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RECIPROCAL CROSS EFFECTS ON AGRONOMIC TRAITS AND HETEROSIS IN SWEET AND WAXY CORN

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SUMMARY

Effect of reciprocal cross is salient information for hybrid testing. Therefore, this study aimed to assess the importance of reciprocal effects, attainable heterosis, and their relationship, emphasizing on agronomic traits, yields, and yield components of sweet-waxy corn F_1 hybrids. 11 parental lines were used comprised of 3 super sweet and 8 waxy corns to generate 48 F_1 progenies using North Carolina II mating scheme. Parental lines, hybrids, and 3 check hybrid varieties were evaluated at the Vegetable Experimental Farm, Khon Kaen University, Thailand in the dry season (2017/2018). Reciprocal cross effect was existed for days to silking, plant height, husked ear length, unhusked yield, and husked yield. Almost all traits exposed quite a small contribution of reciprocal cross advantage, out of which both unhusked and husked yields possessed higher contribution (13.7% or 2.03 ton ha^{-1} and 11.8% or 1.25 ton ha^{-1}, respectively). Reciprocal cross effects significantly impact heterosis (both mid-parent heterosis (MPH) and high-parent heterosis (HPH) for all traits observed as positively strong linear correlation coefficient were revealed. This investigation suggests corn breeders to include reciprocal crosses in their any mating design since it is imperative for high-yielding oriented breeding.

Key words: *Zea mays* L., parental effect, hybrid breeding, hybrid vigour, correlation

Key findings: Reciprocal cross effects study is critical especially if corn breeders faced limit area, time, and labour for generating F_1 hybrid testing in their breeding program. In case, assigning sweet corn inbred lines carrying *sh2* gene as maternal side occasionally experienced poor germination that is unfavorable for commercial hybrid seed production. Reciprocal cross effects gave a small contribution for agronomic traits (plant architecture) suggesting that either non-*sh2* mutant sweet corn or waxy corn inbred lines could be designated as mother parent for hybrid seed production purpose. Meanwhile, the quite significant impact of reciprocals were resided in yields implying corn breeders pursuing that reciprocal crosses are worthwhile for high-yielding oriented breeding.

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INTRODUCTION

Waxy corn is popular due to its stickiness containing high amylopectin in its endosperm (Fergason, 2001) whereas sweet corn possessing high sugar content and tenderness is well-known as well (Tracy, 2001). However, waxy corn normally has several shortcomings such as low yield, agronomic performance, as well as susceptible to environmental stresses. Apart from naturally cross-pollinated crop, hybrid variety is proposed to be a good solution for dealing with these problems due to high hybrid vigour potentially expressed (Hallauer *et al*., 2010; Acquaah, 2012).

Heterosis is the phenomenon in which the hybrid population obtained by the crossing of the two genetically dissimilar gametes or individuals shows increased or decreased vigour over either the better parent or mid-parental value (Rai, 1979). As a rule in maize and sweet corn, breeders intended to attain positive heterosis for plant height (Revilla and Tracy, 1997), ear height (Zhang *et al*., 2017), grain yield (Makumbi *et al*., 2011; Adebayo *et al*., 2017), and other yield components such as ear weight, ear diameter, ear length, ear width, and kernel depth (Dickert and Tracy, 2002; Assunção *et al*., 2010; Solomon *et al*.,2012) and negative heterosis for days to silking, days to anthesis (Wegary *et al*., 2013), and disease incidence and severity (Abera *et al*., 2016). Hence, high heterosis could be utilized as an indicator for assuring that superior hybrids may be achieved.

On the any conventional corn breeding framework, crossing block followed by F_1 hybrid testing is imperative. Corn breeders mostly faced problems constraining their works such as limited labor, area, and cost in an effort to generate full-sib crosses or all possible F_1 hybrid combinations. In this situation, a question is arisen whether they should perform reciprocal crosses in their mating scheme. Since long time ago, reports have been published that inclusion of reciprocal crosses significantly affected agronomic performance in maize such as days to silk, plant height, ear height, and grain yield (Kalsy and Sharma, 1972; Khehra and Bhalla, 1976), pest resistance (Dhliwayo *et al*., 2005), and disease severity (Mukanga *et al*., 2010). Fan *et al*. (2013) found reciprocal cross advantages by identifying additional high grain yield in maize. In contrary, several studies using different maize germplasms and environments concluded that reciprocal effects were not significant for ear resistance to pink stem borer (Butrón *et al*., 1998), grain yield, lodging, and flowering traits (Jumbo and Carena, 2008) and unstable with low magnitude for kernel yield, plant height, and ear height (Pollmer *et al.*, 1979), forage traits (Seitz *et al.*, 1995), and yield (Machida *et al.*, 2010).

In any corn type, in which kernel yield is largely determined by endosperm, reciprocal cross is crucial to understand what impact the inclusion or non-inclusion of it will reside in yields and yield components. Investigation about the reciprocal cross effect on vegetable corns is still limited. Worrajinda *et al.* (2013) recently found that the reciprocal effect gave only a small contribution to total variations for ear number and whole ear weight among super sweet corn genotypes. However, none of the above studies reported on the impact of reciprocal crosses of waxy corn germplasm, focusing on economically important agronomic traits, yields, and yield components. Therefore, the objectives of this study were to (i) assess the importance of reciprocal effects for agronomic traits, yields, and yield components of sweet-waxy corn F_1 hybrids, (ii) estimate attainable heterosis among normal and reciprocal cross F_1 hybrids, and (iii) determine the impact of reciprocal effects on heterosis magnitude. Answering these aims helps corn breeders to enhance breeding efficiency and productivity especially in selecting suitable mating design whether a full-scale testing of reciprocal hybrids is required.

MATERIALS AND METHODS

Plant material

Eleven parental lines were used for this study. These parental lines (Table 1) consisted of 3 and 8 lines of sweet corn and waxy corn, respectively. Briefly, 3 sweet corn inbred lines belong to super sweet group having double recessive genes (*btbt Sh2Sh2wxwx*) and triple recessive genes (*btbtsh2sh2wxwx*). Double recessive genes group, 101 LBW, have good adaptation due to originated from Thailand and perform well in terms of agronomic traits whereas triple recessive genes, 101L/TSC-4 and 101L/TSC-10, show early maturity since these lines derived from combined Thailand and USA germplasm. Additionally, all of these sweet corn inbred lines have white kernels and variation in maturity (early and late). Besides, 8 waxy corn inbred lines belong to a normal waxy group having one recessive gene (*BtBt Sh2Sh2 wxwx*). Furthermore, these waxy corn inbred lines have various kernel colors (monocolor and bicolor) and maturities (early, medium, and late).

Both normal and reciprocal crosses were generated using North Carolina Design II (NCII) mating scheme (Comstock and Robinson, 1948; Hallauer *et al.*, 2010; Acquaah, 2012). Basically, concept of NCII design is crossing each member of the parent group to each member of another one. For normal crosses, the 11 parental lines were divided into two groups, one as female (3 sweet lines) and another as male (8 waxy lines), to obtain 24 F_1 hybrids. For reciprocal cross effects purpose, the same number of crosses were derived with the opposite sex (8 waxy lines as female parents and 3 sweet lines as male parents). Hence, 48 crosses had been accomplished during the rainy season 2017 at the Vegetable Experimental Farm, Khon Kaen University, Thailand. In generating

Table 1. Parental lines used in the study.

Lines	Type	Genotype	Origin	Maturity	Kernel color
101 LBW	Supersweet corn	*btbtSh2Sh2wxwx*	Thailand	Late	White
101 L/TSC-4	Supersweet corn	*btbtsh2sh2wxwx*	Thailand/USA	Early	White
101 L/TSC-10	Supersweet corn	*btbtsh2sh2wxwx*	Thailand/USA	Early	White
YINNUO 18	Waxy corn	*BtBtSh2Sh2wxwx*	China	Medium	White
CAITIANNUO 13-1	Waxy corn	*BtBtSh2Sh2wxwx*	China	Medium	White-purple
HONGYU 2	Waxy corn	*BtBtSh2Sh2wxwx*	China	Medium	White-purple
HJ	Waxy corn	*BtBtSh2Sh2wxwx*	Thailand/China	Late	White
ORANGE WAXY 13	Waxy corn	*BtBtSh2Sh2wxwx*	Thailand	Late	Orange
KV/mon	Waxy corn	*BtBtSh2Sh2wxwx*	Thailand/USA	Early	White
KV/3473	Waxy corn	*BtBtSh2Sh2wxwx*	Thailand/USA	Early	White-yellow
KNM102	Waxy corn	*BtBtSh2Sh2wxwx*	Thailand	Medium	Purple

single cross hybrid, compatible flowering date between male and female parents is imperative. Due to various maturity levels residing our parental lines, staggered planting was conducted for 3 times in each plot to prevent incompatible pollination across different types of maturity level among these parents.

Field experiment

A set of genetic materials (11 parental lines, 48 genotypes, and 3 check varieties) was evaluated at the Vegetable Experimental Farm, Khon Kaen University, Thailand in the dry season (November 2017 – January 2018). A Randomized Complete Block Design (RCBD) with 3 replications was used. Each plot consisted of 2 rows of 5 m in length with a spacing of 0.75 m between rows and 0.25 m between hills, hence the plot size was 7.5 m^2 with 40 plants within the plot.

Crop management

The crop field managements applied in this experiment was according to the Thailand agricultural recommendations including fertilization, irrigation, and pest, disease, and weed control. Land clearing and soil preparation (two times for tillaging and one time for sloping) have been done before planting. Corn was oversown 3-5 seeds per hill and thinned in to 1 plant per hill at two weeks after planting. Fertilizer formula 15-15-15 of NPK was applied at the rate 312.5 kg ha^{-1} before planting and fertilizers formula 46-0-0 at the rate 156.25 kg ha^{-1}were applied twice at 20 and 40 days after planting, respectively. Weeds were controlled by both herbicide and manual weeding at critical periods of crop whereas pest and disease were controlled if only exceeding the economic injury level (EIL). Plants were harvested at R4 growth stage (milking stage with 70% kernel moisture) for each plot without borders.

Data collection

Ten randomly selected plants (5 from each row in a plot in each replication) excluding any plant surrounding a missing hill and border plants were used for observation on agronomic traits according to IBPGR (1991), mainly plant height (cm), from ground level to the base of the tassel after milk stage; and ear height (cm), from ground level to the node bearing the uppermost ear after milk stage. For following traits, plot basis of each experimental unit was performed, such as days to tasseling (DAP), number of days from sowing to when 50% of the plants have shed the pollen; and days to silking (DAP), number of days from sowing to when silks have emerged on 50% of the plants.

Yield and yield component traits were measured after harvest at fresh stage (21 days after pollination). These following traits represented yield components, namely husked ear weight (g), using digital weight without the husk; husked ear diameter (cm), using digital caliper without the husk; and husked ear length (cm), using ruler without the husk. Those of traits were based on ear weight (gram per ear) averaged from the best ten ears for each plot and then converted in to (ton ha^{-1}) unit.

Statistical model and analysis

Error assumption (normality and homogeneity of variances) tests were performed before data analysis. Then, analysis of variance (ANOVA) was computed according to Gomez and Gomez (1983) following this additive linear model:

$$Y_{ij} = \mu + \tau_i + \beta_j + \varepsilon_{ij}$$

where Y_{ij} = response of genotype -i and replication –j, μ = grand mean, τ_i = genotype effect (i = 1, 2, 3, …, 62), β_j= replication effect (j = 1, 2, 3), ε_{ij} = experimental error.

Further, genotype effect was partitioned into reciprocal crosses differences effect by orthogonal contrast (normal vs reciprocal crosses). In case of significant differences detected, paired t-test was carried out to compare the mean difference between normal crosses and reciprocal crosses. This following formula (Bulant *et al.*, 2010) was used for calculating reciprocal crosses advantages (R):

$$\mathbf{R} = \frac{\mathbf{RC - NC}}{\mathbf{NC}} x\ \mathbf{100}$$

where R = reciprocal crosses advantage **(%)**, RC = reciprocal cross mean, NC = normal cross mean.

Both mid-parent heterosis (MPH) and high-parent heterosis (HPH) were calculated using the means of the hybrids and inbred lines. These calculations were performed in both a normal cross hybrid population and a reciprocal cross hybrid population.

Mid Parent Heterosis (MPH)

$$\mathbf{MPH} = \frac{\mathbf{F1 - MP}}{\mathbf{MP}}\ \mathbf{x\ 100}$$

$$\mathbf{MP} = \frac{\mathbf{P1 + P2}}{\mathbf{2}}$$

where F_1 is the mean of the F_1 hybrid performance; P_1 and P_2 are the means of the two inbred parents.

High Parent Heterosis (HPH)

$$\mathbf{HPH} = \frac{\mathbf{F_1 - BP}}{\mathbf{BP}} x\ \mathbf{100}$$

where BP is the mean of the best parent.

Pearson simple linear correlation coefficient was generated to estimate the relationship between hybrid performance, reciprocal crosses advantages (R), and heterosis (MPH and HPH). The range of coefficient from -1 to +1, where – representing negative correlation and + representing positive correlation (Walpole, 1982). Coefficient of determination (R^2) calculated as the square of simple linear correlation coefficient (r) represented the contribution of the linear function of independent variable to the variation in dependent variable (Gomez and Gomez, 1983). The coefficient of variation (CV) was included as the ratio of the standard deviation to the mean. Mean values of each cross combination were compared with LSD (Least Significant Difference)'s test at a 5% level of probability.

RESULTS AND DISCUSSION

Orthogonal linear contrast analysis

Analysis of variance showed genotype factor was highly significant for all traits (Tables 2 and 3). Due to significance, genotype variation was partitioned into parental line vs F_1 hybrid, F_1 hybrid vs check variety, and F_1 normal cross vs F_1 reciprocal cross. Parental line vs F_1 hybrid was highly significant for all traits. F_1 hybrid vs check variety was highly significant for almost all traits excluding husked ear diameter and husked yield. The main focus of this study, F_1 normal cross vs F_1 reciprocal cross, was highly significant for almost all traits except for days to anthesis and husked ear diameter indicating that the reciprocal cross effect was resided among hybrids. In addition, F_1 normal cross vs F_1 reciprocal cross could be partitioned in to normal cross vs reciprocal cross (within tester a), normal cross vs reciprocal cross (within tester b), normal cross vs reciprocal cross (within tester c). Tester a, b, and c were super sweet corn lines (101LBW, 101L/TSC-4, 101L/TSC-10, respectively). Reciprocal cross effects among hybrid combinations within tester 101LBW and tester 101L/TSC-4 were significant for plant height, ear height, unhusked and husked yields whereas not significant for the rest traits observed. Meanwhile, reciprocal cross effect among hybrid combinations within tester 101L/TSC-10 was significant for days to silking, plant height, husked ear length, unhusked and husked yields.

Reciprocal cross advantages

Since the variation of F_1 normal cross vs F_1 reciprocal cross was highly significant for almost all traits, paired student t-test for reciprocal cross mean differences was calculated. Based on this analysis (Tables 4 and 5), there were significant for days to silking, plant height, husked ear length, unhusked yield, and husked yield, whereas not significant for days to anthesis, ear height, and husked ear diameter.The significant difference between normal cross and reciprocal cross depicted that reciprocal effect was existed. Owing to the existing reciprocal effect, hybrid performance for related traits was dependent on the cross direction (Machida *et al.*, 2010). This result confirmed earlier studies of reciprocal cross effect reported by Khehra and Bhalla (1976) and Kalsy and Sharma (1972) on maize crop for plant height, ear height, and days to silking. Principally reciprocal differences are attributable to maternal and non-maternal effects in which maternal effect is caused by cytoplasmic genetic factors, while maternal effect is explained by the interaction between nuclear genes and cytoplasmic gene effects (Evans and Kemicle, 2001). In practical breeding terms, the choice of the female parent in a single cross hybrid may influence agronomic performance and yields in case major contribution of maternal effect instead of non-maternal effect is revealed.

Table 2. Analysis of variance with genotype partitioned by orthogonal linear contrasts for important agronomic traits.

SOV	Df	Mean Square			
		Days to anthesis	Days to silking	Plant height	Ear height
Replication	2	2.26**	2.30**	81.54ns	2.88ns
Genotype	61	46.97***	49.15***	1831.69***	801.49***
Parental line vs F_1 hybrid	1	1150.00***	1417.81***	34409.22***	8940.37***
F_1 hybrid vs Check variety	1	12.23***	7.23***	1962.22***	1316.89***
F_1 normal cross vs reciprocal cross	1	0.84ns	8.51***	2624.94***	204.30**
N_F_1 vs R_F_1 (cross with tester a)	1	0.75ns	0.08ns	2417.69***	405.13***
N_F_1 vs R_F_1 (cross with tester b)	1	0.02ns	0.75ns	660.60***	94.36*
N_F_1 vs R_F_1 (cross with tester c)	1	0.33ns	15.19***	192.32*	25.86ns
Error	122	0.35	0.40	81.54	23.31
CV (%)		1.2	1.3	3.8	6.2

df = degree of freedom; CV = coefficient of variation; N_F_1 vs R_F_1 = F_1 normal cross vs F_1 reciprocal cross; *** = data significant at $P \leq 0.001$; ** = data significant at $P \leq 0.01$; * = data significant at $P \leq 0.05$; ns = data not significant at $P \leq 0.05$.

Table 3. Analysis of variance with genotype partitioned by orthogonal linear contrasts for yields and yield components.

SOV	Df	Mean Square			
		Husked ear length	Husked ear diameter[a]	Unhusked yield	Husked yield
Replication	2	2.80**	48.03**	0.69 ns	0.27ns
Genotype	61	9.28***	415.44***	32.15***	17.08***
Parental line vs F_1 hybrid	1	335.26***	9316.82***	900.50***	477.04***
F_1 hybrid vs Check variety	1	4.15**	29.38ns	9.92***	0.82ns
F_1 normal cross vs reciprocal cross	1	4.31**	0.10ns	147.99***	56.43***
N_F_1 vs R_F_1 (cross with tester a)	1	0.20ns	1.20ns	57.73***	32.03***
N_F_1 vs R_F_1 (cross with tester b)	1	1.30ns	8.80ns	53.83***	19.83***
N_F_1 vs R_F_1 (cross with tester c)	1	4.04*	12.35ns	37.65***	8.40***
Error	122	0.36	9.06	0.62	0.22
CV (%)		3.5	2.0	5.3	4.5

[a] = mean square value x 1000; df = degree of freedom; CV = coefficient of variation; N_F_1 vs R_F_1 = F_1 normal cross vs F_1 reciprocal cross; *** = data significant at $P \leq 0.001$; ** = data significant at $P \leq 0.01$; * = data significant at $P \leq 0.05$; ns = data not significant at $P \leq 0.05$.

Table 4. Reciprocal cross mean differences for important agronomic traits among 48 sweet-waxy corn F_1 hybrids.

	Days after planting		Height (cm)	
	Anthesis	Silking	Plant	Ear
Normal cross mean	47.65	46.94	170.21	79.56
Reciprocal cross mean	47.50	47.43	178.75	81.94
(R-N) difference	-0.15^{ns}	0.49*	8.54**	2.38^{ns}
$\hat{R}$ (%)	-0.32	1.04	5.02	2.99

(R-N) = The difference between reciprocal cross mean and normal cross mean; $\hat{R}$= relative reciprocal cross advantage [(reciprocal cross mean-normal cross mean)/normal cross mean] x 100; ** = data significant at $P \leq 0.01$; * = data significant at $P \leq 0.05$; ns = data not significant at $P \leq 0.05$.

Table 5. Reciprocal cross mean differences for yields and representative yields components among 48 sweet-waxy corn F_1 hybrids.

	cm		Yield (t ha^{-1})	
	Husked ear length	Husked ear diameter	Unhusked	Husked
Normal cross mean	18.12	4.76	14.83	10.57
Reciprocal cross mean	17.77	4.76	16.85	11.82
(R-N) difference	-0.35*	0.00^{ns}	2.03***	1.25***
$\hat{R}$ (%)	-1.91	0.03	13.66	11.83

(R-N) = The difference between reciprocal cross mean and normal cross mean; $\hat{R}$= relative reciprocal cross advantage [(reciprocal cross mean-normal cross mean)/normal cross mean] x 100; *** = data significant at $P \leq 0.001$; * = data significant at $P \leq 0.05$; ns = data not significant at $P \leq 0.05$.

For answering the importance of reciprocal cross effects for agronomic traits, yields, and yield components of sweet-waxy corn F_1 hybrids, relative reciprocal cross advantage was carried out. The relative reciprocal cross advantages were negatively low on days to anthesis and husked ear length, and positively low on days to silking, plant height, ear height, and husked ear diameter. Only on unhusked and husked yields, these values were relatively higher than other traits mentioned before, namely 13.66% and 11.83%, respectively. These negative magnitudes in this study indicate that inclusion of reciprocal crosses tended to accelerate male flower for anthesis and shorten ear length. In contrary, these positive magnitude designates that involving reciprocal crosses was prone to delay female flower for silking, raise plant and ear height, enlarge husked ear diameter, and increase yields.

Emphasizing on yields (Table 5), the average of additional fresh-harvested yield was noticed as much as 2.03 ton ha^{-1}and 1.25 ton ha^{-1} for unhusked and husked yields, respectively. Then, 12 and 10 of 24 hybrid combinations showed the highest difference in unhusked and husked yields, respectively, which are superior to those additional yield means (Figures 1 and 2). Even there were some cross combinations revealing the widest difference as much as 5.21 ton ha^{-1} (101LBW/H.2) and 3.62 ton ha^{-1} (101LBW/C.13-1) for unhusked and husked yields, respectively. This finding was quite surprising since additional yield of 1.00 ton ha^{-1}

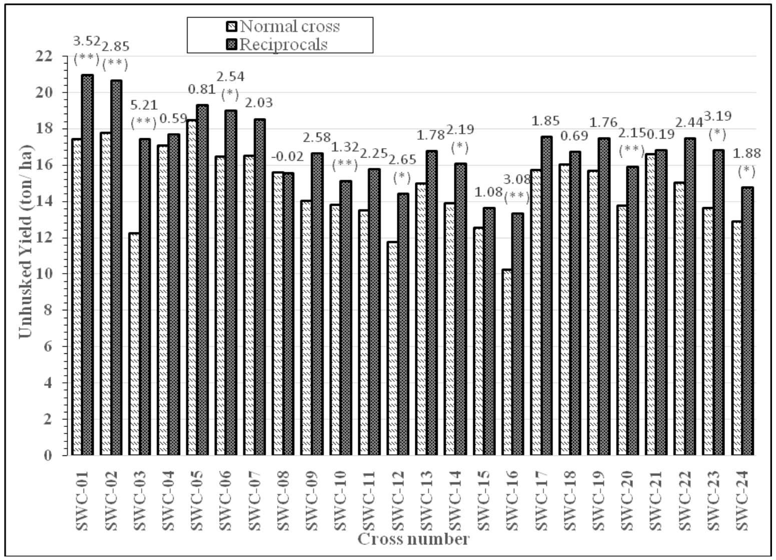

Figure 1. Unhusked yield of 48 sweet waxy corn hybrids deriving from 24 combinations (normal cross and reciprocals). Bar height represents the mean. Upper case number above the bars stands for the difference (reciprocals-normal cross). Significant difference between reciprocal revealed by ** (*P < 0.01*) and * (*P < 0.05*) within parentheses for each combination.SWC-01 : 101LBW x Y.18; SWC-02 : 101LBW x C.13-1; SWC-03 : 101LBW x H.2; SWC-04 : 101LBW x HJ; SWC-05 : 101LBW x OWX.13; SWC-06 : 101LBW x KV/mon; SWC-07 : 101LBW x KV/3473; SWC-08 : 101LBW x KNM102; SWC-09 : 101L/TSC-4 x Y.18; SWC-10 : 101L/TSC-4 x C.13-1; SWC-11 : 101L/TSC-4 x H.2; SWC-12 : 101L/TSC-4 x HJ; SWC-13 : 101L/TSC-4 x OWX.13; SWC-14 : 101L/TSC-4 x KV/mon; SWC-15 : 101L/TSC-4 x KV/3473; SWC-16 : 101L/TSC-4 x KNM102; SWC-17 : 101L/TSC-10 x Y.18; SWC-18 : 101L/TSC-10 x C.13-1; SWC-19 : 101L/TSC-10 x H.2; SWC-20 : 101L/TSC-10 x HJ; SWC-21 : 101L/TSC-10 x OWX.13; SWC-22 : 101L/TSC-10 x KV/mon; SWC-23 : 101L/TSC-10 x KV/3473; SWC-24 : 101L/TSC-10 x KNM102.

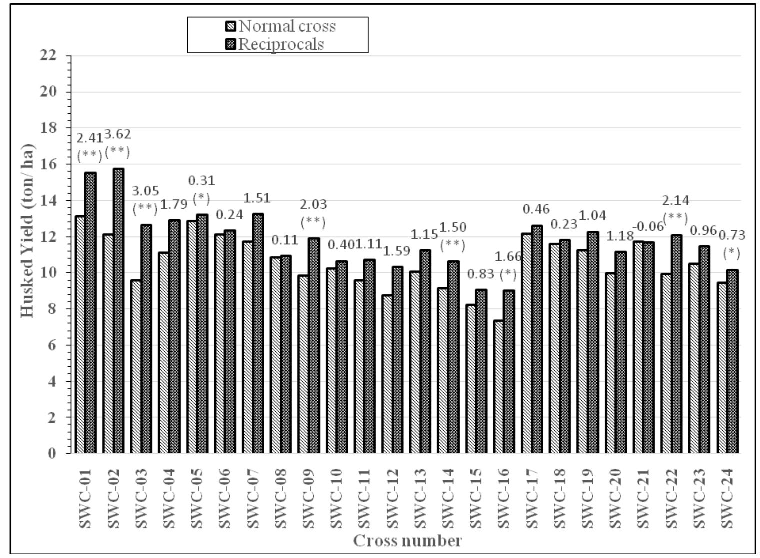

Figure 2. Husked yield of 48 sweet waxy corn hybrids deriving from 24 combinations (normal cross and reciprocals). Bar height represents the mean. Upper case number above the bars stands for the difference (reciprocals-normal cross). Significant difference between reciprocal revealed by ** (*P < 0.01*) and * (*P < 0.05*) within parentheses for each combination.SWC-01 : 101LBW x Y.18; SWC-02 : 101LBW x C.13-1; SWC-03 : 101LBW x H.2; SWC-04 : 101LBW x HJ; SWC-05 : 101LBW x OWX.13; SWC-06 : 101LBW x KV/mon; SWC-07 : 101LBW x KV/3473; SWC-08 : 101LBW x KNM102; SWC-09 : 101L/TSC-4 x Y.18; SWC-10 : 101L/TSC-4 x C.13-1; SWC-11 : 101L/TSC-4 x H.2; SWC-12 : 101L/TSC-4 x HJ; SWC-13 : 101L/TSC-4 x OWX.13; SWC-14 : 101L/TSC-4 x KV/mon; SWC-15 : 101L/TSC-4 x KV/3473; SWC-16 : 101L/TSC-4 x KNM102; SWC-17 : 101L/TSC-10 x Y.18; SWC-18 : 101L/TSC-10 x C.13-1; SWC-19 : 101L/TSC-10 x H.2; SWC-20 : 101L/TSC-10 x HJ; SWC-21 : 101L/TSC-10 x OWX.13; SWC-22 : 101L/TSC-10 x KV/mon; SWC-23 : 101L/TSC-10 x KV/3473; SWC-24 : 101L/TSC-10 x KNM102.

significantly makes an impression on vegetable corn production especially in large scale. In any case, this was comparable to what Ordás *et al.*(2008) found for reciprocal differences study for yield (2.50 ton ha^{-1}) in sugary x sugary enhancer sweet corn hybrids. In agreement with Ordás *et al.* (2008), Fan *et al.* (2013) fortunately noticed the potential superior hybrids in which reciprocal crosses inclusion established additional high grain yield in maize. However, almost all traits excluding unhusked and husked yields exhibited small contribution (15 reciprocals of all possible combinations possessed not significant difference for those traits mentioned as shown in Table 6). Thus, the reciprocal cross effect played a minor role for agronomic traits and yield components among sweet-waxy corn hybrids. Hence, those main findings implied conventional corn breeders that routine testing for reciprocal differences among hybrids is not recommended (Seitz *et al.*, 1995) especially when resources are limited (Machida *et al.*, 2010) since it might be difficult to exploit them commercially (Pollmer *et al.*, 1979).In case of sweet corn hybrid breeding program, several problems occasionally are arisen, two of which are poor germination (especially in *sh2* mutant type) and susceptible to diseases at seedling stage. Hence, information of either insignificant or low reciprocal cross effects can be applied by breeders to designate either the waxy corn or non-*sh2* sweet corn lines as mother parent instead of *sh2* sweet corn lines to achieve better maternal vigour and economically becomes a benefit for sweet-waxy corn hybrid seed production. In addition, this small contribution expectantly could help the breeders in order to collect the data on plant architecture.

Mid-parent heterosis

A wide variation was recognized for the mid-parent heterosis (MPH) percentage prevailing among the observed traits (Table 7), namely plant height (-1.67% to 42.63% in normal cross), ear height (15.17% to 66.60% and 11.76% to 63.04% in normal and reciprocal cross, respectively), unhusked yield (-2.22% to 98.06% and 39.41% to 132.18% in normal and reciprocal cross, respectively), and husked yield (6.19% to 135.45% and 35.00% to 153.51% in normal and reciprocal cross, respectively) of the sweet waxy corn F_1 hybrids. These findings confirmed Solomon *et al.* (2012) suggesting the MPH estimates range was wider for yield and smaller for flowering traits.

Mid-parent heterosis denotes relative performance of a hybrid compared to its parental mean value. In both normal and reciprocal crosses, mean percentage MPH was positive for plant height (26.22%; 32.16%), ear height (37.67%; 41.14%), husked ear length (24.06%; 21.58%), husked ear diameter (12.68%; 12.68%), unhusked yield (51.39%; 72.39%), and husked yield (55.23%; 73.02%) but negative for days to anthesis (-9.57%; -9.86%) and days to silking (-11.74%; -10.81%).The highest mean MPH percentages were derived mostly from yields. Both unhusked and husked yields exposed the highest (72.39% and 73.02%, respectively), whereas flowering traits exhibited the smallest mean estimate, -11.74% for days to silking and -9.86% for days to anthesis.

Reasonable explanation for high heterosis among these sweet waxy corn hybrids was possibly promoted

Table 6. Mean comparison from each combination (normal cross and reciprocals) of 48 sweet waxy corn hybrids for agronomic traits.

Cross	Days after planting		Height (cm)		Husked ear (cm)	
	Anthesis	Silking	Plant	Ear	Length	Diameter
101LBW x Y.18	53.00[a]	52.33[a]	206.55[a]	103.50[a]	19.75[a]	5.08[a]
Y.18 x 101LBW	52.00[a]	52.00[a]	205.73[a]	100.37[a]	18.05[a]	5.18[a]
LSD 5%	1.43	1.43	15.02	11.31	5.23	0.26
CV (%)	0.67	0.78	2.07	3.16	7.87	1.44
101LBW x C.13-1	49.33[a]	48.00[b]	183.75[b]	94.83[a]	19.67[a]	4.98[b]
C.13-1 x 101LBW	50.67[a]	50.33[a]	202.97[a]	101.23[a]	20.48[a]	5.22[a]
LSD 5%	2.87	1.43	10.23	11.06	1.42	0.24
CV (%)	1.63	0.83	1.51	3.21	2.02	1.32
101LBW x H.2	49.33[a]	49.00[a]	149.00[b]	84.50[a]	18.04[a]	4.80[a]
H.2 x 101LBW	48.67[a]	49.67[a]	188.01[a]	96.83[a]	17.94[a]	4.83[a]
LSD 5%	3.79	2.87	9.82	21.63	1.49	0.33
CV (%)	2.20	1.66	1.66	6.79	2.36	1.98
101LBW x HJ	53.00[a]	51.00[a]	205.83[a]	100.67[a]	19.05[a]	4.85[a]
HJ x 101LBW	53.00[a]	51.67[a]	208.88[a]	109.03[a]	18.39[a]	4.82[a]
LSD 5%	2.48	3.79	15.45	10.05	2.64	0.23
CV (%)	1.33	2.10	2.12	2.73	4.02	1.36
101LBW x OWX.13	52.33[a]	52.00[a]	197.50[b]	102.75[b]	18.60[a]	5.09[a]
OWX.13 x 101LBW	51.00[a]	50.33[b]	221.59[a]	116.53[a]	19.11[a]	4.99[a]
LSD 5%	1.43	1.43	10.93	8.36	2.28	0.21
CV (%)	0.79	0.80	1.48	2.17	3.43	1.19
101LBW x KV/mon	46.67[a]	44.67[a]	188.75[a]	83.33[a]	17.65[a]	4.94[a]
KV/mon x 101LBW	46.47[a]	45.00[a]	198.00[a]	89.83[a]	18.55[a]	5.01[a]
LSD 5%	2.48	1.43	15.76	30.15	1.94	0.41
CV (%)	1.52	0.91	2.32	9.91	3.04	2.34
101LBW x KV/3473	48.00[a]	47.00[a]	181.50[b]	86.33[a]	19.07[a]	4.92[a]
KV/3473 x 101LBW	47.33[a]	46.33[a]	190.37[a]	89.33[a]	18.79[a]	4.81[b]
LSD 5%	1.43	1.43	3.39	17.86	3.63	0.07
CV (%)	0.86	0.87	0.52	5.79	5.47	0.38
101LBW x KNM102	50.00[a]	51.67[a]	195.75[a]	93.83[a]	17.63[a]	4.84[a]
KNM102 x 101LBW	50.33[a]	51.00[a]	206.63[a]	93.07[a]	17.13[a]	4.71[a]
LSD 5%	1.43	3.79	30.02	35.35	1.29	0.15
CV (%)	0.81	2.10	4.25	10.77	2.11	0.89
101L/TSC-4 x Y.18	47.67[a]	47.00[a]	180.75[a]	86.25[a]	18.23[a]	4.84[a]
Y.18 x 101L/TSC-4	47.67[a]	47.67[a]	179.93[a]	84.17[a]	17.35[a]	4.90[a]
LSD 5%	2.48	1.43	15.68	3.69	2.00	0.30
CV (%)	1.48	0.86	2.47	1.24	3.20	1.77
101L/TSC-4 x C.13-1	46.00[a]	45.67[a]	150.00[a]	69.17[a]	18.30[a]	4.84[a]
C.13-1 x 101L/TSC-4	47.00[a]	47.00[a]	165.93[a]	67.70[a]	16.97[a]	4.77[a]
LSD 5%	1.43	1.43	30.27	4.59	2.39	0.45
CV (%)	0.12	0.88	5.45	1.91	3.86	2.63
101L/TSC-4 x H.2	47.00[a]	46.33[a]	167.00[a]	75.00[a]	18.67[a]	4.61[a]
H.2 x 101L/TSC-4	46.67[a]	47.00[a]	168.13[a]	81.27[a]	17.48[b]	4.48[a]
LSD 5%	1.43	1.43	26.27	15.93	0.79	0.24
CV (%)	0.87	0.87	4.46	5.80	1.26	1.48
101L/TSC-4 x HJ	49.00[a]	48.00[a]	180.83[a]	73.00[a]	16.90[a]	4.41[b]
HJ x 101L/TSC-4	49.33[a]	48.00[a]	179.03[a]	78.80[a]	16.53[a]	4.51[a]
LSD 5%	1.43	1.43	42.69	15.88	1.56	0.10
CV (%)	0.83	0.18	6.75	5.96	2.65	0.64
101L/TSC-4 x OWX.13	48.00[a]	47.00[a]	182.83[a]	87.33[a]	17.39[a]	4.67[a]
OWX.13 x 101L/TSC-4	47.67[a]	46.00[a]	187.31[a]	90.90[a]	18.06[a]	4.58[a]
LSD 5%	1.43	1.43	39.04	1.98	1.98	0.25
CV (%)	0.85	0.80	6.01	4.90	3.18	1.56

Table 6. (cont'd).

Cross	Days after planting		Height (cm)		Husked ear (cm)	
	Anthesis	Silking	Plant	Ear	Length	Diameter
101L/TSC-4 x KV/mon	44.33[a]	43.33[a]	152.25[a]	64.50[a]	17.00[a]	4.35[b]
KV/mon x 101L/TSC-4	43.00[a]	43.33[a]	169.06[a]	69.80[a]	17.62[a]	4.67[a]
LSD 5%	1.43	1.43	25.49	8.79	0.62	0.26
CV (%)	0.93	0.34	4.52	3.72	1.03	1.65
101L/TSC-4 x KV/3473	44.33[a]	43.00[a]	153.50[a]	64.67[a]	16.77[a]	4.28[a]
KV/3473 x 101L/TSC-4	45.00[a]	44.67[a]	158.50[a]	68.50[a]	17.25[a]	4.28[a]
LSD 5%	1.43	2.87	19.58	12.41	1.11	0.20
CV (%)	0.91	1.86	3.57	5.30	1.86	1.34
101L/TSC-4 x KNM102	45.67[a]	47.67[a]	157.75[a]	70.25[a]	17.61[a]	4.26[a]
KNM102 x 101L/TSC-4	45.33[a]	46.33[a]	176.37[a]	71.47[a]	16.96[a]	4.29[a]
LSD 5%	1.43	1.43	19.74	13.21	2.38	0.17
CV (%)	0.90	0.87	3.36	5.31	1.13	3.13
101L/TSC-10 x Y.18	48.00[a]	47.33[a]	150.50[b]	64.17[a]	18.64[a]	5.18[a]
Y.18 x 101L/TSC-10	48.00[a]	49.33[a]	179.65[a]	74.70[a]	17.33[b]	5.05[a]
LSD 5%	2.48	2.48	15.77	13.45	1.00	0.29
CV (%)	1.47	1.46	2.72	5.51	1.66	6.40
101L/TSC-10 x C.13-1	46.00[a]	45.33[b]	150.17[a]	69.25[a]	18.80[a]	4.99[a]
C.13-1 x 101L/TSC-10	47.00[a]	47.67[a]	155.80[a]	62.73[a]	17.42[a]	4.84[a]
LSD 5%	2.48	1.43	17.88	15.66	2.65	0.45
CV (%)	1.52	0.88	3.33	6.75	4.16	2.62
101L/TSC-10 x H.2	47.00[a]	45.67[a]	158.25[a]	76.00[a]	18.63[a]	4.87[a]
H.2 x 101L/TSC-10	45.00[a]	46.33[a]	150.07[a]	74.60[a]	17.99[a]	4.79[a]
LSD 5%	2.48	1.43	28.52	5.47	0.95	0.45
CV (%)	1.54	0.89	5.27	2.07	1.48	4.04
101L/TSC-10 x HJ	48.00[a]	47.33[a]	163.33[a]	77.33[a]	17.63[a]	4.65[a]
HJ x 101L/TSC-10	48.67[a]	48.33[a]	154.69[a]	72.67[a]	17.12[a]	4.66[a]
LSD 5%	2.87	2.48	32.46	12.47	0.95	0.24
CV (%)	1.69	1.48	5.81	4.73	1.56	1.48
101L/TSC-10 x OWX.13	48.00[a]	47.00[a]	168.25[a]	85.50[a]	18.33[a]	4.99[a]
OWX.13 x 101L/TSC-10	47.67[a]	47.67[a]	176.45[a]	76.90[a]	17.78[a]	4.75[b]
LSD 5%	1.43	1.43	12.37	16.58	1.89	0.19
CV (%)	0.85	0.86	2.04	5.81	2.98	1.10
101L/TSC-10 x KV/mon	44.33[a]	42.33[a]	154.50[a]	63.33[a]	17.65[a]	4.66[a]
KV/mon x 101L/TSC-10	43.00[a]	43.00[a]	160.90[a]	67.70[a]	17.43[a]	4.87[a]
LSD 5%	1.43	1.43	13.34	9.06	1.07	0.38
CV (%)	0.93	0.96	2.41	3.94	1.74	2.25
101L/TSC-10 x KV/3473	44.00[a]	42.33[a]	153.50[a]	67.00[a]	18.30[a]	4.49[a]
KV/3473 x 101L/TSC-10	44.67[a]	43.33[a]	146.97[a]	69.97[a]	18.66[a]	4.70[a]
LSD 5%	1.43	1.43	21.98	16.88	0.49	0.26
CV (%)	0.92	0.67	4.16	7.01	0.75	1.63
101L/TSC-10 x KNM102	44.67[a]	45.67[a]	153.00[a]	67.00[a]	16.47[a]	4.71[a]
KNM102 x 101L/TSC-10	44.67[a]	46.33[a]	159.00[a]	58.57[b]	16.08[a]	4.63[a]
LSD 5%	2.48	1.43	27.14	6.82	2.06	0.27
CV (%)	1.58	0.89	4.95	3.09	3.60	1.66

Means followed by the same letter in the column within each cross do not differ significantly at 5% level of probability according to LSD (Least Significant Difference)'s test; CV (%): coefficient of variation.

Table 7. Mid-parent heterosis of 48 sweet-waxy corn F_1 hybrids derived from normal and reciprocal crosses for agronomic traits, yields, and yield components.

Trait	Cross type	Mid-parent heterosis (%)			CD	
		Mean ± SE	Min.	Max.	5%	1%
Days to anthesis	Normal	-9.57 ± 0.27	-12.13	-6.47	0.55	0.75
	Reciprocal	-9.86 ± 0.28	-12.34	-8.14	0.58	0.79
Days to silking	Normal	-11.74 ± 0.46	-16.72	-8.01	0.95	1.29
	Reciprocal	-10.81 ± 0.37	-14.75	-8.36	0.76	1.03
Plant height	Normal	26.22 ± 2.09	-1.67	42.63	4.32	5.87
	Reciprocal	32.16 ± 1.15	23.91	42.86	2.39	3.24
Ear height	Normal	37.67 ± 3.05	15.17	66.60	6.31	8.56
	Reciprocal	41.14 ± 2.73	11.76	63.04	5.64	7.65
Husked ear length	Normal	24.06 ± 1.86	8.33	47.23	3.86	5.23
	Reciprocal	21.58 ± 1.54	11.45	41.80	3.19	4.33
Husked ear diameter	Normal	12.68 ± 1.26	2.68	29.24	2.60	3.53
	Reciprocal	12.68 ± 1.02	4.75	26.79	2.11	2.87
Unhusked yield	Normal	51.39 ± 4.46	-2.22	98.06	9.22	12.51
	Reciprocal	72.39 ± 4.90	39.41	132.18	10.14	13.76
Husked yield	Normal	55.23 ± 5.94	6.19	135.45	12.29	16.68
	Reciprocal	73.02 ± 5.79	35.00	153.51	11.97	16.24

SE = standard error; CD = critical difference.

by parental lines used in this study had great genetic distance (Revilla and Tracy, 1995) and may have been more inbred than which used in other studies (Revilla and Tracy, 1997). Those values were consistent and comparable to diallel cross study on sweet corn hybrid populations (negatively low MPH for male and female flowering, positively low MPH for the plant and ear height, and positively high MPH for ear weight, ear length and yield) (Assunção *et al.*, 2010). Revilla *et al.* (2006) also reported that days to anthesis and silking possessed negatively low MPH, however, only positively medium MPH for plant height and positively low MPH for ear height, ear length, and yield can be attained. Revilla and Tracy (1997) gave more constricting evidence by positively medium for yield and positively low for plant height and days to silking among open-pollinated sweet corn cultivars.

High-parent heterosis

A broad range was also identified for the high-parent heterosis (HPH) percentage existing among the observed traits (Table 8), namely plant height (-14.13% to 28.92% in normal cross), ear height (-17.10% to 46.46% and -21.39% to 48.99% in normal and reciprocal cross, respectively), unhusked yield (-11.88% to 78.38% and 5.95% to 85.16% in normal and reciprocal cross, respectively), and husked yield (-6.27% to 108.92% and 6.61% to 107.77% in normal and reciprocal cross, respectively) of the hybrids. In both normal and reciprocal crosses, mean percentage HPH was positive for plant height (12.14%; 17.41%), ear height (13.15%; 16.31%), husked ear length (16.67%; 14.32%), husked ear diameter (6.25%; 6.30%), unhusked yield (29.83%; 48.12%), and husked yield (31.69%; 47.01%) but negative for days to anthesis (-2.89%; -3.19%) and days to silking (-5.95%; -4.95%).

Table 8. High-parent heterosis (heterobeltiosis) of 48 sweet-waxy corn F_1 hybrids derived from normal and reciprocal crosses for agronomic traits, yields, and yield components.

Trait	Cross type	High-parent heterosis (%)			CD	
		Mean ± SE	Min.	Max.	5%	1%
Days to anthesis	Normal	-2.89 ± 0.87	-10.30	4.26	1.81	2.46
	Reciprocal	-3.19 ± 0.94	-11.52	4.96	1.94	2.63
Days to silking	Normal	-5.95 ± 0.90	-13.25	1.41	1.86	2.52
	Reciprocal	-4.95 ± 0.90	-13.13	2.07	1.87	2.54
Plant height	Normal	12.14 ± 2.24	-14.13	28.92	4.64	6.30
	Reciprocal	17.41 ± 1.64	2.64	31.98	3.39	4.60
Ear height	Normal	13.15 ± 3.23	-17.10	46.46	6.69	9.08
	Reciprocal	16.31 ± 3.48	-21.39	48.99	7.20	9.76
Husked ear length	Normal	16.67 ± 1.64	1.25	29.67	3.40	4.61
	Reciprocal	14.32 ± 1.24	2.23	25.44	2.57	3.49
Husked ear diameter	Normal	6.25 ± 1.17	-1.98	19.02	2.42	3.29
	Reciprocal	6.30 ± 1.18	-3.72	15.66	2.43	3.30
Unhusked yield	Normal	29.83 ± 4.18	-11.88	78.38	8.64	11.72
	Reciprocal	48.12 ± 4.82	5.95	85.16	9.98	13.54
Husked yield	Normal	31.69 ± 5.49	-6.27	108.92	11.35	15.40
	Reciprocal	47.01 ± 5.50	6.61	107.77	11.38	15.45

SE = standard error; CD = critical difference.

Table 9. Pearson correlation coefficients of reciprocal cross difference and hybrid performance with heterosis for agronomic traits, yields, and yield components among bulked-48 sweet-waxy corn F_1 hybrids.

Trait	Determination coefficient (R^2)			Pearson correlation coefficients (r)			
	R-MPH	R-HPH	MP-F_1	R-MPH	R-HPH	F_1-MPH	F_1-HPH
Days to anthesis	0.99^{**}	0.99^{**}	0.92^{**}	0.99^{**}	0.99^{**}	0.33^{*}	0.02^{ns}
Days to silking	0.99^{**}	0.99^{**}	0.85^{**}	0.99^{**}	0.99^{**}	0.66^{**}	0.20^{ns}
Plant height	0.98^{**}	0.97^{**}	0.71^{**}	0.99^{**}	0.98^{**}	0.08^{ns}	0.24^{ns}
Ear height	0.98^{**}	0.97^{**}	0.77^{**}	0.99^{**}	0.98^{**}	-0.11^{ns}	0.28^{*}
Husked ear length	0.99^{**}	0.99^{**}	0.31^{**}	0.99^{**}	0.99^{**}	0.06^{ns}	0.31^{*}
Husked ear diameter	0.99^{**}	0.99^{**}	0.57^{**}	0.99^{**}	0.99^{**}	-0.07^{ns}	-0.07^{ns}
Unhusked yield	0.85^{**}	0.87^{**}	0.47^{**}	0.92^{**}	0.93^{**}	-0.05^{ns}	0.08^{ns}
Husked yield	0.90^{**}	0.93^{**}	0.46^{**}	0.94^{**}	0.96^{**}	-0.07^{ns}	0.06^{ns}

R = reciprocal cross differences; MPH = mid-parent heterosis; HPH = high-parent heterosis; MP = mid-parent value; F_1 = hybrid performance; ** = data significant at $P \leq 0.01$; * = data significant at $P \leq 0.05$; ns = data not significant at $P \leq 0.05$.

Comparing to MPH mean, HPH showed a significant reduction for all traits observed even higher than 50% for days to anthesis, ear height, and husked ear diameter. However, HPH is well known also as heterobeltiosis (Fonseca and Patterson, 1968) is favoured by plant breeders than MPH since it has more commercial value in hybrid breeding program. Plant breeders (including in corn) are advised to use HPH as practical definition of heterosis, thus representing the real hybrid vigour expression over the better parent (Rai, 1979). Linking to genetic basis at loci level, over-dominance hypothesis is assumed as a responsible explanation for HPH. Acquaah (2012) explained the over-dominance hypothesis in which a heterozygote being superior to the best performing homozygote and that vigor increases in proportion to the amount of heterozygosis at particular loci.

Impacting reciprocal cross on heterosis

Comparing to normal cross hybrids, reciprocal cross hybrids were disposed to possess higher mean MPH percentage of almost all characters excluding the husked ear length, husked ear diameter, and days to anthesis. In the same pattern of MPH, reciprocal cross hybrids were disposed to possess higher mean HPH percentage of almost all characters excluding the husked ear length and days to anthesis comparing to normal cross hybrids. Interestingly, there is significant mean HPH inflation of reciprocal cross to normal cross in unhusked yield.

A shortage previous report of reciprocal cross effects impacting on heterosis in any corn type was arisen. Young and Virmani (1990) studied that topic in rice and reported inconsistent reciprocal cross effects on MPH for agronomic traits such as yield, days of flowering, and plant height. In this study, reciprocal cross effects significantly impact heterosis (both MPH and HPH) for all traits observed as positively strong linear correlation coefficient were detected (Table 9). This result is reasonable since both vegetable corn (sweet and waxy corn) and maize (field corn) are naturally cross-pollinated crops, whereas rice belongs to self-pollinated crop. Thus, as one of the general feature, the phenomenon of heterosis occurs more frequently in a number of naturally cross-pollinated crop species as compared with the self-pollinated ones (Allard, 1960;Rai, 1979).

CONCLUSION

Reciprocal cross effect was significanty revealed for days to silking, plant height, husked ear length, unhusked yield and husked yield. Despite that, almost all traits excluding unhusked and husked yields showed quite small contributions representing the reciprocal cross effect played a minor role for agronomic traits and yield components. However, both unhusked and husked yields possessed higher contribution. Under corn breeder's perspective, small negative contributions have been exposed for days to silking, plant height, and husked ear length. Reciprocal cross effects significantly impact heterosis (both MPH and HPH) for all traits observed as positively strong linear correlation coefficient were revealed. Considering both high heterosis percentage and significant reciprocal effect on yields, superior hybrids were potentially derived from sweet-waxy corn F_1 hybrids tested. This investigation suggests corn breeders to include reciprocal crosses in their any mating design since it is imperative for high-yielding oriented breeding.

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