once the supersweet gene is chosen. These have been discussed thoroughly in section II C. A major complaint with supersweets is the lack of a glutinous texture common in *sugary-1* and *sugary-enhancer* hybrids and in well-cooked *waxy-1* hybrids. Breeding methods always begin with simple field taste-tests and eliminate off-flavors that have, in fact, been encountered rarely despite the use of very diverse field corns in their parentage. Several tropical American races of maize are harvested immature and roasted or boiled. These and modern field corns harvested immature often have a very robust and satisfying corn flavor, suggesting genes that sweet corn breeders in the tropics have yet to exploit. Quantification of sweetness in the supersweets is usually adequate from taste-tests. In Hawaii we choose three ears per plot, husk them and have 3-5 tasters munch each and rate 1 to 5. Replication is achieved "in time" rather than "in space", with repeated unreplicated trials surveying annual variations in climate.

Kernel Color. Corns eaten at the sweet stage have historically had white endosperm (*y/y*) and no pericarp or aleurone colors. Andean sweet races like 'Chullpi' also have white endosperm but often have red and brown pericarps. A prevailing attitude is that white corn is for humans, as in rice, but that yellow or other colors are for animal feed. The reverse is true in much of the tropics where lack of essential proVitamin A carotenoids is associated with macular degeneration, blindness and other deficiency symptoms (Harjes et al. 2008). Also common is the attitude that yellow corns have an 'unusual' (unpleasant) taste, an attitude that is dispelled when near-isogenic lines can be compared. It seems to be an attitude rooted in the historic fact that white corns were selected for food quality, while yellows were selected largely for feed quantity. Tropical maize varies widely in endosperm

carotenoid colors, with three major common loci *Y1* (Chrom. 6L-30), *y8* (Chrom.7S-34) and *y11* (not mapped), the last two being pale yellows. The *y11* gene segregates in some Hawaiian supersweets and creates a type of bicolor preferred by growers, largely as it identifies best stage for harvest. White isogenic versions have been released of Hawaii's inbreds (Brewbaker 2010) and of #9 as 'Hawaiian Supersweet Silver'. Fresh markets currently feature bicolors (yellow and white) as much as the homozygotes, e.g. 'Hawaiian Supersweet #9 Bicolor" 'Orange' (dark-yellow) endosperms are the subject of cxtensive research to maximize betacarotenoids in tropical field corns, notably in Africa (Harjes et al. 2008; Vallabhaneni and Wurtzel 2009; Chandler et al. 2013; O'Hare and Martin, pers. commun.). Field corn colors range from pale yellows of many temperate dents to a few dark yellow or 'orange' types found in Caribbean races like 'Cuban Yellow', 'Coastal Tropical Flint', and 'Cateto'. There is some corresponding interest in 'orange' (very dark yellow) sweet and waxy corns. Research is focused on the conversion of phytoene-derived compounds into betacarotenoids and notably into betacarotene and betacryptoxanthin. Each step in this long pathway has been studied enzymatically and notable "switch" loci underscored (Harjes et al. 2008). An alternate pathway to that of betcarotenoids is that of alpha carotenoids and lutein, of less importance as proVitamin A. Also involved are later enzymatic steps that convert the betacarotenoids into zeaxanthin and ultimately to abscisic acid. Favored are richly colored 'orange' or 'supergold' endosperms with high levels of provitamin A carotenoids (Chandler et al. 2013; T. O'Hare and I. Martin, unpubl.) Variations to dark-yellow colors occur in many tropical flints and in a few tropical sweets like Australian selections (I. Martin, unpubl.) and Hawaii's Hi37 (*brittle-1*). The inheritance is not well known but suspected to be polygenic. Also observed have been richly colored ("orange") field corns like Hi35 that appear to have normal betacartinoids but have alleles of the *P* (*pericarp and cob color*) locus.

Aleurone and pericarp colors offer interesting new opportunities for marketing sweet and waxy corns. Endosperms in waxy varieties are white (y/y). However the aleurones often have anthocyanins that make them purple or red, representing segregation of genes *A1, A2, C1, R1,* and *Pr1* (Figure 14). White waxy is the most common in markets, followed by light purple. Bicolor (and tricolor) hybrids are rarely marketed, as in Figure 14. Some black or intensely-colored waxy varieties are coming out of the breeding (M.H. Lee and T. Pulam, unpubl.), probably representing pericarp colors based on the many alleles of the *P1* locus. Such alleles have been found in Peruvian floury races (J. L. Brewbaker unpubl.). As noted earlier aleurone and pericarp colors are obviated in supersweets by the close linkage of *sh2* to *a1* and of *bt1* to *a2*. The mutant *bt2* that resembles *sh2* has no such color linkage, and a red cob variety was released by Banafunzi and Brewbaker (1975) as 'Hawaiian Supersweet *6' and can occasionally be seen in Asian markets. An allele of the *bt1* locus named *btA* lacks the *a2* allele, i.e., is *(bt1 A2)* (Hannah and Basset 1977; Bae et al. 1990). Breeding of *britle* supersweets is underway to use this genotype to breed supersweet corns of diverse aleurone and pericarp colors as found in waxies (Figure 14). A red supersweet, presumably *brittle1* lacking the *a2* block, named 'Siam Ruby Queen' has been released by T. Pulam (unpubl.). Research is needed to determine effects of maturity during the harvestable stages on these colors, as some are poorly expressed at typical sweet corn harvest stage.

Plant Color. Plant colors vary greatly in tropical races of maize, and are suspected to be associated with insect and disease tolerance. Temperate sweet corns normally have no plant color since the *sh2* gene is tightly-linked to gene *a1* that suppresses plant colors. 'Hawaiian Supersweet #9' is of the *brittle-1* genotype, linked to a2 allele that suppresses color in kernels. However #9 was converted into the purple-plant (A, B, Pl), red-cob (*P-wr*) variety and named 'Kalakoa' (Brewbaker 2011). It has yellow endosperm but cooks to release a disarming red juice similar to red beets that luckily is water-soluble.The color of silks in corn is generally inherited independently from plant and kernel. Colorless silks are greatly preferred for attractive marketing of vegetable corns, since colored silks turn dark brown when cooked. Most tropical field corns have deeply colored silks associated with the pericarp-and-cob color *P* locus. This involves the compound maysin that confers some tolerance of earworms. All of our original tropical sweets had colored inner silks. They continue to dominate production despite preference for green inner silks. Genetic control of silk color appears to be digenic.

V. PRODUCTION AND PRODUCTS

A. Production.

Tropical vs. Temperate Production. Tropical production of sweet and waxy corns differs in many respects from that in temperate regions. This is not only for variations in climate and year-round growth, but extends to farmers' choices of corn genotypes and local disease and pest challenges. In contrast to temperate sweet corns, a much more diverse array of production methods and products occurs in the tropics (Pulam 1997, 2002; Brewbaker 2003). Production knows no 'seasons' in much of the tropics, and sweet corn is often grown in an 'off-season', e.g. after a crop of rice or field corn. Experiments on maximizing farm income at IRRI in the 1970s revealed that sweet corn made the most profit among the four major crops grown (rice, beans, melons, corn) (R. A. Bradfield, unpubl.). Low inputs are common on tropical farms and human diets can be extremely variable. Corn is consumed often as a major source of energy by working farmers in the tropics who eat immature field corn, waxy corn, and very mature sweet corns for energy. Highly favored are white endosperm corns that, however, fail to provide essential carotenoids in human diets. However, in some countries (e.g., Thailand and Guangdong, China) high-input production of tropical supersweets is increasing for fresh, canning, shrink-wrapped or frozen markets. In Australia most sweet corn is packaged attractively in "four-packs" with a few husks removed and kept chilled.

During this time of transition in tropical food uses of sweet-stage corns, breeders and extension personnel and growers must work with several different genotypes and harvest demands under varying field conditions (Brewbaker 1985). Weekly or even daily plantings will become increasingly common to permit fresh marketing daily. An essential adjunct to evaluation for market acceptance is the economic assessment of the many difference methods of preparing food products from vegetable corn. Focus is often on corn products that contribute to a diverse cuisine, rather than simply as fresh ears to be eaten on the cob.

The tropical-farmer demand for open-pollinated (OP) varieties emphasizes the continuing importance of public-sector breeding and evaluation for the tropics. Private companies may breed composites and synthetics, but do not release these as OP cultivars. The 27 open-pollinated populations released by Hawaii Foundation Seeds amount to about half those of the entire tropical industry (Brewbaker 1998). Thailand has two widely grown OP cultivars including TSSC1DMR. International centers including CIMMYT and AVRDC have not worked with sweet corns. As national economies are changing in the tropics, it is typical to find elderly people favoring the starchy heirloom OP cultivars and children favoring the supersweet types of modern hybrids.

World Production. Production of sweet and supersweet corns occupies about one million hectares, with 80% still in temperate North America (Tracy 1997). Any estimates of tropical acreage are fragile since there is no accurate accounting of the predominately on-farm and backyard production. In Thailand (Pulam 1997, 2002) many hybrids like ATS-2 and WAN68 (*brittle-1*) and Sugar-73 and WAN54 (*shrunken 2*) are produced year-round largely for Thailand's $60 million canning industry. Queensland's Hi-Brix 5 (Martin *et al*, 1993) outyields all competitors in subtropical Australia, a $50 million fresh market. Virtually no markets exist for sweet corns in Latin America or Africa or India, although immature field corns are often cooked locally but without economic importance. Hawaii's farmers plant supersweet hybrids weekly and market year-round, often with high net incomes (>US$10,000 per acre). There is preference for pairs of hybrids, one early and one late, that can be co-planted but harvested over a two-week period. Canned corn is valued around $500 million in the U.S.A., with frozen and vacuum-wrapped ears valued around $200 million. Americans consume an average of 2.5 kg annually per person (fresh ears with cob), but importation is largely excluded except from Hawaii. Despite the potentially huge winter market, it is presently not feasible economically to send Hawaii's tropically-grown hybrids to the mainland. Estimates of acreage grown in waxy corns approaches half-million hectares, much of it in temperate China and Korea (Brewbaker et al. 2007). Here also an attractive market is in winter for tropical hybrids.

'Baby corn' is an immature ear product largely of S. E.   Asia, and can be produced from any type of corn, sweet or field. The canned product is a $30 million crop in Thailand and Vietnam. Maximum quality requires the growth of male-sterile hybrids, since quality decreases rapidly following fertilization. Although a common treat for hungry grad students, there is no evidence that a sweet or super sweet cob (a maternal tissue) has any higher quality than a field corn. We found no published evidence on breeding and selection.

Nutrients in Production. Nutrients present a major problem to corn growers throughout the tropics, somewhat less so for corn harvested fresh than as dry grain (Brewbaker 2003). Nitrogen (N) is the most significant factor for tropical corn, as tropical soils have ~90% of their N above ground, in contrast to temperate soils with ~90% of N in the ground. As a result the levels of N are universally limiting, and with no supplementation crop failure is to be expected. N Levels of 150 to 200 kg ha^{-1} are typical for commercial production. However, small farmers can often double yield and reduce costs with only 30 to 50 kg ha^{-1}. Crop rotation that is typical of corn farming in temperate regions is not so important in the tropics if major nutrients are addressed. Research trials have been grown effectively without crop rotation over a 40-year period in Hawaii, but with care to plow down crop residues snd supplement major elements like N (Brewbaker 2003). Companion plantings with woody legumes like the leucaenas is common with field corn. Use of green manure from N-fixing plants has also been an historic practice. Common examples are in Indonesia and Philippines, where legume shrubs are planted as an alley crop with maize planted between. Green manure is applied well before corn planting, to initiate N release. Leucaena is a major crop for this use (Shelton and Brewbaker 1994). Phosphorus (P) is a major deficiency of most tropical soils, often having been fixed by iron or aluminum in lateritic soils and only made available by mycorrhizae. Levels of 0.05 to 0.10 ppm in the soil solution are required lest vegetable corn yields be significantly reduced. Deficiency of P greatly reduces early growth, often exacerbating greatly the losses from viruses and fungal pathogens (Pulam 2002). Genotypic differences for P response can be quite large among corn inbreds, some showing high tolerance (Pulam 2002) and others showing monogenically controlled high intolerance (Nourse 2002). Sweet corns commonly appear to react similarly to field corns for deficiencies of minor elements such as zinc, boron, and manganese.

Plant densities range widely from those of small farmers to commercial production, the latter averaging about 75,000 plants ha^{-1} with N rates >175 ha^{-1}. Weeds in the tropics thrive year-round and under high rates of N. Most herbaceous weeds can be controlled inexpensively by herbicides such as 2-4D or by hand weeding. Grasses and sedges are more challenging and can dominate weed pressure. Their effects can be minimized with repeated rotovation or by specific but often expensive herbicides (notably Roundup, Sedgehammer, and Fusilade). Challenges for tropical breeders include improved tolerance to stresses imposed by nutrients, drought, light deficiency and pressures from diseases and pests (Section IV). It can be assumed that, as transgenes of several types come off patent, they will be used in tropical sweet corns for weed or insect control. Currently they are restricted to temperate sweet corns with BT and Liberty-Link transgenes.

B. Products.

The products and uses of tropical sweet and waxy corns are expected to become as varied as the five billion people who live in the tropics. Field days in Hawaii (Figure 15) always involve local Asian-Pacific chefs, like Alfredo Cabacungan and students shown in the figure. Their recipes range from fritters (often beer-battered as here) and freeze-dried kernels to ice creams and milks. Focus is often on corn products that contribute to a diverse cuisine, rather than simply as fresh ears to be eaten on the cob. Very sweet cakes, pies, and supersweet corn that are typical of American markets generally are not favored in the tropics. Vegetable corn is an energy food in most of the tropics, thus favoring delayed harvests of sweet or waxy corns having kernels with much higher levels of starch (e.g. 24-28 days after pollination). In Hawaii all farm markets sell two types of corn, haole (white) and pilipino (Philippines & E Asia). Kernel dry weights increase linearly with time (A. D. Josue, unpubl.), with moisture levels of ~75% at 18 DAP, ~55% at 24 DAP, and ~36% at 38 DAP (physiological maturity of flint corns). The glutinous

texture of waxy maize is first evident around 24 DAP, and often harvested at this maturity. Waxy, field, and well-matured sweet ears are often grilled or parched to enhance their carmelized flavors. A common product is from boiling for extended periods. Coblets of waxy and sweet corn are commonly cut for addition to stews and soups. Coconut- or curry- or peanut-flavored corn dishes are regional favorites. All of these observations on products and uses reinforce breeding approaches that favor high corn flavor and yield with less emphasis on sweetness and tenderness. Commercial products can also be much more diverse, including in Thailand highly popular cups, cartons and pouches.

Many unusual products are based on tropical supersweet varieties. Prominent in Thailand is a nutritious fresh corn milk made from supersweet ears and marketed widely by Kasetsart University. Many Asians have lactose intolerance, and since corn milk lacks lactose it might even come to challenge soy milks. InThailand the milks are valued at $1,000,000 annually and growing. Research is underway to produce and market ultra-high temperature (UHT) products. Ice cream based on supersweet corn also has become very popular in Thailand and the Philippines. Sample tests were very well received in Hawaii, based on liquids created by blending and centrifuging relatively mature *brittle1* supersweets. Freeze-dried kernels make an excellent, healthy snack, unlike the *sugary-1* corns that can be frozen fresh but not freeze-dried. We've samples of our freeze-dried *brittle-2* hybrids that are still edible tracing to production in the 1970's (Banafunzi 1974, Brewbaker and Banafunzi 1975; Brewbaker 1984). These freeze-dried supersweet kernels appear regularly in popular Asian dishes. An excellent dried noodle soup, Sapporo's 'Ichiban Chicken Flavor Oriental Noodle Soup', usually contains ~28 kernels of freeze-dried *shrunken-2* corn. Cooked ears in vacuum-packed plastic (Figure 8) now appear also in tropical markets. A single ear of a vacuum-packed *su se* hybrid from Japan sells for about $5 in Singapore, a week's wages for many in the tropics. Experienced chefs in Hawaii find extraordinary ways to use supersweet corn to enhance Asian and 'fusion' cuisine (Figure 15).

Improved waxy corn hybrids for fresh harvest are increasingly common in S.E.Asia (Anonymous 2007). They occur in a great variety of products. One meal in Suwon, Korea, was entirely based on waxy—soups, mixed vegetables, cold milky-juice, cakes, etc. (J. L. Brewbaker unpubl.). Expanded international production of adapted tropical waxy hybrids will assure much wider acceptance of this fine vegetable and energy source. It is to be hoped that international agriculture centers and global seed companies will finally come to support the development of tropical vegetable corns. Focus must be on high beta-carotenoid yellow corns for health purposes. New options include a wide array of colors, including black and red pericarped varieties and hybrids (e.g., 'Siam Ruby'" waxy hybrid; T. Pulam unpubl.).

7VI   CONCLUSIONS

We emphasize throughout this review the two primary challenges for tropical vegetable corn breeders--diseases and low incident light. Often of equal importance are specific tropical insects or such oddities as cockatoos and turkeys. Only rarely has industry effectively marketed temperate hybrids in the tropics, and international crop improvement organizations have ignored these vegetables. However, breeding of tropically-adapted sweet and waxy corns has made substantial progress in the past half-century, largely confined to the Asian and Pacific arena. Hybrids from Thailand dominate canning worldwide, and fresh ears are marketed in an expanding region of East and Central Asia. Here we argue that the genetic base of superior temperate inbreds is too narrow to permit direct conversion to the challenges of the tropics. Temperate vegetable corns are highly susceptible to most tropical pests and diseases (Table 3) and are uniquely marked by genes like *grassy tiller* (Brewbaker and Josue 2007). Our tropical vegetable breeding suggests that industry focus on introgressing genes for superior quality (Tracy 1997; Gerdes and Tracy 1994) into adapted germplasm discussed here (e.g., Table 1). Failing support to public sector vegetable breeding demands expanded investment by seed companies and international institutes. In reverse, continued breeding advance in quality would be welcomed in tropical material. These challenges are formidable but can be reduced greatly by exploiting germplasm discussed in this review. Introgression of desired genes is most

effective if from adapted inbreds and hybrids. It becomes successively more difficult to introgress from inbred-based synthetics and from tropical sweet composites, that are often referred to as 'inbreeding-resistant' due to segregation of deleterious alleles when selfed. Many of the requisite genes occur in field corn populations of the tropics, making extended inbreeding and evaluation essential.

It is extremely important that open-pollinated cultivars described here remain open-pedigree and available. Very few of the five billion people in the tropics can pay US or Japanese prices for hybrids. Collaborative yield trials by public and private sector breeders in Thailand provide a fine model for future growth. Private sector investment unfortunately requires excessive security of germplasm. Suitable arrangements with the private sector might assure the requisite public-sector participation. This type of collaboration has essentially failed with field maize due to issues of transgenics and intellectual-property rights. It will be unfortunate if such issues require private companies to re-invent the wheel as they try to bring their ill-adapted hybrids to the tropics and even choose to avoid the use of public lines.

Economic prospects for success of tropical vegetable corn production are very great. Year-round production assures efficient use of labor, land, water, factories and supplies. Emerging economies provide attractive markets for a high-value and high-yielding vegetable matured in ten weeks. Emergence of high pro-vitamin A hybrids and varieties ensures added nutritional value to a crop widely enjoyed by people of all ethnicities. Genetic advance appears to involve quantitative inheritance for most agronomic, pest and disease, quality, stress tolerance and yield traits in tropical vegetable corns. This is almost inevitable in an ancient tropically-evolved amphidiploid like *Zea mays*. The breeder's use of large segregating populations under controlled environments with careful personal (preferably weekly) scrutiny will continue to be essential to ensure genetic progress. Breeders in the tropics can plant almost weekly and there is no substitute for regular nurseries with large populations of segregating germplasm that are viewed (and tasted) almost daily. As an example more than 800 and 300 research nurseries of vegetable corns, respectively, have been planted in Thailand and Hawaii in the last 30 years (T. Pulam and J. L. Brewbaker, unpubl.). Concurrently this affords developmental genetic advance for many significant traits. This is for some of us the most enjoyable and rewarding profession available and the prospects for development throughout the tropics are extremely exciting.

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Table 1. Sweet synthetic and composite populations bred in Hawaii

Name	Gene	Color*	Origin
HS	*su1*	Yellow	'Hawaiian Sugar' (HS) (A. J. Mangelsdorf , unpubl., 1945)

HibtCOMP3m	bt1	Yellow	Inbreds from HS converted to bt1, 'Haw'n Supersweet #9'
HibtCOMP4k	bt1	Yellow	Crosses of HS x flint composite Suwan 1
HibtCOMP6n	bt1	Yel/White	'Kalakoa Supersweet', HibtCOMP3 as purple plant (A B Pl)
HibtCOMP9aa	bt1	White	'Haw'n Supersweet Silver' (y1, not y8 or y11)
HibtSYN2h	bt1	Yellow	15 high-quality inbreds from COMP3
HibtSYN3h	bt1	Yellow	Three outstanding inbreds (Hi36,H937,Hi38) from COMP3
HibtSYN7o	bt1	Yellow	Broad base of hybrids of tropical sweets x flints
HibtSYN9f	bt1	Yel/White	Six UH field corn synthetics x HibtSYN3
Hish2COMP2o	sh2	Yellow	'Haw'n Supersweet #1', broad temp x trop base
Hish2SYN2k	sh2	Yellow	Hish2SYN6 x commercial temperate hybrids
Hish2SYN6f	sh2	Yellow	23 Haw'n sh2 inbreds x 5 temperate inbreds
Hibt2COMP1m	bt2	Yellow	Lines from HS x bt2 source; 'Haw'n Supersweet #6'
HisuSYN3i	su1	Yellow	16 inbreds from HS
HisuSYN4h	su1	Yellow	14 best temp x trop singlecrosses
HisuCOMP6g	su1	Yellow	HS x N28 dent, stiff-stalk
HisuCOMP10f	su1	Yel/White	HibtCOMP1 x tropical flints BCd to HS
HisuCOMP12n	su1	Blue	Blue-seeded HS
HisuCOMP13g	su1	Yellow	HS x HisuSYN3

Table 2. Development of inbred Hi80

Stage	Cycles	Year	Inbred	Approach and Major Emphases
1	16	1966	AA8	Inbreeding from 'Hawaiian Sugar' (sugary-1), Yield
2	14	1979	Hi38A	Conversion to brittle-1, Resistance to fusarium
3	12	1989	Hi38B	Rust resistance, C rf4 conversion, Tenderness
5	17	1996	Hi38C	Green silk, Roots, Erect habit, Yield
6	16	2013	Hi80	Resistance to MCMV and Southern rust, Staygreen

Table 3. Relative importance of maize diseases in wet lowlands (WL), dry lowlands (DL) and highlands (HI) of the tropics.

Disease	Pathogen	WL	DL	HI
Fusarium rot	Fusarium moniliforme	3	2	2
Gibberella rot	Gibberlla fujikori	0	0	1
Aspergillus rot	Aspergillus flavus	1	0	1
Southern rust	Puccinia polysora	3	1	2
Common rust	Puccinia sorghi	0	0	2
Turcicum blight, NCLB	Setosphaeria turcica	1	0	3
Maydis blight, SCLB	Cochliobolis heterostrophus	1	1	2
Yellow leaf blight	Ascochyta sp	0	0	1
Common smut	Ustilago maydis	0	0	1
Head smut	Sphacelotheca sp.	0	0	1
Downy mildews	Sclerospora sp.	2	1	0
Brown spot	Physoderma sp.	1	1	0
MMV	Maize mosaic virus	3	1	0
MDMV	Maize dwarf mosaic virus	2	1	2
MSV	Maize streak virus	3	2	2

MCMV	*Maize chlorotic mottle virus*	2	1	2
MRDV	*Maize rough dwarf virus*	0	0	1
Corn stunt	*Spiroplasma sp.*	1	1	1
Bacterial stalk rot	*Pectobacterium sp.*	2	1	1
Bacterial leaf blight	*Pseudomonas avenae*	1	0	0
Bacterial leaf stripe	*Pseudomonas andrapogonis*	1	1	0
Stewart's wilt	*Erwinia stewartii*	0	0	1