Combining Ability and Acceptability of Temperate Sweet Corn Inbreds Derived from Exotic Germplasm

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Abstract. **Excellent table quality is an essential characteristic of commercial sweet corn (*Zea mays*) and commonly held paramount as a selection criterion. As a consequence, breeding for improved agronomic performance in sweet corn has been limited in comparison with United States dent corn breeding efforts. The narrowness of genetic diversity within modern sweet corn germplasm suggests potential exists for yield enhancement through new heterotic combinations and introgression of sources of improved agronomic performance. The objective of this study was to examine the results of incorporating nonsweet germplasm in the development of improved temperate sweet corn cultivars. Five inbreds derived from crosses between nonsweet germplasm and temperate supersweet (*shrunken2, sh2*) inbreds were crossed with three temperate *sh2* testers to make 15 experimental hybrids. The hybrids were evaluated in four environments with three replications per environments. Experimental entry Wh04038V × Tester2 yielded 18.1 Mg·ha^{-1} in 2009 and 16.6 Mg·ha^{-1} in 2010, significantly out-yielding the top producing commercial control, 'Overland', in both years. An additional six entries derived from exotic-by-temperate crosses yielded significantly more than all commercial checks in 2009. Four specific experimental entries consistently exhibited superior resistance to root lodging, northern corn leaf blight (*Exserohilum turcicum*), and *Maize dwarf mosaic virus* (MDMV) compared with 'Marvel' and 'Supersweet Jubilee Plus'. Ten of the 15 experimental entries exhibited similar quality for flavor relative to 'Marvel' and 'Overland', however 'Supersweet Jubilee Plus' outperformed all entries for both flavor and tenderness, suggesting that while incorporation of nonsweet germplasm in sweet corn breeding programs may provide valuable contributions for yield and agronomic performance, flavor and tenderness must be carefully regarded.**

Excellent table quality, defined by desirable flavor, tenderness, and visual appearance, is an essential characteristic of sweet corn cultivars and is commonly held paramount as a selection criterion (Tracy, 1990a). With such emphasis on table quality, selection for other desirable characteristics such as enhanced yield, improved plant vigor, strong roots and stalks, and pest resistance has been considerably restricted in comparison with U.S. dent corn (Treat and Tracy, 1993), rendering sweet corn deficient in a number of agronomic traits. The selection limitations arising from the importance of table quality are compounded by the narrow genetic diversity within sweet corn germplasm as several bottlenecks occurred over the course of sweet corn development.

Development of sweet corn cultivars in the 19th century focused primarily on white kernel types (Huelsen, 1954; Tracy, 1997) from the race Northern Flint, which itself has a highly restricted germplasm base relative to other races of corn (Doebley et al., 1988). The success of 'Golden Bantam', released by the Burpee Company (Philadelphia, PA) in 1902, stimulated a transition in preference toward cultivars with the allele for yellow (*Y1*) endosperm and 'Golden Bantam' was subsequently incorporated in the development of new cultivars (Galinat, 1971; Gerdes and Tracy, 1994; Marshall and Tracy, 2003). 'Golden Bantam' possesses an essentially pure Northern Flint background and has contributed significantly to modern sweet corn germplasm, serving as an ancestor of almost all modern yellow endosperm hybrids (Galinat, 1971; Gerdes and Tracy, 1994). As a result, the background of many of today's sweet corn cultivars includes a significant portion of, if not 100%, Northern Flint (Tracy, 2000), suggesting sweet corn breeding populations might be enhanced through the addition of new sources of genetic diversity.

It has been advocated (Goodman et al., 2000; Nelson and Goodman, 2008; Taller and Bernardo, 2004; Whitehead et al., 2006) that genetic gains may be achieved in competitive U.S. dent corn breeding programs through incorporation of exotic germplasm in an effort to address the narrowing diversity of the germplasm base that has resulted from inbred recycling among elite hybrids predominantly derived from the Stiff Stalk and Lancaster genetic backgrounds (Taller and Bernardo, 2004; Tallury and Goodman, 1999). Evaluation of the introgression of exotic germplasm in breeding of U.S. dent corn has been conducted in efforts to mine exotic germplasm for favorable alleles and to provide rationale for tapping the high species diversity within corn that is not represented in U.S. dent corn production. The screening trials of Holland and Goodman (1995) provide evidence that superior tropical corn accessions may serve as a useful germplasm source for commercial corn breeding in the United States. Taller and Bernardo (2004) identified four exotic populations as donors of favorable alleles to an elite Corn Belt Dent single cross, concluding that suitable exotic germplasm could contribute to improvement of U.S. dent corn germplasm. Yield data produced by Goodman (2004) revealed that certain largely tropical or completely tropical

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inbreds when crossed with domestic inbreds result in hybrids competitive with commercial cultivars, suggesting a potential for use of largely tropical germplasm as compared with the more common practice of introducing small segments of exotic material into breeding programs. Evaluations of Whitehead et al. (2006) suggested germplasm having a background of 25% elite exotic material can be incorporated in the stiff stalk and nonstiff stalk heterotic groups without disruption of combining ability. Nelson and Goodman (2008) provided additional evidence that there is yield potential to be realized using germplasm exotic to U.S. dent corn, but conceded that breeders working with tropical-exotic germplasm face challenges pertaining to photoperiod sensitivity and ultimate success is largely attributed to choice of germplasm.

Because the available sweet corn germplasm base is even further restricted relative to U.S. dent corn, introgression of nonsweet germplasm into sweet corn breeding may provide new beneficial heterotic combinations and improved sources of disease and pest resistance (Tracy, 2000). Successful incorporation of nonsweet germplasm has proved useful in several instances throughout the development of improved sweet corn cultivars (Galinat, 1971; Tracy, 1999) with the discovery of *sugary enhancer1* (*se1*) as one of the most striking examples of the potential of exotic germplasm in sweet corn development (Gonzales et al., 1976). The success of historic sweet corn cultivars including Stowell's Evergreen and Golden Bantam developed from crosses with nonsweet cultivars provide examples of successful utilization of nonsweet germplasm in sweet corn breeding (Tracy, 1999). Another early example of successful incorporation of nonsweet germplasm in sweet corn development is 'Spanish Gold' (Jones and Singleton, 1931). 'Spanish Gold' was the product of a cross between an early maturing high-rowed flint named 'Cinquantino' of the Pyrenees Mountains of Spain and several sweet corn cultivars (Galinat, 1971) and is found in the ancestry of many early maturing inbreds such as C2A, C3, C4, and C5 (Galinat, 1971; Tracy, 2000). It has been shown that Spanish field corn can be useful in the improvement of *sugary1* (*su1*) sweet corn heterotic patterns (Revilla et al., 2000). Butrón et al. (2008) crossed *su1*, *sh2*, and *se1* populations with 'Lazcano', 'Oroso', and 'Rastrojero' Spanish field corn populations, demonstrating that nonsweet populations may improve yield and agronomic traits of sweet corn, but selection of the contributing nonsweet population should be based on target growing conditions and may require subsequent selection for improved quality. The narrowness of modern sweet corn germplasm suggests there may be potential for yield enhancement through new heterotic combinations, improved agronomic performance, and increased resistance to pests through efforts to increase genetic diversity in breeding programs (Goodman et al., 2000; Haber, 1945; Tracy, 1990a, 1990b). The objective of this study was to examine the potential for utilization of exotic sources of germplasm in competitive sweet corn breeding programs by assessing the performance of five *sh2* sweet corn inbreds derived from crosses between temperate sweet corn and nonsweet germplasm.

Materials and Methods

Germplasm. Experimental entries consisted of 15 hybrids developed in a NC Design II factorial mating design (Comstock and Robinson, 1952), in which five sweet corn inbreds derived from sweet by nonsweet breeding populations were crossed with three proprietary *sh2* temperate inbred testers (Tester1, Tester2, and Tester3) that have been commonly used in the Wisconsin Sweet Corn Breeding Program. The five inbreds derived from sweet by nonsweet crosses included Wh92047, Wh04030V, Wh04036V, Wh04038V, and Wh01001. Wh04030V, Wh04036V, and Wh04038V were developed from 'NTZ Mexican Dent *sh2*'. 'NTZ Mexican Dent *sh2*' was derived from 'NTZ Mexican Dent' (93% Mexican, 7.0% temperate) (Gerrish, 1980; Tracy, 1990a) crossed to C68*sh2,* a *su1* inbred developed in Connecticut and converted to *sh2* in Wisconsin. The progeny of this cross were intermated and only *sh2* kernels were saved. The *sh2* population underwent an additional four generations of sibmating. Wh04030V, Wh04036V, and Wh04038V were the result of eight to nine generations of self-pollination and selection for ear appearance, agronomic performance, and resistance to MDMV. Wh92047 and Wh01001 possess backgrounds that include U.S. dent corn. Wh92047 was derived from a cross between A632 × Ia5125*sh2* followed by nine generations of inbreeding. A632 is a field corn inbred from Minnesota and Ia5125 is *su1* sweet corn inbred from Iowa and converted to *sh2* in Wisconsin. Wh01001 is a product of a cross between 'Dairyland ST 1180' and 'Contender', which was subsequently self-pollinated for nine generations. 'Dairyland ST 1180' is a single-cross field corn hybrid and 'Contender' is a supersweet sweet corn hybrid. Although initial crosses resulted in F_1 progeny that consisted of at least 50% nonsweet germplasm, during inbreeding there was selection for ear appearance in early generations that may have diminished the percentage of the exotic parent. Three commercial *sh2* hybrid cultivars, Overland (Syngenta; Basel, Switzerland), Supersweet Jubilee Plus (Syngenta), and Marvel (Crookham Co.; Caldwell, ID) served as checks within the experiment. 'Supersweet Jubilee Plus' was not included in 2009.

Experimental design. The experiment was conducted in 2009 and 2010 at the University of Wisconsin West Madison Agricultural Research Station (lat. 43°04'N, long. 89°32'W) and the Arlington Agricultural Research Station (lat. 43°18'N, lat. 89°21'W). Soil type at both locations is a Plano silt loam (fine-silty, mixic mesic Typic Argiudoll). The experimental design was a randomized complete block design (RCBD) with three replications at each environment. Plots consisted of two rows in 2009 and four rows in 2010. Row length excluding the alleys was 3.5 m with 0.76 m between rows.

Experimental entries were planted at the West Madison Agricultural Research Station on 26 May 2009 and 19 May 2010 and at the Arlington Agricultural Research Station on 29 May 2009 and 25 May 2010. Limited seed quantity resulted in the exclusion of the following entries in a third replication at both the Arlington, WI 2009 and West Madison, WI 2009 environments: Wh04036V × Tester1, Wh04038V × Tester1, and Wh04036V × Tester2. Preemergence herbicide and insecticide were applied at all environments. Entries were overplanted to ≈30 seeds/row (113,000 seeds/ha) and were subsequently thinned to 15 plants/row at the V5 growth stage (Ritchie et al., 2003), resulting in a population density of 56,455 plants/ha. In 2009, the commercial control 'Marvel' suffered severe raccoon (*Procyon lotor*) feeding damage in all three replications at the 2009 Arlington, WI environment, and was excluded in analysis of traits pertaining to yield or ear characteristics.

Susceptibility to common rust (*Puccinia sorghi*) was examined in independent trials in 2010. A single-row plot of each of the 18 entries was arranged in an RCBD with one row of 'Supersweet Jubilee Plus' (a cultivar susceptible to common rust) bordering each entry to allow for a more even distribution of secondary inoculum of *P. sorghi*. Three full replications of those 18 experimental entries were planted at the West Madison Agricultural Research Station on 19 May 2010 and at the Arlington Research Station on 25 May 2010. Plots were overplanted and thinned to a density of 45,000 plants/ha (12 plants/row) at the V5 growth stage. Common rust evaluation trials were inoculated with a mixture of three strains of *P. sorghi* at the V8 to V12 leaf stage via application of a urediniospore suspension consisting of 15 mg urediniospores in 11 mg H_2O with 5 drops of Tween 20 (Sigma-Aldrich, St. Louis, MO) added to prevent clumping, directed into the leaf whorls (Chandler and Tracy, 2007). The West Madison common rust trial was inoculated with *P. sorghi* urediniospores on 28 June 2010. The corresponding common rust trial at Arlington was inoculated on 15 July 2010. Common rust infection was quantified visually and assigned a severity rating of 0% to 100% based on area of leaf tissue infected on the first five bordered plants (consecutive evenly spaced plants in the plot not bordering the alley).

An MDMV screening trial including all 18 experimental entries arranged in a single-row RCBD was planted at West Madison at the same time as the common rust trial and was inoculated on 9 June 2010 and again on 10 June 2010 using a motorized backpack sprayer (Solo 450; Solo, Newport News, VA) and MDMV solution prepared from leaves infected with MDMVa and MDMVb, also known as *Sugarcane mosaic virus*. A single row of 'Supersweet Jubilee Plus', which is susceptible to both strains of MDMV, bordered each plot. A second application of inoculum prepared from bulked leaves within the trial identified as showing a positive susceptible reaction to the initial inoculation was applied using "hand clappers" (tongs) on 24 June 2010 to ensure a more uniform distribution of inoculum. The hand clappers were engineered to include one tong holding a sponge that absorbed the inoculum solution and a corresponding tong, which held small nails serving to puncture the leaf and draw solution from the sponge into the wound. A second environment artificially inoculated with MDMV at Arlington, WI in 2010 was discarded as northern corn leaf blight (NCLB) disease pressure was too severe to accurately score hybrid response to MDMV.

Data collection. Evaluation of traits of interest was conducted on the first five bordered plants. Data were collected within the left row of all two-row plots in 2009 and the center two rows of the four-row plots in 2010. Primary ears from each of the first five bordered plants were harvested once all entries had reached physiological maturity as determined by black layer and were then dried to constant moisture. To evaluate yield, which was measured as wet weight of the ear after the husks were removed, ear moisture was calculated on a wet basis [(wet weight – dry weight)/wet weight] with wet weight per plot standardized to 70% moisture. Harvested ears were also measured for mean ear length and diameter. Many entries at the Arlington, WI 2010 environment suffered severe root lodging, and ears were harvested only from plants judged to be harvestable by mechanical picker (having an angle of 30° or greater between the soil surface and the main stalk. Plant height was measured from the soil surface to the tassel tip and ear height was measured from the soil surface to the ligule of the leaf subtending the ear. Plant and ear heights were recorded individually on five consecutive plants and plot means were calculated.

Days to anthesis were recorded as the number of days from planting to the day on which 50% of the tassels of plants from the two center rows of a plot had exerted 50% of their anthers and served as a basis for harvest of ears to be evaluated for table quality characteristics 23 d after anthesis and as a predictor of physiological maturity. Growing degree days (GDD) were recorded as an average of the maximum and minimum daily temperatures with a base temperature of 10 °C and an upper limit of 30 °C.

Because satisfactory table quality is an essential characteristic of commercial sweet corn cultivars, entries were evaluated for flavor and tenderness. Primary ears were harvested from bordered plants 23 d after anthesis and were immediately sampled raw and rated for both flavor and tenderness by an experienced taste-testing panel consisting of five individuals. Ratings for both flavor and tenderness were based on a 1–5 scale in which a rating of 1 = undesirable flavor or tenderness, 2 = subpar flavor or tenderness, 3 = average flavor or tenderness, 4 = desirable flavor or tenderness, and 5 = highly desirable flavor or tenderness. The commercial control 'Marvel' was designated as a standard established as having a flavor of "3" and a tenderness of "3" and was provided at the onset of each day's taste testing. Staggered planting dates of 'Marvel' allowed for this standard to be provided unannounced during testing, serving as a quality control on the ratings submitted by each individual. Flavor and tenderness ratings were analyzed as the average value of the ratings provided by the five individuals serving on the testing panel.

The percentage of plants within the center two rows of each plot identified for root lodging was analyzed exclusively at the Arlington 2010 environment as two severe storms provided an ideal screening environment for genotypic variation for susceptibility to root lodging. Root-lodged plants were distinguished as those plants for which the angle between the stalk and the soil surface was estimated to be less than or equal to 45° and entries were evaluated based on the percent of plants within the center two rows found to be identified as root lodged.

Experimental entries were assigned a visual rating for susceptibility to common rust based on the total percentage of leaf area found to be infected with rust (*P. sorghi*) pustules. Environments for which susceptibility to common rust was examined included West Madison 2009, Arlington 2010, West Madison 2010 under natural disease pressure, and the artificially inoculated trials at Arlington in 2010 and West Madison in 2010. Susceptibility to common rust was not analyzed for the Arlington 2009 environment as disease pressure at that environment was found to be inadequate to provide for distinguishable variation of interaction phenotypes. Southern rust (*Puccinia polysora*) was identified at both the Arlington 2010 and West Madison 2010 environments in addition to common rust.

Experimental entries were examined for reaction to natural disease pressure of *E. turcicum*, the causal agent of NCLB in 2010 at both Arlington and West Madison, with susceptibility rated on visual assessment of the percentage of leaf area infected. NCLB pressure was notably severe in 2010, providing an excellent screening environment, as two of the checks were identified as highly susceptible with greater than 75% leaf area infected. Susceptibility to NCLB was not analyzed for the Arlington 2009 and West Madison 2009 environments as disease pressure was inadequate to differentiate susceptible hybrids from resistant hybrids.

Susceptibility to MDMV was examined exclusively at the West Madison 2010 MDMV artificial inoculation trial. A second artificially inoculated MDMV environment at Arlington in 2010 was found to be too-heavily infected with NCLB to score response to MDMV and no significant natural MDMV pressure was identified in any other environment. MDMV susceptibility was rated on a 0–3 scale in which 0 = no apparent symptoms, 1 = either faint mosaic symptoms or severe mosaic symptoms restricted to portions of only one or two leaves, 2 = an obvious mosaic on most but not all leaves, and 3 = an intense mosaic, identified as systemic (Pataky et al., 1990).

Statistical analysis. An analysis of variance (ANOVA) was calculated for plot means of all recorded traits using PROC MIXED in the SAS statistics package (version 9.2; SAS Institute, Cary, NC). Environment and entry were considered fixed effects while replication within environment was random. To account for missing data points within the factorial design, least square means were estimated for all traits in PROC MIXED. Entries were partitioned into males (testers), females (inbreds derived from temperate by exotic crosses), and male by female interactions, for all traits for which entry was found to be significant ($P \leq 0.05$). Environments were pooled for all traits for which no significant ($P \leq 0.05$) environment by hybrid effect was identified or in the case where a Spearman rank correlation revealed that a significant environment by hybrid interaction was attributed to a change in magnitude and not a change in rank. Data for all traits were evaluated for normality and equal variance in advance of performing an ANOVA. Non-normal data were analyzed with logarithmic or square root transformations. To determine the average performance of a line in hybrid combination, general combining ability (GCA) of all male and female parents included in the North Carolina Design II mating scheme was estimated for traits of interest in which the hybrid entry was found to be significant ($P \leq 0.05$). For those traits with significant ($P \leq 0.05$) entry effects, specific combining abilities (SCA) were estimated to identify those hybrid combinations that performed relatively better or worse than would be predicted based on the average performance of the parent lines at those specific environments (Griffing, 1956). Two-tailed *t* tests using false discovery rate (FDR) as a multiple testing correction method were conducted to determine significance of GCA and SCA effects.

Results and Discussion

Environment effects were significant ($P \leq 0.05$) for all traits measured across the 15 experimental hybrids and three commercial checks, excluding rating for flavor and susceptibility to NCLB. Hybrid effects were significant ($P \leq 0.05$) for all traits. Significant ($P \leq 0.05$) female parent effects were also identified for all traits examined. Male parent effects were significant ($P \leq 0.05$) for all traits examined except rating for tenderness and susceptibility to NCLB. The interaction of male and female parents was significant ($P \leq 0.05$) for all traits excluding ear length, rating for flavor, and susceptibility to root lodging. Replication within environment was found to be significant ($P \leq 0.05$) for yield, plant height, ear height, ear length, ear diameter, susceptibility to root lodging, susceptibility to rust, and susceptibility to NCLB.

The least square estimate for overall mean yield pooled across 2010 environments was 14.6 $Mg{\cdot}ha^{-1}$ standardized to 70% moisture (Table 1). Across 2009 environments, the least square estimate for the mean overall yield at 70% moisture was 17.3 $Mg{\cdot}ha^{-1}$ (Table 1). Entry Wh04038V × Tester2 performed notably well in both 2009 and 2010, yielding significantly more than the highest yielding commercial control, 'Overland', when pooled separately across both the 2009 and 2010 environments (Table 1). An additional nine hybrids were not significantly different from the highest yielding commercial control in 2010. Across 2009 environments, 7 of 15 experimental entries significantly out-yielded 'Overland' (the highest yielding commercial hybrid), while an additional six experimental entries were not significantly ($P \leq 0.05$) different from 'Overland', with Wh29047 × Tester2 performing notably well. Across the 2010 environments, Wh04038V exhibited significant ($P \leq 0.05$) positive GCA for yield relative to the remaining four female parents (Table 2). Wh01001 was identified as having significant ($P \leq 0.05$) negative combining ability for yield across both the 2009 and 2010 pairs of environments. Wh01001 hybrids were among the earliest flowering (Table 2). Hybrids derived from Wh01001 had consistently poor tip fill.

Plant height least square estimates ranged from 210.6 cm for the commercial control 'Overland' to 248.6 cm for Wh92047 × Tester2 (Table 1). Wh04038V × Tester2, which was the highest yielding hybrid across both the 2009 and 2010 environments, was not significantly ($P \leq 0.05$) different from the tallest hybrid. Female parents Wh92047 and Wh04038V produced the tallest hybrids with highly significant ($P \leq 0.001$) positive GCAs for late season plant height when pooled across all environments (Table 2). Wh04036V revealed highly significant ($P \leq 0.001$) negative GCA for plant height, producing hybrids ≈17 cm below the mean plant height. Ear height pooled across all environments was found to be highly variable with least square mean estimates ranging from 74.8 cm for Wh04036V × Tester3 to 114.9 cm for Wh92047 × Tester2.

Growing degree days to anthesis ranged from 555 for the earliest flowering hybrid, 'Marvel', to 630 for Wh92047 × Tester1 when pooled across the 2009 and 2010 environments at West Madison, WI (Table 1). Nelson and Goodman (2008) conceded that breeders experimenting with tropical exotic germplasm face challenges pertaining to photoperiod sensitivity. Because none of the 18 experimental hybrids were found to flower significantly earlier than 'Marvel', the earliest flowering hybrid in this study, or significantly later than 'Overland', the second latest flowering hybrid in this study, it was concluded that hybrids developed from the lines derived from exotic germplasm included in this study were well adapted to temperate climates. Yield was correlated with GDD to anthesis ($P = 0.06$, Pearson's $r = 0.47$). At the West Madison, WI 2009 and 2010 environments, Wh01001 had a highly significant ($P \leq 0.001$) GCA for earlier flowering relative to the other female parents (Table 1). Across those same environments, Wh92047 had a highly significant ($P \leq 0.001$) GCA for later flowering, as hybrids developed from Wh92047 flowered 26 GDD later than the least square mean of 598 GDD (Table 2). Despite highly significant GCA for earlier and later flowering, respectively, Wh01001 and Wh92047 produced hybrids that did not flower earlier than 'Marvel' or later than 'Overland'.

Hybrids Wh04030V × Tester3 and Wh01001 × Tester2 had the longest ears when data were pooled across all environments and the ears were significantly longer than those of 'Overland',

Table 1. Least square means for agronomic and quality traits for 15 sweet corn hybrids developed in a 5 × 3 North Carolina Design II mating design and three commercial checks across specific environments.

	Yield		Plant ht	Ear ht	Date of anthesis	Ear length	Ear diam	Flavor rating	Tenderness rating
Hybrid	ARL2010[z] and WM2010 (Mg·ha^{-1})	ARL2009 and WM2009 (Mg·ha^{-1})	All (cm)	All (cm)	WM2009 and WM2010 (GDD)[y]	All (cm)	All (cm)	WM2009 and WM2010 (1–5 scale)[x]	WM2009 and WM2010 (1–5 scale)[x]
Wh01001 × Tester1[w]	13.6 (6)[v]	14.5 (6)	237.4 (12)	94.0 (12)	577 (6)	16.5 (12)	4.6 (12)	2.9 (6)	2.9 (6)
Wh04030V × Tester1	13.5 (6)	18.4 (6)	229.2 (12)	91.9 (12)	611 (6)	16.0 (12)	4.7 (12)	2.5 (6)	2.5 (6)
Wh04036V × Tester1	15.2 (6)	17.7 (4)	212.8 (10)	79.7 (10)	597 (5)	14.8 (10)	4.8 (10)	2.4 (5)	2.3 (5)
Wh04038V × Tester1	15.1 (6)	16.8 (4)	247.2 (10)	106.4 (10)	601 (5)	15.2 (10)	4.7 (10)	2.6 (5)	2.3 (5)
Wh92047 × Tester1	13.9 (6)	16.5 (6)	243.1 (12)	114.3 (12)	630 (6)	15.3 (12)	4.6 (12)	2.6 (6)	2.3 (6)
Wh01001 × Tester2	13.9 (6)	17.1 (6)	237.1 (12)	92.1 (12)	581 (6)	17.1 (12)	4.7 (12)	2.8 (6)	3.1 (6)
Wh04030V × Tester2	16.3 (6)	17.9 (6)	230.6 (12)	92.4 (12)	605 (6)	16.4 (12)	4.7 (12)	2.9 (6)	2.5 (6)
Wh04036V × Tester2	15.7 (6)	19.1 (4)	220.9 (10)	81.6 (10)	600 (5)	15.0 (10)	4.8 (10)	2.6 (5)	2.7 (5)
Wh04038V × Tester2	16.6 (6)	18.1 (6)	248.4 (12)	96.3 (12)	590 (6)	16.5 (12)	4.8 (12)	2.7 (6)	2.3 (6)
Wh92047 × Tester2	15.8 (6)	19.7 (6)	248.6 (12)	114.9 (12)	620 (6)	16.4 (12)	4.8 (12)	2.7 (6)	2.9 (6)
Wh01001 × Tester3	12.0 (6)	14.3 (6)	216.6 (12)	81.4 (12)	567 (6)	17.0 (12)	4.3 (12)	2.9 (6)	2.9 (6)
Wh04030V × Tester3	15.7 (6)	17.2 (6)	219.0 (12)	83.4 (12)	603 (6)	17.2 (12)	4.4 (12)	2.0 (6)	2.1 (6)
Wh04036V × Tester3	15.3 (6)	18.3 (6)	211.5 (12)	74.8 (12)	590 (6)	15.4 (12)	4.5 (12)	2.3 (6)	2.7 (6)
Wh04038V × Tester3	15.5 (6)	17.0 (6)	233.5 (12)	86.8 (12)	578 (6)	17.0 (12)	4.3 (12)	2.6 (6)	2.5 (6)
Wh92047 × Tester3	15.7 (6)	18.5 (6)	244.4 (12)	110.4 (12)	621 (6)	16.3 (12)	4.4 (12)	2.3 (6)	3.4 (6)
'Marvel'	12.5 (6)	16.2 (3)	218.4 (12)	78.4 (12)	555 (6)	15.9 (12)	4.4 (9)	3.1 (6)	3.0 (6)
'Overland'	15.6 (6)	16.6 (6)	210.4 (12)	86.4 (12)	627 (6)	16.4 (12)	4.6 (12)	2.3 (6)	3.0 (6)
'Supersweet Jubilee Plus'	11.5 (6)	NA[u]	226.8 (6)	87.5 (6)	611 (3)	16.2 (6)	4.3 (6)	4.2 (3)	4.0 (3)
Least significant difference (0.05)	1.0	1.3	5.7	4.3	9.6	0.7	0.1	0.6	0.6
Overall least square mean	14.6	17.3	229.8	91.8	598	16.1	4.6	2.7	2.7

[z]All = all trial environments; ARL2009 = Arlington, WI 2009; ARL2010 = Arlington, WI 2010; WM2009 = West Madison, WI 2009; WM2010 = West Madison, WI 2010.
[y]Growing degree days (GDD) were recorded as an average of the maximum and minimum daily temperatures with a base temperature of 10 °C and an upper limit of 30 °C.
[x]1 = undesirable flavor or tenderness, 2 = subpar flavor or tenderness, 3 = average flavor or tenderness, 4 = desirable flavor or tenderness, and 5 = highly desirable flavor or tenderness.
[w]Tester1, Tester2, and Tester3 represent three proprietary inbreds used extensively within the Wisconsin Sweet Corn Breeding Program.
[v]The number of plot observations (*N*) examined is included in parenthesis.
[u]NA = least square mean estimate not available.

Table 2. General combining ability of the female parent and specific combining ability of the hybrid for agronomic and quality traits for 15 sweet corn hybrids developed in a 5 × 3 North Carolina Design II mating design measured in Arlington, WI and West Madison, WI in 2009 and 2010.

	General combining ability								
	Yield		Plant ht	Ear ht	Date of anthesis	Ear length	Ear diam	Flavor rating	Tenderness rating
Female parent	ARL2010[z] and WM2010 (Mg·ha^{-1})	ARL2009 and WM2009 (Mg·ha^{-1})	All (cm)	All (cm)	WM2009 and WM2010 (GDD)[y]	All (cm)	All (cm)	WM2009 and WM2010 (1–5 scale)[x]	WM2009 and WM2010 (1–5 scale)[x]
Wh01001	–1.7***[w]	–1.9**	–2.1*	–4.4***	–24***	0.7**	0.0	0.3	0.4*
Wh04030V	0.3	0.6	–5.9***	–3.8**	9*	0.5*	0.0	–0.2	–0.3
Wh04036V	0.5	1.0	–16.7***	–14.6***	–3	–1.1***	0.1*	–0.1	–0.1
Wh04038V	0.8*	–0.3	10.5***	3.0**	–8	0.1	0.0	0.0	–0.3**
Wh92047	0.2	0.7	14.1***	19.7***	26***	–0.2	0.0	–0.1	0.2*
Overall least square mean	14.6	17.3	229.8	91.8	598	16.1	4.6	2.7	2.7
Hybrid	*Specific combining ability*								
Wh01001 × Tester1[v]	1.1*	NS	5.4*	NS	NS	NS	NS	NS	0.2**
Wh04030V × Tester1	–1.0*	NS	NS	NS	NS	NS	NS	NS	NS
Wh04036V × Tester1	NS	NS	NS	NS	NS	NS	NS	–0.1*	NS
Wh04038V × Tester1	NS	NS	NS	6.2*	7*	NS	NS	NS	0.2*
Wh92047 × Tester1	NS	NS	NS	NS	NS	NS	NS	NS	–0.4**
Wh01001 × Tester2	NS	NS	NS	NS	NS	NS	NS	NS	NS
Wh04030V × Tester2	NS	NS	NS	NS	–8*	NS	NS	NS	NS
Wh04036V × Tester2	NS	NS	NS	NS	NS	NS	NS	NS	0.1*
Wh04038V × Tester2	NS	NS	NS	NS	5*	NS	NS	NS	NS
Wh92047 × Tester2	NS	NS	NS	NS	–7*	NS	NS	NS	NS
Wh01001 × Tester3	–1.1*	NS	5.8*	NS	NS	NS	NS	NS	NS
Wh04030V × Tester3	NS	NS	NS	NS	9***	NS	0.1**	NS	NS
Wh04036V × Tester3	NS	NS	NS	NS	3***	NS	NS	NS	NS
Wh04038V × Tester3	NS	NS	NS	–4.6*	–12*	NS	NS	NS	NS
Wh92047 × Tester3	NS	NS	5.8*	NS	NS	NS	NS	NS	0.4*

[z]All = all trial environments; ARL2009 = Arlington, WI 2009; ARL2010 = Arlington, WI 2010; WM2009 = West Madison, WI 2009; WM2010 = West Madison, WI 2010.
[y]Growing degree days (GDD) were recorded as an average of the maximum and minimum daily temperatures with a base temperature of 10 °C and an upper limit of 30 °C.
[x]1 = undesirable flavor or tenderness, 2 = subpar flavor or tenderness, 3 = average flavor or tenderness, 4 = desirable flavor or tenderness, and 5 = highly desirable flavor or tenderness.
[w] NS, *, **, *** Nonsignificant or significant at $P \leq 0.05, 0.01, 0.001$, respectively.
[v]Tester1, Tester2, and Tester3 represent three proprietary inbreds used extensively within the Wisconsin Sweet Corn Breeding Program.

Table 3. Least square means for susceptibility to root lodging, common rust, northern corn leaf blight (NCLB), and *Maize dwarf mosaic virus* (MDMV) for 15 sweet corn hybrids developed in a 5 × 3 North Carolina Design II mating design and 3 commercial checks across specific environments.

	Susceptibility to root lodging	Susceptibility to common rust	Susceptibility to NCLB	Susceptibility to MDMV
Hybrid	ARL2010[z] (% plants lodged)	ARL2010, ARL2010-R, WM2009, WM2010, and WM2010-R (% leaf area infected)	ARL2010 and WM2010 (% leaf area infected)	WM2010-M (0–3 scale)[y]
Wh01001 × Tester1[x]	16.1 (3)[w]	17 (15)	40 (6)	1.0 (3)
Wh04030V × Tester1	0.0 (3)	13 (15)	20 (6)	0.0 (3)
Wh04036V × Tester1	0.0 (3)	19 (14)	30 (6)	0.0 (3)
Wh04038V × Tester1	44.4 (3)	38 (14)	40 (6)	0.0 (3)
Wh92047 × Tester1	23.3 (3)	25 (15)	57 (6)	0.0 (3)
Wh01001 × Tester2	92.9 (3)	16 (15)	57 (6)	2.0 (3)
Wh04030V × Tester2	40.3 (3)	14 (15)	23 (6)	0.0 (3)
Wh04036V × Tester2	6.7 (3)	14 (14)	27 (6)	0.0 (3)
Wh04038V × Tester2	98.9 (3)	21 (15)	20 (6)	0.0 (3)
Wh92047 × Tester2	61.2 (3)	27 (15)	70 (6)	1.0 (2)
Wh01001 × Tester3	77.8 (3)	13 (15)	50 (6)	2.5 (3)
Wh04030V × Tester3	54.4 (3)	19 (15)	20 (6)	0.0 (3)
Wh04036V × Tester3	2.2 (3)	15 (15)	33 (6)	0.0 (3)
Wh04038V × Tester3	90.0 (3)	28 (15)	40 (6)	0.7 (3)
Wh92047 × Tester3	84.4 (3)	25 (15)	70 (6)	0.0 (3)
‘Marvel’	94.4 (3)	23 (15)	80 (6)	3.0 (1)
‘Overland’	1.2 (3)	1 (15)	10 (6)	2.0 (3)
‘Supersweet Jubilee Plus’	56.8 (3)	NA[v]	87 (6)	3.0 (3)
Least significant difference (0.05)	38.3	7	14	0.6
Overall least square mean	47.0	20	43	0.8

[z]ARL2009 = Arlington, WI 2009; ARL2010 = Arlington, WI 2010; ARL2010-R = Arlington, WI 2010 inoculated common rust trial; WM2009 = West Madison, WI 2009; WM2010 = West Madison, WI 2010; WM2010-R = West Madison, WI 2010 inoculated common rust trial; WM2010-M = West Madison, WI 2010 inoculated MDMV trial.

[y]0 = no apparent symptoms, 1 = faint mosaic symptoms or severe mosaic symptoms restricted to portions of only one or two leaves, 2 = an obvious mosaic on most but not all leaves, and 3 = an intense mosaic, identified as systemic.

[x]Tester1, Tester2, and Tester3 represent three proprietary inbreds used extensively within the Wisconsin Sweet Corn Breeding Program.

[w]The number of plot observations (*N*) examined is included in parenthesis.

[v]NA = least square mean estimate not available.

the longest eared and highest yielding commercial control (Table 1). Wh01001 and Wh04030V had significant ($P \leq 0.05$) positive GCA for ear length (Table 2). The mean ear diameter for hybrids pooled across all environments was 4.6 cm with eight of the 15 experimental hybrids having significantly wider ears than ‘Overland’, which produced the widest ears of the commercial checks (Table 1). Ear width is an important consideration in breeding for processing sweet corn as yield gains from wider ears may not translate into good ear types for processing. Despite significant differences for increased ear width, no hybrid produced ears that averaged greater than 0.2 cm wider than ‘Overland’, and thus, should not pose any problems in processing.

No experimental hybrid received a mean rating for flavor that was significantly ($P \leq 0.05$) worse than ‘Overland’ and three entries were found to have significantly better flavor than ‘Overland’. However, ‘Supersweet Jubilee Plus’, which received the highest mean rating for flavor, was significantly ($P \leq 0.05$) superior to all experimental entries (Table 1). Similarly, ‘Supersweet Jubilee Plus’ was rated the most tender in 2010, with a mean tenderness that exceeded the tenderness of all the experimental hybrids (Table 1). Five of the 15 experimental entries received ratings for tenderness that were significantly ($P \leq 0.05$) poorer than the lowest rated commercial cultivar, Overland. This suggests that while exotic germplasm may result in sweet corn cultivars with improved yield or agronomic performance, particular attention must be paid to flavor and tenderness during inbred and hybrid development. The parent Wh01001 contributed positively ($P \leq 0.05$) to favorable tenderness relative to the other female parents (Table 2).

The Arlington, WI 2010 environment was an excellent screening environment for susceptibility to root lodging as hybrid response to two severe wind storms was found to be highly variable. No plants root lodged across the three replicates for both Wh04030V × Tester1 and Wh04036V × Tester1, with four additional entries not found to be significantly different from 0% root lodging. Ninety percent or greater of plants were root lodged for Wh01001 × Tester2, Wh04038V × Tester2, Wh04038V × Tester3, and ‘Marvel’, with two additional entries found not to significantly differ from the most susceptible entry at 98.9% susceptibility to root lodging (Table 3). Inbred Wh04036V produced hybrids with a 43% reduction

Table 4. General combining ability of the female parent for susceptibility to root lodging, common rust, northern corn leaf blight (NCLB), and *Maize dwarf mosaic virus* (MDMV) for 15 sweet corn hybrids developed in a 5 × 3 North Carolina Design II mating design measured in Arlington, WI and West Madison, WI in 2009 and 2010.

	General combining ability			
	Susceptibility to root lodging	Susceptibility to common rust	Susceptibility to NCLB	Susceptibility to MDMV
Female parent	ARL2010[z] (% plants lodged)	ARL2010, ARL2010-R, WM2009, WM2010, and WM2010-R (% leaf area infected)	ARL2010 and WM2010 (% leaf area infected)	WM2010-M (0–3 scale)[y]
Wh01001	16.1	–4	9***	1.3
Wh04030V	–14.6	–7**[x]	–19***	–0.5
Wh04036V	–43.2	–4**	–10*	–0.5
Wh04038V	31.6	9**	–6	–0.2
Wh92047	10.1	6**	26***	–0.2
Overall least square mean	47.0	20	43	0.8

[z]ARL2010 = Arlington, WI 2010; ARL2010-R = Arlington, WI 2010 artificially inoculated common rust trial; WM2009 = West Madison, WI 2009; WM2010 = West Madison, WI 2010; WM2010-M = West Madison, WI artificially inoculated MDMV trial; WM2010-R = West Madison, WI 2010 artificially inoculated common rust trial.

[y]0 = no apparent symptoms, 1 = faint mosaic symptoms or severe mosaic symptoms restricted to portions of only one or two leaves, 2 = an obvious mosaic on most but not all leaves, and 3 = an intense mosaic, identified as systemic.

[x]*, **, *** significant at $P \leq 0.05$, 0.01, 0.001, respectively.

in susceptibility to root lodging relative to the overall trial mean of 47% (Table 4). Although the GCA for root lodging was nonsignificant ($P \leq 0.05$), the raw P value of 0.0178 was corrected to 0.0632 after FDR for multiple testing and this inbred may prove useful in contributing to resistance to root lodging. Significant ($P \leq 0.05$) SCA for susceptibility to root lodging was identified for only a single hybrid entry. No significant correlation between yield and susceptibility to lodging was identified at the Arlington, WI 2010 environment ($P = 0.20$, Pearson's $r = -0.32$).

Susceptibility to common rust was analyzed at the Arlington, WI 2010 and West Madison, WI 2009 and 2010 environments and also under separate trials artificially inoculated with *P. sorghi* at both Arlington, WI and West Madison, WI in 2010 (Table 3). The commercial control 'Overland' exhibited nearly complete resistance to common rust, with the only noticeable pustules attributed to southern rust. All other entries were found to be significantly ($P \leq 0.05$) more susceptible to rust pressure when grown at an environment favorable for *P. sorghi.* Pooled across the five environments in which rust was rated, Wh04038V × Tester1 was identified as the most susceptible entry with a least square mean estimate of 38% leaf area infected (Table 3). Wh04030V and Wh04036V showed significant ($P \leq 0.01$) GCA for a reduction in hybrid susceptibility to common rust (Table 4).

Susceptibility to NCLB from natural disease pressure was scored in 2010 at both the Arlington, WI and West Madison, WI environments. At those 2010 environments, yield was negatively correlated to susceptibility to NCLB ($P = 0.013$; Pearson's $r = -0.58$). Least square mean estimates for susceptibility to NCLB ranged from 10% leaf area infected for 'Overland' to 87% leaf area infected for 'Supersweet Jubilee Plus' (Table 3). Four of the 15 experimental entries were not significantly ($P \leq 0.05$) different from 'Overland' in exhibiting resistance to NCLB and 13 of 15 entries demonstrated significantly ($P \leq 0.05$) greater resistance to NCLB than both 'Marvel' and 'Supersweet Jubilee Plus'. Hybrids developed from Wh04030V exhibited relatively strong resistance to NCLB with a highly significant ($P \leq 0.001$) GCA estimate of –19% from a mean NCLB severity rating estimate of 43% leaf area infected (Table 4).

Resistance to MDMV was scored at only one artificially inoculated environment in 2010 as a second artificially inoculated environment suffered from severe NCLB pressure. All three commercial checks were susceptible to MDMV while 10 of the 15 experimental hybrids showed no evidence of any symptoms to MDMV (Table 3). An additional three entries were more resistant ($P \leq 0.05$) to MDMV overall commercial checks. No significant GCA or SCA estimates for susceptibility to MDMV were identified.

Conclusions

Examination of the performance of 15 hybrids derived from nonsweet germplasm suggests introgression of exotic germplasm may be useful in the development of sweet corn hybrids that yield competitively with commercial hybrids 'Marvel', 'Overland', and 'Supersweet Jubilee Plus' and may offer comparable quality to 'Marvel' and 'Overland'. Yields of 10 of the 15 experimental entries were not different from the top-yielding control, 'Overland', in 2010 and seven entries yielded more than 'Overland' in 2009. Results indicate Wh04030V, Wh04036V, Wh04038V, and Wh92047 hold potential as female parents and may contribute to improved yield in sweet corn. Hybrids developed from Wh04030V and Wh04036V had improved resistance to common rust, NCLB, and MDMV. Wh92047 had favorable combining ability for improved tenderness in addition to yielding competitively with all checks, but hybrids developed from this parent tend to be tall with high ear placement. Most entries examined in this study showed improved resistance to root lodging, common rust, NCLB, and MDMV relative to 'Marvel' and 'Supersweet Jubilee Plus'. 'Supersweet Jubilee Plus' had better flavor and tenderness than all entries, revealing that while nonsweet germplasm holds potential as a source of improved agronomic performance, recovery of exceptional flavor and tenderness can be elusive.

However, lack of significant ($P \leq 0.05$) differences for flavor or tenderness between 'Overland' and most entries suggests that sweet corn hybrids having at least some component of exotic germplasm can be successful processing sweet corn cultivars.

The narrowness of modern sweet corn germplasm in breeding programs suggests potential exists for yield enhancement through new heterotic combinations and a reduction in the susceptibility of sweet corn to pathogen pressures through increased genetic diversity (Haber, 1945; Holland and Goodman, 1995; Taller and Bernardo, 2004; Tracy, 1990a, 2000). Although development of acceptable temperate inbreds derived from exotic germplasm may provide for yield enhancement, breeding with exotic germplasm remains a costly and time consuming endeavor, and ultimate success is largely attributed to choice of germplasm (Nelson and Goodman, 2008). Although nonsweet germplasm may contribute to improved yield or disease resistance, sweet corn breeders must pay careful attention to photoperiod sensitivity, undesirable increases in plant or ear height, and loss of flavor or tenderness when introgressing nonsweet germplasm.

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