Disease-resistant Tropical Supersweet Corn Populations

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Temperate sweet corn hybrids cannot be grown year-round in Hawaii, or in most other tropical climates, because of disease susceptibility and low yields under conditions of low incident light and high levels of diseases and pests (Brewbaker, 1983; Brewbaker et al., 1966). A primary problem in Hawaii is maize mosaic virus (MMV), to which no temperate sweet corns are resistant (Brewbaker, 1981a). Additionally, no temperate sweet corns are sufficiently tolerant of common rust (*Puccinia sorghi* Schw.), seedling and kernel rot (*Fusarium moniliforme* Sheld.), Northern leaf blight [*Exserohilum turcicum* (Pass.) Leonard & Suggs], and corn earworm [*Helicoverpa zea* (Boddie)] for year-round production (Kim et al., 1988). The populations described here were bred to make production cost-effective in Hawaii with minimal or no use of pesticides.

In 1961, breeding was initiated of tropically adapted open-pollinated populations and hybrids based on the *sugary1* gene (Brewbaker, 1968). Emphasis shifted to high-sucrose genes, such as *shrunk2*, for enhanced postharvest quality (Banafunzi, 1974). The high-sucrose mutant that has been exploited most extensively in Hawaii is *brittle1*, with the first varietal release in 1977 (Brewbaker, 1977). The 17 populations described represent >200 cycles of recurrent mass and backcross selection for quality and disease and pest resistance. They are marked by resistance to MMV and high tolerance of fusarium seedling and kernel rot, common rust, and earworms. They also segregate for general resistance to Southern rust (*Puccinia polysora* Underw.), bacterial leaf blight, maize dwarf mosaic virus, and Northern leaf blight. Four types of sweet corn are represented, based on genes *sugary1*, *shrunk2*, *brittle1*, and *brittle2*.

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Origin

The 17 populations described here were bred largely at the Waimanalo Research Station of the Univ. of Hawaii on Oahu at sea level, lat. 20°N. They differ greatly from temperate sweet corns, as they are derived largely from tropical field corns (notably, the Caribbean Flints), which they resemble in height and stature, prolificacy, sensitivity to photoperiod (Brewbaker, 1981b), husk number, and the rarity of tillers and flag leaves. Corn breeding is conducted year-round in Hawaii. No insecticide or fungicide treatments have been applied in almost four decades to experimental fields at Waimanalo, Oahu, creating ideal conditions for natural epidemics of diseases and insect pests. Summer corn grain yields are twice winter yields at Waimanalo, even in the absence of disease, because of fluctuations in incident light (Jong et al., 1982). A shuttle breeding strategy was used, in which cycles of selection were continued year-round, from the warm, dry, long-day summers to cool, wet, low-light winters. Disease and insect epibiotics were cyclical, usually short-lived, rarely severe, and abiotic stresses were transient. Bottleneck-breeding (Mangelsdorf, 1952), a form of periodic intensive selection, was practiced whenever conditions were optimum, e.g., roguing during a brief increase in populations of corn leaf aphid (*Rhopalosiphum maydis* Fitch) before predators eliminated them (Chang and Brewbaker, 1976).

Genetic advance was achieved largely through recurrent mass selection (RMS) using the two following methods. 1) Populations of 2000 to 4000 plants at a density of 250,000/ha were hand-sibbed, rogued, and thinned prior to pollination, retaining from 150 to 250 ears. Ear quality selection was often achieved by bite-testing in the field at 20 d after pollination (Ito and Brewbaker, 1981) and carefully drying selected ears for the next generation. 2) High-density plantings of 3000 to 10,000 plants were rogued prior to anthesis to 30% to 50% stand, open-pollinated under isolation, and rogued again at sweet corn stage and at harvest to retain 200 to 500 ears.

Populations based on open-pollinated (OP) parents were designated as composites (COMP); those based entirely on inbred parents or singlecross hybrids were designated synthetics (SYN). Selection focused on the six following traits, for which the new releases

excel in comparison with most temperate sweet and supersweet corns.

1) Common rust—Severe epiphytotics occur in wetter months at Waimanalo. Hawaiian COMPs and SYNs averaged 2.1 on a 1–9 scale vs. an average of 6.3 for 98 mainland hybrids (Kim et al., 1988). All specific resistance genes except *rp-677A* are ineffective in Hawaii (Kim and Brewbaker, 1987). Resistance to Southern rust is also high among these populations due to their Caribbean ancestry, but cannot be evaluated well in Hawaii.

2) Maize mosaic virus—Hawaiian COMPs and SYNs are homozygous or carry high gene frequencies of the resistant allele *Mv* (Brewbaker, 1981a; Ming et al., 1997), an allele not found in temperate sweets. The aphid-transmitted maize dwarf mosaic virus is uncommon in Hawaii, but resistance to this virus is also known to segregate in these populations when grown abroad. Virus resistance of any type is less common in temperate corns (Brewbaker et al., 1991).

3) Earworms—Hawaiian COMPs and SYNs have high tolerance to this omnipresent and nonseasonal insect, primarily because of increased numbers and tightness of husks (Brewbaker and Kim, 1979).

4) Fusarium rots—are epidemic in Waimanalo soils where corn has been grown and the stubble plowed down continuously over 30 years. Under cool winter conditions, nontreated temperate supersweet seeds fail to emerge. Germination of nontreated seeds of Hawaiian COMPs and SYNs was reduced 45% by fusarium in 1992 winter trials, vs. a 93% reduction for the temperate *sugary1* control 'Jubilee' (Table 1). Kernel rots due to fusarium were common in temperate populations but rare in the Hawaiians.

5) Northern leaf blight—This disease is occasionally severe at Waimanalo. No monogenes for specific resistance (e.g., *Ht1*) are effective in Hawaii. Most UH COMPs and SYNs have intermediate levels of general resistance adequate to permit sweet corn harvest without yield loss. Southern blight [*Bipolaris maydis* (Nisik.) Shoem.] is uncommon in Hawaii, but tolerance of these populations is also reportedly high.

6) Low light stress—Selection advance in the shuttle breeding appeared to have been especially effective for yield under the limiting light conditions of Hawaii's winter (Jong et al., 1982).

Description

Several horticultural traits of the 17 populations are summarized in Table 1, based on trials planted between January and September in Waimanalo. The controls included a common commercial temperate hybrid and the OP variety 'Hawaiian Sugar' (Brewbaker, 1968). All populations achieved commercial yields in plantings between September and January, while none of the temperate hybrids evaluated could be grown commercially in this season.

1) Populations based on the gene *brittle1*. The high-sucrose gene used most extensively in Hawaii's breeding is *brittle1* (Chromosome

Table 1. Agronomic and disease tolerance traits of Hawaiian sweet and supersweet corn cultivars.

Name	Gene	Color	Kernel			Ear length (cm)	Plant height (cm)	Ear height (cm)	Resistance ^a		
			Depth (mm)	Mass (mg)	Row no.				MMV	Rust	Fus
HibtSYN2	<i>bt1</i>	Y	9.9	125	14.7	12.3	179	56	R	2	39
HibtSYN3	<i>bt1</i>	Y	10.0	101	14.7	11.3	169	56	R	2	41
HibtCOMP3	<i>bt1</i>	Y/W	9.8	125	13.4	11.9	179	70	R	3	13
HibtCOMP4	<i>bt1</i>	Y	9.4	112	13.2	10.8	182	75	R	2	55
HibtCOMP6	<i>bt1</i>	Y/W	7.9	123	13.8	9.5	197	76	R	4	60
HibtCOMP7	<i>bt1</i>	Y/W	10.5	142	14.5	12.5	195	79	R	4	63
HibtCOMP8	<i>bt1</i>	Y	9.4	117	13.5	12.0	184	68	R	3	57
Hibt2COMP1	<i>bt2</i>	Y	8.6	146	13.5	11.2	191	63	R	5	69
Hish2SYN6	<i>sh2</i>	Y	8.9	95	12.9	11.5	189	76	R	4	77
Hish2COMP2	<i>sh2</i>	Y	9.5	158	13.5	14.2	190	77	R	4	44
HisuSYN3	<i>su1</i>	Y	10.0	193	14.1	13.1	212	94	R	4	54
HisuSYN4	<i>su1</i>	Y	9.5	234	13.4	12.0	203	79	R	4	52
HisuCOMP6	<i>su1</i>	Y	9.6	195	13.7	13.1	207	74	R	5	41
HisuCOMP10	<i>su1</i>	Y/W	9.4	211	13.6	13.6	203	80	R	3	19
HisuCOMP12	<i>su1</i>	B	10.0	171	13.5	13.0	202	75	R	4	30
HisuCOMP13	<i>su1</i>	Y	9.2	139	13.9	12.9	197	77	R	4	26
Mean			9.4	154	13.6	12.2	195	76			47
Haw'n Sugar	<i>su1</i>	Y	8.9	222	12.9	13.7	206	93	R	5	24
Jubilee	<i>su1</i>	Y	10.8	158	14.8	12.5	138	49	S	8	93

^aMMV = Maize mosaic virus, R = Resistant, S = susceptible; Rust = Common rust resistance on 1 (resistant)–9 (susceptible) score; Fus = percent reduction of germination by the fungus *Fusarium moniliforme*, winter nursery.

5L-42). The allele was obtained from Maize Genetics Coop stock 63-3023-8 x 3033-10 (*al bt1 pr A C R*). Despite the dominance of *shrunk2* in temperate supersweet marketing, tropical field germination and organoleptic tests (Banafunzi, 1974; Zan, 1995; Zan and Brewbaker, in press) led us to abandon this genetic background in favor of *brittle1*. The only supersweet corns presently marketed with this gene (Hawaii, Australia, Thailand, Nigeria) trace back to Hawaiian germplasm. The gene has been sequenced and is believed to control membrane transport phenomena in the endosperm (Sullivan et al., 1991).

Five *bt1* COMPS and two *bt1* SYNS are being released. Hi bt SYN 2 was derived from crosses of SYN 1 (a 5-inbred synthetic) to 10 other inbreds out of Hi bt COMP 3. Hi bt SYN 2 was advanced through four cycles of recurrent mass selection (RMS) followed by selfing four generations and recombining inbreds selected for tenderness and field performance. This synthetic is our best present genetic base for inbreeding, with a wide array of tolerances to diseases and pests.

Hi bt SYN 3 was bred from five outstanding *bt1* inbreds derived from Hi bt COMP 3. Three of these (Hi36, Hi37, Hi38) serve as the basis of commercial hybrids 'Waimanalo Supersweet' (SX) and 'Hawaiian Supersweet #10' (3X). It was advanced through six cycles of high-intensity selection among 3000 plants in winter months, retaining ≈200 ears per cycle. The synthetic is low in variability, short in stature, and high in rust resistance (Table 1).

Hi bt COMP 3 ('Hawaiian Supersweet #9') was derived from two earlier COMPS (1 and 2) that were five-backcross conversions of *sugary1* composites introgressed with the *Ht1* gene (effective in Hawaii until about 1975). It was named after eight cycles of RMS (Brewbaker, 1977). Several later cycles of RMS were based on bite test scores and peri-

carp thickness measurements (Ito and Brewbaker, 1981). Subsequent selection cycles included one S1, one S2 and 12 RMS (eight hand-sibbed), with emphasis on kernel quality, silk color, disease and earworm resistance. Hi bt COMP 3 has been grown commercially throughout the tropics, and enters the pedigree of all other Hawaiian *bt1* COMPS, SYNS, and inbreds. It is marked by high tenderness, high flavor scores, good uniformity and yields (Kratky et al., 1989). It has superior tolerance to soilborne fungi (Table 1), and yield losses to common rust, Northern leaf blight, and earworms are very small under no-pesticide regimes. A conversion to *y1/y1* (white kernel) was marketed in 1998 as '#9 Silver'.

Hi bt COMP 4 derives from crosses of Hi bt COMP 3 with inbreds from a superior Thai composite, 'Suwan 1'. It was advanced through seven cycles of RMS (hand-sibbed). This composite resembles Hi bt COMP 3 but has a palette of disease and pest resistances not available or rare in American supersweets, including some tolerance to borers and to the downy mildew (*Sclerospora* spp.), Stewart's bacterial wilt [*Erwinia stewartii* (E.F. Smith) Dye], curvularia leaf spot (*Curvularia* spp.), Southern rust, and maydis leaf blight.

Hi bt COMP 6 is a six-backcross conversion of Hi bt COMP 3 to the genes *A1*, *B1*, and *P1* for purple stalk, husks and cob, with four cycles of RMS. This was released in 1996 as 'Kalakoa Supersweet' ('kalakoa' is the Hawaiian name for colorful, as in calico prints). Seed mass and ear length are reduced somewhat under low light conditions, but it performs well in the summer (Table 1). Silks are colorless and kernels are yellow or bluish-colored at sweet corn stage. Both a *y1/y1* (white seed) and an *Og1* (Old gold stripe) version of this composite have been bred, and a bicolor hybrid is marketed.

Hi bt COMP 7 was derived from *bt1* seg-

regants among testcrosses of Mo17 to 46 high-yielding tropical field corn inbreds. After seven cycles of RMS, this composite had good lodging tolerance, deep kernels, and high stalk and ear quality (Table 1). It segregates white kernels and ranges widely in kernel tenderness.

Hi bt COMP 8 is a daylength-insensitive (DI) selection initiated in 1978 from Hi bt COMP 3, which in turn had about 5/16 temperate DI germplasm in its pedigree. It was derived from four cycles of selection under 16-h days in Hawaii (Brewbaker, 1981b), followed by one cycle of selection at Madison, Wis., by Dr. W. Tracy, and segregates some daylength-sensitive plants. Five additional cycles of RMS under normal Hawaiian daylength are in the pedigree of Hi bt COMP 8, that generally mimics Hi bt COMP 3 (Table 1).

2) *Population based on brittle2*. One composite, Hi bt2 COMP 1, was generated using the *brittle2* gene (Chromosome 4S-48) from a Maize Genetics Coop stock that was introduced into tropical flint inbred Hi27 and then crossed to an assortment of *su1* COMPS and SYNS. Near-isogenic lines of Hi27 exist for ≈120 genetic markers, including *bt1*, *bt2*, *sh2*, and *su1*; all of the lines with this background germinate slowly (Zan and Brewbaker, in press). Subsequent crosses were made to *sugary1* inbred AA8, and the composite was advanced through 11 cycles of RMS and made homozygous for the *bt2* allele. It segregates for red cob and silk, but has excellent stature, small ears and kernels, and high general disease and pest resistance (Table 1). The *bt2* and *sh2* genes both affect ADPG-pyrophosphorylase activity and germinate poorly in high-fusarium soils (Zan and Brewbaker, in press). An early version was released as 'Hawaiian Supersweet #6' (Brewbaker and Banafunzi, 1975) and is available in Asian markets.

3) *Populations based on shrunk2*. A series of six inbred-based synthetics and two composites were bred with the *shrunk2* gene (Chromosome 3L-149.2), of which only one of each has been retained (Table 1). Hawaiian inbreds based on the *shrunk2* (*sh2*) allele were direct conversions of Hawaiian *su* inbreds. All were marked by absence of anthocyanin, because of close linkage of *sh2* to the *al* allele. Synthetic sh2SYN2 was released to growers in 1970 as 'Hawaiian Supersweet #4' after seven cycles of RMS (Brewbaker, 1971). 'Thai Supersweet' evolved from sh2SYN5, which was released as sh2COMP1 in Thailand in 1968. Although advanced through seven cycles of RMS, sh2SYN5 was marked by poor form and quality. However, it was crossed to Suwan 1, and the extracted supersweet variety, 'Thai Supersweet', resists downy mildew and has provided a foundation, along with Hi bt COMP 3, for the \$40 million Thai supersweet industry (Pulam, 1997). More *sh2* inbreds were derived from crosses of sh2SYN3 x 12 Mainland hybrids. These were recombined and advanced through nine cycles of RMS as sh2SYN4. All of these early synthetics were difficult to germinate in Hawaii, suffered high fusarium damage to seed and seedling, and were discarded.

Hi sh2 SYN 6 (Table 1) was created by combining sh2SYN2 (based on 23 inbreds from 'Hawaiian Sugar' x AA8sh2) and sh2SYN4 (25% AA8sh2 and 75% from inbreds 2256sh2, R819, R821, R825, R839, and R853). It was advanced through five cycles of RMS. With a broad tropical x temperate base and high table quality, it is a useful genetic resource for *shrunk*-2 inbreds. However, ears are short, kernels are small, and fusarium tolerance is low (Table 1).

Two composites were based on *shrunk*-2, of which Hi sh2 COMP 2 (Table 1) survived. It was bred from hybrids of the sh2 version of *sugary1* Hawaiian inbred AA8 with a wide range of tropical flints (Antigua 2d, Mexican and Philippine hybrids, Guatemalan and Caribbean composites, Indian flint inbreds). Six RMS cycles were grown under isolation in blocks of 1000 to 8000 plants, with 250 to 500 ears harvested from disease-resistant plants. Eight cycles of selection involving sib matings or chain crosses were added for more intense selection. This composite is largely daylength-sensitive with long ears and large kernels (Table 1), and should be a rich resource of pest, disease, and stress resistance genes.

4) *Populations based on sugary1*. Two synthetics and four composites (Table 1) have been retained from 15 *sugary1* populations bred in Hawaii. All trace back in part to 'Hawaiian Sugar', released by Mangelsdorf (Brewbaker, 1968) in 1945 from crosses of a Puerto Rican population, USDA34, with 'Golden Cross Bantam'. 'Hawaiian Sugar' was chosen for its tolerance to low-light conditions, resistance to MMV, and tolerance of other diseases and earworms. It handily outyielded all U.S. hybrids tested in Hawaii and the Philippines in the 1960s (Brewbaker et al., 1966). Relatively few other tropical sweet corn varieties were available at this time, among them Pajimaca (Cuba), USDA34 (Puerto Rico), Chulpi and related races (Andes) and Maize Chiripo Dulce (= Maize Dulce, Mexico). Although grown regularly in Hawaiian trials, they had too many negative features to encourage their use in breeding.

The two *sul* synthetics were based on inbreds derived from 'Hawaiian Sugar' introgressed with genes *Ht1* and *Rp1-d*. Hi su SYN 3 represents 20 generations of RMS and closely mimics parent 'Hawaiian Sugar' in performance (Table 1), but excels in uniformity of maturity and quality. Hi su SYN 4 was based on 15 outstanding singlecrosses in 1966 of Hawaiian and Mainland inbreds (190a, 442, 637, 650, C42, C53, P39, P51, and T33), selected through eight cycles in Thailand and Hawaii for low ear position and improved kernel quality and mass (Table 1). Highly variable in horticultural characters, it is a useful repository of tropical and temperate genes for table quality, yield, and resistance.

Four composites were retained on the *sul*

background (Table 1). Stiff stalk and lodging tolerance were introduced into Hi su COMP 6 from inbred N28, along with alleles *Ht1* and *Rp1-d*, during seven cycles of RMS. Hi su COMP 10 excels in fusarium tolerance (Table 1), with large kernels and tender pericarps. It has a complex 23-generation pedigree that includes 5/8 'Hawaiian Sugar', 1/8 Hi bt COMP 1, and 1/8 inbred IL677A. The inbred 677A is *sul sel* (sugary-enhancer) and provides the only specific resistance gene effective against common rust in Hawaii, allele *rp-677a* (Kim and Brewbaker, 1987). The broad tropical base of this composite included many types of disease and pest resistance.

Hi su COMP 12 is blue-seeded through seven BC conversion of 'Hawaiian Sugar' to genes *ACRPr* from marker stock Hi27 (Brewbaker, 1995). This composite showed high table quality following five additional cycles of RMS, and had green plant and silk color, low ear position and good lodging tolerance. Composite Hi su COMP 13 was based entirely on 'Hawaiian Sugar' and its inbreds, involving 25% AA8 (*Ht1* conversion), and was advanced through seven cycles of RMS (Table 1). Like other early *sugary1* populations, it is late, small seeded, and poorly rooted, but high in fusarium tolerance, husk number, and general disease resistance.

Intended Use

Hawaii's composites of supersweet and sweet corns have been assembled on a broad genetic base of tropical field corns, which they mimic, as a genetic resource for breeders. They are comparable to CIMMYT's populations and pools of field corn. The synthetics were designed as a basis for inbred and hybrid development and for direct use as cultivars. Many have entered international vegetable corn breeding, and several are marketed commercially under other names.

Availability

All seeds are open-pedigree and available at cost from Hawaii Foundation Seed Facility, Dept. of Tropical Plant and Soil Science, College of Tropical Agriculture and Human Resources, Univ. of Hawaii, Honolulu, HI 96822. Earlier informal releases of some of these lines must be considered obsolete.

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