NE-EDR*su1* and NE-EDR*b1*, Disease-resistant Sweet Corn Populations with *sugary1* and *brittle1* Endosperms

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The development of broadly based, open-pollinated populations as genetic resources for sweet corn improvement was proposed in 1976 under USDA–CSRS Regional Project NE66 (now NE124). The population NE-EDR (“Northeast, Exotic Disease Resistance”) was bred in Hawaii from crosses of temperate sweet corns with tropical populations chosen for high tolerance of diseases, insects, and stresses (Brewbaker et al., 1991; Kim et al., 1988a). Two counterpart populations, NE-HY-13A and -13B, were selected for high yield based on crosses with elite temperate field corns (Davis et al., 1988). The base population for NE-EDR was a yellow sweet corn with the *sugary1* endosperm gene. Since 1989 this base was converted by backcrossing into sub-populations homozygous for the “supersweet” genes *shrunk2* and *brittle1*, reflecting the shift of consumer interest from *sugary1* to high-sucrose genotypes for enhanced postharvest quality. A germplasm release of the *shrunk2* subpopulation, NE-EDR*sh2*, has been made by Scully et al. (2001). The high-sucrose mutant preferred in the tropics has been *brittle1* (Zan and Brewbaker, 1999).

Origin

The NE-EDR populations were created as a genetic resource for breeders, comparable to CIMMYT’s populations and pools of field corn. They represent >60 cycles of recurrent mass and backcross selection. The primary intent was to expand the genetic base of sweet corn for disease tolerances, a base that largely involved three open-pollinated northeastern American cultivars (Tracy, 1994). Genetic background of NE-EDR is about one-half tem-

perate and one-half tropical sweet corn, the latter derived from tropical field corns (Brewbaker, 1978). The tropical parents were chosen for their resistance to important diseases (Brewbaker, 1979). These include the seedling, stalk, and kernel rots caused by *Fusarium moniliforme* Sheld., and maize mosaic virus (MMV) and maize dwarf mosaic virus (MDMV). Tropical lines also incorporate racially nonspecific tolerance of common rust, southern rust, bacterial leaf blight, northern leaf blight, brown spot, and southern leaf blight. Causal agents are *Puccinia sorghi* Schw., *Puccinia polysora* Underw., *Pseudomonas avenae* Mains, *Exserohilum turcicum* (Pass.) Leonard & Suggs, *Physoderma maydis* Miyabe, and *Bipolaris maydis* (Nisik.) Schoem., respectively.

The NE-EDR*su1* base population and the derivative *b1* and *sh2* sub-populations were bred largely at the Waimanalo Research Station of the Univ. of Hawaii on Oahu at sea level, 20°N lat. Breeding of the *sh2* sub-population was initiated in Hawaii and completed by Scully (Scully et al., 2001) at the Everglades Research Station of the Univ. of Florida at sea level, 26°N lat. Breeding of the NE-EDRs was started in 1976 using *sugary1* lines with yellow endosperm. Conversions were begun in 1989 to supersweet genes *shrunk2* and *brittle1* in populations with both yellow and white endosperm.

Ten elite American sweet corn hybrids (*sugary1* gene) that dominated the industry in 1975 were chosen as the base population of NE-EDR (Table 1). All were temperate except for Hawaii’s H68 or ‘TropIII’ (Brewbaker, 1968), a hybrid of Hawaii’s AA8 (tropical) and Illinois’ 442 (temperate). All except H68 showed high susceptibility to maize mosaic virus, fusarium seedling rot, common and southern rust, and other diseases common in Hawaii (Brewbaker, 1998). While some of these problems were peculiar to the tropics, many were simply intensified by year-round corn production in Hawaii’s congenial climate.

The 10 temperate hybrids were crossed in a diallel with 12 subtropical *sugary1* populations developed through 6 to 12 cycles of

recurrent mass selection (RMS) in Hawaii (Table 1), using four ears of each population as females to each temperate hybrid as male. Most of the subtropical populations appear in the pedigree of 16 composites and synthetics (6 *sugary1*, 7 *brittle1*, 1 *brittle2*, 2 *shrunk2*) released previously (Brewbaker, 1998). These populations included composites and synthetics, the latter based on inbreds from the cultivar Hawaiian Sugar, or from hybrids among Hawaiian inbreds and publicly available U.S. inbreds. The composites were derived from crosses of temperate sweet corns with tropical field corns chosen for their tender pericarp. Many tropical races and cultivars of field corn evolved as *elote* or green food corns, and customarily have thin pericarp and high consumer acceptability (Brewbaker et al., 1996). In contrast, Corn Belt Dents of the United States have pericarps much thicker than tropical corn races (Wang and Brewbaker, 2001).

Aliquots of the 480 hybrid ears were bulked to create NE-EDR, and were planted 1 Nov. 1976, as a population of 3300 plants from which 500 open-pollinated ears, comparable to an F₃, were selected. Hardy–Weinberg estimates of gene frequencies in this population were *Mv* 50%, *Rp1-d* 50%, *Ht1* 40%, and *o2* 8%. Thirteen cycles of recurrent mass selection followed in the base population, which was made homozygous for the *su1* allele in cycle 6. Selection for agronomic quality and disease resistance was made insofar as possible prior to hand-pollination and at an intensity of ≈10% among >1000 plants per cycle.

No insecticide, fungicide, or seed treatment is ever applied to corn at Waimanalo Research Station. During the 25 years of year-round breeding and evaluation of NE-EDR, 320 nurseries were planted that averaged 590 plots (5 m in length) per month. This maximized the frequency and severity of natural epidemics of diseases and insect pests. A temporal shuttle breeding strategy for the base population of NE-EDR was combined with selection, alternating from the warm, dry, long-day summers to the cool, wet, low-light winters (Jong et al., 1982). All epidemics were cyclical and more severe in winter. Five of the 13 cycles were conducted in winter months, under heavy selection pressure for diseases. Seven of the 13 cycles involved hand-sib pollination, with significant selection prior to silking, while six were conducted in isolation for open-pollination.

Table 1. Temperate sweet corn hybrids and tropical sweet corn populations that were crossed to form base population NE-EDR.

Temperate hybrids	Tropical populations
Bonanza	Hawaiian Sugar [*]
Gold Winner	Hi su SYN2
Golden Cross Bantam	Hi su SYN4 [*]
Iobelle	Hi su COMP 6 [*]
Jubilee	Hi su COMP 7
Midway	Hi su COMP 8
NK 51036	Hi su COMP 9
Silver Queen	Hi su COMP 10 [*]
Stylepak	Hi su COMP 11
Trop III (H68)	Hi o2su COMPs 1,2,3

^{*}Described by Brewbaker (1998).

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NE-EDR sub-populations

Two major sub-populations based on the “supersweet” genes *brittle1* and *shrunk2* have been bred in addition to the base population NE-EDR*su1*. NE-EDR*bt1* originated in 1990 from crosses of NE-EDR*su1* Cycle 8 with Hi bt COMP 3 as the *bt1* donor (Brewbaker, 1998). The accelerated conversion involved 14 cycles of breeding that included five backcrosses followed by sibbing, selfing, and open-pollination in isolation. The fifth backcross involved a large population of the recurrent parent. Eight of the 14 cycles occurred in the winter, providing high selection pressure for viability of the high-sucrose seeds and disease resistance. Although the double mutant, *sugary1 brittle1*, could be recovered from advanced cycles of selection, it was eliminated from the population due to its poor viability. NE-EDR*sh2* also originated from crosses made in 1990 between NE-EDR*su1* Cycle 8 and temperate *shrunk2* hybrids, with five backcrosses and five sib cycles in Hawaii followed by backcrosses and sibs summarized by Scully et al. (2001).

Description

Horticultural traits. The NE-EDR populations emerged silks between 48 and 60 d in Hawaii, and were harvested as fresh corn in ≈10 weeks. They ranged widely in maturity during the year, and would be considered “mid- to late-mid” season relative to commercial U.S. hybrids. For comparison, the hybrid Jubilee silks in 46 to 50 d in Hawaii. The NE-EDRs are segregating for daylength sensitivity, and some plants would be delayed 1 week or more to silk by 16-h days. Field emergence rates of NE-EDR populations appear to follow those reported by Zan and Brewbaker (1999) for near-isogenic lines, with *su1* 85%, *bt1* 74%, and *sh2* 52%.

The NE-EDRs appear similar to field corns, with rare tillers and flag leaves, strong brace roots, and high tolerance of lodging tolerance and stalk breakage. Leaf-area indices are high, and a small fraction of plants have erect leaves and delayed senescence or stay green. Plant and ear heights range widely in the NE-EDRs, with summer averages (maximal in Hawaii) of 2.34 m (top of tassel) and 0.76 m (base of uppermost ear). Ears also show wide variability in length and row number. Husk numbers are higher (9 to 13) than in temperate hybrids. Husks extend well over the slightly tapered ears, providing high tolerance to earworms (*Helicoverpa zea*), and husk- or flag-leaves are absent or reduced in size. The *opaque2* gene is expected to be present in all sub-populations at low frequency. The base population of NE-EDR*su1* has only yellow kernels, but NE-EDR*bt1* cycle 14 segregated 18% white kernels (*y1/y1*) and 35% pale yellow kernels, believed to be based on allele *y8*. A detailed description of horticultural properties in Florida of sister composite NE-EDR*sh2* has been published by Scully et al. (2001).

Disease tolerances. The NE-EDR populations were grown for breeding or evaluation in

Table 2. Empirical scores for nine diseases (1 highly resistant to 9 highly susceptible) averaged over two decades of observations in Hawaii of populations NE-EDR*su1* and NE-EDR*bt1* sweet corn.

Disease common name	Disease causal organism	Score
MMV	Maize mosaic virus	1
MDMV	Maize dwarf mosaic virus	3
Ear and kernel rot	<i>Fusarium moniliforme</i>	2
Common rust	<i>Puccinia sorghi</i>	2
Southern rust	<i>Puccinia polysora</i>	4
Northern leaf blight	<i>Exserohilum turcicum</i>	4
Southern leaf blight	<i>Bipolaris maydis</i>	6
Brown spot	<i>Physoderma maydis</i>	2
Bacterial leaf blight	<i>Pseudomonas avenae</i>	3

≈120 of the ≈320 Waimanalo corn nurseries since 1976, of which there were 22 breeding nurseries for *su1*, 25 for *bt1*, and 19 for *sh2*. Disease and insect epibiotics varied greatly within and among these years (Brewbaker, 1974; Moon et al., 1999), and selection often dramatically improved resistance within populations for diseases, e.g., MMV, fusarium kernel rot, southern rust, or physoderma brown spot. Assessments of disease tolerances (Table 2) were based largely on empirical observations on a 1–9 scale of these 120 trials. In many trials commercial U.S. hybrids were also grown as susceptible checks, with scalar averages of 7 to 9 (Kim et al., 1988a). High resistance characterized most Univ. of Hawaii field corns in these trials, which are grown commercially in Hawaii without pesticides. MMV resistance (Brewbaker, 1998) did not occur in any American sweet corn in 1975. Thus, NE-EDR breeding focused initially on selection for resistance, shown by Ming et al. (1997) to involve chromosome 3 locus *Mv*. In Nov. 2000 the gene frequency of resistant allele *Mv* was 62.4% among 500 plants of the two NE-EDRs, while >90% of temperate checks were virus-infected. Resistance to the aphid-transmitted MDMV occurs among the tropical parents of NE-EDR, but aphid predation prevents spread of MDMV in Waimanalo nurseries. Virus resistance of any type is uncommon in temperate corns (Brewbaker et al., 1991), and other resistance genes expected to occur in NE-EDR include those to the corn stunt complex of Mesoamerica.

The NE-EDRs express high tolerance of fusarium kernel, ear, and seedling rots, since seeds are never fungicide-treated and *Fusarium moniliforme* Sheld. is epidemic in fields dedicated to corn at Waimanalo. Under the wet winter conditions of 1992, untreated seeds of temperate *sh2/sh2* and *se/se* hybrids germinated 7%, while NE-EDR germination exceeded 60%. Ears harvested in May 2001 for National Seed Storage Laboratory showed kernel rot in 6% of NE-EDR*su1* and 27% of NE-EDR*bt1*, generally confirming experience in Hawaii with these endosperm genes. Occasional viviparous seeds occurred in 1% of *su1* ears and in 9% of *bt1* ears. Ears of a Jubilee Supersweet check revealed 85% kernel rot and 12% vivipary. NE-EDR and other Hawaii-bred populations uniquely show little or no damage to thrips (*Frankliniella* sp.), which are abundant and a serious problem on temperate germplasm in Hawaii’s seed industry. Thrips

are a similar problem in Queensland, Australia, where Hawaii’s hybrids show high tolerance (I. Martin, personal commun.). Actual injury to corn by thrips is believed to be minimal, but they are suggested to provide an avenue for entry by fusarium. Thus the selection for fusarium resistance may have conferred some thrip tolerance on Hawaii-bred populations.

High general resistance occurs in NE-EDR (Table 2) to the mixture of races of common rust that are epidemic in wet winter months at Waimanalo. In 1988, an NE-EDR population in cycle 7 averaged 3.2 on a 1–9 rust scale vs. an average of 6.3 for 98 temperate sweet corn hybrids (Kim et al., 1988b). In 2000, 100 temperate hybrids averaged 7.2 on this scale (Pataky et al., 2001) and produced no marketable ears. A nearby population of NE-EDR*su* ranged widely but averaged 3.6 on this scale. All specific resistance genes except *rp-677A* (Kim and Brewbaker, 1987) are ineffective in Hawaii. The resistance allele *Rp1-d* is present in NE-EDR but is now widely ineffective (Pataky et al., 2001). Southern rust can be very severe at Waimanalo in dry cool winters, and major QTLs for resistance have been identified in tropical field corns at this location (Moon et al., 1999). Mature-plant resistance is rare in temperate sweet corns but common to all Hawaii-bred sweet corns (Table 2).

Northern leaf blight is occasionally severe at Waimanalo, where monogenes for specific resistance such as *Ht1*, *Ht2*, and *HtN* are ineffective. Tropical parents of the NE-EDRs had high general resistance (Brewbaker, 1998), and temperate parents were susceptible or carried *Ht1*. In Florida, the NE-EDR populations averaged 1.6 on the 0 to 9 scale of Scully et al. (2001), vs. 3.3 for ‘Florida Staysweet’ and 0.9 for ‘Waimanalo Supersweet’. Southern blight is uncommon in Hawaii, but tolerance has been observed (Table 2). Brown spot is common throughout the year at Waimanalo, and the NE-EDRs appear to be highly tolerant (Table 2). Tolerance of bacterial leaf blight, caused by *Pseudomonas avenae* Manns, is also high (Table 2), with fewer than 4% infected plants in a 2001 spring nursery showing >90% infection of susceptible inbreds.

Tolerance for several diseases should segregate in the NE-EDR populations, but have not been assessed. Common smut, caused by *Ustilago maydis* (DC) Cda, is an example, for which NE-EDR may segregate susceptible plants at rather high frequencies, since suscep-

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tibility is common among tropical lines. Also among the tropical parents of the NE-EDRs are composites or varieties that had tolerance of Stewarts' bacterial wilt (Ming et al., 1999), head smut, caused by *Sphacelotheca reiliana* (Kuhn) Clint, downy mildew diseases, and other stalk and kernel rots.

Availability

All seeds are open-pedigree and available at cost from Hawaii Foundation Seed Facility, Dept. Tropical Plant and Soil Science, College of Tropical Agriculture and Human Resources, Univ. of Hawaii, 3190 Maile Way, Honolulu, HI 96822. The two NE-EDR populations are stored at the U.S. National Seed Storage Laboratory, Ft. Collins, Colo., and are registered (NE-EDRsu1 = PI 619435, NE-EDRbt1 = PI 619436), and the *sh2* population is registered as PI 614830 (Scully et al., 2001). Recipients are requested to acknowledge the use of these materials in research, patenting, or germplasm development.

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