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Relationships among phenotypic traits of sweet corn and tolerance to crowding stress

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ABSTRACT

Crowding stress tolerance is defined as the extent to which the crop maintains yield per unit area as plant population density increases beyond standard levels. Sweet corn (*Zea mays* L.) hybrids grown for processing vary widely in tolerance to crowding stress; however, the mechanisms involved in crowding stress tolerance are unknown. The objective of the study was to determine the extent to which crop traits, individually and in combination, relate to crowding stress tolerance in processing sweet corn. Twenty-six modern shrunken-2 processing hybrids from eight sources were grown under conditions of crowding stress (i.e. 72,000 plants ha^{-1}) over a three-year period. Seventeen crop traits measured from emergence to harvest were related to four measures of crowding stress tolerance, including ear mass, recovery, case production, and gross profit margin. Of individual crop traits, kernel mass $plant^{-1}$ was among the best predictors of crowding stress tolerance in processing sweet corn, as long as sweet corn lines were grown at a uniformly high plant population. Two categories of traits related to crowding stress tolerance in sweet corn, including a 'source-sink relationship' factor and a 'photosynthetic capacity' factor. Factor regression showed the combination of traits loading into the source-sink relationship factor was positively related to ear mass, case production, and gross profit margin. This research points to the underlying mechanisms involved in crowding stress tolerance in processing sweet corn.

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1. Introduction

Crowding stress tolerance (also known as plant density tolerance) is defined as the extent to which the crop maintains yield per unit area as plant population density (hereafter simply called 'population density') increases beyond standard levels. Genetic contributions to gains in field corn (*Zea mays* L.) productivity over the last 80 years have been driven largely by improvements in stress tolerance in modern hybrids (Duvick, 2005; Tokatlidis and Koutroubas, 2004; Tollenaar and Wu, 1999). Crowding stress tolerance over a range of environmental conditions has played a major role in genetic improvement, as evidenced by corn hybrid 'era' studies. Such studies show yield potential per plant has remain unchanged for decades while yield potential per unit area has increased as a function of both higher population density and year of hybrid introduction (Carlone and Russell, 1987; Duvick et al., 2004; Russell, 1991). Adaptation to continual increases in population density not only explains much of the relationship between population density and historic U.S. field corn yields, but also opens debate about how to improve future yields (Duvick, 2005; Lobell et al., 2014).

While the epicenter of processing sweet corn production is in the United States of America, several other countries grow processing sweet corn, including Australia, Brazil, Canada, China, Europe, New Zealand, and South Africa. Recent work in the U.S. has shown that modern sweet corn hybrids grown in temperate regions vary widely in tolerance to crowding stress (Shelton and Tracy, 2013; Williams, 2012). Across six processing hybrids popular in the U.S. cornbelt, Williams (2012) showed a positive relationship between optimal population density and maximum yield. Field surveys show population densities used by sweet corn growers corresponds to optimal population density of hybrids with intermediate tolerance to crowding stress, yet may be insufficient for crowding stress tolerant hybrids (Williams, 2012).

The sweet corn seed and processing industries are interested in not only identifying top performing hybrids that yield well under elevated population densities, but also traits involved in crowding stress tolerance. Several crop traits are believed to relate to tolerance to intense competition, including plant height, tiller number, and ear width (Shelton and Tracy, 2013; Zystro et al., 2012). However, individual traits are unlikely to be a useful indi-

Abbreviations: GDD, growing degree days; IPAR, intercepted photosynthetically active radiation; LAI, leaf area index; WAP, weeks after planting.

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Table 1
Description, unit of measure, range of hybrid means, and variation among hybrids of 17 predictor traits and four processor variables for sweet corn grown under conditions of crowding stress (72,000 plants ha^{-1}).[a]

Type	Trait	Timing	Description	Unit	Range of hybrid means	*P*-value[b]
Predictor trait	Initial emergence	1 WAP	Initial seedling counts as percentage of seed planted	%	37–86	<0.001
	Final emergence	3 WAP	Final seedling counts as percentage of seed planted	%	73–93	0.041
	Early height	V6	Plant height at V6	cm	39–66	<0.001
	Early chlorophyll	V6	Chlorophyll measured with SPAD meter at V6	–	44–54	<0.001
	Mid-silk	R1	Time to mid-silk	GDD	620–830	<0.001
	Late height	R1	Plant height at R1	cm	150–230	<0.001
	Late chlorophyll	R1	Chlorophyll measured with SPAD meter at R1	–	50–57	<0.001
	LAI	R1	Leaf area index at R1	–	3.5–6.6	<0.001
	IPAR	R1	Intercepted photosynthetically active radiation at R1	%	72–94	<0.001
	Leaf N	R1	Leaf nitrogen content at R1	%	2.6–3.0	<0.001
	LAI case^{-1}	R1 & R3	LAI per case	LAI case^{-1}	31–91	<0.001
	Ears plant^{-1}	R3	No. marketable ears per plant	no. plant^{-1}	0.58–0.90	<0.001
	Ear mass plant^{-1}	R3	Green ear mass per plant	g plant^{-1}	180–300	<0.001
	Kernel mass plant^{-1}	R3	Kernel mass per plant	g plant^{-1}	66–120	<0.001
	Plant lodging	R3	Percent of plants lodged	%	0–3	<0.001
	Ear length	R3	Ear length	cm	18–21	<0.001
	Filled ear length	R3	Filled ear length	cm	16–20	<0.001
Processor variable	Ear mass	R3	Mass of marketable ears per ha	Mt ha^{-1}	13–21	<0.001
	Recovery	R3	Fraction of ear mass accounted by kernel mass	%	32–46	<0.001
	Case production	R3	Number of cases of cut corn per ha	cases ha^{-1}	760–1340	<0.001
	Gross profit margin	R3	Value of cases ha^{-1} less cost of ear mass per ha	$ ha^{-1}	7900–14,400	<0.001

[a] Abbreviations: GDD, growing degree days; IPAR, intercepted photosynthetically active radiation; LAI, leaf area index; R1, silk emergence; R3, milk stage; V6, 6-collar corn; WAP, weeks after planting.
[b] *P*-values report significance in variation among hybrids.

cator for breeding greater crowding stress tolerance into sweet corn, as multiple factors are probably involved. A recent survey of maize germplasm revealed several categories of traits involved in crowding stress tolerance, including photosynthetic capacity, plant architecture, and source-sink relations (Mansfield and Mumm, 2014).

In recent work in field corn, the range of crop yields among hybrids widened as population density increased beyond normal levels. Yield declined in hybrids with poor crowding stress tolerance whereas yield improved in hybrids with superior crowding stress tolerance (Mansfield and Mumm, 2014). This concept was applied to sweet corn to develop a simplified research method to identify processing hybrids with superior tolerance to crowding stress (Williams, 2015). The general approach involved growing a diversity of modern hybrids under a uniformly high population density and comparing hybrids in terms of variables important to the processor, collectively called 'processor variables'. In addition to processor variables, 17 additional crop traits from emergence to harvest were measured. The objective of the present study was to determine the extent to which these crop traits, individually and in combination, relate to crowding stress tolerance in processing sweet corn.

2. Materials and methods

2.1. Experimental approach

Field experiments were conducted in 2012, 2013, and 2014 at the University of Illinois Vegetable Crop Research Farm near Urbana, IL. The field each year followed the soybean phase of a corn-soybean rotation. Soils were a Flanagan silt loam (fine, smectitic, mesic Aquic Argiudoll) averaging 3.0% organic matter.

Twenty-six modern shrunken-2 (sh2) processing hybrids from eight sources were used (Supplemental Table 1). Although not the focus of the current study, one objective of the previous study (Williams, 2015) was to determine if an interaction exists between N fertilization and hybrid on crop response to crowding stress. Therefore, hybrids were grown under a suboptimal N rate (67 kg N ha^{-1}) and supraoptimal N rate (202 kg N ha^{-1}) in a factorial arrangement of treatments. Nitrogen fertilization treatments were determined from a soil-specific fertility recommendation of 135 kg N ha^{-1} (Fritz et al., 2010; Laboski and Peters, 2014) and applied as urea immediately prior to incorporation with a field cultivator and sweet corn planting. Hybrids and fertility treatments were applied to subplots and main plots, respectively, of a split plot randomized complete block with four replications. Subplots measured 3 m (i.e. four rows on 0.76 m spacing) by 9 m. To accommodate N application, main plots measured 9 m (i.e. 12 rows) by 87 m.

Experiments were planted May 17, 15, and 20 in 2012, 2013, and 2014, respectively. Hybrids were over-seeded 35% at planting, and then at three weeks after planting (WAP), hand thinned to a target population of 72,000 plants ha^{-1}. The target population was selected based on previous research that showed 72,000 plants ha^{-1} was just beyond the optimal population of the most crowding stress tolerant hybrid (Williams, 2012).

Insect pests were controlled with an at-planting t-band application of tefluthrin ((1*S*,3*S*)-*rel*-2,3,5,6-Tetrafluoro-4-methylbenzyl 3-((*Z*)-2-chloro-3,3,3-trifluoroprop-1-en-1-yl)-2,2-dimethylcyclopropanecarboxylate) and, as needed, a foliar application of permethrin (3-phenoxybenzyl (1RS) cis,trans-3-(2,2-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate). Weed control was accomplished by a preemergence application of atrazine (6-chloro-N-ethyl-N′-(1-methylethyl)-1,3,5-triazine-2,4-diamine) plus metolachlor (2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl) acetamide) followed by a single interrow cultivation prior to canopy closure and, as needed, handweeding. Fields were sprinkler irrigated ~2 cm as needed to ensure crop growth during exceptionally dry periods. Total water applied was 13.3 and 3.7 cm in 2012 and 2013, respectively.

2.2. Data collection

Data were taken from the center two rows of each subplot (Table 1). One and three weeks after planting (i.e. prior to thinning), crop emergence was determined from seedling counts made along two meters of crop row per subplot. Plant height, measured from the soil surface to plant apex, was measured on five plants per subplot at the V6 and R1 stages (crop growth stages defined by Abendroth et al., 2011). A relative measure of leaf chlorophyll concentration was quantified using a chlorophyll meter (SPAD 502, Spectrum Technologies, Aurora, IL) on five plants per subplot at the mid-length of the oldest emerging leaf (at V6) or primary ear leaf (at R1). Thermal time to mid-silk was determined as cumulative growing degree days (GDD) from planting to mid-silk, whereby GDD was determined using a base temperature of 10 °C and daily temperature data from a nearby weather station (Illinois State Water Survey, Champaign, IL). At R1, leaf area index (LAI) and photosynthetically active radiation (PAR) were measured within 1.5 h of solar noon with a linear ceptometer (LP-80 AccuPAR, Decagon Devices, Pullman, WA). Five above-canopy measurements and five below-canopy measurements per plot were used to calculate intercepted photosynthetically active radiation (IPAR); specifically, [(mean above-canopy PAR minus mean below-canopy PAR) divided by mean above-canopy PAR] × 100. At R1, six primary ear leaves per subplot were cut along the collar, oven-dried at 65C to a constant weight, ground, and submitted for assessment of total leaf nitrogen content (A&L Great Lakes Laboratories, Fort Wayne, IN).

At 21 days after mid-silk (R3 growth stage), marketable ears (e.g., measuring >4.4 cm in diameter) were hand harvested from the center two rows of each subplot, 6 m in length. Total ear number and green ear mass per subplot were recorded. Ear mass consisted of whole earshoots, including husks, shanks, kernels, and cobs. Twelve ears per subplot were randomly selected and measured for ear length (distance from butt to tip) and filled ear length (distance from butt to the extant of fully developed kernels). Ear samples were then husked with an industry-grade husking bed (A&K Development, Eugene, OR), and fresh kernels were cut from cobs with an industry-grade hand fed corn cutter (A&K Development, Eugene, OR). Kernel moisture was determined gravimetrically for each subplot. Kernel mass per sample was quantified as the difference in husked ear mass per sample and cob mass per sample, then adjusted to 76% kernel moisture.

Processor variables determined include: (1) ear mass, defined as mass of marketable ears ha^{-1}, (2) recovery, calculated as the fraction of ear mass accounted by kernel mass, (3) case production, calculated as the number of cases of sweet corn ha^{-1} (assuming 6.13 kg of kernels case^{-1}), (4) gross profit margin, calculated as the value of case production ha^{-1} minus cost of ear mass ha^{-1} paid by the processor to the grower. Estimates of case production ($12 case^{-1}) and cost of ear mass ($110 M ton^{-1}) were obtained from the sweet corn processing industry (Nick George, Midwest Food Processors Association; personal communication).

Plant populations observed at harvest, in combination with yield data, were used to quantify ears plant^{-1}, ear mass plant^{-1}, and kernel mass plant^{-1}. In addition, subplots were scored for stalk or root lodging at R3 by determining the percent of plants lodged at harvest.

2.3. Data analyses

With one exception, diagnostic tests of residuals indicated data met ANOVA assumptions of homoscedasticity and normality. No transformation improved distribution of lodging data; therefore, the Kolmogorov-Smirnov test of frequency distributions was used to determine if hybrids differed in lodging response. For all other response variables, data were analyzed using the Mixed procedure in SAS (Version 9.3, SAS Institute Inc., Cary, NC). Fixed effects included hybrid, N fertilization, and their interaction. Random effects included year and replicate nested within year.

Pearson correlation analysis between predictor traits and processor variables was conducted. Probability values for correlations were calculated using the Bonferroni correction at $\alpha = 0.05$ (Neter et al., 1996).

Covariance was observed among several of the predictor traits. Principle component factor analysis is useful in describing the covariance relationships among many variables in terms of a few underlying, yet unobservable, 'factors' (Johnson, 1998). In theory, principle component factor analysis could reduce various predictor traits to a handful of categories of traits (i.e. factors) previously implicated in crowding stress tolerance in field corn. Therefore, principal component factor analysis was conducted and factors were retained using Cattell's Scree Plot Test (Johnson, 1998). Relationships among predictor traits loading into each factor were quantified using Pearson correlation analysis. Principal component factor and correlation analyses were performed in SYSTAT 13.0 (SYSTAT Software Inc., Chicago, IL). An additional advantage of principal component factor analysis is that factor loadings can be used in further analyses. For instance, relationships between factors and measures of crowding stress tolerance can be elucidated. Therefore, processor variables were fitted individually to a linear model as a function of loadings of each factor using least-squares regression. Model performance was documented by reporting P-values and coefficient of determination (R^2) values. Regression analyses were performed in Sigmaplot 11.0 (SYSTAT Software, Inc., Chicago, IL).

3. Results

3.1. Phenotypic variability

Few interactions were observed between hybrid and N fertilization (data not shown); therefore, data were pooled across N fertilization in additional analyses. A wide range of phenotypic variability was observed among the 26 hybrids used in this study. Hybrids differed significantly in every predictor trait measured (Table 1). Emergence 1WAP ranged from 37 to 86% among hybrids. By V6, the tallest hybrid was 27 cm greater than the shortest hybrid. Differences continued throughout the growing season. By R1, hybrid LAI ranged from 3.5 to 6.6, IPAR ranged from 72 to 94%, and LAI case^{-1} ranged from 31 to 91. Lodging, which occurred at a very low level (≤3%), was differentially expressed among hybrids.

Crowding stress tolerance, as measured by processor variables in this experimental design, varied widely among hybrids, too. Ear mass of the highest-yielding hybrid was 62% greater than the lowest-yielding hybrid (Table 1). Case production among hybrids ranged from 760 to 1340 cases ha^{-1}. Gross profit margin, the single most important economic metric for hybrid comparisons, revealed a nearly two-fold difference among hybrids.

3.2. Correlation analysis

Under conditions of crowding stress, many predictor traits were associated with processor variables. Eleven of the predictor traits were positively correlated with ear mass, case production, and gross profit margin, while mid-silk and LAI case^{-1} were negatively correlated with the same three processor variables (Table 2). Not only were correlations significant, but particularly large for certain predictor traits. Correlations with ear mass were 0.90, 0.93, and 0.97 for kernel mass plant^{-1}, ears plant^{-1}, and ear mass plant^{-1}, respectively. Additionally, kernel mass plant^{-1} was highly correlated ($\rho = 0.97$) with case production and gross profit margin. In contrast, few predictor traits were highly correlated with recovery ($\rho \leq 0.51$).

Table 2
Pearson correlations between select predictor traits and processor variables across hybrids, N treatments, and environments for sweet corn grown under conditions of crowding stress (72,000 plants ha^{-1})[a].

Trait	Ear mass	Recovery	Case production	Gross profit margin
Kernel mass $plant^{-1}$	0.90***	0.51***	0.97***	0.97***
Ear mass $plant^{-1}$	0.97***	0.23*	0.85***	0.83***
Ears $plant^{-1}$	0.93***	0.23**	0.83***	0.80***
Late chlorophyll	0.82***	−0.08	0.70***	0.66***
Leaf N	0.67***	0.26***	0.63***	0.61***
Early height	0.51***	0.08	0.41***	0.38***
Filled ear length	0.54***	−0.07	0.40***	0.36***
LAI	0.49***	0.04	0.37***	0.34***
Early chlorophyll	0.52***	−0.08	0.37***	0.34***
Ear length	0.50***	−0.07	0.36***	0.32***
IPAR	0.38***	−0.05	0.26***	0.23**
Mid-silk	−0.49***	−0.09	−0.48***	−0.46***
LAI $case^{-1}$	−0.61***	−0.40***	−0.67***	−0.67***

[a] *, **, *** Significant at 0.05, 0.01 and 0.001 probability, respectively.

Table 3
Mean factor loadings and cumulative variance accounted by 17 predictor traits.

Trait	Factor 1	Factor 2	Factor 3
Ear mass $plant^{-1}$	0.93	–	–
Ears $plant^{-1}$	0.89	–	–
Late chlorophyll	0.84	–	–
Kernel mass $plant^{-1}$	0.82	–	–
Filled ear length	0.74	–	–
Ear length	0.73	–	–
Early height	0.68	–	–
Leaf N	0.68	–	–
LAI	0.65	–	–
Early chlorophyll	0.64	–	–
LAI $case^{-1}$	–	0.71	–
Mid-silk	–	0.69	–
Late height	–	0.59	–
IPAR	–	0.59	–
Final emergence	–	–	0.83
Initial emergence	–	–	0.76
Plant lodging	–	–	–
Cumulative variance (%)	42	57	67

Table 4
Pearson correlation coefficients among 10 predictor traits that loaded into Factor 1. All coefficients are significant at $\alpha = 0.05$.

	Ear mass $plant^{-1}$	Ears $plant^{-1}$	Late chlorophyll	Kernel mass $plant^{-1}$	Filled ear length	Ear length	Early height	Leaf N	LAI
Ears $plant^{-1}$	0.95	–							
Late chlorophyll	0.81	0.80	–						
Kernel mass $plant^{-1}$	0.91	0.87	0.71	–					
Filled ear length	0.58	0.49	0.49	0.45	–				
Ear length	0.56	0.48	0.47	0.43	0.89	–			
Early height	0.52	0.46	0.46	0.43	0.54	0.57	–		
Leaf N	0.65	0.66	0.67	0.62	0.38	0.32	0.24	–	
LAI	0.50	0.46	0.46	0.39	0.43	0.47	0.50	0.42	–
Early chlorophyll	0.52	0.51	0.55	0.39	0.44	0.37	0.56	0.36	0.43

3.3. *Factor analysis*

Factor analysis reduced the 17 predictor traits to three principal factors that accounted for as much as 67% of the inherent variation among traits. The first factor loaded highly ($\geq$0.64) for 10 traits, specifically: ear mass $plant^{-1}$, ears $plant^{-1}$, late chlorophyll, kernel mass $plant^{-1}$, filled ear length, ear length, early height, leaf N, LAI, and early chlorophyll (Table 3). The first factor accounted for 42% of the variation among traits. Correlation among the 10 traits loading into Factor 1 ranged from 0.24 to 0.95 (Table 4). Traits loading into Factor 1 with the highest correlations ($\rho \geq 0.91$) were measurements of yield reported on a per-plant basis; specifically, ears $plant^{-1}$ and kernel mass $plant^{-1}$.

Variables that loaded into Factor 2 were traits that largely described the mature architecture of the plant, including LAI $case^{-1}$, mid-silk, late height, and IPAR (Table 3). The second factor accounted for an additional 15% of the variation among traits. All traits loading into Factor 2 were positively correlated to each other, ranging from 0.11 to 0.53 (data not shown).

Two traits related to seedling establishment loaded into Factor 3, specifically, initial emergence and final emergence. Factor loadings for these two traits ranged from 0.76 to 0.83 (Table 3). The third

Table 5
Significance (*P*-values) of analysis of processor variables regressed on factor loadings derived from factor analysis (see Table 3). Linear regression parameter estimates and goodness of fit (R^2) are included.

Factor	Processor variable	*P*-value	Intercept	Slope	R^2
1	Ear mass	<0.001	17.3	5.39	0.82
	Recovery	0.001	37.2	0.71	0.03
	Case production	<0.001	954	273	0.61
	Gross profit margin	<0.001	10,050	2,820	0.55
2	Ear mass	<0.001	17.3	−1.65	0.08
	Recovery	<0.001	37.2	−0.96	0.06
	Case production	<0.001	954	−137	0.15
	Gross profit margin	<0.001	10,050	−1,543	0.16
3	Ear mass	0.225	17.3	0.39	<0.01
	Recovery	0.252	37.2	0.25	<0.01
	Case production	0.089	954	33	<0.01
	Gross profit margin	0.079	10,050	367	<0.01

factor accounted for an additional 10% of variation among traits. A positive correlation ($\rho = 0.58$) was observed between these two measures of crop emergence.

3.4. Factor regression

Regression analysis was used to quantify functional relationships between factors of crop traits and the four processor variables. Regressions were highly significant (≤ 0.001) between all four processor variables and the first two factors identified in the factor analysis (Table 5).

Positive slope coefficients indicated all measures of crowding stress tolerance were improved as Factor 1 loadings increased. Each unit increase in Factor 1 corresponded to >5% increase in ear mass (Table 5). Furthermore, model performance was relatively high for the relationships between Factor 1 and three of the processor variables. Specifically, R^2 values for model fit between Factor 1 and ear mass, case production, and gross profit margin were 0.82, 0.61, and 0.55, respectively.

Factor 2 also was associated with all four processor variables. Negative slope coefficients indicated all measures of crowding stress tolerance responded negatively to increases in Factor 2 loadings (Table 5). While relationships were significant for Factor 2 ($P < 0.001$) and processor variables, linear regressions were relatively weak, as evidenced by R^2 values ranging from 0.06 to 0.16.

Little relationship was observed between Factor 3 loadings and processor variables. Only marginal relationships (e.g. $P = 0.079$) were observed and model fit was poor (Table 5).

4. Discussion

The experimental approach used in this study provided an opportunity to evaluate the extent to which processing sweet corn hybrids yield when grown at an above-standard population density. This increased population created conditions of crowding stress, as evidenced by the lack of multiple marketable ears per plant in these normally prolific hybrids. Therefore, yield response of each hybrid characterized the hybrid's relative degree of crowding stress tolerance in central Illinois conditions. Regardless of the yield measurement (i.e. processor variable), hybrids varied widely in crowding stress tolerance. For instance, ear mass of hybrids grown at 72,000 plants ha^{-1} ranged from 13 to 21 Mt ha^{-1} (Table 1); a far wider range than observed previously on Illinois farms at the typical population of 57,000 plants ha^{-1} (Williams et al., 2009). Under elevated population density, hybrids yielding nearly 21 Mt ha^{-1} were considered to have greater crowding stress tolerance than those yielding considerably less. Details on individual hybrid response, as well as crop response to N fertilization, are reported by Williams (2015).

Factor analysis used covariance relationships among predictor traits to identify a few underlying, yet unobservable, factors. Because Factor 1 was loaded with several traits characterizing potential for light interception (e.g. early height, leaf N, and LAI) and yield components (e.g. per-plant ear number, ear mass, and kernel mass), it was interpreted as a 'source-sink relationship' factor. The source:sink ratio is the supply and demand of assimilates within the plant during grain fill (Rajcan and Tollenaar, 1999). Increasing population density influences the source:sink ratio by differentially affecting light interception and yield components. In general, measures of yield of individual plants (e.g. ear size, kernels $plant^{-1}$, and kernel weight) decline with increasing population density (Hashemi et al., 2005; Lashkari et al., 2011).

Traits loading into Factor 2 largely described the crop's efficiency in light interception and conversion into assimilates. Factor 2 was interpreted as a 'photosynthetic capacity' factor. Improved light interception throughout the canopy, not just among the uppermost leaves, is believed to be responsible for increased dry matter production and assimilate partitioning to the ear. Modern field corn hybrids have more upright leaves and smaller tassels compared to their predecessors (Duvick, 2005). Such structural changes are believed to have improved photosynthetic capacity by enabling more light to penetrate deeper into the crop canopy (Brekke et al., 2011; Duvick and Cassman, 1999).

Emergence data, taken prior to thinning of seedlings to 72,000 plants ha^{-1}, loaded into factor 3. Factor 3 was interpreted as a 'crop establishment' factor. Endosperm mutation is known to influence emergence characteristics of sweet corn (Azanza et al., 1996; Zan and Brewbaker, 1999). However, all hybrids in the present work carried the sh2 endosperm mutation. Variation in seedling emergence was likely driven in large part by germination differences among seed lots, which ranged from 90 to 98%.

Plant traits in field corn, similar to traits measured here in sweet corn, were classified into categories previously implicated in crowding stress tolerance. Factor 1 (source-sink relationship) is comparable to the source-sink category described by Mansfield and Mumm (2014). In their work, several traits in the source-sink category, including upper leaf area and kernels per plant, had among the highest positive correlations to grain yield across 32 hybrids grown in population densities ranging from 47,000 to 133,000 plants ha^{-1}. Moreover, Factor 2 (photosynthetic capacity) of the present work is comparable to the photosynthetic capacity category also described by Mansfield and Mumm (2014). They showed leaf area to produce one gram of grain was negatively correlated ($\rho = -0.62$) to grain yield. A comparable ratio measured in the present work, LAI $case^{-1}$, quantifies the efficiency of sweet corn to convert sunlight into cases of fresh cut kernels. Efficiency increases as the LAI $case^{-1}$ ratio decreases since less leaf area is required to produce a case of kernels. Consistent with previous research on field corn, LAI to produce one case of sweet corn was negatively correlated ($\rho = -0.61$ to -0.67) to ear mass and case production.

To what extent can crop traits measured in this work, either individually or in combination, relate to crowding stress tolerance in sweet corn? Factor regression revealed the strongest relationships between processor variables and factors (R^2 up to 0.82) was for the source-sink relationship, Factor 1 (Table 5). The combination of traits loading into the source-sink relationship factor was positively related to ear mass, case production, and gross profit margin (Table 5). A similar analytical approach was used to assess sweet corn's ability to tolerate interspecific (i.e. weed) competition. A factor regression using 18 crop traits in 23 hybrids identified relationships among crop canopy factors and tolerance to wild-proso millet (*Panicum miliaceum* L.) competition (So et al., 2009). The improved fit between crop factors and crowding stress tolerance observed in the present work is likely due to the variability inherent in crop-weed competition studies driven by factors such as weed emergence timing, community composition, and weed population density (Zimdahl, 2004).

Certain individual traits, namely kernel mass plant^{-1} and ear mass plant^{-1}, were highly associated ($\rho = 0.97$) with ear mass, case production, and gross profit margin. Previous research on linkages between crop traits and processor variables showed weaker relationships than observed here. Williams (2014) reported a correlation coefficient of 0.661 between ears plant^{-1} and gross profit margin to the processor. However, population densities varied widely in that dataset, which was drawn from various studies across 22 different growing environments over an 8-year period. The large associations reported in the current research were undoubtedly made possible by the uniformly high population density used in the present experimental approach. Since plant population was constant across all experimental units, even subtle changes in per-plant ear measurements directly influenced yield per unit area.

5. Conclusions

Crowding stress tolerance likely involves multiple, complex mechanisms within the plant. Two categories of traits measured in the present work, and previously implicated in crowding stress tolerance in field corn, related to crowding stress tolerance in sweet corn. Progress is being made towards identifying the underlying genetics of crowding stress tolerance in field corn, which will likely benefit sweet corn. In the meantime, and from a practical perspective, this work shows certain individual plant measurements, including kernel mass plant^{-1}, may be among the best predictors of crowding stress tolerance in processing sweet corn, as long as sweet corn lines are grown at a uniformly high plant population. With a constant population density, individual plants within plots, rather than entire plots, could be harvested. This would reduce labor needs and costs associated with hybrid development and evaluation. Moreover, with a population that is sufficiently high to suppress prolificacy (i.e. $\leq$1.0 ear plant^{-1}), crowding stress tolerant hybrids could be identified based on kernel mass plant^{-1}. The extent to which plant populations can be increased in crowding stress tolerant hybrids needs to be studied.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2015.10.022.

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