Gene action, heterosis of agronomic traits and variable resistance to Turcicum leaf blight in sweet corn (*Zea mays saccharata* L.)

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Abstract

Wider ranges of variation were observed for most agronomic traits both in the parents and their F_1 experimental cross combinations of sweet corn. Four hybrids SC sel 3 × SC sel 1, SC sel 2 × SC Synthetic, SC Sel 2 × SC sel 3 and SC sel 2 × MRCSC 9 recorded higher green ear yield than best standard check hybrid which ranged from 12.21 to 12.48 tons per hectare. A substantial amount of heterosis over better parent and standard checks in a favourable direction was observed for all the characters. Against the best standard check Misti, heterosis was observed only in three hybrids for green ear yield (GEY), two hybrids for total soluble solids (TSS) and thirteen hybrids for green fodder weight (GFW). The ear length (EL) and kernel row number (KRN) heterosis maintained significantly positive correlation with heterosis values of different cob characters whose heterosis would uniquely describe the GEY. Thus, if there is a heterosis for EL and KRN, one would expect greater heterosis for GEY. The potence ratio indicated the presence of a high degree of overdominance in most hybrids for all traits studied suggesting the traits under the control of non-additive gene effects. However, the predominance of both partial dominance and overdominance for green fodder weight, ear height and TSS reveal that these traits are governed by both additive and non-additive gene effects.

Abbreviations

BP: better parent
BPH: better parent heterosis
CD: critical difference
°C: degree Celsius
DEW: dehusked ear weight
DFS: days to 50% silking
DFT: days to 50% tasseling
EH: ear height
EL: ear length
EG: ear girth
FAOSTAT: Food and Agriculture organization statistics
GEY: green ear yield
GFW: green fodder weight
IIMR: Indian Institute of Maize Research
KR: kernels per row
KRN: kernel row number
MP: mid-parent
PH: plant height
RBD: randomized block design
SC: standard check
SH: standard heterosis
TLB: *Turcicum* leaf blight
TSS: total soluble solids

Introduction

Maize (*Zea mays* L. 2n=20) is considered as the queen of cereals, cultivated in more than 150 countries. In India, it is extensively grown in Karnataka, Andhra Pradesh, Maharashtra, Bihar, Rajasthan and Madhya Pradesh (Sujay Rakshit 2017). There is an emphasis on diversification of cultivated crops and finding alternative crops as a suitable strategy for the problems faced by the Indian farmers. Among various speciality corns, sweet corn (*Zea mays saccharata* L. 2n=2x=20) is evolving very fast as a vegetable crop and has a very huge market potential in India and the world as well, especially if the processing and packing are taken care of. It is one of the most popular vegetables in United States of America (USA), Europe and other developed countries; cultivated in an area of 1.17 million hectares with a global production and productivity of 11.85 million tons and 9.84 tons per hectare. The USA is the largest producer (4.01 million tons) with 1.95 lakh hectares (FAOSTAT 2019).

Sweet corn is consumed at immature grain stages at 20 days after fertilization. Its flavour is determined largely by sweetness, which in turn affected by the amount of sugar and starch in the endosperm (Tracy 1994; Halluer 2001). The total sugar at milky stage ranges from14-24% (Wahba *et al*.. 2016) compared to 2-5% in normal corn. It contains 14% carbohydrates, 5% dietary fibre, 6% protein, 7% total fat and 4% energy. It is also a good source of vitamin 'C' and 'A' (Lertrat and Pulam 2007). It is differentiated from other maize types by the presence of genes that alters endosperm starch synthesis. There are one or more homozygous recessive endosperm mutations in maize that influence kernel carbohydrate metabolism (Coe and Polaco 1994). Several mutants such as sugary (*su*), sugary 2 (*su2*), shrunken 4(*sh4*), sugary enhancer (*Se*), amylase extender (*ae*), dull (*du*), waxy (*wx*), which confer high sugar content in the endosperm of the immature kernel by increasing sugar content and decreasing starch content (Hannah *et al*.. 1993). Compared to field corn, sugary endosperms accumulates more and highly branched, water-soluble forms of starch known as phytoglycogen which gives a creamy texture to the kernel at harvest.

In the recent past, sweet corn has gained commercial importance and evolving as an important vegetable crop in India due to the change in food consumption pattern of both rural and urban population. The area under cultivation is increasing significantly at a faster rate depicting its high market value. However, very little attention has been received so far in genetic improvement of the crop. Hence, there is a scope and need for developing cultivars with high green ear yield (GEY) and total soluble solids (TSS) that can meet the diverse requirements of direct consumption, processing, the potential utility for extraction of products such as ethanol, and to ensure security to farmers in changing climatic conditions. Development and identification of high yielding hybrids acceptable for farmers and consumers necessitate the expensive task of generation and testing of a large number of experimental hybrids (Betran *et al*. 2003; Solomon *et al*.. 2012). It is more complicated in this crop wherein heterotic patterns are poorly established (Revilla and Tracy 1997). Understanding the relationships among genetic effects, heterosis and hybrids performance will have a direct benefit to the improvement of GEY (Suzukawa *et al*.. 2018). The present study was undertaken to identify the nature and magnitude of different kinds of heterosis and to determine the nature of gene action and dominance effects for agronomic traits.

Materials and methods

Plant materials and experiments set up

Seven inbred lines were selected out of 37 lines based on lower anthesis to silking interval to achieve synchronization of lines. All seven inbred lines were sown during the second fortnight of December 2018 during *rabi /summer* season at Main Agricultural Research Station, University of Agricultural Sciences, Dharwad (22.3597° N, 88.4318° E at an elevation of 678 meter above sea level). Each inbred line was sown in 7 rows of 2 m length. The crossing was performed between all 7 inbred lines in all possible combinations in 7×7 diallel fashion. Simultaneously, each inbred line was selfed to evaluate along with experimental hybrids. The 42 experimental hybrids and their 7 parental lines; and 3checks *viz*., Misti (best national check), Madhuri (popular national check) and Central Maize VL Sweet Corn 1 (station/local check) were grown in a randomized block design (RBD) in three replications during *Kharif* 2019 with a spacing of 60cm × 20cm. Each entry was raised in two rows of 4m length by dibbling two seeds per hill and later thinned to single seedling after 15 days of sowing. The recommended set of practices to raise a good and healthy crop was followed. The average temperature throughout the experimental period ranged 28-35°C maximum and 11-16°C minimum.

Screening of hybrids for reaction to Turcicum leaf blight (TLB) disease

The productivity of corn including sweet corn is less due to biotic stresses such as TLB, Maydis Leaf Blight, Downy mildew, charcoal rot and infestation by stem borer, armyworm and earworms including the new invasive pest fall armyworm (Tippannavar *et al*.. 2019). Among various diseases, TLB caused by *Exserohilum turcicum* reduces the yield significantly. Therefore, to identify a high yielding hybrid with resistance to TLB, a separate set of all hybrids were sown in RBD with two replications and screened their reaction under artificial epiphytotic condition.

Recorded traits

At the pre-flowering stage, five random competitive plants in each entry were tagged in each replication. The observations on days to 50% tasseling (DFT) and days to 50 % silking (DFS), ear height (EH in cm), plant height (PH in cm) were recorded. The reaction of hybrids to TLB was scored as per the standard scale of 1 to 9 (Hooda *et al*.. 2018). The green ears in each hybrid were harvested at 22-23 days after silking to maintain the uniformity among all genotypes; weighed immediately and the total weight was expressed as green ear yield (GEY in tons ha^{-1}). Further, green ears in each entry were dehusked, weighed and the total weight was recorded as de-husked ear weight (DEW in tons ha^{-1}). On the day after the harvest of green ears, green fodder weight (GFW- tons ha^{-1}) in each entry per plot was documented. The total soluble solids (TSS in %) was recorded immediately after harvest from seeds of fresh ear in three selfed cobs in each test entry with the help of hand refractometer. The ear traits such as ear length (EL in cm), ear girth (EG in cm), kernel rows number per ear (KRN) and kernels per row (KR) were documented as per the standard procedures.

Statistical analysis

ANOVA was performed for each trait; heterosis and potence ratio estimations were performed as follows. The heterosis percentages relative to better parents (Heterobeltiosis/better parent heterosis) and standard checks (Standard heterosis) for different traits were estimated using the procedure illustrated by Mather and Jinks (1971) as Better Parent (BPH%) =[(F_1-BP)/BP] × 100 and Standard heterosis (SH%) =[(F_1-SC)/SC] × 100; Where, F_1 is the mean performance of the new hybrid, BP is mean value of the best performing parent in the cross combination and SC is mean of the standard checks. The potence ratio was computed as per the suggestion of Mather (1949) and Smith (1952) to determine the degrees of various dominance effects as $P= \{(F_1-MP)/[0.5(P_2 – P_1)]\}$, Where, P = relative potency of the group of genes, F_1 = hybrid mean of the first generation, P_1 = mean of the low yielding parent, P_2 = mean of the high yielding parent, MP = mean value of the mid parent $(P_1 + P_2)/2$. The estimated potence ratio values equal to +1 indicate complete dominance; values between −1 and +1 indicate partial dominance. Over dominance effect is indicated when the values exceed ±1, and values equal to zero reveals the absence of any kind of dominance. All the positive and negative signs reflect the direction of the dominance of either parent. Further, the correlations of yield using SPSS and heterosis using IndoStat software were computed.

Results

Phenotypic performance

Wider ranges of variation were observed for most agronomic traits both in the parents and their F_1 cross combinations (data not shown). However, the range for TSS was relatively smaller compared to other traits. The realization of good hybrids was significantly different for the majority of traits. The GEY of four cross combinations namely SC sel 3 × SC sel 1, SC sel 2 × SC Synthetic, SC Sel 2 × SC sel 3 and SC sel 2 × MRCSC 9 was better than best standard check Misti as they recorded 12.21, 12.45, 12.46 and 12.48 tons per hectare (Table S1) respectively. Though these crosses documented lesser yield advantage of 1.58 to 3.82% over Misti, they registered a significantly higher yield performance of 27.45 to 30.27% over next best check Central Maize VL sweet corn 1. In light of important yield contributing trait DEW, the hybrid SC sel 2 × SC Synthetic outperformed Misti with 9.34 tons per hectare, while above other three hybrids recorded on par performance. In contrary, hybrid SC Syn × SC Sel 2 recorded good DEW (9.15 tons/ha) though it exhibited lesser GEY (11.82 tons/ha). For the majority of other yield-related cob traits such as EL, EG, KRN and KR the hybrids SC Sel 2 × SC sel 3 and SC sel 2 × SC Synthetic showed on par mean performance with best two standard checks. Concerning the important quality trait, two good hybrids SC Sel 2 × SC sel 3 and SC sel 2 × SC Synthetic recorded on par TSS of 11.15% and 12.23% compared to Misti (12.48%). Furthermore, the hybrid MRCSC9 x SC Sel 2 manifested significantly higher GFW of 14.25 tons per hectare compared to Misti (10.40 tons per hectare) followed by SC Sel 2×MRCSC9 (13.71 tons per hectare). Though none of the new cross combinations showed a resistant reaction to TLB, most were moderate resistant except 4 hybrids which recorded moderate susceptible reaction.

Heterosis

A substantial amount of heterosis over the better parent and standard checks was observed with a diverse degree for all characters and significance was in the direction favourable for the respective trait. The mean BPH percentage across all the traits ranged from -31.2 for TLB to 5.6 for EL (Table 1). For flowering characteristics, the BPH varied from 2 to 13%; for growth traits, it was -6 to 38 for PH and -21 to 87% for EH; for yield attributing traits, it was -8 to 54 for EL, -6 to 33 for EG, -11 to 28 for KRN, -3 to 85 for KR, -37 to 250 for DEW, -38 to 160 for GFW and -19 to 208 for GEY. The range of heterobeltiosis for TSS content of cob, the precious quality characteristic ranged from -18 to 14%. Although the range for TLB was - -54 to 14%, only one hybrid showed BPH.

Lesser number of hybrids expressed heterosis for different traits against standard checks and better parent. The KRN, EL and EH heterosis was observed in >50% hybrids against Misti and better parent as well. In conversely, heterosis over the standard check Misti was observed only in three hybrids for GEY; two hybrids for TSS; and thirteen hybrids for GFW. Withal four F_1 hybrids were identified which recorded heterosis outperforming the commercial checks. Their expressed heterosis over better parent and standard checks is presented in the (Table 2). The hybrids *viz.*, SC sel 2 × MRCSC 9, SC Sel 2 × SC Sel 3, SC sel 2 × SC Synthetic and SC sel 3 × SC sel 1 registered a large magnitude of BPH for GEY and other ear traits. The commercial heterosis of these hybrids for KRN and GEY over Misti was positive significant. Besides, these hybrids displayed desirable negative heterosis for DFT and DFS. In addition, the heterosis values showed an improvement in resistance of these crosses to TLB over the checks.

Correlation

Network visualization of the correlation between BPH and commercial heterosis for distinct traits revealed several trends. The commercial heterosis for EL, EG, KRN, KR, and DEW including TSS were associated with GEY (Table 3). Indistinguishably, the better parent heterosis for EG, KRN and DEW were positive significantly correlated with GEY; EL and KR showed positive but non-significant association with GEY. However, TSS exhibited a negative correlation with GEY. The heterosis of EL and KRN held a strongly positive correlation with the heterosis characteristics of various cob characters. The outperforming F_1 cross combinations SC sel 2 × SC sel 3 and SC sel 2 × SC Synthetic continued to maintain high better parent and standard heterosis (Central Maize VL Sweet corn 1) for EL and KRN (Table 2).

Potence ratio

The estimates of potence ratio indicated the presence of varying degrees of dominance effects for different traits of F_1 hybrids. It was evident that most traits however controlled by overdominance gene action, followed by partial dominance. Infrequent regulation of traits by complete dominance and no-dominance gene action was also observed. GEY for all 42 crosses exhibited dominance gene effects with potence ratio for 19 crosses each greater than 1.0 but both in the positive and negative directions (Figure 1, Table S2). Thirty-eight crosses manifested overdominance, whereas four crosses showed partial dominance with potence ratio between +1.0. Similar patterns have been observed for traits such as DFT, DFS, PH, EL, EG, KRN, KR, DEW, and resistance to TLB where twenty-nine (GFW) to forty (EL) hybrids exhibited overdominance. Moreover, it was interesting to note that the direction of potence ratio in all these traits was both in negative and positive directions in almost equal proportions (Figure 2, Table S3). Conversely, three traits *viz.*, GFW, EH and TSS registered partial dominance in more than 10 hybrids ranging from eleven to sixteen F_1 hybrids and overdominance in twenty-five to twenty-nine hybrids, respectively. Potence ratio of +1.0 was observed in few crosses *viz.*, SC Sel 3 × SC Sel 2 and SC Ind × SC Sel 2 for DFT; SC Sel 1 × SC Sel 2 for DFS; MRCSC 9 × SC Ind for KRN and SC Syn × SC Sel 1 for resistance to TLB. Not often, for all traits other than EL, EG, DEW, GFW and GEY no dominance gene action was observed where only one to five F_1 hybrids recorded zero potence ratios

Table 1 - Mean and range values of per cent heterobeltiosis and standard heterosis with frequencies of F_1 hybrids for 13 traits

Traits	Heterobeltiosis			Standard heterosis					
				Central Maize VL Sweet Corn 1			Misti		
	Mean	Range	F1	Mean	Range	F1	Mean	Range	F1
DFT	-8.2	-12 to -4	4	0.8	1 to 16	38	-1.8	-7 to 8	8
DFS	-7.6	-13 to 2	5	2.7	1 to 14	37	-0.1	-5 to 8	10
PH	1.8	-6 to 38	28	4.8	-7 to 26	20	1.9	-12 to 19	7
EH	-7.3	-21 to 87	26	71.3	17 to 131	42	-1.2	-30 to 49	26
EL	5.6	-8 to 54	31	-7.7	-20 to 16	12	-13.6	-28 to 5	23
EG	-3.7	-6 to 33	32	-2.2	-13 to 8	18	-4.5	-17 to 4	7
KRN	-3.7	-11 to 28	29	-5.2	-19 to 10	4	-1.7	-13 to 19	24
KR	-2.8	-3 to 85	41	-6.2	-19 to 24	21	-11.0	-27 to 12	4
DEW	-15.5	-37 to 250	38	-16.0	-45 to 26	13	-25.5	-56 to -1	0
TSS	-7.7	-18 to 14	4	-8.2	-21 to 9	9	-10.3	-24 to 4	2
GFW	-11.0	-38 to 160	31	42.5	-9 to 108	39	-6.3	-40 to 37	13
TLB	-31.2	-54 to 14	1	54.0	16 to 112	42	-6.7	-15 to 55	28
GEY	-3.3	-19 to 208	37	-9.8	-35 to 30	18	-20.4	-48 to 4	3

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, DEW-dehusked ear weight, TSS-total soluble solids ,GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield

Discussion

Per se performance

The presence of divergence and genetic variation among the genotypes has been evidenced by considerable difference between the values of most traits. The high degree of range values for each trait revealed the plenitude of variability which can be substantiated by the report of Ghosh *et al.* (2018). The existence of low TSS range among the parents as well as hybrids studied reflected limited genetic variability for this trait. The lower superiority of GEY of top four hybrids over Misti suggests the need for use of more genetically divergent parents than presently used in this study for better realization higher hybrid vigor. Although the hybrid SC Syn × SC Sel 2 produced lesser GEY, its DEW was second-best among the test hybrids demonstrating the compensating mechanism in operation in consistent with prior observations from Zarei *et al.* (2012) and Kumar *et al.* (2017). The enhanced general performance of the hybrids SC Sel 2 × SC sel 3 and SC sel 2 × SC Synthetic in line with the top two best checks for most of the yield contributing cob traits EL, EG, KRN, KR demonstrated the significant contribution of these traits in enhancing GEY. The on par TSS content of these hybrids with the check along with high yield is much desired; such hybrids would be preferred by end-users and will have high market potential.

Apart from GEY and TSS, identification of hybrids with resistance to TLB and high GFW are important traits to be considered. The green fodder ensures additional income to the farmer whereas the resistance to TLB helps to realize the good yield with lesser or no disease incidence in the crop. The hybrids SC Sel 2×SC Syn and SC Sel 2×SC Sel 3 exhibited moderate resistance reaction to TLB. Due to far excess rainfall during the evaluation season, the weather was very congenial for TLB; the disease severity was pronounced. The documentation of moderate reaction in most of the hybrids in such situation indicates the true resistance of these hybrids wherein the chances of escape to the disease is practically less.

Heterosis

Utilization of heterosis is critical in maize breeding for boosting grain yield (Yi *et al.* 2019). It is evident from the study that the exploitation of heterosis in any hybrid was dependent on the direction of heterosis favourable for traits considered. BPH directly reflects the superiority of hybrids over comparable line cultivars (Barth *et al.*. 2003; Li *et al.*, 2018). The nature and extent of heterobeltiosis assists in the discovery and processing of successful cross combinations. The analysis of heterosis for several agronomic traits revealed that sweet corn hybrids exhibit the BPH for almost all the traits. These results are analogous to the previous observations (Amanullah, 2011; Ali *et al.* 2012; Rajeev Kumar *et al.*. 2013). The economic heterosis varied substantially for different traits. The manifestation of positive commercial heterosis for KRN and negative for few other ear traits by the outperforming hybrids revealed that negative heterotic expression for some cob characters is countered by positive heterosis of some observed characters, resulting in no ultimate loss in green ear yield.

Table 2 - Percent heterosis of selected hybrids against better parent and standard checks

Traits	Heterobeltiosis				Standard heterosis							
					SC Sel 2 × MRCSC9		SC Sel 2 × SC Sel 3		SC Sel 2 × SC Syn		SC Sel 3 × SC Sel 1	
	SC Sel 2 × MRCSC9	SC Sel 2 × SC Sel 3	SC Sel 2 × SC Syn	SC Sel 3 × SC Sel 1	Misti	Central Maize VL Sweet Corn 1	Misti	Central Maize VL Sweet Corn 1	Misti	Central Maize VL Sweet Corn 1	Misti	Central Maize VL Sweet Corn 1
DFT	-13.13	-8.06	-10.16	-8.51	-2.82	4.87**	-3.38	4.26**	-5.08	2.43**	-2.82	4.87**
DFS	-12.14	-8.63	-8.04	-7.61	-1.09	4.62**	-1.63	4.04*	0.01	5.78**	-0.54	5.20**
PH	15.76**	38.39**	24.10**	8.13*	2.05	7.92	5.60	11.67**	4.25	10.25**	6.67	12.81**
EH	-3.77	7.54**	- 6.90	3.06*	0.01	54.54**	11.76**	72.72**	5.88**	63.63**	9.80**	69.69**
EL	23.54**	35.89**	35.27**	42.47**	-15.65	-6.44	-7.21	2.91**	-7.64	2.44**	-4.46	5.96**
EG	28.27	15.26	7.71	7.63	0.72	4.20	0.95	4.44	-3.34	0.00	-5.72	-2.47
KRN	13.79**	12.06**	15.51**	12.5**	6.45**	-1.49	4.83**	-2.98	8.06**	0.00	1.61	-5.97
KR	52.7**	84.57**	53.08**	49.51**	-7.25	2.67**	12.08**	24.08**	-2.41	8.02**	-6.04	4.01**
TSS	-4.40	-12.20	6.07**	-4.33	-12.82	-8.80	-10.62	-6.49	-2.00	2.51**	-2.60	1.88*
DEW	249.54**	127.09**	202.93**	96.35**	-3.01	21.75**	0.32	25.95**	-2.83	21.97**	-13.25	8.90**
GFW	101.22**	49.21**	67.36**	72.03**	31.86**	100.60**	-4.40	45.42**	7.21**	63.10**	13.42	72.56
TLB	-37.43	-28.68	-37.43	-28.87	15.41**	57.97**	31.56**	80.07**	15.41**	57.97**	10.31**	51.00**
GEY	158.96**	143.14**	208.10**	138.23**	3.81**	30.26**	3.65**	30.06**	3.58**	29.97**	1.55	27.44**

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, TSS-total soluble solids, DEW-dehusked ear weight, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield

Table 3 - Association between heterosis values of better parent and best standard check (Misti) for green ear yield and its component traits

Traits	DFT	DFS	PH	EH	EL	EG	KRN	KR	DEW	TSS	GEY	GFW
DFT	1.00	0.34*	-0.07	-0.10	-0.09	-1.00	-0.18	0.29	-0.29	-0.22	-0.05	0.03
DFS	0.64*	1.00	-0.12	-0.21	-0.19	-0.60	-0.30	0.09	-0.31	-0.15	-0.19	-0.13
PH	0.51*	0.42*	1.00	0.55*	0.78*	0.29	0.99*	0.36*	0.71*	0.71*	0.73*	0.38*
EH	-0.64	-0.64	-0.14	1.00	-0.42	0.02	-0.45	-0.14	-0.28	-0.34	-0.25	0.34*
EL	0.40*	0.03	0.59*	0.16	1.00	0.53*	0.99*	0.51*	0.61*	0.83*	0.70*	0.08
EG	-0.69	-0.50	-0.03	-0.09	0.50*	1.00	0.84*	0.27	0.94*	0.78*	0.66*	0.33*
KRN	-0.69	-0.75	-0.23	0.09	0.92*	0.20	1.00	0.02	0.34*	0.30*	0.48*	0.27
KR	-0.24	-0.05	-0.31	-0.02	0.22	-0.26	0.18	1.00	0.97*	0.97*	0.97*	0.11
TSS	-0.61	-0.71	-0.42	-0.04	0.41*	0.37*	0.48*	0.81*	1.00	0.48*	0.33*	0.02
DEW	-0.48	-0.58	-0.47	-0.07	0.12	0.40*	0.49*	0.54*	0.26	1.00	0.95*	0.55*
GEY	0.05	-0.15	0.47*	0.37*	0.05	0.52*	0.46*	0.12	0.95*	-0.01	1.00	0.50*
GFW	-0.4	-0.1	-0.3	-0.2	0.2	-0.6	0.1	0.1	-0.3	0.38*	-0.2	1.00

Note: Correlation values: Upper diagonal- Standard check (Misti), Lower diagonal- Better parent, *. Significant at 0.05 level, DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, TSS-total soluble solids, DEW-dehusked ear weight, GEY-green ear yield, GFW-green fodder weight.

The positive significant heterosis for EH of best hybrids was also previously observed (Alam *et al.* 2008; Patil *et al.* 2017). Negative heterosis by these hybrids for flowering traits is desirable as they have gene combinations that enhance early maturity (Gissa *et al.* 2007). Disease resistance allows end-users to grow a profitable crop. Problems arising from the use of pesticides have forced farmers to find an alternative ecological approach to control disease (Pandiarana *et al.* 2015). Genetic resistance is considered as an important and successful component of integrated disease management as it is relatively inexpensive, biologically safe and convenient for cultivators; the high heterotic resistant hybrids reduce the yield loss and stabilize the farmers' income.

Correlation

It was further confirmed from correlation analysis that heterosis for ear traits was significantly and positively correlated with heterosis for GEY. The strong positive correlation of EL and KRN heterosis with important cob traits illustrate that their heterosis would uniquely describe the GEY in green corn which was in agreement with the work of Sadaiah *et al.* (2013). Thus, if there is heterosis for EL and KRN, one would expect greater

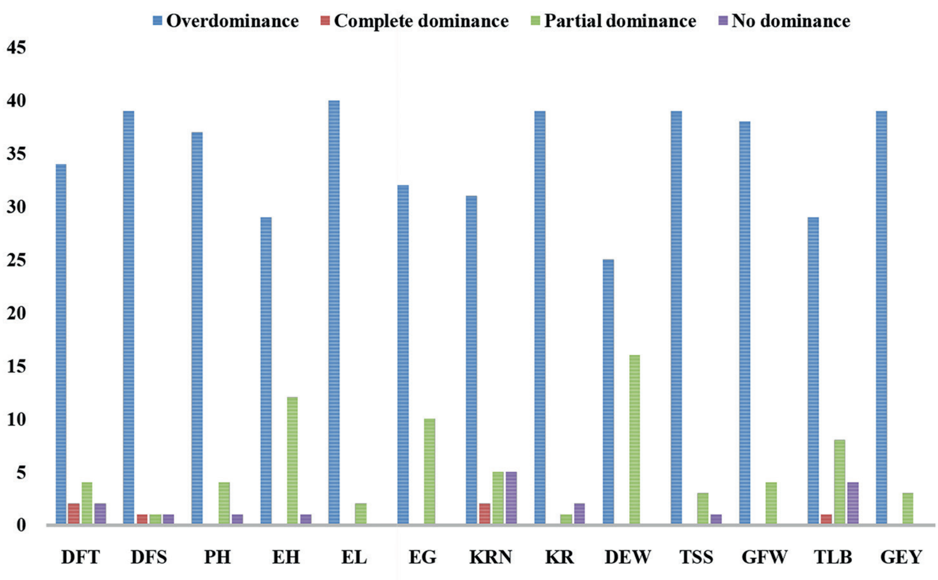

Fig. 1 - Number of hybrids showing different type of gene effects for different traits

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, DEW-dehusked ear weight, TSS-total soluble solids, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield heterosis for GEY. The manifestation of a high better parent and commercial heterosis (Central Maize VL Sweet corn 1) for EL and KRN traits by outperforming F_1 hybrids SC sel 2 × SC sel 3 and SC sel 2 × SC Synthetic reveal the fact that GEY heterosis can be predicted based on these traits. It was also substantially reported by earlier workers that GEY is influenced by many cob characters (Jayakumar and Sundaram 2007; Ghosh et al 2014) and breeding for these traits enhances the GEY. The low level of correlation of TSS with GEY could potentially be a result of low correlation for the hybrid performance, the better parent performance or both.

Potence ratio and gene action

High heterosis is known to be a result of the effects of non-additive genes. Potence ratios can be used to suggest the dominance of inherited traits (Pandiarana *et al.* 2015). In this study, the presence of all four kinds of dominance effects for different traits of F_1 hybrids was indicated by potence ratio. The degree of dominance ranging from partial to overdominance is specified by positive values of ratio and degree of recessiveness ranging from partial to under dominance by negative values of ratios (Solieman *et al.* 2013). The manifestation of dominance gene effects in 38 out of 42 hybrids for green ear yield with potence ratio more than 1.0 indicated that inheritance of trait was exclusively due to over dominance. Further, an exhibition of gene effects in these 19 out of these 38 hybrids negative directions indicates that this direction may camouflage the breeder in the selection of genotypes. These results corroborate with similar findings in green corn for ear yield (Jelena *et al.* 2011). The four crosses that showed partial dominance with potence ratio between +1.0 indicated the importance of non-additive gene action in the inheritance of GEY in those hybrids which were earlier reported by Sadiah et al (2014) in few F_1 hybrids. Analogously, in all other traits except GFW, EH and TSS prevalence of overdominance highlighted the significance of non-additive gene action in the inheritance of above traits which can be supported by earlier observations of Jelena et al (2011), Elayraja et al (2014) in green corn, El-Badawy (2012) and Ghosh et al (2018) in maize where they also noticed over dominance in the inheritance of these traits. The documentation of partial dominance in more than 10 hybrids in GFW, EH and TSS indicated that these traits are under the control of both partial and overdominance gene effects. Combining productivity with acceptable visual ear traits and eating quality requires the prevalence of genetic varia-

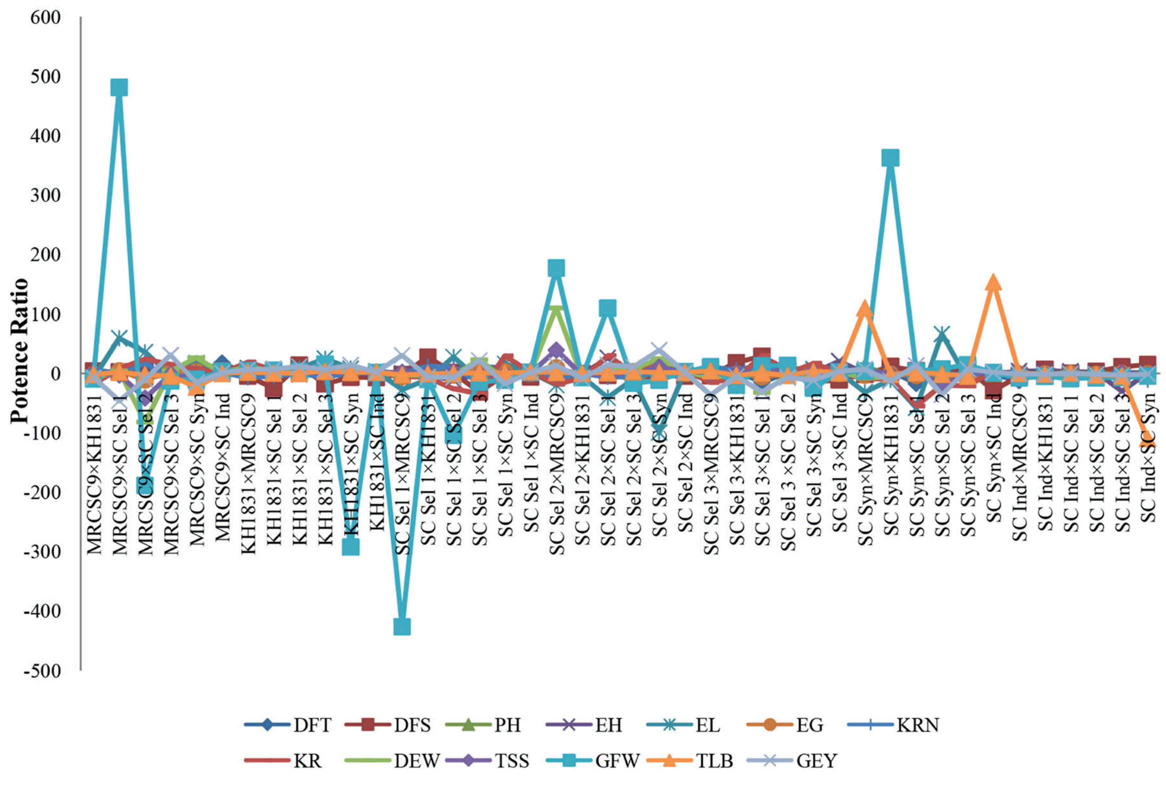

Fig. 2 - Potence ratio of different traits for 42 F1 experimental hybrids

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, DEW-dehusked ear weight, TSS-total soluble solids, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield bility and knowledge of genetic trait regulation. The contribution of additive genetic effect was small in the expression of TSS which corroborate with the findings for this trait (Solomon *et al*. 2012). The influence of both additive and non-additive gene effects was observed in two different crosses in green corn (Wahba *et al.* 2015). The findings are following Solieman (2009) where it was observed that the number of fruits per plant in tomato was governed by partial dominance. Yi *et al* .(2019) detected the display of additive effects for the traits which showed low or no significant dominance. The presence of exactly +1.0 potence ratio in SC Sel 3 × SC Sel 2 and SC Ind × SC Sel 2 for DFT; SC Sel 1 × SC Sel 2 for DFS; MRCSC 9 × SC Ind for KRN and SC Syn × SC Sel 1 for resistance to TLB indicate that these traits were controlled by complete dominance gene action in these five hybrids.

From the above discussion, a few important trends in the inheritance pattern of different traits emerge. All hybrids recorded a high degree of overdominance for almost traits studied. Except for green fodder weight, ear height and TSS, all traits showed the predominance of overdominance in more than 80 per cent hybrids. According to Russell et al (1978), the average degree of dominance would decrease and most loci contributing to heterosis would likely to be coupled with repulsion phage linkage with partial dominance. Ghosh et al (2018) also observed for traits like TSS. The estimate of positive or negative potence ratio with >1.0 value is the indication of the prevalence of overdominance in desirable direction and importance of overdominance for expression of heterosis in a majority of hybrids for maximum traits becomes apparent and hybrid development can be carried out in green corn.

Conclusions

It could be concluded from the results that a particular hybrid cannot perform better for all the desirable traits. The direction of heterosis was trait dependent and desirable BPH, as well as superiority over the checks, were observed among the tested crosses. The heterosis for EL was positively associated with heterosis for GEY suggesting that it is an important trait to be considered while breeding for higher GEY in green corn Potence ratio indicated the presence of a high degree of overdominance in most hybrids for all traits studied indicating the traits under the control of non-additive gene effects. However, a predominance of both partial dominance and overdominance for GFW, EH and TSS indicates that these traits are governed by both additive and non-additive gene effects. We were able to identify two promising hybrids SC sel 3 × SC sel 1, SC sel 2 × SC Synthetic based on mean performance, heterosis for GEY along with high TSS apart from moderate resistance to TLB. Further, this information could be used to identify good general and specific combiners for the genetic improvement of such characters.

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Conflict of Interest

All the authors declare that they have no conflict of interest to the manuscript content.

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Table S 1 - Phenotypic performance of top 10 yielding hybrids with commercial checks

Sl. No.	Hybrids	DFT	DFS	PH	EH	EL	EG	KRN	KR	TSS	DEW	GFW	TLB	GEY
1	SC Sel 2×MRCSC9	57.3	60.3	126.33	51	15.33	4.69	14.7	34.11	10.88	9.03	13.71	48.19	12.48
2	SC Sel 2×SC Sel 3	57.0	60.0	130.73	57	16.87	4.70	14.4	41.22	11.15	9.34	9.94	54.93	12.46
3	SC Sel 2×SC Syn	56.0	61.0	129.07	54	16.79	4.50	14.9	35.89	12.23	9.04	11.15	48.19	12.45
4	SC Sel 3×SC Sel 1	57.3	60.7	132.07	56	17.37	4.39	14.0	34.56	12.15	8.07	11.79	46.06	12.21
5	SC Syn×SC Sel 2	57.3	62.0	121.87	60	15.29	4.57	14.4	33.78	12.95	9.15	11.42	46.06	11.82
6	SC Sel 2×SC Sel 1	59.0	63.3	138.47	71	16.86	4.23	14.0	34.44	11.68	8.75	10.88	41.81	11.69
7	SC Sel 3×SC Ind	58.3	60.7	120.13	53	15.72	4.36	15.3	30.44	11.45	9.06	11.14	54.93	11.57
8	SC Ind×SC Sel 3	60.7	60.7	130.53	63	15.57	4.37	13.6	31.67	12.23	8.52	13.25	37.45	11.52
9	KH1831×SC Syn	56.7	61.3	123.53	52.33	17	4.54	15.1	37.22	12.10	7.79	9.06	48.19	11.41
10	SC Sel 3×SC Syn	60.0	61.3	124.33	52.33	15.03	4.33	14.7	32.22	10.93	8.38	11.13	43.94	11.01
Grand Mean	58.70	61.71	128.45	56.53	15.79	4.46	14.3	33.32	11.29	6.97	9.78	47.00	9.82	
Mean of top 10 hybrids	57.96	61.13	127.70	56.97	16.18	4.47	14.5	34.55	11.78	8.71	11.35	46.97	11.86	
Checks														
1	Misti	59.0	61.0	123.80	51.00	18.18	4.66	13.8	36.78	12.48	9.31	10.40	41.75	12.02
2	Central Maize VL Sweet Corn 1	54.6	57.7	117.07	33.00	16.39	4.50	14.9	33.22	11.93	7.41	6.83	30.51	9.58
3	Madhuri	56.0	59.3	124.80	48.00	15.36	4.09	13.1	32.33	11.60	3.97	3.42	39.63	7.41
Mean of checks	56.5	59.3	121.89	44.00	16.64	4.42	13.93	34.11	12.00	6.90	6.88	37.30	9.67	
	Yield Improvement													
Top 10 hybrids over checks	-	-	-	-	-2.7	1.1%	4.1%	1.3%	-1.8%	26.2%	65.0%	-	22.6%	
Best hybrid over checks	-	-	-	-	4.4%	6.3%	9.8%	20.8%	7.9%	35.4%	99.3%	-	29.0%	
Best hybrid over best check	-	-	-	-	-4.4	0.9%	2.7%	12.1%	3.7%	0.3%	31.8%	-	3.8%	
CD @ 0.05	3.15	3.06	11.71	2.30	2.26	0.40	1.63	5.89	1.09	2.53	2.42	9.36	3.06	
CD @0.01	4.17	4.05	15.50	3.05	3.00	0.54	2.16	7.80	1.45	3.35	3.20	12.40	4.05	

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, TSS-total soluble solids, DEW-dehusked ear weight, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield

Table S 2 - Number of hybrids showing different gene effects for agronomic traits

Type of gene effect	DFT	DFS	PH (cm)	EH (cm)	EL (cm)	EG (cm)	KRN	KR	DEW	TSS	GFW	TLB	GEY
Overdominance	34	39	37	29	40	32	31	39	25	39	38	29	39
Complete dominance	2	1	0	0	0	0	2	0	0	0	0	1	0
Partial dominance	4	1	4	12	2	10	5	1	16	3	4	8	3
No dominance	2	1	1	1	0	0	5	2	0	1	0	4	0

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, TSS-total soluble solids, DEW-dehusked ear weight, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield

Table S 3 - Potence ratio of 13 agronomic traits for 42 F_1 experimental hybrids

Crosses	DFT	DFS	PH (cm)	EH (cm)	EL (cm)	EG (cm)	KRN	KR	DEW	TSS	GFW	TLB	GEY
MRCSC9×KH1831	1.67	3.73	-2.08	-7.89	-8.84	-2.27	6.0	-18.08	-8.73	0.38	-8.97	-2.16	-6.96
MRCSC9×SC Sel 1	2.40	2.40	3.37	3.00	58.75	4.31	0.0	7.63	4.00	-2.53	481.00	1.81	-46.35
MRCSC9×SC Sel 2	1.10	2.69	-5.22	2.86	35.50	-10.82	17.0	24.17	-82.11	-41.67	-188.55	-2.36	-10.50
MRCSC9×SC Sel 3	2.83	4.11	-2.78	-1.24	-3.81	2.00	-11.0	15.33	4.16	-1.41	-12.85	-4.45	30.85
MRCSC9×SC Syn	1.73	3.00	-11.05	0.79	17.00	2.87	1.3	7.55	26.40	-12.14	-9.75	-23.08	-15.83
MRCSC9×SC Ind	17.00	5.00	1.44	-1.23	-0.10	0.76	1.0	0.77	0.60	4.91	3.72	0.00	0.70
KH1831×MRCSC9	-1.29	-4.09	2.11	8.78	7.65	3.19	-7.0	18.85	11.31	0.60	4.82	1.97	6.64
KH1831×SC Sel 1	-3.00	-25.00	1.07	0.56	6.36	2.02	-5.0	5.25	4.02	0.00	5.10	0.35	7.22
KH1831×SC Sel 2	0.00	14.00	3.85	-1.87	8.27	2.62	0.0	9.16	8.02	0.72	3.47	0.00	11.43
KH1831×SC Sel 3	-3.67	-18.00	5.80	0.00	24.68	1.71	-7.0	11.32	3.86	0.68	15.91	3.35	5.93
KH1831×SC Syn	-2.40	-6.50	2.58	0.11	7.96	1.55	2.3	8.09	8.13	1.60	-292.00	1.61	13.78
KH1831×SC Ind	-1.74	-7.00	0.95	-1.51	3.10	0.94	3.4	2.51	1.29	0.86	1.03	1.97	1.61
SC Sel 1×MRCSC9	-2.80	-2.00	-2.78	-0.22	-27.75	-5.46	0.0	-5.11	-3.08	1.60	-426.00	-2.61	30.42
SC Sel 1×KH1831	2.27	27.00	-1.26	-2.70	-10.27	-1.80	12.0	-7.06	-2.82	-0.68	-9.88	-0.61	-6.14
SC Sel 1×SC Sel 2	1.36	1.00	-1.38	-11.50	27.30	-2.42	10.0	-26.14	-3.28	1.96	-104.00	-0.35	-7.17
SC Sel 1×SC Sel 3	11.00	-31.00	-2.01	-1.62	-10.53	7.17	-15.0	-34.43	22.56	-1.29	-14.43	0.77	21.70
SC Sel 1×SC Syn	9.00	-2.33	-2.13	1.22	16.17	2.43	0.2	29.67	-8.93	-0.95	-11.31	0.17	-17.55
SC Sel 1×SC Ind	-3.75	-6.00	4.43	-0.94	1.34	0.39	2.4	2.00	0.53	-0.22	1.67	2.42	0.94
SC Sel 2×MRCSC9	-1.48	-2.85	3.35	-0.14	-19.79	9.45	-9.0	-18.67	110.15	39.00	177.45	1.59	13.55
SC Sel 2×KH1831	0.00	0.00	-3.69	-0.98	-5.37	-3.35	0.0	-7.80	-5.98	-2.83	-7.51	0.00	-8.46
SC Sel 2×SC Sel 1	-1.00	-3.00	2.18	26.00	-41.00	2.08	-6.0	30.14	8.01	-0.48	109.86	1.13	14.36
SC Sel 2×SC Sel 3	-2.33	-7.50	-12.22	-1.38	-9.72	2.87	-5.7	0.00	7.34	-1.34	-16.53	2.60	10.61
SC Sel 2×SC Syn	-2.80	-4.33	6.26	-0.60	-99.50	1.84	2.0	23.40	24.26	10.33	-11.50	1.61	38.97
SC Sel 2×SC Ind	-1.11	-4.14	0.74	-2.00	3.40	0.94	1.8	4.35	1.46	3.09	2.80	1.58	1.66

SC Sel 3×MRCSC9	-2.17	-3.44	2.00	1.60	6.09	-3.42	11.0	-15.17	-5.46	0.85	11.40	4.01	-36.90
SC Sel 3×KH1831	3.44	18.00	-6.77	1.63	-21.32	-1.14	5.0	-9.08	-3.65	0.44	-19.68	-3.31	-5.33
SC Sel 3×SC Sel 1	-15.00	29.00	1.58	1.15	13.94	-5.67	15.0	30.43	-32.34	5.29	13.09	0.80	-31.01
SC Sel 3 ×SC Sel 2	1.00	5.50	10.34	2.13	6.61	-2.17	5.7	0.00	-4.53	0.02	13.47	-3.69	-7.20
SC Sel 3×SC Syn	-13.00	-14.00	3.54	0.57	6.81	4.11	1.4	16.80	-8.58	2.02	-24.72	3.24	-11.86
SC Sel 3×SC Ind	-3.20	-11.00	0.62	20.33	1.97	0.06	2.5	1.98	3.23	0.32	2.38	0.96	3.26
SC Syn×MRCSC9	-0.27	-1.57	11.81	0.17	-31.60	-3.13	-0.3	-10.00	-8.37	5.57	4.10	110.27	6.79
SC Syn×KH1831	3.60	11.50	-3.30	-0.37	-10.95	-1.15	-2.0	-8.83	-5.62	-0.82	362.67	-2.00	-12.86
SC Syn×SC Sel 1	-17.00	4.33	1.76	2.09	-58.17	-3.76	0.0	-55.00	4.22	-0.65	3.70	1.00	13.45
SC Syn×SC Sel 2	2.00	3.33	-4.75	-1.80	65.75	-2.01	-1.3	-19.60	-24.66	-20.00	7.73	-1.80	-36.11
SC Syn×SC Sel 3	0.60	8.00	-2.95	-1.20	-11.07	-9.89	-0.8	-21.20	3.78	0.79	14.64	-4.56	7.03
SC Syn×SC Ind	-2.33	-29.00	0	-0.37	2.33	0.74	-1.0	3.00	1.08	1.34	1.20	153.87	1.59
SC Ind×MRCSC9	-12.0	-4.33	-2.67	3.50	-1.50	-1.31	1.0	-2.02	-0.88	-0.55	-7.96	0.00	-1.30
SC Ind×KH1831	1.42	7.00	-1.07	4.20	-2.57	-0.71	-3.0	-1.97	-1.43	-1.29	-4.95	-1.37	-1.86
SC Ind×SC Sel 1	0.75	0.50	-8.19	3.11	-2.60	-0.46	-0.4	-3.05	0.85	-1.43	-8.65	0.20	-0.10
SC Ind×SC Sel 2	1.00	3.29	-1.40	1.57	-3.20	-1.37	-2.2	-3.20	-1.06	-5.78	-7.56	-2.75	-1.52
SC Ind×SC Sel 3	1.80	11.00	-1.14	-30.40	-1.86	-0.11	-0.5	-2.43	-2.76	0.50	-7.21	-4.45	-3.22
SC Ind×SC Syn	0.56	15.00	-0.86	1.33	-0.25	-0.37	-11.0	-3.56	-1.07	-2.52	-4.58	-110.2	-1.18

Note: DFT-days to 50% tasseling, DFS-days to 50% silking, PH-plant height, EH-ear height, EL-ear length, EG-ear girth, KRN-kernel row number, KR-kernels per row, TSS-total soluble solids, DEW-dehusked ear weight, GFW-green fodder weight, TLB-Turcicum leaf blight, GEY-green ear yield