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Article

Recurrent Selection and Participatory Plant Breeding for Improvement of Two Organic Open-Pollinated Sweet Corn (*Zea mays* L.) Populations

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Abstract: Organic growers face unique challenges when raising sweet corn, and benefit from varieties that maintain high eating quality, germinate consistently, deter insect pests, and resist diseases. Genotype by environment rank changes can occur in the performance of cultivars grown on conventional and organic farms, yet few varieties have been bred specifically for organic systems. The objective of this experiment was to evaluate the changes made to open-pollinated sweet corn populations using recurrent selection and a participatory plant breeding (PPB) methodology. From 2008 to 2011, four cycles of two open-pollinated (OP) sweet corn populations were selected on a certified organic farm in Minnesota using a modified ear-to-row recurrent selection scheme. Selections were made in collaboration with an organic farmer, with selection criteria based on traits identified by the farmer. In 2012 and 2013, the population cycles were evaluated in a randomized complete block design in two certified organic locations in Wisconsin, with multiple replications in each environment. Significant linear trends were found among cycles of selection for quantitative and qualitative traits, suggesting the changes were due to recurrent selection and PPB methodology for these populations. However, further improvement is necessary to satisfy the requirements for a useful cultivar for organic growers.

Keywords: organic; participatory plant breeding; sweet corn; open-pollinated; recurrent selection

1. Introduction

As organic agriculture has grown in recent years, so too has an interest in breeding crop and vegetable varieties adapted specifically for organic farming systems. Varieties bred for conventional agriculture often perform differently when grown in organic systems [1–5]. In addition to yield, organic farmers place a priority on crops that are disease and insect resistant, can compete with weeds, are adapted to intercropping and biologically diverse systems, and exhibit a positive yield response to organic fertility sources [6]. A survey of organic growers in the United States conducted in 2010 by the Organic Seed Alliance found that 83% agreed or strongly agreed with the statement, "varieties bred for organic system management are important to the overall success of organic agriculture" [7]. However, developing effective breeding strategies for organic agriculture is challenging. For cultivars in which the important traits under selection exhibit minimal genotype by environment interaction, indirect selection on conventional breeding stations may be the most efficient breeding method. When there is low genetic correlation between a genotype's performance on-station and on-farm, however, direct selection in organic conditions is preferred [8]. The diversity of cultural practices found on organic farms, especially regarding fertility practices and pest management, further complicate the choice of appropriate selection environments [9]. Although numerous studies have shown the effect of conventional versus organic environments on genotype performance, few studies have been conducted to understand potential genotype x production system interactions among organic farms [10]. Adding to the challenge, plant breeders who have been trained in conventional farming systems may be unaware of the most important traits for successful production in organic systems.

One strategy that has been used to breed varieties adapted to organic farming systems is participatory plant breeding (PPB) [11–14]. With this methodology, breeders and farmers work collaboratively throughout the breeding process, often making selections and evaluating progeny on organic farms. PPB was first described by name in the peer-reviewed literature in 1996 by Witcombe *et al.* [15], and was originally developed to breed useful varieties for small-scale farmers situated on marginalized land in developing countries. Advantages of PPB can include exploiting genotype by environment interactions by selecting superior lines in the target environment, involving farmers in the initial planning stages to facilitate development of varieties that suit their particular requirements, and, in the case of open-pollinated (OP) populations and diverse mixtures of self-pollinated pure-lines, allowing farmers to continually adapt and improve the variety [16].

Initial examples of successful PPB projects tended to involve self-pollinating grain crops, such as barley and rice, in part because of the relative ease with which these crops could be bred on-farm [17–20]. After the initial crosses are made to generate variability in the breeding population, no further controlled pollinations are required in successive cycles of selection. Because the grain used for human and/or animal consumption is the same as the seed, participating farmers do not need to significantly alter normal harvesting techniques to produce both a food crop and breeding seed for the next year. Examples of PPB projects with cross-pollinating grain crops, such as maize and sorghum can also be found in the literature [21–23]. Cross-pollinating crops increase the complexity of the breeding scheme because selections are often made after fertilization has occurred, and unless the pollinations have been controlled by hand, pollen from both desirable and undesirable genotypes within the population contributes to the next cycle of selection. Selections made on half-sib progeny decrease the gain from selection made with each progressive cycle relative to full-sib progeny [24]. PPB projects tend to focus almost exclusively on non-hybrid cultivars, with some exceptions such as a hybrid maize PPB experiment in southwest China [25]. In general, the large amount of labor and capital required to effectively breed and produce seed of hybrids is a limiting factor for PPB [26].

Organic PPB projects, while initially focusing on grain crops, have also increasingly explored the feasibility of improving OP vegetable crops [12,14,27]. However, no examples are cited in the scientific literature quantifying the actual gains made during cycle selections of an organic vegetable crop using a PPB methodology. A successful breeding project begins with the selection of high-quality parents, but minimal information may be available regarding the best cultivars for organic systems. When breeding on-farm, space limitations for trial plots, lack of homogeneity in field conditions, and the use of single site selections can make improvement of traits with low heritability difficult [8]. These challenges may explain the lack of peer-reviewed literature in this discipline.

Sweet corn (*Zea mays* L.) is an example of a vegetable crop that, until recently, has not been bred for organic production systems. Organic sweet corn is grown for both the fresh and processing markets, and its narrow window of seasonal availability make it particularly attractive to consumers at direct sales venues such as farmers' markets [28]. While kernel flavor and tenderness are critical for all markets, ear quality traits are particularly important for the fresh market, as the kernels are eaten directly off of the cob. Important traits include number of kernel rows, row configuration (straightness and arrangement), tip fill, ear shape, and ear size [29]. However, the field space and labor required to grow sweet corn organically deter many farmers from producing it [30]. Controlling weeds is a significant challenge, as are insect and disease pressures, and the difficulty of achieving a uniform distribution of the high nitrogen requirements of sweet corn [28,31,32]. Breeding sweet corn for organic production could help to minimize some of these production issues.

The purpose of this study was to evaluate the gains made in two organic OP sugary-enhancer sweet corn populations, developed with a modified ear-to-row recurrent selection scheme and PPB. After the initial populations were developed, all selection occurred on a certified organic farm in Minnesota from 2008 to 2011. The agronomic and quality traits under selection were those identified by the participating farmers as important to their organic sweet corn production system, and consistent with the general needs of organic farmers listed above.

2. Experimental Section

2.1. Breeding History

Two sugary-enhancer sweet corn populations were developed at the University of Wisconsin's West Madison Agricultural Research Station (WMARS). The earlier maturing of the two populations, designated "early", was produced by crossing four publicly available sugary-enhancer sweet corn hybrids: Sugar Buns, Mystique, Miracle, and Ambrosia. Progeny were cross-pollinated by hand, followed by a cycle of self-pollination. The later maturing population, designated "late", was also produced by crossing four publicly available sugary-enhancer sweet corn hybrids: Ambrosia, Incredible, Argent, and Delectable. Progeny were alternately cross-pollinated by hand, followed by a cycle of self-pollination, for a total of four years of recombination. The early and late populations were maintained at approximately 150 plants per population, and share one common hybrid parent.

Beginning in 2008, each population underwent five cycles of a modified ear-to-row recurrent selection scheme. The original ear-to-row procedure, developed by C.G. Hopkins [33], involved planting a population in an isolated unreplicated plot, allowing the population to open pollinate, saving seed from the superior female parents, and replanting the selected half-sib families for further evaluation and selection. In the modified ear-to-row procedure used in this experiment, 136 ears from cycle 0 (C0) of the early population, and 92 ears from C0 of the late population were planted in unreplicated plots on a certified organic farm in Farmington, Minnesota. Prior to planting, Suståne (Cannon Falls, MN, USA) 5-2-4 organic fertilizer was applied to the field at the rate of 667 kg·ha^{-1}. Soil type is a Kanaranzi loam (fine-loamy, mixed mesic Typic Hapludoll). Twenty-five kernels from each ear were planted in single row plots, measuring 3.5 m long and 0.9 m wide. Alleys between plots were 0.9 m. At the V6 growth stage, plants were side-dressed with Suståne 5-2-4 organic fertilizer at a rate of 445 kg·ha^{-1}. Initial weed flushes were controlled with a tractor-mounted cultivar, followed by hand weeding throughout the season.

Each plot was evaluated for germination by counting the total number of plants emerged. Plots were thinned at the V5 growth stage to a final density of 15 plants·plot^{-1}. The breeders and farmer evaluated each open-pollinated row at the fresh eating stage (approximately 21 days after silk emergence) for the following traits: resistance to common rust (*Puccinia sorghi*), husk protection (amount of husk covering the ear tip), tip fill (complete kernel development extending to the tip of the ear), ear shape, kernel flavor, and kernel tenderness. All traits were identified by the farmer as important to his production system, and were evaluated on a 1–5 scale, with 5 as the best. Any rows that exhibited corn smut (*Ustilago maydis*) were immediately discarded. Flavor and tenderness ratings were weighted heaviest in selection, and no progeny rows with flavor and tenderness ratings below 3 were recombined. Unplanted remnant seeds from the best 11 ear rows from each population were planted in an off-season nursery in Chile, enabling two growing seasons in a single calendar year (one season for selection and the other for recombination). In Chile, plants were cross-pollinated by hand to create the next cycle of full-sib families. This procedure was repeated each year in both the early and late populations.

2.2. Experimental Methods

An experiment was conducted to evaluate the differences among populations and cycles of selection for quantitative and qualitative plant and ear traits in 2012 and 2013 on certified organic land at WMARS and the University of Wisconsin's Arlington Agricultural Research Station (AARS). Soil type at both locations is a Plano silt loam (fine-silty, mixed mesic Typic Argiudoll). The experiment was arranged as a randomized complete block design (RCBD) with four replications per environment. Rows measured 3.5 m long and 0.8 m wide. Each plot consisted of four rows; alleys between plots were 0.9 m. Seed for cycles 0–3 (C0–C3) of the early and late population was produced at WMARS in 2011. Seed for cycle 4 (C4) of both populations was taken directly from the ears returning from the off-season nursery for use in 2012, and was produced at WMARS in 2012 for use in 2013.

In 2012, all cycles of the early and late populations were planted at WMARS on 18 May and at AARS on 23 May. In 2013, all cycles of the early and late populations were planted at WMARS on 16 May and at AARS on 3 June. Prior to planting, the 2012 and 2013 WMARS location was prepared with Suståne

8-2-4 organic fertilizer applied at the rate of 280 kg·ha^{-1}. The 2012 AARS location was prepared with organic poultry compost applied at the rate of 4484 kg·ha^{-1}. The 2013 AARS location was prepared with liquid dairy manure applied at the rate of 75 kL·ha^{-1}. Initial weed flushes were controlled with a tractor-driven rotary hoe, followed by hand weeding throughout the season at all locations. All entries were planted at 30 kernels·row^{-1} and evaluated for germination by counting total number of plants emerged. Plots were then thinned to the desired density of 15 plants·row^{-1} (53,800 plants·ha^{-1}) at the V5 leaf stage.

Morphological data were taken from the first five bordered plants in the left-center row of each plot. Flowering dates were recorded for all locations (except at AARS in 2012) and used as a predictor of fresh eating maturity. Silk emergence was recorded when fifty percent of the plants in the center two rows of a plot showed silk emergence from the husk. All calendar dates were converted to growing degree days (GDD), and calculated from planting date by subtracting 10 °C from the average daily temperature, with minimum temperatures set no lower than 10 °C, and maximum temperatures set no higher than 30 °C. Plant height, ear height, and ear leaf width were measured post-anthesis. Plant height was measured as the distance from the soil surface to the tassel tip and ear height was measured as the distance from the soil surface to the ligule of the leaf subtending the uppermost ear. Ear leaf width was measured at the widest section of the leaf subtending the uppermost ear.

To evaluate ear characteristics, 10 ears from bordered plants in the left-center row were harvested at the fresh eating stage as determined by flowering dates. Five ears were husked, and data were collected on ear length, ear width, and number of kernel rows. Using a numeric rating scale of 1–5, with 5 as the best, the ears were further evaluated for their husk appearance, husk protection, tip fill (kernel development to end of ear), ear shape, and row configuration. Five ears were tasted and evaluated for their flavor and tenderness. All plants in the right-center row were harvested, husked, and counted to determine the total number of marketable ears (ears measuring greater than 15 cm in length). Because flowering dates were not recorded in the 2012 AARS location, the ears in that environment were not evaluated for flavor and tenderness.

Experiments were also conducted to evaluate resistance to common rust (*P. sorghi*) among the populations and cycles of selection, as well as to evaluate tolerance to cold germination. Results were non-significant, and the data is not presented here.

2.3. Data Analysis

Data analysis was performed using the SAS 9.2 statistics package (SAS Institute, Cary, NC, USA) and R version 3.0.3 (R Foundation for Statistical Computing, Vienna, Austria). Environments and genotypes (cycles of selection in both populations) were evaluated as fixed effects, while replication within environment was considered random. Normality and equal variance tests were conducted on the entry residuals, with no deviations found. For all traits measured, an analysis of variance (ANOVA) was calculated on plot means using the SAS MIXED procedure. No significant ($p \leq 0.05$) genotype-by-environment interactions were found, with the exception of days to silking. Spearman rank correlations indicated differences in magnitude rather than rank, and entries were pooled across all environments. Entry means were compared using Fisher's protected least significant differences (LSD) at the $p \leq 0.05$ significance level. Orthogonal polynomial contrasts were performed to compare overall means between the early and late populations. A second ANOVA was calculated for each population, and cycles of selection were partitioned into linear and quadratic contrasts to test for trends in response to selection. Inference on statistical significance of linear and quadratic responses to selection was made based on F-tests of polynomial contrasts to increase the power to detect trends. Intercepts and polynomial coefficients were estimated based on population cycle means using the SAS REG procedure.

3. Results and Discussion

3.1. Evaluation of Populations and Cycles of Selection

Significant differences were found between population means and/or among cycles of selection for all quantitative traits except for stand count percentage and number of marketable ears (Table 1). In the late population, plants were significantly taller, ears were higher on the stalk, ear leaves were wider, and the maturity (measured by GDD to silking) was later, compared to the early population. In the early population, plant height tended to decrease with successive cycles of selection, with a significant change from C0 at 162.2 cm to C4 at 138.9 cm. The late population plant height remained unchanged from C0–C3, then increased to 173.9 cm in C4. In the early population, ear height tended to decrease with successive cycles of selection, with a significant change from C0 at 48.3 cm to C4 at 42.0 cm. Ear height in the late population tended to increase, with a significant change from C0 at 52.3 cm and C4 at 58.6 cm. In the early population, ear leaf width decreased in C3, then increased slightly. There was no significant difference between C0 and C4. In the late population, ear leaf width tended to increase across cycles of selection, with a significant increase from 8.7 cm in C0 to 9.1 cm in C3. The early population became earlier from C0 at 589.2 GDD to C4 at 565.4 GDD. In the late population, maturity increased significantly from 605.4 GDD in C0 to 632.4 GDD in C4.

Ear length was significantly greater in the late population, with an overall population mean of 19.5 cm compared to 18.8 cm in the early population. Ear length in the early population did not change significantly. Ear length in the late population increased steadily and significantly from 19.1 cm in C0 to 19.9 cm in C4. The early and late populations did not differ for average number of kernel rows (Table 1). In the early population, there was a significant difference between C1 at 14.7 kernel rows, and C3 (15.6) and C4 (15.5). In the late population, with 16.5 kernel rows, C4 had more rows than all other cycles.

Significant differences were found between population means and/or among cycles of selection for all qualitative traits except for husk appearance and tenderness (Table 2). The amount of husk covering the ear was rated on a 1–5 scale, with 5 as the best husk protection. The overall mean of the late population, 3.8, was significantly greater than the early population mean, 2.9. Husk protection decreased significantly in the early population from a rating of 3.4 at C0 to a minimum of 2.5 at C3. Husk protection in the late population did not change significantly.

Tip fill is a measure of complete kernel development, and describes the kernel coverage at the ear tip. This trait was rated on a 1–5 scale, with 5 being a completely filled ear. Tip fill was significantly better in the late population, with an overall mean rating of 3.5 compared to 2.8 in the early population. This trait showed no significant differences among cycles of selection in the early population. In the late population, tip fill improved from 2.9 in C0 to 3.8 in C4.

Table 1. Means for quantitative plant and ear traits of cycles 0–4 from two sweet corn populations (early and late) grown in Arlington, WI and West Madison, WI in 2012 and 2013.

Entry	Plant Height (cm)	Ear Height (cm)	Ear Leaf Width (cm)	Stand Count (%)	Days to Silking † (GDD)	Ear Length (cm)	Kernel Rows (average)	Marketable Ears (average)
Early: C0	162.2	48.3	8.5	77.1	589.2	19.2	15.1	11.0
Early: C1	153.9	51.6	8.5	75.8	580.1	19.3	14.7	11.1
Early: C2	148.9	43.7	8.7	69.8	577.6	18.6	15.2	10.8
Early: C3	141.6	42.4	8.1	76.0	561.7	18.6	15.6	10.7
Early: C4	138.9	42.0	8.4	80.6	565.4	18.6	15.5	11.4
Late: C0	166.2	52.3	8.7	78.1	605.4	19.1	15.2	11.0
Late: C1	164.5	53.3	8.7	73.5	618.8	19.2	14.8	10.3
Late: C2	166.2	49.7	8.7	75.4	617.4	19.4	15.1	12.0
Late: C3	164.6	54.3	9.1	79.4	619.2	19.8	15.4	11.6
Late: C4	173.9	58.6	9.0	72.9	632.4	19.9	16.5	11.4
CV %	6.9	15.2	6.1	15.8	1.7	6.4	7.2	18.1
F ratio	18.2 **	8.6 **	4.9 **	1.1 ns	75.8 **	2.9 *	3.4 **	1.0 ns
LSD (0.05)	7.7	5.3	0.4	8.4 ns	8.1	0.8	0.8	1.4 ns
Orthogonal contrast of overall means between the early and late populations								
Early Pop.	149.1	45.6	8.4	75.9	574.8	18.8	15.2	11.0
Late Pop.	167.1	53.7	8.8	75.9	618.6	19.5	15.4	11.2
F ratio	107.9 **	45.5 **	26.1 **	0.0 ns	577.6 **	10.0 **	0.8 ns	0.6 ns

† Trait not evaluated in Arlington, WI in 2012; *, ** Significant at 0.05, 0.01 probability levels, respectively; ns = no significant differences; LSD = Fisher's protected least significant difference, labeled "ns" if the *F*-test was not significant; GDD = growing degree days in Celsius; CV% = Relative coefficient of variation.

Ear shape was rated on a 1–5 scale, with 5 being a perfectly cylindrical ear. Ears were more cylindrical in the late population, with an overall mean rating of 3.7 compared to 3.3 in the early population. Both populations tended to improve with successive cycles of selection, although the differences were not significant.

Row configuration was rated on a 1–5 scale, with 5 being the straightest rows. Rows were straighter in the early population, with an overall mean rating of 3.3 compared to 3.0 in the late population. Differences were not significant among cycles of selection in the early population. In the late population, rows become straighter from C0 at 2.6 to C2 at 3.3. C4 did not differ from C0 or C2.

Flavor was rated on a 1–5 scale, with 5 being the best. Flavor was significantly better in the early population, with an overall mean rating of 3.2 compared to 2.7 in the late population. In the early population, improvement was observed with successive cycles of selection, from 2.8 at C0 to 3.6 at C4. In the late population, flavor improved significantly from C0 at 2.3 to C2 at 3.1. C4 did not differ from C0 or C2.

Table 2. Means for qualitative ear traits rated on a 1–5 scale (5 is the best) of cycles 0–4 from two sweet corn populations (early and late) grown in Arlington, WI and West Madison, WI in 2012 and 2013.

Entry	Husk Appearance	Husk Protection	Tip Fill	Ear Shape	Row Configuration	Flavor †	Tender-ness †
Early: C0	3.4	3.4	2.8	3.2	3.6	2.8	3.3
Early: C1	3.1	3.0	2.8	3.8	3.5	3.3	3.6
Early: C2	2.8	2.6	3.1	2.9	3.1	2.9	3.6
Early: C3	2.8	2.5	2.6	3.3	3.1	3.4	3.6
Early: C4	2.9	2.7	2.6	3.4	3.4	3.6	3.6
Late: C0	3.3	3.9	2.9	3.4	2.6	2.3	3.4
Late: C1	3.1	3.7	3.6	3.8	2.9	2.5	3.6
Late: C2	2.5	4.1	3.5	3.8	3.3	3.1	3.6
Late: C3	3.3	3.5	3.6	3.7	3.1	2.5	3.9
Late: C4	3.2	3.8	3.8	3.8	2.8	2.9	3.8
CV %	37.5	30.1	28.4	24.5	28.7	31.9	19.7
F ratio	1.0 ns	5.4 **	4.3 **	2.0 *	2.0 *	2.3 *	0.7 ns
LSD (0.05)	0.8 ns	0.7	0.6	0.6	0.6	0.8	0.6 ns
Orthogonal contrast of overall means between the early and late populations							
Early Pop.	3.0	2.9	2.8	3.3	3.3	3.2	3.5
Late Pop.	3.1	3.8	3.5	3.7	3.0	2.7	3.7
F ratio	0.2 ns	36.1 **	25.7 **	7.1 **	7.4 **	9.7 **	1.1 ns

† Trait not evaluated in Arlington, WI in 2012; *, ** Significant at 0.05, 0.01 probability levels, respectively; ns = no significant differences; LSD = Fisher's protected least significant difference, labeled "ns" if the *F*-test was not significant; CV% = Relative coefficient of variation.

In the early population, positive linear responses to selection, as indicated by a significant linear coefficient, were observed for the flavor rating (0.2) and number of kernel rows (0.2) (Table 3). Negative linear responses were observed for plant height (−5.9 cm), ear height (−2.2 cm), days to silking (−6.6 GDD), ear length (−0.2 cm) and the husk protection rating (−0.2). A positive quadratic response was found for stand emergence (1.7%).

In the late population, positive linear responses to selection were found for plant height (1.5 cm), ear height (1.4 cm), ear leaf width (0.1 cm), days to silking (5.4 GDD), number of kernel rows (0.3 cm), the tip fill rating (0.2), and the tenderness rating (0.1) (Table 4). Positive quadratic responses were also found for plant height (1.3 cm) and number of kernel rows (0.2). The only negative response in the late population was the quadratic coefficient for the row configuration rating (−0.1).

Table 3. Intercepts and significant linear and quadratic coefficients for response to selection among cycles 0–4 from the early sweet corn population grown in Arlington, WI and West Madison, WI in 2012 and 2013.

Early Population	**Plant Height** (cm)	**Ear Height** (cm)	**Emergence** (%)	**Days to Silking †** (GDD)	**Ear Length** (cm)	**Kernel Rows** (average)	**Husk Protection** (rating)	**Flavor †** (rating)
Intercept	147.8	45.7	72.5	573.0	18.8	15.1	2.6	3.2
Linear coefficient	−5.9 **	−2.2 **	-	−6.6 **	−0.2 *	0.2 *	−0.2 *	0.2 *
Quadratic coefficient	-	-	1.7 *	-	-	-	-	-
R^2	0.99	0.68	0.76	0.89	0.73	0.89	0.99	0.70

† Trait not evaluated in Arlington, WI in 2012; *, ** Significant at 0.05, 0.01 probability levels, respectively; - = non-significance; GDD = growing degree days in Celsius.

Table 4. Intercepts and significant linear and quadratic coefficients for response to selection among cycles 0–4 from the late sweet corn population grown in Arlington, WI and West Madison, WI in 2012 and 2013.

Late Population	**Plant Height** **(cm)**	**Ear Height** **(cm)**	**Ear Leaf Width** **(cm)**	**Days to Silking †** **(GDD)**	**Row Configuration** **(rating)**	**Kernel Rows** **(average)**	**Tip Fill** **(rating)**	**Tenderness †** **(rating)**
Intercept	164.4	51.5	8.8	618.0	3.2	14.9	3.6	3.7
Linear coefficient	1.5 *	1.4 *	0.1 *	5.4 **	-	0.3 **	0.2 **	0.1 *
Quadratic coefficient	1.3 *	-	-	-	-0.1 *	0.2 **	-	-
R^2	0.80	0.81	0.58	0.81	0.95	0.99	0.84	0.83

† Trait not evaluated in Arlington, WI in 2012; *, ** Significant at 0.05, 0.01 probability levels, respectively; - = non-significance; GDD = growing degree days in Celsius.

3.2. Discussion

The differences found among cycles of selection for quantitative and qualitative traits suggest the effectiveness of the modified recurrent selection and PPB methodology. However, some of the changes observed could also be caused by genetic drift, which are random changes in allele frequencies that can occur from one generation to the next, especially in small populations [34]. Genetic drift can be difficult to predict or quantify, although linear and quadratic trends may suggest that the changes observed result from direct or indirect selection. During selection of these populations, a strong emphasis was placed on improving the eating quality of both populations, as the participating farmer and breeders agreed that first and foremost, a new sweet corn variety must be enjoyable to eat. Sugary-enhancer sweet corn is based on a mutation of the *sugary enhancer1* (*se1*) allele, which has the unique ability among sweet corn mutants to accumulate high levels of sucrose and phytoglycogen simultaneously in a *sugary* (*su1*) background [29,35]. As a result, sugary-enhancer sweet corn (*su1 se1*) maintains both the sweetness associated with the supersweet (*sh2*) varieties, and the creamy texture characteristic of traditional sugary (*su1*) sweet corn. While the genetics determining maximum sugary-enhancer quality are not fully understood, it is clear that multiple recessive modifier genes contribute to high eating quality [36]. The early population showed a significant linear response to direct selection for flavor improvement, while the late population exhibited a significant linear response to direct selection for tenderness.

The only other qualitative trait that showed a significant positive linear response to direct selection was the improvement of tip fill in the late population, an important trait for consumers. Husk protection showed a significant negative linear response to direct selection in the early population, while it remained unchanged in the late population with a high average rating of 3.8. Husk protection serves an important function for organic farmers because a long, tight husk extending beyond the ear can help deter the corn earworm (*Heliothis zea*) [37].

A number of quantitative traits, while not under direct selection, did respond linearly and, in some cases quadratically (Tables 3 and 4). The changes observed in these traits could be a result of genetic linkage among traits, pleiotropy, or genetic drift such as inbreeding depression. While both populations were not significantly different from each other in C0, by C4 the late population was significantly taller, with a higher ear placement, wider ear leaves, and longer ears with more kernel rows compared to the early population. These agronomic qualities make the late population a better choice for an organic cultivar, as plant height and leaf width have been associated with weed suppression in sweet corn [38], and larger ear size is generally preferred. Inbreeding depression tends to reduce plant height, ear size and days to maturity, suggesting that the early population may be suffering from this effect [39].

This experiment utilized a modified ear-to-row recurrent selection scheme to develop the early and late populations. In addition, selections were made on half-sib ear rows, with remnant seed from full-sibs recombined in a winter nursery to create the next cycle of families. This breeding method attempted to maximize the speed of improvement of recessive quantitative traits such as eating quality given the logistical difficulty of controlling pollinations by hand on-farm. It is important to note that multiple examples of PPB selection schemes for maize exist, including mass selection, full-sib recurrent selection, half-sib recurrent selection, and recurrent selection on self pollinated families [21,22,40–42]. The choice of breeding methods depends on both the goals of the project and the resources available to the participants.

At least two limitations of the study suggest areas for further investigation. First, given the variability inherent in cross-pollinating OP populations, increasing the number of plants evaluated on a per plot basis will yield a more accurate representation of each population cycle. Second, while resource allocation is always a consideration, increasing the number of environments tested, particularly to include the selection environment, would potentially increase the statistical robustness and allow a comparison of performance between the selection and non-selection environments. The locations for this experiment were chosen based on their proximity to the researchers (the selection environment was 440 kilometers away) and the feasibility of collecting numerous data points. However, organic farming systems vary substantially, and given the slow process of building soil quality and structure with organic inputs, the number of years that a piece of land has been managed organically will greatly impact the health of the crop grown on it. The on-farm selection environment in this study has been in organic production for multiple decades, whereas the agricultural research station trial locations have been managed organically for ten years or less. This difference can cause improved crop performance in the selection environment in comparison to the trial locations.

4. Conclusions

The purpose of this study was to evaluate the gains made in two organic OP sugary-enhancer sweet corn populations. Organic growers face unique challenges when raising sweet corn, and benefit from varieties that maintain high eating quality, germinate consistently, deter insect pests, and resist diseases. This study indicates that progress can be made in developing OP sweet corn for organic growers using a modified ear-to-row recurrent selection scheme and on-farm PPB. While changes were observed in both populations, the late population exhibits promising traits including high eating quality, minimized tip blanking, good ear size and shape, and tall plants to help with weed competition. However, further selection is necessary to improve traits that are critical for organic growers, including rust resistance, husk protection and cold soil germination.

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Author Contributions

William F. Tracy developed the breeding populations and designed the recurrent selection method. Adrienne C. Shelton designed and executed the experiment, and wrote the paper. All authors have read and approved the final manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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