Recurrent Full-sib Family Selection for Husk Extension in Sweet Corn

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ABSTRACT. Corn earworm (*Helicoverpa zea*) is a costly and destructive pest in sweet corn (*Zea mays*) production. A recurrent selection experiment was conducted to assess the feasibility of selecting a sweet corn population for longer husks without shortening the ears and to determine whether direct selection for longer husks confers improved resistance to the corn earworm. The initial population was derived from crosses between long- and tight-husked inbred lines (A684su, A685su, and A686su) originally selected for resistance to the european corn borer (*Ostrinia nubilalis*) and a high-quality commercial hybrid parent ('Super Sweet Jubilee Plus'). Three cycles of recurrent full-sib family selection were conducted from 2014 to 2016, with a selection intensity of $\approx 10\%$ per cycle. In 2017, the cycles of selection were evaluated and compared with common commercial cultivars for husk extension, ear length, rate of corn earworm infestation, and extent of corn earworm damage. Ears were artificially infested with corn earworm eggs suspended in an agar solution. The population was successfully selected for longer husk extension without shortening the ears, but the increase in husk extension did not correspond to an increase in corn earworm resistance. Further evaluation is needed to determine whether long husk extension is ineffective as a source of corn earworm resistance, whether it is more effective in combination with other resistance traits, whether greater differences in husk extension are needed to confer biologically significant differences in corn earworm resistance, or whether improved inoculation methods could improve differentiation between genotypes.

Corn earworm is the most destructive pest of sweet corn (Del Valle and Miller, 1963; Pimentel et al., 1997; Snyder, 1967; Yadav, 1980) and one of the costliest of all crop pests in North America (Huang, 2015). The migratory nature of corn earworm makes it unpredictable and challenging to manage on a farm scale, and climate change is likely to expand its overwintering range, increase the number of generations per year, and cause earlier infestations. Corn earworm is ubiquitous; it feeds on more than 200 host plants, including important crops as well as weedy and uncultivated plants (Hardwick, 1965; Huang, 2015; Kennedy and Storer, 2000; Neunzig, 1963; Olmstead et al., 2016; Sudbrink and Grant, 1995). This ubiquity limits the ability to use cultural controls such as crop rotation and increases the pest's adaptability and probability of successful development (Kennedy and Storer, 2000; Olmstead et al., 2016). The oviposition and feeding habits also limit the efficacy of chemical controls (Barber, 1941; Cook et al., 2003, 2004). Plant breeding remains one of the few promising tools for reducing the economic damage caused by corn earworm.

Corn earworm is an especially challenging pest for organic sweet corn growers, because few effective management strategies are permissible under the National Organic Program (Cook et al., 2003, 2004; Ni et al., 2011). Organic producers are in particular need of breeding for resistance to corn earworm since the advent of transgenic *Bacillus thuringiensis* cultivars has supplanted classical breeding for earworm resistance. However, novel forms of corn earworm resistance are of interest to conventional farmers as well, since increasing reports of *Bacillus thuringiensis* resistance indicate a limited lifespan for one of their main management tools (Reisig and

Reay-Jones, 2015; Tabashnik and Carriere, 2015; Tabashnik et al., 2009).

As early as the 1910s, plant breeders have examined husk characteristics as potential mechanisms of resistance to the corn earworm, including husk thickness, husk texture, and presence or absence of flag leaves (Collins and Kempton, 1917). Longer husk extension past the ear tip has been proposed as a resistance mechanism either by increasing the distance the larva must travel before it can feed on the ear and/or due to availability of non-kernel food for the larva to consume (Barber, 1944; Collins and Kempton, 1917; Kyle, 1918). Husk tightness has been considered primarily as a physical barrier: a tight husk leads to tightly bunched silks, which may slow or halt larval penetration to the ear tip. The combination of long and tight husks may improve this physical resistance (Barber, 1941, 1944; Phillips and King, 1923). Husk extension and tightness also have been thought to interact with the cannibalistic behavior of corn earworm larvae to improve resistance. A tighter husk with a "tube-like" silk channel increases the likelihood the larvae will meet and reduce the population through cannibalism (Barber, 1936).

Over the decades, many studies have evaluated husk extension and tightness as corn earworm resistance factors, but results have been mixed. Some studies have shown strong negative relationships between corn earworm damage and husk extension, husk tightness, or both (Collins and Kempton, 1917; Del Valle and Miller, 1963; Douglas, 1947; Kyle, 1918; Ni et al., 2007, 2008). However, a number of studies have shown an inconsistent or absent relationship between corn earworm damage and these husk characteristics (Ni et al., 2012; Painter and Brunson, 1940; Snyder, 1967; Yadav, 1980), or even a positive relationship with corn earworm damage (Widstrom et al., 1970).

One major challenge in assessing husk traits as a corn earworm resistance mechanism is the presence of significant epistatic and environmental interactions. Several of the afore-

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mentioned authors (Del Valle and Miller, 1963; Painter and Brunson, 1940; Widstrom et al., 1970) explained the contradictory evidence on husk traits and earworm damage as effects of genetic background and interactions with other traits that confer resistance or susceptibility. In addition to these epistatic interactions, several studies indicate interactions between genotype and both environmental and management factors (Barber, 1944; Del Valle and Miller, 1963; Dicke and Barber, 1944; Douglas, 1947; Wiseman et al., 1970).

In addition to the inconsistent relationship between husk traits and corn earworm resistance, one challenge in breeding sweet corn for longer husks in particular has been an inverse relationship between husk length and yield. Butron et al. (2002) noted that longer husk extension past the ear tip has frequently been achieved by shortening the ear rather than actually lengthening the husk.

The goals of this research were to determine the feasibility of selecting a sweet corn population for longer husks without shortening the ears, to determine whether direct selection for longer husks indirectly confers improved resistance to the corn earworm, and finally to compare husk extension, ear length, earworm infestation rate, and extent of damage of each cycle of selection to commercial cultivars used on organic farms in Wisconsin.

Materials and Methods

POPULATION DEVELOPMENT. In Summer 2006, crosses were made between three long- and tight-husked inbred lines (A684su, A685su, and A686su) and a high-quality commercial hybrid parent ('Super Sweet Jubilee Plus'). A684su, A685su, and A686su were derived from an Apache/Ia453/B52 background and originally were selected for resistance to the European corn borer (Davis et al., 1993). Progeny from the initial crosses were intermated in Summer 2007 using a "row sib"; full-sib families were planted in rows and plant-to-plant crosses were made between these rows. The resulting population was intermated again in Summer 2013 using a "chain sib." A balanced bulk of three kernels per ear (created from the ears produced in Summer 2007) was planted, and plant-to-plant crosses were made within the bulk. The resulting population was considered Cycle 0 of the recurrent selection experiment.

RECURRENT SELECTION. For three cycles of selection (Summer 2014 to Summer 2016), full-sib families (here defined as seeds from a single ear pollinated by a single other individual) were grown in single-row plots. Rows were 3.5-m long, 12 plants per row, and planted at 76-cm spacing between rows. Two replications were planted at West Madison Agricultural Research Station (Verona, WI). Three ears from each full-sib family were self-pollinated and the rest of the ears were left to open-pollinate. In late August, ear length (from the base of the ear to the tip of the ear) and husk length (from the base of the ear to the tip of the husk) were measured for four of the open-pollinated ears per replication for each full-sib family (for a total of eight ears per family).

Husk extension for each ear was calculated as the difference between husk length and ear length, and the mean husk extension was calculated for each full-sib family. The families with the longest mean husk extension were selected, with the requirement that none of the measured ears within

the family were shorter than 16 cm. For each selection cycle, a selection pressure of $\approx 10\%$ was applied (Table 1). Within each selected plot, a single self-pollinated ear with the most viable seed was selected, and these selected ears were recombined at a winter nursery in Rancagua, Chile. Recombination was achieved by planting each selected family in a single row beside a row containing a balanced bulk of all other selected families; plant-to-plant crosses were made in these paired rows to produce new full-sib families. These families were the basis for the next selection cycle; balanced bulks of kernels from these ears also made up each cycle to be evaluated for the traits of interest. In Winter 2014–15 and Winter 2015–16, all ears with viable seed were included in the next cycle (a mean of six ears per row), but in Winter 2016–17, the two ears with the most seed were selected to prevent the population size from expanding further.

EVALUATION. Balanced bulks were created from the ears recombined in the winter nurseries each year. In Summer 2017, the four selection cycles (Cycles 0 through 3) of the long husk population and three commercial check cultivars were evaluated for ear length, husk length, and corn earworm resistance. The three commercial check cultivars were Mirai, Primus, and Tuxana, which are cultivars commonly grown by organic sweet corn growers in Wisconsin, as identified in grower interviews. The seven entries were planted in single-row plots (3.5-m long, 12 plants per row, and 76-cm between-row spacing) in a randomized complete block design with four replications at two locations with two planting dates (15 May and 1 June) per location. On each planting date, one planting was on certified organic land and the other on nonorganic land. All four plantings were at the West Madison Agricultural Research Station. The planting dates of 15 May and 1 June affected development significantly enough to constitute a separate environment.

To evaluate resistance to corn earworm, ears were artificially infested with corn earworm eggs, since corn earworm pressure is unpredictable in south central Wisconsin. Inoculation took place between 18 July and 1 Aug. in the first planting and 26 July and 7 Aug. in the second planting. Corn earworm eggs were ordered from Benzon Research (Carlisle, PA) every 3 to 4 d. Eggs were suspended in 0.2% agar solution, and the agar-egg solution was applied onto the emerging, fresh corn silks using a pressure applicator at an estimated rate of 15 to 30 eggs per ear (Mihm, 1982; Widstrom and Burton, 1970; Wiseman et al., 1974). Eggs were applied when 75% of plants in a family row had fresh silks emerging on its top ear (nine plants per row, or fewer depending on germination and maturity). Plants were tagged and eggs were reapplied to the same plants 7 d later to ensure uniform infestation (Widstrom and Burton, 1970).

Evaluation took place during milk stage (i.e., 21 d after the first inoculation took place). The tagged ears were harvested, and each ear was evaluated for ear length, husk length, number

Table 1. Selection pressure for each cycle of recurrent selection in the sweet corn population. In each cycle of selection, full-sib families were selected with the longest mean husk extension past the ear tip, given a minimum ear length of 16 cm on all measured ears. A selection pressure of $\approx 10\%$ was applied, with year-to-year variation in selection pressure due to families with the same mean husk extension.

Yr	Cycle	Population size ^z	Selected families (no.)	Selection pressure (%) ^y
2014	1	116	10	8.6
2015	2	148	20	13.5
2016	3	419	42	10.0

^zNumber of full-sib families in previous cycle.

^yThe selection pressure on the previous cycle that produced the listed cycle.

Table 2. Dates of major rain events at West Madison Agricultural Research Station (WMARS) in Summer 2017. Several major rain events occurred when sweet corn ears were being inoculated with corn earworm eggs in Summer 2017.

Date	Total rainfall (mm)
19 July	20
20 July	17
21 July	42
26 July	5
3 Aug.	11

of corn earworms present, number of damaged kernels, and length of damaged area below the ear tip. Length of damaged was assessed using the revised centimeter scale, which has been used widely to rate damage by ear-feeding pests. A rating of 0 corresponds to no damage, a rating of 1 corresponds to damage to silks only, a rating of 2 corresponds to feeding up to 1 cm beyond the ear tip, and the rating increases by one for each additional 1 cm of feeding (Widstrom, 1967).

Two environmental factors were identified as potential confounding factors for earworm damage evaluation—rain events and other silk-feeding insects. During the period in July and Aug. 2017 when the plots were inoculated, there were several major rain events, which could have altered the frequency of successful inoculation (e.g., by washing eggs off the silks). Table 2 shows the dates with major rain events during the inoculation period. There were also infestations of both japanese beetle (*Popillia japonica*) and corn rootworm beetle (*Diabrotica* sp.) feeding on the silks, and these other insects may have altered the frequency of successful inoculation (e.g., by disturbing the eggs during feeding).

DATA ANALYSIS. The two direct targets of selection in the long husk population were increased husk extension and maintaining ear length above a minimum threshold of 16 cm. The two indirect targets of selection were reduced infestation rate and reduced damage on infested ears. We were interested both in measuring change in these variables in the long husk population over the course of selection and in comparing the population with commercial hybrids for each of these variables.

Each of the four targets of selection was evaluated on a plot-mean basis using a linear mixed effect model. The husk extension and ear length models included genotype (*G*), environment (*E*), and *G* × *E* interaction as fixed effects, and block within environment [*B*(*E*)] as a random effect:

$$\text{Husk extension} = G + E + G \times E + B(E) + \text{error}$$

$$\text{Ear length} = G + E + G \times E + B(E) + \text{error}$$

Infestation rate was calculated as the proportion of ears per plot that contained at least one earworm larva. Extent of damage was evaluated using the plot-mean revised centimeter scale rating. In addition to the aforementioned explanatory variables, the infestation rate and extent of damage models included a rain date (*RD*) dummy variable as a covariate. This variable contains values of either 0 or 1, where 1 corresponds to plots inoculated on days with major rain events:

$$\text{Infestation rate} = G + E + RD + G \times E + B(E) + \text{error}$$

$$\text{Extent of damage} = G + E + RD + G \times E + B(E) + \text{error}$$

For each model, Tukey's multiple comparison method was used for pairwise comparisons among genotypes, environments, and the rain date dummy variable (where applicable). Pearson and Spearman correlations were used to calculate correlations between husk extension and the two damage-related variables. Data were analyzed using RStudio version 1.1.383 (RStudio, Boston, MA). Packages used in the analysis include lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), lsmeans (Lenth, 2016), multcomp (Hothorn et al., 2008), MuMIn (Barton, 2018), and plyr (Wickham, 2011).

Results

Effects of selection

HUSK EXTENSION. Genotype and environment were both significant, whereas *G* × *E* interaction and block effects were not (Table 3). Cycle 2 showed a small increase in mean husk extension relative to Cycles 0 and 1, but the difference was not statistically significant. However, Cycle 3 had significantly longer husks than the three previous cycles (Table 4).

Environment was also a significant determinant of husk extension. The 1 June planting in the conventional field had significantly shorter husk extension than all other environments. The field experienced waterlogging in late July and early August, which may explain the shorter husks relative to other environments (Table 5).

EAR LENGTH. None of the factors were significant determinants of ear length (Table 3). None of the cycles or environments were significantly different from each other in terms of ear length (Tables 4 and 5).

INFESTATION RATE. An overall infestation rate of 0.34 was achieved across all plots in the study. Only environment and the rain event dummy were significant; genotype, *G* × *E* interaction, and block effect were not (Table 6).

None of the cycles of selection were significantly different from each other in terms of proportion of ears infested. In terms of environmental effects, the 1 June organic planting had a significantly lower rate of infestation than either the 15 May organic planting or the 1 June conventional planting (Tables 4 and 5). The "rain date" dummy variable, corresponding to plots inoculated on the same date as a major rain event, was expected to correspond to a lower rate of infestation due to eggs washing

Table 3. Analysis of variance for husk extension and ear length of the long husk sweet corn population. The cycles of selection were grown and evaluated in 2017 using a randomized complete block design.

Fixed effects	Numerator df	Denominator df	Husk extension		Ear length	
			F	P	F	P
Genotype (<i>G</i>)	3	47	18.2	5.8 ^{e-08***}	1.4	0.24 ^{NS}
Environment (<i>E</i>)	3	47	6.7	0.0007***	0.3	0.82 ^{NS}
<i>G</i> × <i>E</i>	9	47	1.1	0.40 ^{NS}	0.6	0.81 ^{NS}
Random effects		χ^2 df	Husk extension		Ear length	
			χ^2	P	χ^2	P
Block (<i>E</i>)		1	2.84 ^{e-14}	1 ^{NS}	0	1 ^{NS}

NS, ***Nonsignificant or significant at $P \leq 0.001$, respectively.

off the silks. However, infestation rate was significantly greater in these plots (Table 7). Among the cycles of selection, frequency of infestation did not show a statistically significant correlation with husk extension using either Pearson or Spearman correlation (Table 8).

EXTENT OF DAMAGE. The “rain date” dummy variable was significant at the 5% level and environment was significant but only at the 10% level. Genotype, $G \times E$ interaction, and block effects were not significant (Table 6).

None of the cycles of selection were significantly different from each other in terms of extent of damage. In terms of environmental effects, the 15 May conventional planting had significantly lower damage than the 1 June conventional planting (Tables 4 and 5). Again, contrary to expectations, the extent of damage was significantly greater in the plots inoculated on days with significant rain events (Table 7). Among the cycles of selection, extent of damage was not correlated with husk extension using either Pearson or Spearman correlation (Table 8).

Comparison with commercial check cultivars

To compare the long husk population cycles to the commercial checks, we ran the same models including all seven genotypes (four selection cycles and three checks).

HUSK EXTENSION. ‘Mirai’ had relatively short husk extension (a mean of 3.2 cm), ‘Primus’ had relatively long husk extension (a mean of 6.6 cm), and ‘Tuxana’ had intermediate husk extension (a mean of 5.3 cm). Cycles 0 and 1 were not significantly different from any of the commercial cultivars, but Cycle 2 had significantly longer husk extension than ‘Mirai’, and Cycle 3 had significantly longer husk extension than both ‘Mirai’ and ‘Tuxana’ (Table 9).

EAR LENGTH. Among the commercial cultivars, ‘Tuxana’ had the shortest mean ear length (19.7 cm), ‘Primus’ an intermediate length (20.5 cm), and ‘Mirai’ the longest (22.1 cm). All of the long husk selection cycles were within a 95% confidence interval of ‘Tuxana’ in terms of ear length, and Cycle 3 also showed no significant difference with ‘Primus’. All selection cycles had shorter ears than ‘Mirai’ (Table 9).

Table 4. Mean and SE of husk extension, ear length, infestation rate, and corn earworm damage of the long husk sweet corn population across the cycles of selection. Damage is measured using the revised centimeter scale [RCS (see Table 2)]. There were no significant differences among means for ear length, infestation rate, or damage.

Genotype	Husk extension (cm)		Ear length (cm)		Infestation rate (0–1 scale)		Damage-infested ears only (RCS)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Cycle 0	5.4 a ^z	0.35	18.6	0.23	0.24	0.06	3.5	0.39
Cycle 1	5.4 a	0.35	18.8	0.27	0.39	0.07	4.2	0.26
Cycle 2	6.0 a	0.31	19.1	0.36	0.35	0.05	3.9	0.30
Cycle 3	7.8 b	0.21	19.4	0.28	0.25	0.05	4.7	0.29

^zMean separation performed using the Tukey contrasts multiple comparison method. Within columns, means with the same letter are not significantly different from one another at $P \leq 0.05$.

Table 5. Mean and SE of husk extension, ear length, infestation rate, and corn earworm damage of sweet corn ears within environments. Damage is measured using the revised centimeter scale [RCS (see Table 2)]. There were no significant differences among means for ear length.

Environment	Husk extension (cm)		Ear length (cm)		Infestation rate (0–1 scale)		Damage-infested ears only (RCS)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
15 May organic	6.2 b ^z	0.36	18.9	0.28	0.43 b	0.07	3.9 ab	0.31
1 June organic	6.4 b	0.31	19.0	0.38	0.24 a	0.05	4.3 ab	0.27
15 May conventional	6.8 b	0.34	18.8	0.27	0.25 ab	0.05	3.4 a	0.34
1 June conventional	5.1 a	0.45	19.2	0.25	0.30 b	0.05	4.6 b	0.29

^zMean separation performed using the Tukey contrasts multiple comparison method. Within columns, means with the same letter are not significantly different from one another at $P \leq 0.05$.

Table 6. Analysis of variance for infestation rate and corn earworm damage of the long husk sweet corn population. Damage is measured using the revised centimeter scale [RCS (see Table 2)]. The cycles of selection were grown, inoculated, and evaluated in 2017 using a randomized complete block design.

Fixed effects	Numerator df	Infestation rate (0–1 scale)			Damage-infested ears only (RCS)		
		Denominator df ^z	F	P	Denominator df	F	P
Genotype (<i>G</i>)	3	35.1	0.9	0.5 ^{NS}	30.5	2.2	0.11 ^{NS}
Environment (<i>E</i>)	3	13.2	3.6	0.04*	11.9	3.3	0.06*
Rain date	1	45.9	10.3	0.002**	29.5	4.8	0.04*
$G \times E$	9	34.8	0.9	0.5 ^{NS}	29.4	1.5	0.21 ^{NS}
Random effects	χ^2 df	Infestation rate (0–1 scale)			Damage-infested ears only (RCS scale)		
		χ^2		P	χ^2		P
Block (<i>E</i>)	1	0.3		0.6 ^{NS}	0.006		0.9 ^{NS}

NS, ., *, **Nonsignificant or significant at $P \leq 0.10$, 0.05, or 0.01, respectively.

^zThe denominator df in these regressions have decimal values due to use of the Satterthwaite approximation to calculate df.

Table 7. Infestation rate and mean corn earworm damage of sweet corn ears depending on whether ears were inoculated on a date with a major rain event. Dates with major rain events are listed in Table 3. Damage is measured using the revised centimeter scale [RCS (see Table 2)].

Inoculated on rain date?	Infestation rate (0–1 scale)	Damage-infested ears only (RCS)
Yes	0.50 b ^z	4.7 b
No	0.27 a	4.0 a

^zMean separation performed using the Tukey contrasts multiple comparison method. Within columns, means with the same letter are not significantly different from one another at $P \leq 0.05$.

Table 8. Pearson and Spearman correlations between husk extension and both corn earworm infestation rate and mean damage in sweet corn. Damage is measured using the revised centimeter scale [RCS (see Table 2)]. When only the cycles of selection of the long husk population were included in the analysis, husk extension was not correlated with either infestation rate or damage. However, when the three commercial check cultivars were included in the analysis, husk extension was negatively correlated with infestation rate according to both Pearson and Spearman methods.

Method	Infestation rate (0–1 scale)		Damage-infested ears only (RCS)	
	Cycles only	Cycles + commercial cultivars	Cycles only	Cycles + commercial cultivars
Pearson	–0.10	–0.28**	0.02	–0.06
Spearman	–0.009	–0.26**	0.03	–0.06

**Significant at $P \leq 0.01$.

INFESTATION RATE. There were no significant differences in infestation rate among genotypes (Table 9). According to both Pearson and Spearman methods, when the commercial cultivars were included, there was a significant negative correlation between husk extension and rate of infestation (Table 8).

EXTENT OF DAMAGE. There were no significant differences in damage rating among genotypes (Table 9). According to both the Pearson and Spearman methods, there were no significant correlations between husk extension and damage, even when commercial cultivars were included (Table 8).

Discussion

EFFECTS OF SELECTION. Cycle 3 had significantly longer husk extension than the previous three cycles of selection. There were no significant differences between ear length among any of the cycles. Together, these results indicate that we successfully selected for longer husks without shortening ears. However, longer husk extension did not translate into lower frequency of infestation or less damage on ears that were infested—there were no significant differences in infestation or damage among any of the cycles, nor were there statistically

significant correlations between husk extension and either the infestation or damage variables.

The inability to detect differences in infestation rate between genotypes may have been associated with inconsistency in the inoculation method itself. The total rate of infestation across all inoculated plants was only 0.34. There was a significant infestation of Japanese beetles during the period of corn earworm inoculation. The Japanese beetles were feeding on the corn silks and may have consumed eggs and/or early instar larvae as well. The Japanese beetle infestation likely reduced the overall infestation rate in the experiment, increased variability in the infestation and damage data, and may have limited our ability to detect differences among genotypes.

ENVIRONMENTAL EFFECTS. There were significant differences between environments for husk extension, infestation, and damage. The 1 June conventional planting had significantly shorter husk extension than all other environments, and this planting also had the greatest damage rating and the second greatest infestation rate. We hypothesize that the shorter husks were a result of waterlogging in this field during key developmental periods. It is possible that the greater infestation and damage were direct results of the shorter husks but may also have been a result of other phenotypic changes mediated by the flooding (e.g., reduced production of secondary metabolites due to nutrient deficiency or stress).

Inoculating on days with significant rain events was expected to lead to lower rates of infestation and damage due to eggs being washed off the silks. However, we found the reverse to be true for both infestation and damage. These unexpected results may also be due to interactions with the beetle infestation. If beetles were knocked off the plants during rain events, this may have allowed eggs and early-instar larvae to survive and ultimately lead to greater infestation/damage. Alternately, rain events may also have prevented eggs and early-instar larvae from desiccating and increased overall survival and thus infestation/damage.

Table 9. Mean and SE of husk extension, ear length, infestation rate, and corn earworm damage of the commercial check sweet corn cultivars and long population. Damage is measured using the revised centimeter scale [RCS (see Table 2)]. There were no significant differences among means for infestation rate or damage.

Genotype	Husk extension (cm)		Ear length (cm)		Infestation rate (0–1 scale)		Damage-infested ears only (RCS)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Mirai	3.2 a ^z	0.24	22.1 c	0.36	0.53	0.08	4.3	0.32
Primus	6.6 bc	0.29	20.5 bc	0.35	0.25	0.06	3.2	0.29
Tuxana	5.3 ab	0.25	19.7 ab	0.27	0.43	0.07	4.3	0.18
Cycle 0	5.4 ab	0.35	18.6 a	0.23	0.24	0.06	3.5	0.39
Cycle 1	5.4 ab	0.35	18.8 a	0.27	0.39	0.07	4.2	0.26
Cycle 2	6.0 b	0.31	19.1 a	0.36	0.35	0.05	3.9	0.30
Cycle 3	7.8 c	0.21	19.4 ab	0.28	0.25	0.05	4.7	0.29

^zMean separation performed using the Tukey contrasts multiple comparison method. Within columns, means with the same letter are not significantly different from one another at $P \leq 0.05$.

COMPARISON WITH COMMERCIAL CHECK CULTIVARS. The long husk population started in Cycle 0 with husks of comparable length to the commercial cultivars evaluated (i.e., not significantly different from the three tested commercial cultivars). In three cycles of selection, we were able to select the population for husks that were significantly longer than both ‘Mirai’ and ‘Tuxana’, and with continued selection we may see further increases in husk extension. Ear length did not change with selection for husk extension; the population had significantly shorter ears than ‘Mirai’ but the ears were comparable in length with both ‘Primus’ and ‘Tuxana’. Evidence from this experiment indicates that it is possible to have ears with longer husk extension without compromising commercial marketability by reducing ear size.

There were no significant differences among the genotypes in terms of infestation rate or extent of damage. In contrast to the analysis of the selection cycles alone, when the commercial checks were included in the analysis, there was a negative and significant correlation between husk extension and infestation rate. There are a few possible explanations for these conflicting results; perhaps the differences in resistance/susceptibility were due to genotypic differences other than husk extension (e.g., if the longer-husked commercial cultivars had also been selected for other resistance-conferring traits). It may also be that husk extension improves resistance in combination with other traits, and so differences in infestation rate were not apparent in the long husk population but appear when diverse genotypes were included in the analysis. The difference in husk extension between Cycle 0 and Cycle 3 was significant but not very large (2.4 cm), whereas the difference between ‘Mirai’ and Cycle 3 was larger (4.6 cm). It could be that the increase in husk extension from Cycle 0 to Cycle 3 was simply not large enough to confer significant improvement in corn earworm resistance.

FUTURE PROSPECTS. This study provides evidence that it is indeed feasible to select sweet corn for long husk extension without reducing ear size. However, the value of selecting for long husks as a mechanism of earworm resistance may have limitations. The increase in husk extension did not correspond to a reduction in infestation rate or extent of damage in the population under selection. These results seem to indicate that long husks are ineffective as a source of corn earworm resistance. However, further evaluation is needed to determine whether long husk extension is more effective in combination with other resistance traits, whether greater differences in husk extension are needed to confer biologically significant differences in earworm infestation and/or damage, or whether more consistent inoculation methods might improve detection of differences in resistance between genotypes. Husk extension has been tested for decades as a mode of corn earworm resistance with similarly ambiguous results. It is unlikely to be the silver-bullet solution to the corn earworm problem but may be one tool in the toolbox especially when defending against a combination of ear-feeding insects and birds.

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