



GENETIC ANALYSIS FOR YIELD ATTRIBUTES IN SWEET CORN (*ZEA MAYS* L. VAR. *SACCHARATA*) UNDER DIVERSE ENVIRONMENTS

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SUMMARY

The genotype and environment interaction (GEI) has always been a challenge as these are the main concerns of breeders during the selection of suitable parents for breeding programs. Very little information is available regarding the implication and importance of significant GE interaction, its source, and nature in plant breeding programs and on the net yield and resultant varieties. The study aimed to investigate the gene action and assess the performance of half-diallel populations using eight advanced sweet corn inbred lines for yield-related traits across two environmental conditions, i.e., Nowshera plain and Swat hilly areas, Khyber Pakhtunkhwa, Pakistan. Statistical analyses revealed significant variations among sweet corn genotypes for the studied traits from both locations. Hayman's graphical analysis deduced that majority of traits like grains cob⁻¹, 100-kernel weight, stover yield, and sweet corn grain yield showed over-dominance sort of inheritance at both Nowshera and Swat locations. The additive components were not more in magnitude than the dominance components at both the locations, however, these were lower than their counterparts' (H₁ and H₂) components signifying the major function of a dominant gene action. The dominance effect was unidirectional for all the traits in the sub-tropical plain area, as well as, the temperate hilly area. Asymmetrical gene allocation was found due to their values being lower than 0.25 at both test locations. Broad-sense heritability was higher for most of the traits at both locations except for grains cob⁻¹ and stover yield at Nowshera. It can be incidental that due to the dominant gene action and the least amount of narrow-sense heritability for most of the sweet corn yield-related traits, high yielding hybrids could be utilized for heterotic breeding.

Keywords: Sweet corn, additive-dominance model, genetic analysis, Hayman's half-diallel approach, heritability, gene action

Key findings: The results, thus, emphasized that yield contributing traits of sweet corn at Nowshera and Swat, showed low narrow-sense heritability and dominant type of inheritance. Changes in the genetic magnitude and heritability estimates over the two test locations indicated a significant role of environment on gene expression. Therefore, simultaneous evaluation and selection of wider adaptable sweet corn genotypes across locations will be more effective for hybrid's development.

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INTRODUCTION

Corn is one of the most important cereal crops and globally ranks third in terms of area planted and yield (Kusaksiz, 2010; Shojaei *et al.*, 2022). Sweet corn (*Zea mays* L. var. *saccharata*) is a type of corn with a thin pericarp layer and creamy texture, and is widely consumed throughout the world. Mutant endosperm with high sugar levels in the kernels and less starch content differentiate sweet corn from other types of corn. Its kernel contains about three to eight times more sugar content than the normal field corn and it is also an important source of vitamins, minerals, and fibers (Creech, 1965; Chozin *et al.*, 2017; Sheng *et al.*, 2018). Globally, sweet corn is grown on 1.06 million hectares (ha) of land and the top four producing countries are the USA, Mexico, Nigeria, and France (Lertrat and Pulam, 2007; Puttarach *et al.*, 2016; Revilla *et al.*, 2021). Production is quite low due to limited research work, narrow genetic makeup, susceptible seeds, poor socioeconomic condition of the farmers, and abrupt climatic changes.

Crop enhancement strategy depends upon genetic variability among genotypes, the environment, and the interactions owing to genotype and environment for vital yield contributing traits in maize (Hassan *et al.*, 2006; Harakotr *et al.*, 2016; Pacurar *et al.*, 2018). High-yielding genotypes with wider adaptability are desirable but the genotypes by environment interaction (GEI) make this complicated. Genotypes that performed better under a particular location might not perform well across environments (Kang and Gorman, 1989; Smith *et al.*, 2005; Shojaei *et al.*, 2022). Therefore, breeders and crop producers normally select hybrids that perform well across diverse environments and identify the most stable and best yield performing maize genotypes before their commercial release into a particular target environment (Yan and Hunt, 2001; Mohammed, 2020; Zystro *et al.*, 2021).

The development of new high-yielding varieties is a prerequisite to feeding the ever-increasing population. Hybridization is one of the procedures to identify the nature and magnitude of gene action accountable for the heritage of various grain yields attributes. Gene action and heritability help in understanding the inheritance pattern and gene legacy of yield components. Diallel analysis was employed to select sweet corn parents for crossbreeding and understanding the character and magnitude of the gene action accountable for the inheritance of the

traits and estimation of total genetic variance. Genetic analyses decide the prevalence of dominance mechanism as more significant than the additive sort of gene heritage and vice versa. Corn researchers, Kumari *et al.* (2007); Tabassum *et al.* (2007), and Mural, (2012) concluded that non-additive gene actions govern corn yield attributes in maize. However, some studies suggested that the majority of the yield attributes in maize were under command of the additive nature of gene action (Alamnie *et al.*, 2006; Kumar and Bharathi, 2009; Chohan *et al.*, 2012; Mousa, 2014; Al-Falahy and Mohammad, 2015; Aslam *et al.*, 2015). Similarly, both additive + non-additive forms of gene variances are the main factors in the inheritance of corn.

To overcome climate change and genetic improvement of sweet corn for grain yield-causative traits in Pakistan, high yielding plants along with yield stability across environments are more desirable to escape environmental stresses that generally coincide with flowering and yield traits and its resistance to diseases occurring during later growth stages. Highly considering all these things, the main objective of the study was to assess and evaluate the breeding potential of sweet corn parents and F₁ hybrids to determine gene action for seed yield and yield attributes in the Nowshera and Swat environments of Khyber Pakhtunkhwa, Pakistan.

MATERIALS AND METHODS

Genetic material and development of F₁ hybrids

Eight sweet corn inbred lines viz., NC17, NC19, SS14, SS18, CS29, CS34, KS1, and SOS1, were crossed in a diallel mating design (without reciprocals) at the Cereal Crop Research Institute (CCRI), Pirsabak Nowshera, Khyber Pakhtunkhwa, Pakistan. Parental genotypes, F₁ hybrid combinations along with two checks, CCRI Sweet (open pollinated variety-OPV) and hybrid 'Moon' of sweet corn were sown in randomized complete block design in two replications. The research plot comprised of two entries, each has 5 m length with distance of 25 and 75 cm between the plants and rows, respectively. A total of 38 genotypes (eight inbred lines with 28 F₁ hybrids and two checks) were evaluated at two locations viz., Nowshera with a sub-tropical environment, and the Agriculture Research Institute, Mingora, Swat, Pakistan with a temperate environment. The crop was grown

under uniform conditions and standard cultural practices were adopted throughout the cropping season to minimize possible environmental effects.

Data recording and statistical analyses

In the F_1 generation, data on plant yield-related traits like grains cob^{-1} , 100-kernel weight, stover yield, and grain yield were measured on 10 selected plants. Analysis of variance was done based on Steel and Torrie (1980) and Mather and Jinks (1982), and Hayman's (1954a, 1954b) diallel analysis was performed. Upon significant differences, analysis of $W_r + V_r$ and $W_r - V_r$, and regression analysis were conducted to conclude the adequacy of the Additive-Dominance Model for sweet corn yield traits.

RESULTS AND DISCUSSION

Pooled analyses of variance showed that differences between locations were significant for the majority of yield attributes under both test locations (Table 1). Mean variations due to sweet corn genotypes were highly significant for most of the characters except for 100-kernel weight. Mean variations due to sweet corn genotypes were further partitioned into parents, F_1 hybrids, and their three contrasts comparisons. Parents and F_1 hybrids exhibited significant variation for some of the traits except stover yield and 100-kernel weight. Parents vs. the rest contrast showed significant ratios for all the studied parameters. The same trends were also shown by parents vs. hybrids and hybrids vs. checks contrasts.

The majority of the traits showed highly significant genotype \times location interaction except for grains cob^{-1} and 100-kernel weight. Almost similar results were also manifested for parents \times locations and F_1 hybrids \times locations interactions. Significant GEI for yield traits have also been determined by other researchers in maize (Banik *et al.*, 2010; Zare *et al.*, 2011; Aslam *et al.*, 2015). Similarly, Khalil *et al.* (2010) also observed significant GEI for silking and anthesis, and grain yield in corn. Likewise, Beyene *et al.* (2011) have suggested highly significant effects due to genotypes, environments, and their interaction for most yield contributing traits in corn. Since the interaction of genotype by location was significant for the majority of the characters, independent analysis was conducted under each test location to compute

relevant genetic parameters. Therefore, Hayman's genetic mechanism was conducted for all the yield-related traits under two different agro-ecological environments, and the results are presented in Table 2 and Table 3.

Grains per cob

Sweet corn grains cob^{-1} was validated by the test of adequacy and the model was partially adequate at two test locations. The effect of the environment on grains cob^{-1} was significant both at Nowshera and Swat (Table 2). Similarly, the additive genetic variance for grains cob^{-1} was significant both at Nowshera and Swat locations, but its magnitude was lower than the dominance component at both test locations. Variation in the genetic makeup of sweet corn inbreds might be due to heterozygosity of the parental lines (Hayman, 1954a; Khan, 2003). Aslam *et al.* (2015) observed an additive category of gene heritage for grains cob^{-1} in maize. The dominance effect was positive and significant for grains cob^{-1} at Nowshera and Swat, indicating that dominance was unidirectional. Similarly, Hussain *et al.* (2014) suggested over dominance sort of gene effects for the heritage of the said trait. The difference between dominance and additive variances was negative at each location indicating over dominance legacy for grains cob^{-1} . It was also supported by the average quantity of dominance which was more than unity at both locations. The proportion of positive and negative gene effects expressed asymmetry in their gene distribution. More dominant genes have existed in parents at both locations. Non-additive and dominant types of gene actions for grains cob^{-1} in maize have been estimated by earlier researchers like Saleem *et al.* (2002), Malik *et al.* (2004), Wattoo (2013), and Bisen *et al.* (2017).

Gene groups responsible for the control of grains cob^{-1} were 1.99 and 4.43 at Nowshera and Swat, Pakistan, respectively. Heritability ratios, i.e., broad and narrow sense were 0.48 and 0.06 at Nowshera, while 0.67 and 0.04 at Swat, respectively. Over-dominant kind of gene legacy was detected by graph (V_r , W_r) for parents at Nowshera, and KS1 composed mainly dominant whereas parental line CS29 have more recessive genes for grains cob^{-1} (Figure 1). At the location of Nowshera, parents CS29 and NC17 had near equal values of dominant and recessive genes for the control of this character. In contrast, at the location of Swat, NC19 composed more recessive genes than parental line KS1.

Table 1. Combined ANOVA for grains cob⁻¹, 100-kernel weight, stover yield, and grain yield of 38 sweet corn genotypes evaluated at two locations of Khyber Pakhtunkhwa.

Source	d.f.	Grains cob ⁻¹	100-kernel weight	Stover yield	Grain yield
Locations	1	27004.45**	34.11*	33888697.40**	32076053.70**
Reps w/n Locations	2	6539.08	0.71	1287097.70	6664.56
Genotypes	37	15016.93**	11.30	3249539.00**	1664225.96**
Parents	7	15733.64**	1.00	294744.39	155935.97*
F ₁ hybrids	27	6678.72*	7.35	1337081.65**	1040099.46**
Parents vs. rest	1	249399.88**	198.06**	66169162.68**	27909041.29**
Parents vs. F ₁ hybrid	1	258672.07**	209.57**	68913618.03**	30055241.13**
F ₁ hybrids vs. checks	1	11253.04	17.41	3492307.27**	3844184.42**
Genotype × Location	37	5408.29	2.43	2752797.60**	838980.66**
Parents × Location	7	6281.64	0.41	446027.48	152378.89*
F ₁ hybrids × Location	27	4936.53	2.76	2131026.42**	816482.18**
Error	74	4051.13	8.24	234650.90	61200.10
CV (%)		16.70	17.71	9.42	6.23

* = Significant at $P \leq 0.05$, ** = Significant at $P \leq 0.01$

Table 2. Genetic components of variation for grains cob⁻¹ and 100-kernel weight of 36 genotypes (eight parents and 28 F₁ hybrids) evaluated at two locations in Khyber Pakhtunkhwa.

Components	Grains cob ⁻¹		100-kernel weight	
	Nowshera	Swat	Nowshera	Swat
E	2531.03**± 310.29	1478.92*± 484.53	0.75*± 0.31	0.77**± 0.28
D	2933.83*± 926.72	4063.87*± 1447.12	-0.36± 0.92	-0.27± 0.82
H ₁	10117.03**± 2139.87	14903.05**± 3341.52	7.02*± 2.12	7.41**± 1.90
H ₂	7999.96**± 1861.73	11336.07*± 2907.20	6.07*± 1.85	6.32± 1.65
H ²	15931.64**± 1248.58	50235.16**± 1949.73	16.52**± 1.24	16.38**± 1.11
F	4422.53*± 2199.51	7309.48*± 3434.65	-0.45± 2.18	-0.06± 1.95
D-H ₁	-7183.20	-10839.20	-7.38	-7.68
(H ₁ /D) ^{1/2}	1.86	1.91	2.1	1.9
H ₂ /4H ₁	0.20	0.19	0.22	0.21
((4DH ₁) ^{1/2} +F) ^{1/2} /((4DH ₁) ^{1/2} -F)	2.37	2.77	1.14	1.10
(h ² /H ₂)	1.99	4.43	2.72	2.59
Heritability (bs)	0.48	0.67	0.73	0.73
Heritability (ns)	0.06	0.04	0.19	0.16

* = Significant at $P \leq 0.05$, ** = Significant at $P \leq 0.01$

Similarly, the regression line touched the origin below the W_r axis signifying the role of an over-dominant nature of gene action for grains cob⁻¹ at Swat. Parental line, NC17, had more dominant genes and inbred lines, CS34 and CS29, contained the most recessive for the trait grains cob⁻¹ (Figure 2). Sweet corn inbred line, SS14, showed recessive genes at both the test locations being farthest from the origin.

100-kernel weight

The additive dominance model for 100-kernel weight was partially adequate both at Nowshera and Swat. Chohan *et al.* (2012) also reported a partially adequate model for yield traits like the 100-kernel weight in corn genotypes. Environmental effect for 100-kernel weight showed significant effects and highly (P

Table 3. Genetic components of variation for stover yield and grain yield of 36 genotypes (eight parents and 28 F₁ hybrids) evaluated at two locations in Khyber Pakhtunkhwa.

Components	Stover yield		Grain yield	
	Nowshera	Swat	Nowshera	Swat
E	156279.50**± 33406.01	82210.15\ 152985.45	29323.12± 50239.93	30082.15± 78735.74
D	86958.88± 99771.61	44937.44± 456912.00	14093.63± 150048.10	80659.62± 235155.06
H ₁	119183.04± 230380.38	9381031.80**± 1055045.19	1311236.55*± 346472.80	3045470.85**± 542991.24
H ₂	146920.99± 200436.04	8601334.81**± 917912.72	1042894.40*± 301438.94	2534399.56**± 472414.43
h ²	395619.08*± 134423.38	26343548.26**± 615602.52	1178308.64**± 202161.56	7569806.33**± 316826.97
F	53270.13± 236801.24	104649.88± 1084449.99	66058.28± 356129.23	183230.01± 558124.76
D-H ₁	-32224.16	-9336094.40	-1297142.90	-2964811.20
(H ₁ /D) ^{1/2}	1.17	14.45	9.65	6.14
H ₂ /4H ₁	0.31	0.23	0.20	0.21
((4DH ₁) ^{1/2} +F) ^{1/2} /((4DH ₁) ^{1/2} -F)	1.71	1.18	1.64	1.45
(h ² /H ₂)	2.69	3.06	1.13	2.99
Heritability (bs)	0.20	0.97	0.93	0.97
Heritability (ns)	0.02	0.14	0.27	0.24

* = Significant at P≤0.05, ** = Significant at P≤0.01

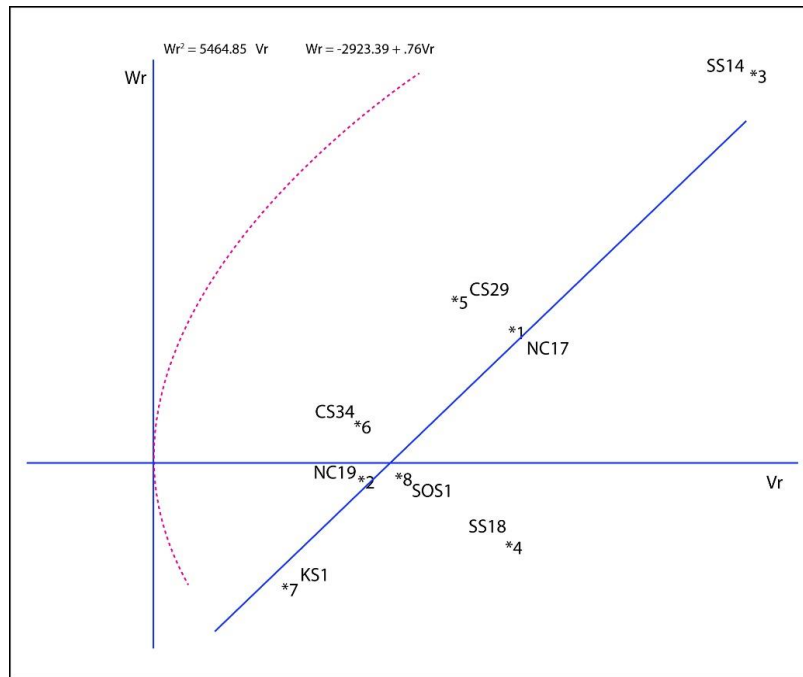


Figure 1. Vr, Wr Graph for grains per cob at Nowshera, Pakistan.

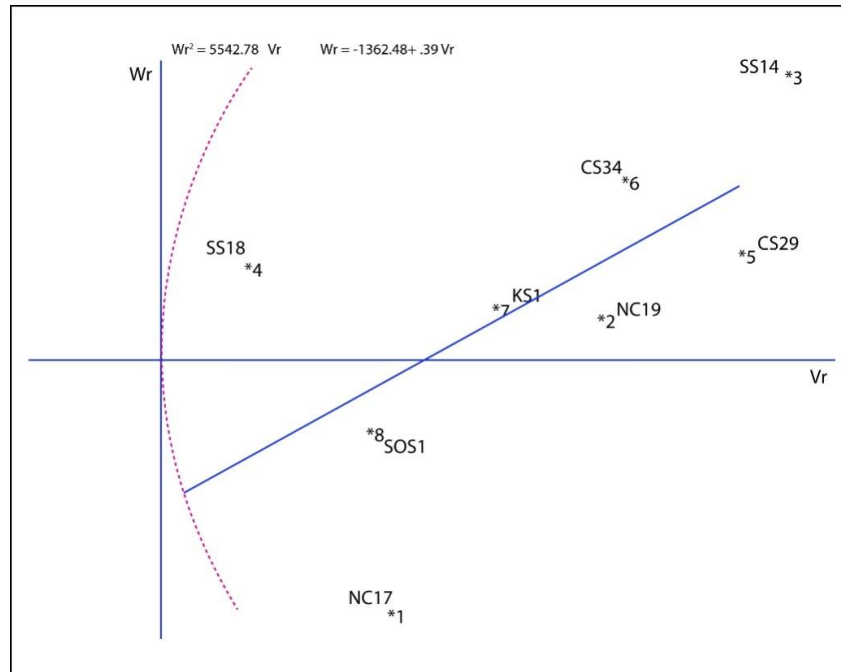


Figure 2. Vr, Wr Graph for grains per cob at Swat, Pakistan.

= 0.01) significant variations at Nowshera and Swat, respectively (Table 2). Additive genetic variance for 100-kernel weight was non-significant and negative at Nowshera and Swat. H_1 and H_2 (dominance components) were more in magnitude as compared with additive genetic variance indicating an over-dominant kind of gene action for 100-kernel weight. H_1 component was larger than H_2 suggesting that both (positive + negative) alleles for 100-kernel weight are not in equal proportions at these loci. Heterozygosity in parental lines is due to variation in the genetic makeup of sweet corn inbreds (Hayman, 1954a; Khan, 2003). The frequency of (dominant + recessive) alleles in sweet corn parents was in favor of recessive alleles at both locations. The difference between additive and dominance components was negative indicating the imperative role of over-dominance in the control of 100-kernel weight. Similarly, Malik *et al.* (2004), Hussain *et al.* (2014), Wattoo *et al.* (2009), and Bisen *et al.* (2017) had also reported an over-dominant gene legacy for 100-kernel weight in maize. On the contrary, Aslam *et al.* (2015) and Tabassum *et al.* (2007) observed an additive sort of gene stroke for 100-kernel weight in maize. The degree of dominance and proportion of genes (dominant + recessive) in the lines was not estimable due to a negative additive genetic value.

An asymmetric sharing of genes, having positive and negative alleles effects, was noticed at Nowshera and Swat locations with values of 0.22 and 0.21, respectively. The number of gene groups at Nowshera and Swat was noted to be 2.72 and 2.59, respectively. A broad sense heritability of 0.73 was recorded at both test locations for 100-kernel weight, although narrow-sense heritability was 0.19 at Nowshera and 0.16 at Swat, Pakistan. The V_r , W_r graph for the parents at Nowshera revealed an over-dominant category of gene stroke involved in 100-kernel weight legacy (Figure 3). Inbred lines, SS18 and CS34, had the most recessive whereas the parent, SOS1 possessed mainly dominant genes for 100-kernel weight. Parental lines, SS14, NC19, and KS1 appeared to have identical frequencies of (dominant and recessive) genes. At the location of Swat, an over-dominant heritage was also manifested for the 100-kernel weight, with parental inbred lines, NC17 and CS34, possessing more dominant, whereas NC19 and SS14, being out of origin, composed mainly of recessive genes for 100-kernel weight. Similarly, the dominant genes component for the trait under study in the inbred line, SS18, was not more in magnitude than inbred line CS29, at the location of Swat (Figure 4). In graphs, CS34 had the most recessive, and parent CS29 exhibited mainly dominant genes for the 100-kernel weight at Nowshera and Swat.

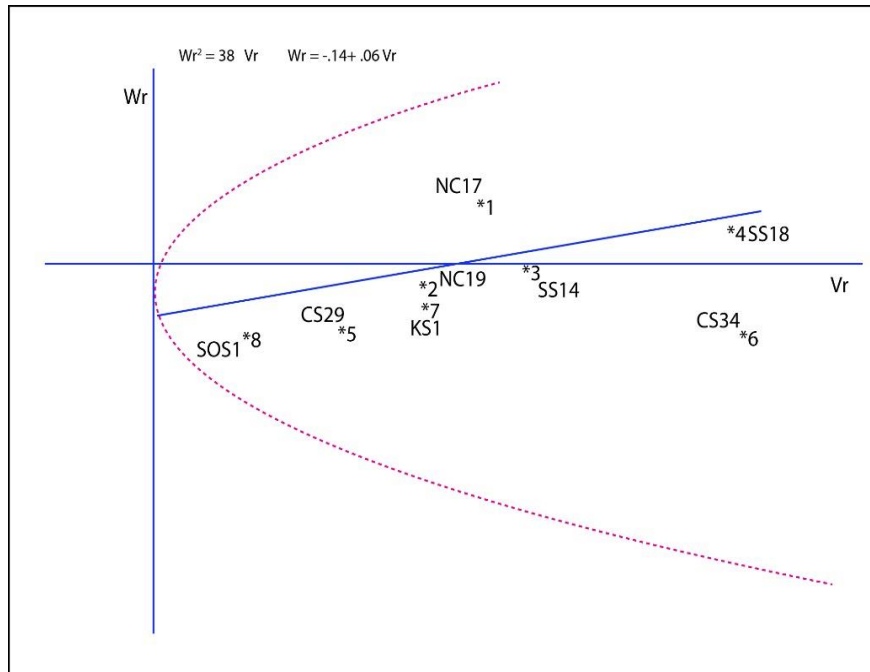


Figure 3. Vr, Wr Graph for 100-kernel weight at Nowshera, Pakistan.

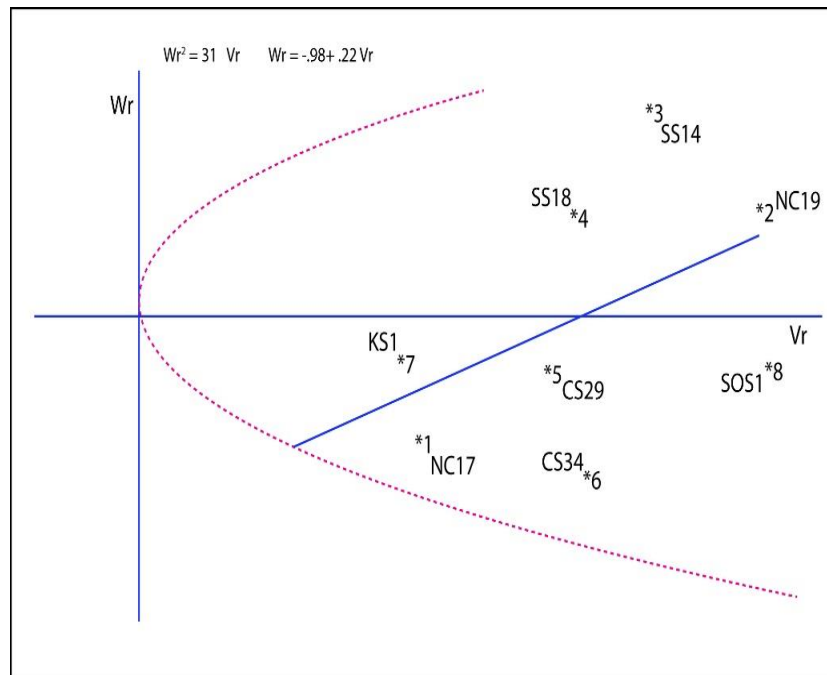


Figure 4. Vr, Wr Graph for 100-kernel weight at Swat, Pakistan.

Stover yield

A partially adequate model was found for stover yield both at Nowshera and Swat. The effect of environment on stover yield was significant at Nowshera, but non-significant at Swat (Table 3). The additive genetic component was non-significant and lower than the H_1 and H_2 dominance mechanism at both locations, indicating a predominance function of a non-additive gene for stover yield. Dominant types of gene actions for stover yield in maize have been estimated by earlier researchers like Tabassum and Saleem (2005), and Singh and Gupta (2009). However, Shabbir and Saleem (2002) reported a dominant sort of gene effect for the supposed traits in maize. On the contrary, Bisen *et al.* (2017) concluded an additive form of gene variances for stover yield trait in maize. The dominance effect was significant and highly significant at Nowshera and Swat, respectively, suggesting that dominance is unidirectional. The positive value of the 'F' component indicated an excess of dominant genes both at Nowshera and Swat. The difference between additive and non-additive constituents was negative at both locations, hence, indicating an over-dominant sort of gene stroke for stover yield. This was correlated with the positive and higher value of the average quantity of dominance at both locations.

Gene proportions having positive and negative effects showed asymmetric interactions as indicated by values 0.31 and 0.23 at Nowshera and Swat, respectively. The number of gene groups for stover yield was 2.69 at Nowshera and 3.06 at Swat. Heritability estimates in the broad sense were 0.20 (Nowshera) and 0.97 (Swat), although the narrow sense was only 0.02 for Nowshera and 0.14 for Swat. Graphical analysis for stover yield at Nowshera displayed a positive intercept which indicated partial dominance for stover yield in the parents, with NC19 and SS14 possessing most of the dominant genes, and CS34 and NC17 composed mainly of recessive genes (Figure 5). Stover yield at Swat, however, showed an over-dominant sort of gene stroke in the parents with parental lines SS18, SOS1, and KS1 possessing more dominant genes, and SS14 having the most recessive genes (Figure 6). Similarly, parental lines, CS29 and NC17, have almost identical frequencies of (dominant and recessive) genes at Nowshera and Swat locations.

Grain yield

Sweet corn grain yield was validated by the test of adequacy for the additive-dominance model and data were partially adequate at two test locations. Environmental variance and additive genetic (D) variance were non-significant at Nowshera and Swat (Table 3). However, dominance components (H_1 and H_2) showed significant variations at both locations. Overall, dominance components were larger in magnitude indicating that an over-dominant sort of gene stroke was involved in grain yield heritage. A significant positive dominance effect (h^2) pointed toward unidirectional dominance. The positive 'F' component indicated more dominant genes at both test locations. The fraction of additive and dominant variance was negative and hence, indicated an over-dominant gene action in the control of this character. This was further confirmed by the average degree of dominance having value more than unity. Past studies manifested that grain yield was predominantly under genetic inheritance of over-dominant mechanism in sweet corn (Wattoo *et al.*, 2009; Zare *et al.*, 2011; Wattoo, 2013; Hussain *et al.*, 2014). Scientists like, Ojo *et al.* (2007), Hussain *et al.* (2009), Chohan *et al.* (2012), Mousa (2014), and Aslam *et al.* (2015) concluded that Hayman genetic analysis showing additive gene inheritance was involved in the genetic legacy of grain yield in maize. Srdic *et al.* (2007), Ngaboyisonga *et al.* (2008), Irshad-ul-Haq *et al.* (2010), Khodarahmpour (2011), Dawod *et al.* (2012), Kumar *et al.* (2012), Agrawal *et al.* (2014), Moradi (2014), Soni and Khanorkar (2014), and Werle *et al.* (2014) have deduced that a non-additive nature of gene action was implicated in the inheritance of grain yield in maize. The genetic legacy of grain yield in maize was under the control of additive and non-additive kinds of gene strokes as suggested by Kumar and Bharathi (2009). The difference in dominance variance (H_1) was larger than the H_2 component signifying that the distribution of positive and negative genes was asymmetrical among sweet corn lines as confirmed by least ratio of $H_2/4H_1$ which was deviated from the expected value (0.25). Variation in the genetic makeup of sweet corn inbred lines might be due to heterozygosity of parental lines (Hayman, 1954a; Khan, 2003).

Gene proportion having positive + negative effects showed asymmetric

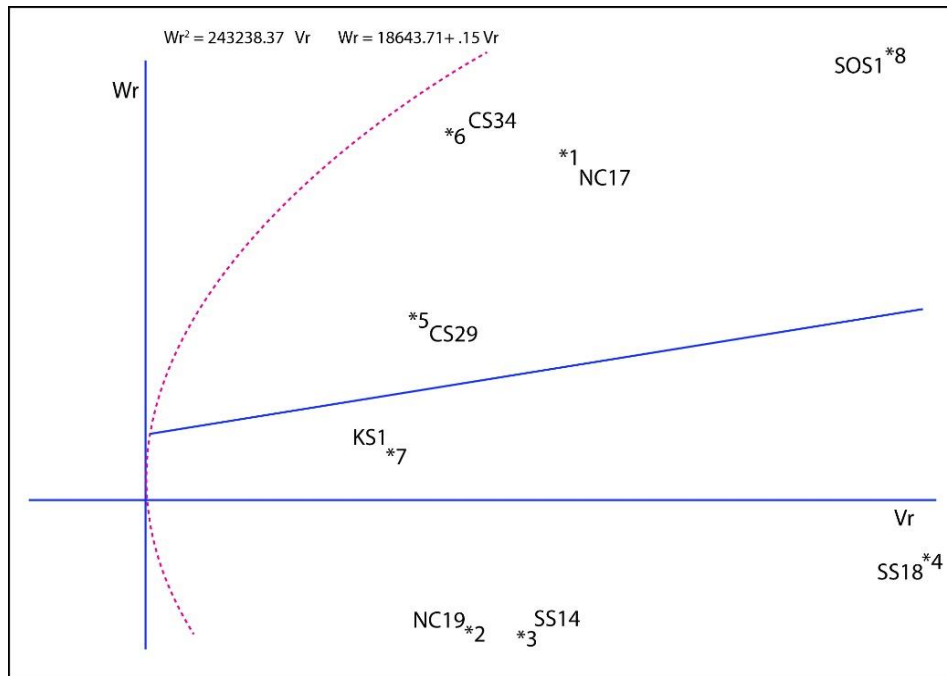


Figure 5. Vr, Wr Graph for stover yield at Nowshera, Pakistan.

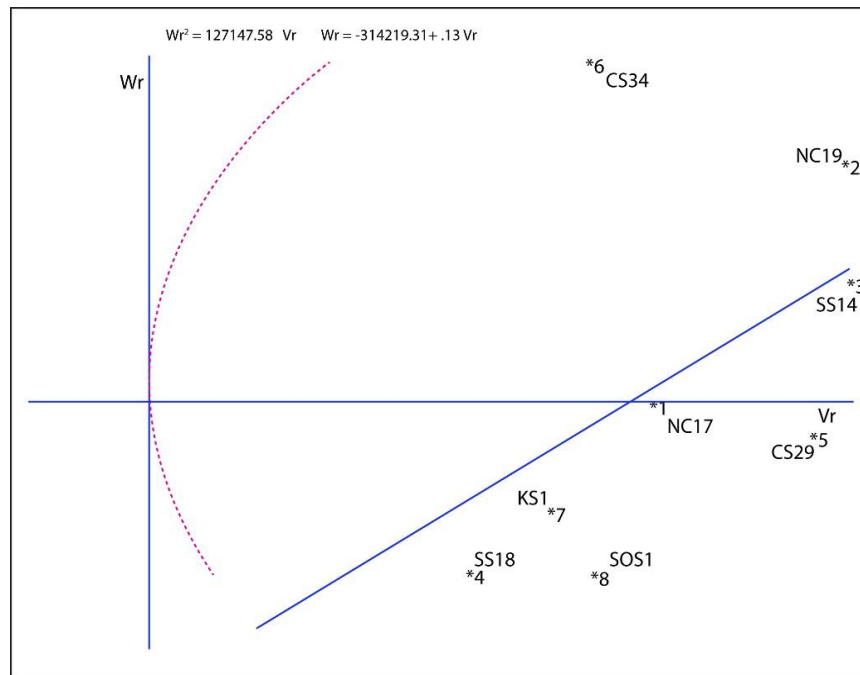


Figure 6. Vr, Wr Graph for stover yield at Swat, Pakistan.

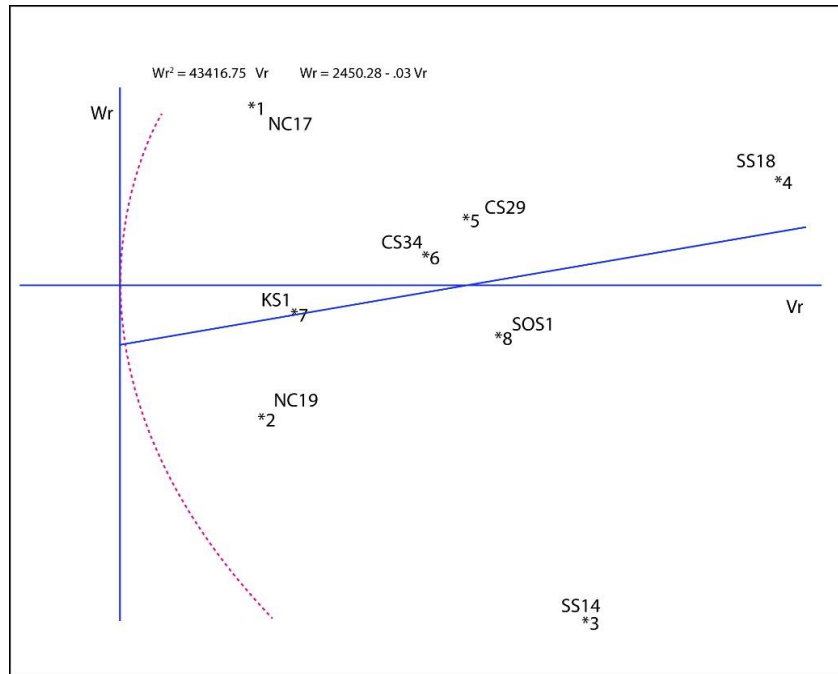


Figure 7. Vr, Wr Graph for grain yield at Nowshera, Pakistan.

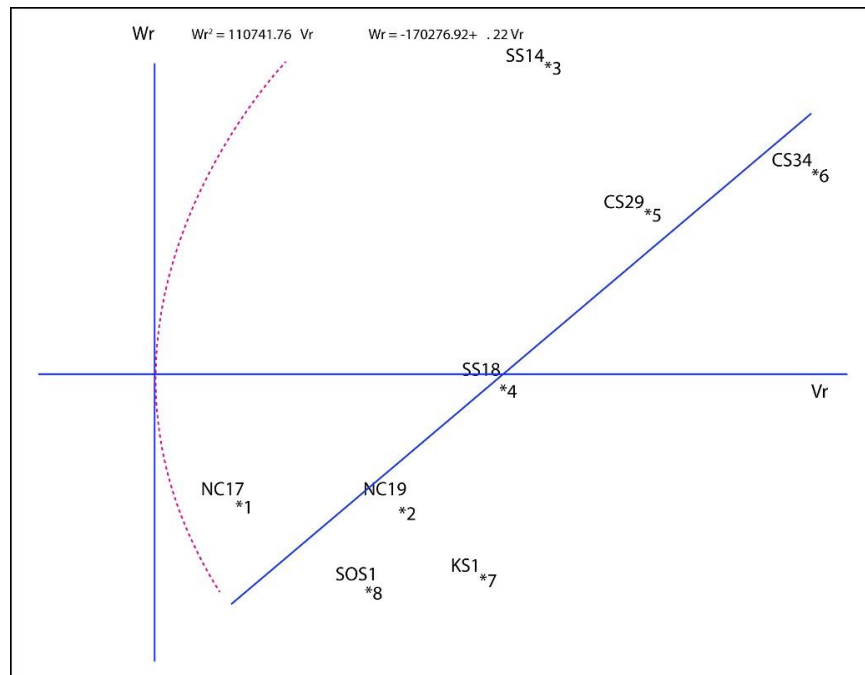


Figure 8. Vr, Wr Graph for grain yield at Swat, Pakistan.

interactions at Nowshera and Swat. The number of genes for the control of grain yield was found to be 1.13 and 2.99 at Nowshera and Swat, respectively. Heritability ratios in a broad sense for grain yield were 0.93 (Nowshera) and 0.97 (Swat), while the narrow sense was 0.27 at Nowshera and 0.24 at Swat. Graphical analysis for grain yield at Nowshera also revealed an over-dominant sort of gene action. Inbred lines KS1, CS34, and NC19 possessed mainly dominant genes, while SS18 and SS14 had more recessive genes for grain yield (Figure 7). A similar picture was portrayed by the parents at Swat with parental inbred lines CS34, SS14, and CS29 possessing the most recessive genes, while NC17, NC19, and SOS1 contained more dominant genes for sweet corn grain yield (Figure 8). At Nowshera, SS18 had the most recessive genes being away from the origin, but the same line possessed almost identical dominant and recessive genes at Swat.

CONCLUSIONS

Genetic analysis of yield traits of sweet corn at Nowshera and Swat test environments deduced that majority of yield causative traits showed low narrow-sense heritability and dominant type of inheritance. It can be inferred that heterosis breeding and wider adaptable sweet corn genotypes can be developed and pursued across different agro-ecological locations with considerable genetic improvements.

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