

COMBINING ABILITY FOR CARBOHYDRATE COMPONENTS ASSOCIATED WITH CONSUMER PREFERENCES IN TROPICAL SWEET AND WAXY CORN DERIVED FROM EXOTIC GERMPLASM

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ABSTRACT

Vegetable corn with an excellent, balance proportion of kernel carbohydrates in relation to good eating quality appeals to consumers. Sweet-waxy corn hybrid is proposed to improve palatability of traditional cooked waxy corn, well known as synergistic corn. We determined genetic effects of sugars, phytyglycogen, total starch, and amylopectin and estimated general combining ability of parents for these traits. Three sweet corn lines assigned as female were crossed with eight waxy corn lines as male following the North Carolina II. About 11 parents, 24 F₁ progenies, and 3 checks were evaluated in randomized complete block design with three replications in two seasons between 2017-2018. Then, entry means of 38 genotypes was clustered with dendogram. Additive effect was important for favored kernel carbohydrates except for phytyglycogen. Two sweet corn lines 101LBW and 101LTSC-10 were proposed as broad-based testers for total sugar and sugar fractions, whereas a waxy corn line KVMON for total starch and amylopectin. Cluster analysis based on amylopectin, total sugar, and phytyglycogen was reliable to discriminate corn genotypes into seven major groups, and two sweet-waxy corn F₁ hybrids 101LTSC-10/C13-1 and 101LTSC-10/KV3473 corresponding to our selection criteria were identified. Implications in plant breeding and suggestions for further investigations are discussed.

Keywords: Amylopectin, hybrid breeding, maize, palatability improvement, phytyglycogen, total sugar

INTRODUCTION

Waxy corn (*Zea mays* L. *ceratina*) is a popular, staple crop consumed as vegetable in East and Southeast Asia. In Thailand, waxy corn has been cultivated as a cash crop, and it is harvested at fresh stage and is cooked for daily consumption (Lertrat and Thongnarin, 2008). Nowadays, the increasing consumption is followed by higher preference of more palatable cooked waxy corn such as stickiness and soft tenderness (Jung et al., 2005). These attributes are associated with high amylopectin content (Ferguson, 2001) and thin pericarp (Jung et al., 2009; So, 2019). Meanwhile, consumer preferences in relation to eating quality of sweet corn are flavor, texture, and aroma (Wann et al., 1971; Flora and Wiley, 1974). Flavor is determined by sweetness, kernel sucrose content, juiciness, and total starch (Azanza et al., 1996a; Reyes et al., 1982), whereas kernel texture is made of pericarp tenderness (Bailey and Bailey, 1938) and phytyglycogen content (Swiader et al., 1992).

Traditional waxy corn is recognized for high stickiness due to predominance of amylopectin content up to 95%

(Ferguson, 2001) with poor sweetness and low sugars (Simla et al., 2016). Sweet-waxy corn hybrid is proposed to improve palatability of traditional cooked waxy corn by applying the synergistic effect of sweet gene combinations (Simla et al., 2009) and maximizing the proportion of sweet kernels among segregating F₂ kernels of individual F₁ ear through Mendelian ratio (Lertrat and Thongnarin, 2008; Simla et al., 2016). The eating quality of vegetable corn can be improved by phenotypic selection based on kernel carbohydrates (Azanza et al., 1996a). Three of seven chemical properties observed in our study namely amylopectin, total sugar, and phytyglycogen are assigned as selection criteria.

Waxy corn is domesticated in Southeast Asia including Thailand (Stamp et al., 2016) from wild-type plants in China (Tian et al., 2009). The introduction of exotic corn germplasm differed in climatic regions is expected to expand the genetic diversity in tropical corn breeding (Menkir et al., 2006). The concept of general combining ability (GCA) and specific combining ability (SCA) for inbred and hybrid selections, respectively

(Sprague and Tatum, 1942) have been common in corn hybrid breeding to date. While the GCA is correlated to additive genetic effect, the SCA is associated with non-additive effects (Falconer, 1989; Rojas and Sprague, 1952). The North Carolina II or factorial mating design (Comstock and Robinson, 1948) is suitable for hybrid formation that involves many parents and avoids intragroup crosses (Hallauer et al., 2010). Previous studies of combining ability analysis and gene action have been conducted with sweet corn x sweet corn for total sugar, sucrose, phytoglycogen, and starch (Has and Has, 2009; Khanduri et al., 2010; Rosenbrook and Andrew, 1971) and waxy corn x waxy corn for starch pasting viscosity properties (Ketthaisong et al., 2014).

Incorporation of sweet genes *su/sh2/bt* to *wx* background through two genes combinations has been investigated among sweet and waxy corn lines (Simla et al., 2016); however, combining ability analysis on these traits of interest by mating scheme between sweet corn x waxy corn has not been reported. Therefore, this current study aimed to estimate the GCA of eleven corn inbred lines for kernel carbohydrates and to identify favored sweet-waxy corn F₁ progenies with an excellent, balance proportion of amylopectin, total sugar, and phytoglycogen. Information obtained in this study helps

breeder working with synergistic sweet-waxy corn hybrids.

MATERIALS AND METHODS

Plant material and mating design

Eleven parental lines comprised of three sweet corn breeding lines and eight waxy corn breeding lines were used in this study (Table 1). Almost tested lines were derived from different origins; however, they had good adaptation to the tropical zone of Thailand. One of three sweet corn lines was 101LBW with two-gene combination (*btbtSh2Sh2wxwx*), whereas other two lines were 101LTSC-4 and 101LTSC-10 with three-gene combination (*btbtsh2sh2wxwx*). Meanwhile, all tested waxy corn lines were equipped with common waxy background (*BtBtSh2Sh2wxwx*). These lines were crossed according to North Carolina Design II by assigning sweet corn lines as female and waxy corn lines as male to produce 24 F₁ progenies. These progenies were expected to possess gene combination of both sweet and waxy genes segregated among kernels within an ear. Also, three commercial F₁ hybrids KNW, SW25, and NTT were used as check. These checks belonged to sweet waxy corn hybrids with slightly different proportion of eating quality.

Table 1. Sweet corn and waxy corn inbred lines used as parents.

Name	Phenotype	Genotype	Origin ^a	Climatic zone
Females				
101LBW	Supersweet corn	<i>btbt Sh2Sh2 wxwx</i>	THA	Tropical
101LTSC-4	Supersweet corn	<i>btbt sh2sh2 wxwx</i>	THA/USA	Tropical/Temperate
101LTSC-10	Supersweet corn	<i>btbt sh2sh2 wxwx</i>	THA/USA	Tropical/Temperate
Males				
Y18	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	CHI	Subtropical
C13-1	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	CHI	Subtropical
HNO2	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	CHI	Subtropical
HJ	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	CHI	Subtropical
OWX13	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	THA	Tropical
KVMON	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	THA/USA	Tropical/Temperate
KV3473	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	THA/USA	Tropical/Temperate
KNM102	Waxy corn	<i>BtBt Sh2Sh2 wxwx</i>	THA	Tropical

^a THA = Thailand; USA = United States of America; CHI = China

Experimental design

11 parental lines, 24 F₁ progenies, and 3 checks were assigned in a randomized complete block design (RCBD) with three replications and were evaluated in the dry season 2017/2018 and in the rainy season 2018 at Khon Kaen University (16°28'27.7" N, 102°48'36.5" E; 190 masl), Thailand. Each plot consisted of 2 rows of 5 m long with 75 cm x 25 cm of plant spacing; thus, the plot size was 7.5 m² with 40 plants within the plot. The crop field managements applied in this experiment was according to the Thailand Department of Agriculture.

Sample preparation and chemical analysis

At milk stage or 19-20 days after pollination the green corn ears were harvested for quantifying kernel

carbohydrates namely total sugar, sucrose, glucose, fructose, phytoglycogen, starch content, and amylopectin content. All harvested ears were derived from controlled sib-pollination to guarantee uniform maturity and genetic purity, and about five ears per plot were selected by following some criteria such as non defective ears with full husk cover. Both procedures for sample preparation and chemical analysis followed Simla et al. (2010) with proper modification. Briefly, the samples were trowled and homogenized in a blender. Each sample in a quantity of 1 g was loaded in a micro-tube for extraction of sugars, phytoglycogen, and starch, using different extraction solvents. Three fractions of total sugar namely sucrose, glucose, fructose were analyzed with high performance liquid chromatography (HPLC) method (Shimadzu™ RID

10A reflexive index detector Japan, Water™ Temperate Control Module II Water™, Column Heater Module). Quantification of phytoglycogen was carried out by using phenol-sulfuric colorimetric method with wavelength of 490 nm. Similarly, quantification of amylopectin and total starch was carried out by using the same method with quantification of phytoglycogen except for the absorbed wavelength being 600 nm instead of 490 nm.

Data analysis

The mean squares for male and female parents are independent estimates of GCA male and GCA female effects, respectively, whereas mean square for interaction between male and female is an estimate of SCA effect (Hallauer et al., 2010). The statistical model for combining ability analysis followed Singh and Chaudhary (1985) with proper modification regarding North Carolina II multi-environment in AGD-R User's guide manual (Rodríguez et al., 2018). The proportional contributions of males (GCA_M), females (GCA_F), and their interaction

($SCA_{M \times F}$) to the total sum of squares of hybrid were assumed to determine gene action on targeted traits (Singh and Chaudhary, 1985). Combining ability estimates (GCA and SCA) including their standard errors were calculated following Singh and Chaudhary (1985). Narrow-sense heritability was estimated on the basis of plot means (Holland et al., 2003) and was adjusted to percentage (%) units. The Pearson correlation coefficient (r) was calculated to estimate the relationship between line per se and GCA, and association among kernel carbohydrates (Figure 1). Dendrogram based on hierarchical Ward's clustering method was constructed, derived from a data matrix of 38 genotype means of three attributes namely amylopectin, total sugar, and phytoglycogen as representative criteria associated with consumer preferences for sweet-waxy corn hybrids. Least significant difference (LSD) at $P < 0.05$ was performed to compare each group mean to the respective checks (Gomez and Gomez, 1984).

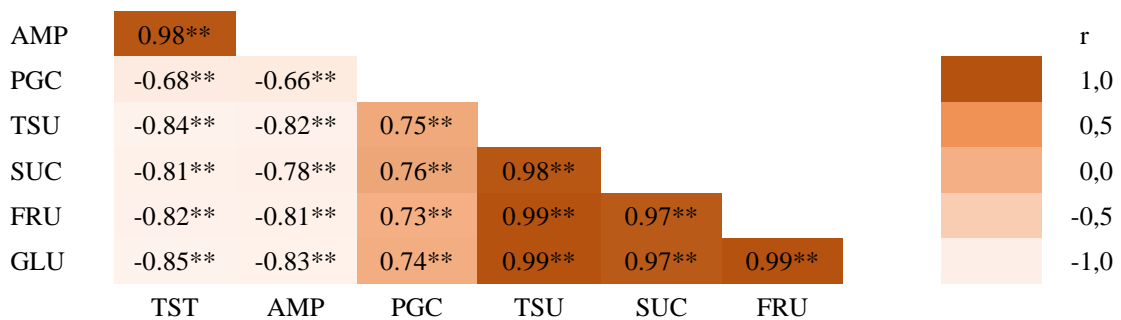


Figure 1. Triangular heat map representing Pearson correlation coefficients (r) among kernel carbohydrate components of sweet and waxy corn genotypes. Means of 38 genotypes (11 parental lines, 24 F1 progenies, and 3 checks) were used as sample size to estimate the correlation. AMP = amylopectin, PGC = phytoglycogen, TSU = total sugar, SUC = sucrose, FRU = fructose, GLU = glucose, TST = total starch. ** level of significance for r value at $P < 0.01$.

The North Carolina II analysis, narrow-sense heritability, and combining ability estimates for all observed traits were computed by using Analysis of Genetic Designs in R (AGD) version 5.0. software (Rodríguez et al., 2018), whereas linear correlation analysis and mean comparison based on LSD's test by using Statistix 10 (Statistix 10, 2013). Dendrogram construction was visualized with JMP Pro software (SAS Institute, 2019).

RESULTS AND DISCUSSION

North Carolina II analysis, gene action, and heritability

North Carolina II multi-season analysis for total sugar (TSU), sucrose (SUC), glucose (GLU), fructose (FRU), phytoglycogen (PHY), total starch (TSA), and amylopectin (AMY) are presented in Table 2. The influence of season was significant for all observed traits except for GLU. GCA of female was significant for all observed traits except for AMY. The effects of hybrid, GCA of male, SCA, interaction between hybrid and

season, and interaction between GCA of female and season were significant for all observed traits. While the interaction between GCA of male and season was significant for all observed traits except for amylopectin, the effect of SCA by season interaction was significant for all traits excluding TSA and AMY.

The significance of hybrid indicated that the genotypic variability on kernel carbohydrates existed, allowing breeders to do selection. In this study, each female has unique recessive allele combination such as *brittle* (*bt*) and *shrunk-2* (*sh2*) affecting composition changing of kernel carbohydrates on segregated F₂ seeds of F₁ plants. The significance of season, H x S, $GCA_F \times S$, $GCA_M \times S$, SCA x S implied that both performances of inbred lines in hybrid formation and F₁ progenies in field trials were obviously influenced by different growing seasons. Previous workers reported the influence of experimental sites differing in soil types and weather conditions on composition changings of both total sugar and the sugar fractions among sweet corn inbred lines with different

endosperm mutations (Azanza et al., 1996b; Wong et al., 1994). Also, two weather profiles namely temperature (Lu et al., 2013) and solar radiation (Yang et al., 2016) were independently reported to affect both starch and amylopectin contents in fresh waxy corn. Thus,

determining the suitable growing season for hybrid seed production and extended field trials emphasizing on carbohydrate composition in fresh kernel of sweet-waxy corn hybrids are encouraged.

Table 2. North Carolina II analysis for kernel carbohydrate components of 24 F₁ progenies evaluated across two seasons between 2017 and 2018

Source	df	Mean squares						
		TSU	SUC	GLU	FRU	PHY	TSA	AMY
Season (S)	1	2,241.1**	940.6**	9.8ns	183.4**	138.3**	238,971.2**	227,799.1**
Hybrids (H)	23	386.1**	13.7**	95.2**	46.6**	3.1**	860.6**	726.9**
GCA _F	2	686.2**	32.0**	182.9**	53.6**	1.1*	2,018.7**	499.1ns
GCA _M	7	633.0**	23.1**	137.8**	84.7**	4.4**	1,225.2**	1,143.4**
SCA	14	219.7**	6.4**	61.3**	26.5**	2.7**	512.9**	551.2*
H × S	23	308.4**	9.0**	81.1**	50.7**	1.5**	628.2**	549.1*
GCA _F × S	2	829.5**	13.5**	172.8**	184.2**	1.1*	1,812.0**	1,260.2*
GCA _M × S	7	272.7**	5.6**	97.0**	35.5**	2.0**	806.0**	627.0ns
SCA × S	14	251.8**	10.0**	60.0**	39.3**	1.3**	370.2ns	408.5ns
Pooled error	92	22.6	0.6	6.7	3.8	0.3	221.1	315.4
%SS GCA _F		15	20	17	10	3	21	6
%SS GCA _M		50	52	44	55	44	43	48
%SS SCA		35	28	39	35	53	36	46
h ² _{ns} (%)		63	61	57	61	19	74	62

TSU total sugar, SUC sucrose, GLU glucose, FRU fructose, PHY phytyglycogen, TSA total starch, AMY amylopectin; df degrees of freedom, GCA_F general combining ability of female parent, GCA_M general combining ability of male parent, SCA specific combining ability, %SS proportional contribution of sum of squares, h²_{ns} narrow-sense heritability; * and ** significant at P < 0.05 and P < 0.01, respectively, ns not significant at P < 0.05.

The effects of GCA and SCA were significant for all observed traits except for AMY (Table 2); however, the proportion of GCA expressed by percentage of sum of squares was greater than that of SCA for all observed traits except for PHY, indicating the predominance of additive gene effect for these traits. This finding corroborated previous reports on sugar components in temperate sweet corn lines (Rosenbrook and Andrew, 1971) and starch properties of pasting viscosity in tropically adapted waxy corn lines (Ketthaisong et al., 2014). Both greater GCA and additive effects on TSU, GLU, SUC, FRU, TSA, and AMY indicated the more favorable alleles (*sh2*, *bt*, and *wx*) shared among parental lines. The absence of additive gene effect for PHY trait was caused by a lack of responsible recessive allele *su1* among parents used. Phytoglycogen (PHY) was greatly accumulated in the corn endosperm containing gene *sugary-1* (*su1*) (Ayers and Creech, 1969; Black et al., 1966). Narrow-sense heritability (h²_{ns}) estimates was moderate (57% - 74%) for all traits of interest except for PHY (19%). The overwhelming additive gene effect with moderate heritability estimates suggested that breeders might obtain rapid breeding values by conducting phenotypic selection at early generations.

General combining ability (GCA) and parental mean

The parental mean and GCA estimates for TSU and the sugar fractions are presented in Table 3, whereas for PHY, TSA, AMY in Table 4. In this study, the selection of sweet and waxy corn lines as parents appealed to consumer preferences on high sweetness, soft tenderness, and stickiness. Favorable sweetness correlated to high TSU, SUC, FRU, and GLU, whereas soft tenderness associated with high PHY. Stickiness was represented by high values of both TSA and AMY. These traits were expressed in both high, positive means and GCA estimates. Two of three female lines, 101LBW and 101LTSC-10, showed overall good general combiners for total sugar and the sugar fractions; however, 101LBW possessed better line per se than the latter. 101LBW had the highest means and positive GCA estimates on TSA (140.0 mg/g; 2.05, P<0.05), SUC (26.3 mg/g; 0.48, P<0.01), GLU (68.1 mg/g; 1.27, P<0.01), and FRU (45.5 mg/g; 0.30, P>0.05). No female with high means and positive GCA estimates for TSA and AMY was noticed. One of eight male lines namely KVMON displayed a good general combiner for TSA (181.6 mg/g; 14.08, P<0.01) and AMY (177.5 mg/g; 14.00, P<0.05). In contrary with female, no male with high means and positive GCA estimates for total sugar and the sugar fractions was revealed. This finding was expected since the female and male corresponded to sweet corn and waxy corn groups, respectively.

Table 3. Parental mean and general combining ability (GCA) estimates for total sugar and the sugar fractions of three sweet corn and eight waxy corn inbred lines evaluated across two seasons between 2017 and 2018

Lines	Total sugar (mg/g)		Sucrose (mg/g)		Glucose (mg/g)		Fructose (mg/g)	
	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA
Females								
101LBW	140.0	2.05*	26.3	0.48**	68.1	1.27*	45.5	0.30ns
101LTSC-4	108.7	-4.36**	17.4	-0.94**	54.7	-2.25**	36.7	-1.17**
101LTSC-10	87.2	2.32*	15.8	0.47**	42.1	0.97*	29.3	0.88*
Males								
Y18	33.8	2.30*	4.2	0.64*	17.2	0.95ns	12.3	0.71ns
C13-1	39.6	8.34**	5.7	1.61**	19.8	4.13**	14.1	2.59**
HNO2	20.3	-9.15**	2.6	-1.51**	10.8	-3.99**	7.0	-3.66**
HJ	39.2	3.46*	3.7	-0.08ns	21.6	2.20*	13.9	1.33*
OWX13	32.1	-6.43**	4.4	-1.35**	16.3	-2.80**	11.5	-2.27**
KVMON	33.1	-4.11*	4.0	-0.49*	16.5	-2.31*	12.5	-1.31*
KV3473	30.2	3.76*	3.6	1.28**	14.7	0.79ns	11.8	1.69*
KNM102	32.7	1.83ns	3.2	-0.10ns	17.5	1.02ns	11.9	0.91ns
LSD 0.05	8.1		1.3		4.7		3.2	
SE female		1.37		0.23		0.75		0.56
SE male		2.24		0.37		1.22		0.91
r	0.09 ns		0.09 ns		0.11 ns		0.09 ns	

LSD least significant difference, SE standard error; LSD 5% is critical value for parental mean; SE male and SE female are assigned as critical value for male and female parents, respectively; ** and * GCA estimates significantly different from zero at $\geq 2SE$ and $\geq SE$, respectively, ns GCA estimates not significantly different from zero at $\geq SE$; ns r not significant at $P < 0.05$.

Table 4. Parental mean and general combining ability (GCA) estimates for phytyloglycogen, total starch, and amylopectin of three sweet corn and eight waxy corn inbred lines evaluated across two seasons between 2017 and 2018

Lines	Phytoglycogen (mg/g)		Total starch (mg/g)		Amylopectin (mg/g)	
	Mean	GCA	Mean	GCA	Mean	GCA
Females						
101LBW	8.7	0.09ns	45.4	-4.86*	38.1	-2.66ns
101LTSC-4	6.4	-0.18*	69.0	7.37*	61.1	3.59ns
101LTSC-10	8.5	0.09ns	68.5	-2.51ns	62.4	-0.92ns
Males						
Y18	4.8	0.47*	157.5	-1.51ns	150.7	-3.34ns
C13-1	4.7	0.57**	145.7	-9.10*	136.6	-9.24*
HNO2	3.6	-0.32*	151.7	-3.46ns	143.4	-0.08ns
HJ	4.8	0.49*	121.9	-11.42*	105.8	-10.51*
OWX13	3.9	-0.44*	132.4	5.66ns	126.3	5.89ns
KVMON	4.1	0.23ns	181.6	14.08**	177.5	14.00*
KV3473	4.1	-0.31*	165.6	1.77ns	153.7	2.54ns
KNM102	4.2	-0.70**	122.2	3.98ns	104.7	0.73ns
LSD 0.05	0.7		12.2		13.5	
SE female		0.15		4.29		5.13
SE male		0.25		7.01		8.37
r	0.21 ns		0.50 ns		0.59 ns	

LSD least significant difference, SE standard error; LSD 5% is critical value for parental mean; SE male and SE female are assigned as critical value for male and female parents, respectively; ** and * GCA estimates significantly different from zero at $\geq 2SE$ and $\geq SE$, respectively, ns GCA estimates not significantly different from zero at $\geq SE$; ns r not significant at $P < 0.05$.

The correlation coefficients (r) between parental mean and GCA estimates were not significant for all observed traits, ranging from poor on TSU (0.09), SUC (0.09), GLU (0.11), FRU (0.09), low on PHY (0.21), and medium on TSA (0.50), and AMY (0.59). This evidence indicated that selection of parental lines based solely on line per se was not recommended especially for sugar contents. For example, in sweet corn lines assigned as female, 101LTSC-4 had higher mean but lower GCA estimates of TSA, SUC, GLU, and FRU than 101LTSC-10. In this

study, none of parental lines used was completely superior for each carbohydrate components. Although recessive allele *wx* has been equipped in all tested sweet corn lines, the expression was masked by either *sh2* or *bt* gene, well known as epistatic effect (Boyer and Hannah, 2001; Creech, 1965). Both 101LBW and 101LTSC-10 could be assigned as broad-based testers for total sugar and the sugar fractions, whereas KVMON for total starch and amylopectin. 101LTSC-10 and KVMON possessed half pedigree from temperate USA, indicating that the use of

exotic germplasm followed by some cycles of recurrent selection could improve the genetic gains of local genotypes.

Trait associations among kernel carbohydrate components

Total starch (TSA) was significantly correlated with AMY ($r = 0.98$, $P < 0.01$). Total sugar (TSU) had strong, positive correlations with GLU ($r = 0.99$, $P < 0.01$), FRU ($r = 0.99$, $P < 0.01$), and SUC ($r = 0.98$, $P < 0.01$). The strong, positive correlations were also noticed among sugar fractions namely between SUC and GLU ($r = 0.97$, $P < 0.01$), SUC and FRU ($r = 0.97$, $P < 0.01$), and FRU and GLU ($r = 0.99$, $P < 0.01$). Phytoglycogen (PHY) was significantly correlated with TSU, GLU, FRU, and SUC with moderate, positive coefficients ranging from 0.73 to 0.75. Both TSA and AMY had significant, negative correlations with TSU, SUC, FRU, and GLU with medium ($r = -0.66$, $P < 0.01$) to high ($r = -0.85$, $P < 0.01$) coefficients.

Our study used sufficient sample size ($n = 38$) to estimate trait linear associations, consisting of normal waxy corn inbreds, supersweet corn inbreds, and sweet-waxy corn hybrids. As the total sugar increased, other sugar fractions like glucose, fructose, and sucrose increased; thus, suggesting breeders to use total sugar as a quantitative parameter in simultaneous selection for sweetness. Glucose, fructose, and sucrose are three of four sugar fractions composing total sugar in corn (King et al., 2017). These sugar fractions are expressed as the effects of different structural genes i.e. *sh1* and *bt* for the respective enzyme activities within the same class mutants in starch biosynthesis pathway (Boyer and Hannah, 2001), explaining the strong, positive correlations among them. Amylopectin mainly constituted about three fourth of normal starch and up to 95% of waxy starch (Ferguson, 2001), revealing a strong, positive correlation between total starch and amylopectin. In carbohydrate synthesis pathway, both *shrunkened* and *brittle* genes grouped in the first mutant class are epistatic to *waxy* gene belonged in the second mutant class (Boyer and Hannah, 2001), addressing the negative correlation between starch (TSA, AMY) and sugars (TSU, GLU, FRU, SUC).

Cluster analysis based on hybrid performance

A dendrogram based on amylopectin, total sugar, and phytoglycogen clustered 38 corn genotypes into seven major groups denoted from group A to G (Figure 2). There was only a sweet corn inbred 101LBW in group A, having the lowest amylopectin and the highest values of both total sugar and phytoglycogen. Group B covered two sweet corn inbreds 101LTSC-4 and 101LTSC-10, having low amylopectin and high values of both sugar and phytoglycogen. Group C comprised four waxy corn inbreds Y18, KV3473, HNO2, and KVMON, having high amylopectin, low total sugar, and moderate

phytoglycogen. Group D consisted of three sweet-waxy corn F₁ progenies 101LTSC-4/Y18, 101LTSC4/OWX13, and 101LTSC-10/KVMON, possessing high amylopectin, moderate total sugar, and high phytoglycogen. There were seven corn genotypes in group E including three waxy corn inbreds (C13-1, OWX13, and HJ), two F₁ progenies (101LTSC-4/HNO2 and 101LTSC-10/HNO2), and a hybrid check KNW. This group had moderate amylopectin, low total sugar, and moderate phytoglycogen. Group F was the largest group with eleven F₁ progenies (101LBW/HNO2, 101LTSC-10/KNM102, 101LBW/KVMON, 101LTSC-4/KVMON, 101LBW/KV3473, 101LBW/KNM102, 101LTSC-10/Y18, 101LBW/OWX13, 101LTSC-4/KV3473, 101LTSC-4/KNM102, 101LTSC-10/OWX13) and a check (NTT), having moderate values of both amylopectin and total sugar and low to poor phytoglycogen. Group G comprising eight F₁ progenies (101LBW/Y18, 101LTSC-10/C13-1, 101LTSC-10/KV3473, 101LBW/HJ, 101LBW/C13-1, 101LTSC-10/HJ, 101LTSC-4/HJ, and 101LTSC-4/C13-1) and a check (SW25) had moderate amylopectin and high values of both total sugar and phytoglycogen.

Hybrid selection was directed to meet consumer preferences on high sweetness, soft tenderness, and stickiness. Since combining both sweetness and stickiness in a single kernel of vegetable corn is impossible due to epistatic effect of gene controlling sweetness (*bt*, *sh2*) over waxy gene (*wx*) (Boyer and Hannah, 2001), the possible way of eating quality improvement is to maximize the proportion of sweet kernels among segregating F₂ kernels of individual F₁ ear (Lertrat and Thongnarin, 2008; Simla et al., 2016). We favored a hybrid group with balance proportions of AMY, TSU, and PHY as high as possible to obtain. Grouping of all corn genotypes in this study based on AMY, TSU, and PHY was reliable since the extreme genotypes either waxy corn inbreds with high AMY or waxy corn inbreds with high TSU and PHY were placed in different major groups. The rest groups (D, E, F, and G) were sweet-waxy corn F₁ progenies, having significantly divergent compositions of AMY, TSU, and PHY (Table 5). Appealing consumer preferences is quite challenging since the parameters of eating quality in vegetable corn are complex that cannot be considered by an attribute alone. Also, three hybrid checks used were clustered in separate groups, indicating preferability of consumers was diverse. Although group G was chosen as representative ideal sweet-waxy corn hybrids due to balance proportions of kernel carbohydrates, other F₁ progenies in group E and F should not be omitted from selection because their performances were similar to the respective checks. Therefore, further investigation of sensory blind test to validate consumer acceptance among sweet-waxy corn tested hybrids is encouraged.

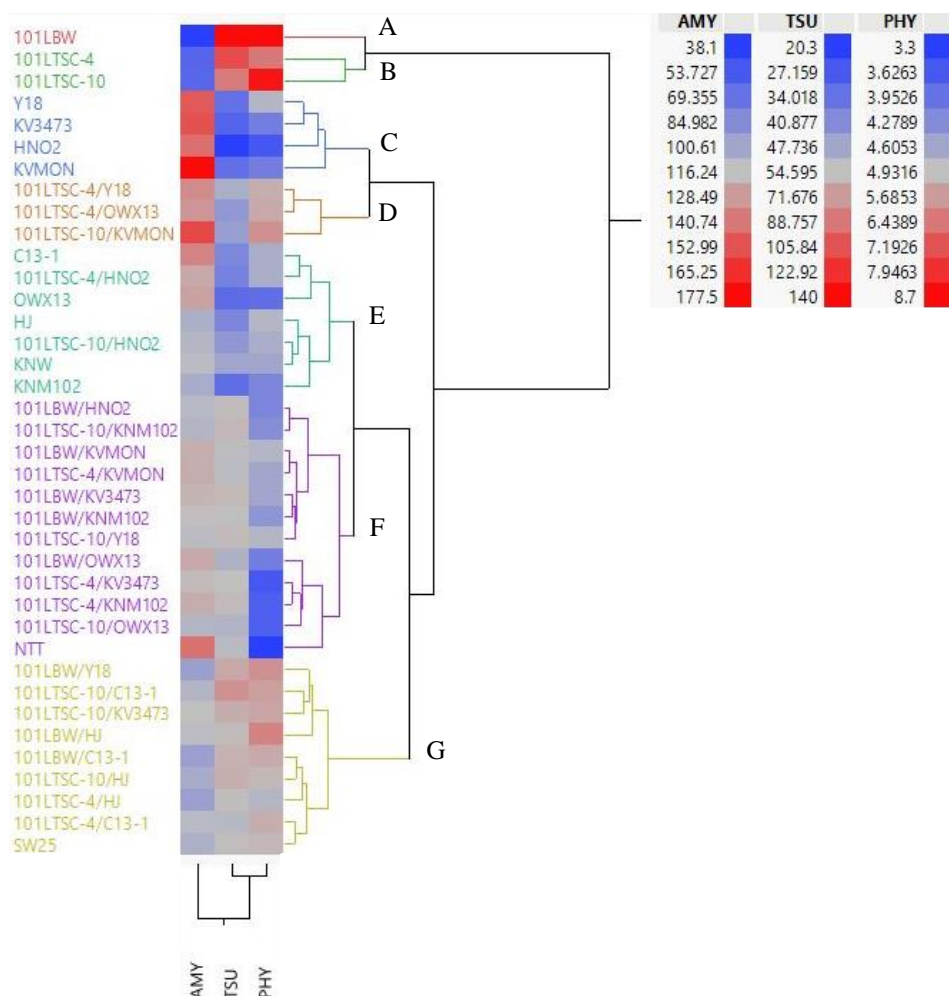


Figure 2. Dendrogram of genetic relationships among 3 sweet corn inbreds, 8 waxy corn inbreds, 24 sweet-waxy corn F1 progenies, and 3 hybrid checks, constructed by hierarchical Ward's clustering method based on amylopectin (AMY), total sugar (TSU), and phytoglycogen (PHY). Different line color represents different major group.

Table 5. Major group means of 24 sweet-waxy corn F1 progenies derived from cluster analysis based on amylopectin, total sugar, and phytoglycogen

Genotypes/Groups	N ^a	Amylopectin (mg/g)	Total sugar (mg/g)	Phytoglycogen (mg/g)
<i>Groups</i>				
D	3	140.23 ± 14.53	46.53 ± 3.13	5.53 ± 0.32
E	2	117.40 ± 10.04	40.80 ± 4.10	4.70 ± 0.00
F	11	117.38 ± 5.39	54.98 ± 2.58	4.25 ± 0.44
G	8	105.94 ± 8.27	61.84 ± 7.40	5.48 ± 0.44
<i>Checks</i>				
KNW		113.20	47.80	4.60
NTT		142.80	53.10	3.30
SW25		106.50	56.10	5.10
^b LSD 5%		22.16	5.44	0.61

^a only sweet-waxy corn F1 progenies are included (the genotype means of parents and checks are omitted from major group means). ^b LSD 5% is critical value to compare each major group mean to the checks.

CONCLUSIONS

Additive gene effect was responsible for total sugar, sugar fractions, total starch, and amylopectin, whereas non-additive gene effects for phytoglycogen of sweet-waxy corn lines. The use of exotic germplasm contributed to better GCA estimates and hybrid performance. We proposed 101LBW and 101LTSC-10 as broad-based

testers for total sugar and the sugar fractions, and KVMON for total starch and amylopectin. Cluster analysis based on amylopectin, total sugar, and phytoglycogen was reliable to discriminate all corn genotypes into seven major groups. Two of eight F1 progenies in group G namely 101LTSC-10/C13-1 and 101LTSC-10/KV3473 were identified as sweet-waxy corn

hybrids with excellent, balance proportion of favored carbohydrate components.

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