Original Paper Open Access

Genetic behavior for kernal yield and its physio-agronomic attributes in maize at normal and high temperature regimes

Muhammad Akbar[1], Jehanzeb Farooq[2*], Yasin Ashraf[3]

[1]Wheat Research Institute, AARI, Jhang road, Faisalabad, Pakistan
[2]Cotton Research Institute, AARI, Jhang road, Faisalabad, Pakistan
[3]Nuclear Institute for Agriculture and Biology, Jhang road, Faisalabad, Pakistan
*Corresponding author: E-mail: jehanzeb1763@hotmail.com

Abstract

Cell membrane thermostability and seedling plant biomass were used to select suitable parents for hybridization against high temperature stress from 77 inbred lines. Six diverse parents with respect to high temperature stress tolerance viz; two high temperature tolerant (935006, R2205-5-4), two moderately tolerant (F-165-2-4, F101-7-2-6) and two high temperature susceptible maize inbred lines (F113-1-1-1 and R2304-2) were selected and crossed in a full diallel fashion to evaluate inheritance pattern of physio-agronomic traits. Data regarding physiological traits *viz*., osmotic potential, transpiration rate, growing degree days (GDDs) to 50% tasseling and agronomic traits *viz*; number of kernels plant^{-1} and kernels yield plant-1recorded were at normal and high temperature stress regimes. Analysis of variance revealed highly significant variation ($P < 0.01$) for all the traits studied except osmotic potential at normal temperature regime which was significant at $P < 0.05$. Transpiration rate, growing degree days to 50% tasseling, number of kernels plant^{-1} and kernel yield plant^{-1} showed partial fitness of the data either at normal or higher temperature regime while osmotic potential showed partial fitness of the data by regression analysis in both temperature regimes. Genetic components of variance and Wr/Vr graph for traits studied depicted preponderance of over dominant gene action except osmotic potential at normal temperature regime which reflected additive gene control at normal temperature regime. High temperature stress modified gene expression in most of polygenic traits.

Keywords: Over dominant and complete dominant gene effects, physio-agronomic traits, global warming and maize kernel yield improvemen

Introduction

Plants with 4-carbon assimilation pathway are efficient user of CO_2 and water. Maize is a C4 plant that is grown from tropical to temperate regions and geographically from 58° North latitude (in Canada and Russia) to 40° South latitude (in Southern hemisphere). In Pakistan it is mainly grown in provinces of Punjab and NWFP in February and July/August. Its world average yield is much higher than that of Pakistan (Anonymous, 2005-2006).

Maize has gained a special position in the crop husbandry of Pakistan and its area under cultivation and yield has significantly increased during the last few years (Anonymous, 2005-2006). The optimum day temperature ranges from 25 to 32°C and night temperature ranges 16.7 to 23.3°C for maize plant. At optimum temperature, the photosynthetic rate is more rapid than respiration resulting in enhanced plant growth. The crop faces high temperature stress particularly at reproductive stage in maize which is a serious problem causing drastic kernel yield reduction so potential kernel yield cannot be achieved from the crop. Therefore, breeders need to develop maize hybrids/synthetics tolerant to high temperature stress in tropical and subtropical regions including Pakistan for getting potential kernel yield.

Growth is affected adversely when temperature decreases to 5°C or increases from 32°C. Net photosynthesis is inhibited at the leaf temperature above 38°C due to thermal inactivation of enzymes. Activity of RUBISCO decreases at the temperature exceeding 32.5°C with nearly complete inactivation at 45°C if temperature increases rapidly. At 54°C, maize plant dies (Steven et al, 2002).Variation in temperature is often misleads in calculating crop period. Therefore, growing degree days to vegetative growth period (Growing degree days to 50% tasseling) and physiological maturity can provide precise estimates in calculating heat units requirement for a crop instead number of days.

High temperature stress and low humidity lead to water stressed condition due to higher evaporation and transpiration. It reduces water potential which compels the plant to osmotic adjustment. Osmotic adjustment is the difference between osmotic potential and water potential at full turgor in irrigated and non-irrigated plants. The highest value of minimum leaf water potential is recorded for plants grown under normal temperature, as a response to the highest soil potential in a cropping system. Pressure potential

 RECEIVED 8/28/2016

and the osmotic potential at full turgor were reduced as a response to water deficit, resulting in an osmotic adjustment. The minimum leaf water potential showed sensitivity to water deficit which makes it a good indicator of water status in maize plants. Maize showed tolerance to water deficit through osmotic adjustment.

High temperature stress can desiccate exposed silk and pollen kernels when they are released from the anthers due to thin outer membranes (Sinsawat, 2004). Prolonged exposure to higher temperature above 32.5°C reduced pollen germination of many genotypes near to a zero level in maize (Herrero, et al, 1980; Hussain et al, 2006) resulted reduction in number of kernels plant^{-1}. The degree of damage depends upon the intensity and the duration of high temperature spell. Continuously rising temperature, less frequency and uneven distribution of rainfall coupled with usual canal–closure in Pakistan has been significantly reducing the kernel yield particularly loss of pollen viability leading to poor seed set. Smith (1996) also reported that corn could survive brief exposures to 112°F (44°C). Corn yield may be reduced by 1.5 bushels acre^{-1} (101 kg ha^{-1}) for each day if the temperature reaches 95°F (35°C) or higher during pollination and kernel filling (Smith, 1996). This problem could be overcome by developing high temperature tolerant maize hybrids.

Genetic variations provide base of improvement in any crop to plant breeders. Success in hybridization program depends upon the choice of suitable parental inbred lines, which will combine well to generate superior hybrids. Knowledge of inheritance pattern influencing yield and its components has become increasingly important for plant breeders in the choice of suitable parental inbred lines for developing potential hybrids in cross pollinated crop (Kruvadi, 1991). Suitable inbred lines thus may be selected on the basis of gene action with their better mean performance to accumulate dominant genes in development of productive hybrids/synthetics.

Therefore, understanding of genetic mechanism at high temperature tolerance is necessary for the development of heat tolerant hybrids and synthetics for sustainable agriculture.

Materials and Methods

The manuscript is part of PhD thesis finally approved in Nov 15, 2008. The research was conducted at the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad and Nuclear Institute for Agriculture and Biology (NIAB) during 2005-07. Two high temperature tolerant (935006, R2205-5-4), two moderately tolerant (F-165-2-4, F101-7-2-6) and two high temperature susceptible maize lines (F113-1-1-1 and R2304-2) were chosen on the basis of cell membrane thermostability seedling plant biomass from 77 inbred lines and crossed in a complete diallel fashion during winter, 2005. Seeds of F_0 including reciprocal crosses and parental lines were sown in triplicate RCBD in two sets after seed treatment with Benomyl 50 WP mixed with Confidar 70 WS @ 5 g kg^{-1} seed for the control of shoot fly. One set was sown on February 08, 2006 (sowing time of maize) in the field while 2nd on March 14, 2006 to expose it to high temperature stress at reproductive stage. Two seeds hill were planted with a dibbler, keeping plant-to-plant and line-to-line distances of 18 and 75 cm, respectively. After germination, thinning was done to have a single healthy seedling hole^{-1}. All cultural practices were kept uniform for both the sets. Twelve irrigations were applied to avoid both the trials from drought stress. Nitrogen, P_2O_5 and K_2O @ 75, 130, 100 kg ha^{-1} respectively were applied at the time of sowing. Nitrogen @ 85 kg ha^{-1} at the time of second irrigation and 100 kg ha^{-1} at tasseling stage was also applied. Premextra gold 720 SC @ 1,200 ml ha^{-1} was applied for control of weeds. Data regarding physiological traits *viz*., growing degree days (GDDs) to 50% tasseling, osmotic potential (-MPa), transpiration rate (µg cm^{-2} second^{-1}) and agronomic traits viz; number of kernels plant^{-1} and kernels yield plant^{-1} (g) were recorded from each entry from each repeat of both the sets at maturity. Third leaf of the plant was cut and frozen in a freezer bellow –20°C for 7 days, then the frozen material was thawed and cell sap was extracted with the help of disposable syringe. The sap so extracted was directly used for the determination of osmotic potential with the help of osmometer.

Transpiration rate measured with the help of steady state Porometer (Model L-1 1600 SSP1674 Li^ Cor Ink, USA) after adjusting it with the prevailing environment with help of Null gain adjustment at prevailed temperature and light quantum from set 1 grown in February 11, 2006 and from set 2 grown in March 14, 2006 in the same field in adjacent plot. Growing degree-days for days to 50% tasseling were calculated as the average daily temperature minus 10 according to the formula:

$$\{GDDs = ½ (T_{max} + T_{min}) -10\}$$

If the maximum daily temperature (T_{max}) was greater than 30°C, then 30°C temperature was used to determine the daily average. Similarly, if the minimum daily temperature (T_{min}) was less than 10°C, then 10°C temperature was used to determine the daily average. Growing degree-days are calculated daily and summed over time to define thermal time for a particular stage of the crop.

Number of kernels per plant were counted and weighed after harvesting and sun drying and averaged of ten were used for analysis. Analysis of variance was carried out to test the significant differences among 36 genotypes resulting from 6×6 diallel cross following Steel and Torrie (1984). Gene action was determined following Hayman (1954a), Jinks (1954) , and Whitehouse et al (1958). Two scaling tests were employed to fulfill the assumptions of absence of epistasis, no multiple allelism and independent gene

Table 1 - Parental inbred lines performance for CMT %age and fresh plant biomass in a complete 6×6 diallel cross in maize.

Parental inbred lines	Injury %age 25°C	Injury %age 45°C	Fresh plant Biomass at 25°C	Fresh plant Biomass at 45°C
935006	40.4	37.67	2.122	1.840
R2205-5	38.9	36.29	1.608	1.467
F101-7-2-6	55.7	51.98	1.934	1.683
F165-2-4	58.3	54.39	1.876	1.697
F113-1-1-1	75.7	70.62	2.099	1.391
R2304-2	75.0	70.00	2.178	1.585

distribution. The first test was an analysis of regression coefficient. Variances (of each array) and covariances (arrays with its parental values) were estimated from the mean diallel table. Then the regression of covariance on the variances was computed. The regression coefficient is expected to be significantly different from zero but not from unity. Analysis of variance of $W_r + V_r$ and $W_r - V_r$ was conducted as a second test for the adequacy of the additive dominance model. If one of two scaling tests fulfills the assumptions, the additive dominance model was considered partially adequate and was analyzed further. Components of variance for such type of partially adequate models have also been estimated by various scientists (Johnson and Aksel, 1964; Azhar and McNeilly, 1988). The genetic components of variation were calculated using the procedures given by Hayman (1954b) and Mather and Jinks (1982) followed by Singh and Chaudhary (1985) in diallel analysis.

Results

Seventy-seven inbred lines obtained from CIMMYT, Mexico and local sources were screened for high temperature tolerance using cell membrane thermostability (Sullivan, 1972) and seedling biomass. Six inbred lines of maize of diverse origin (Table 1) were selected and crossed in full diallel fashion. Genotypic mean squares exhibited highly significant differences among genotypes (parents, their crosses and reciprocals) for all the traits studied (Table 2). Osmotic potential was partially adequate due to adequacy only in regression analysis at both temperature regimes for additive dominant model (Table 3).

Estimation of genetic components of variation for osmotic potential displayed significant additive variation (**D**) only for osmotic potential at normal temperature regime (Tables 4) while the significant dominant variation ($\mathbf{H_1}$ and $\mathbf{H_2}$) at high temperature regime (Table 5). Equal values of $\mathbf{H_1}$ and $\mathbf{H_2}$ at high temperature regime were calculated. Value of **F** was significant and positive at normal temperature regime it turned negative and non significant under high temperature stress. $\mathbf{h^2}$ was non significantly negative. Heritability in broad sense was low at normal temperature regime (44.91%) that increased up to 89.77% at high temperature regime. Narrow sense heritability was comparatively low (40.35 and 17.6%).

Graphical presentation of the data (Figure 1A) also displayed significant additive gene action for osmotic potential at normal temperature regime while over dominant type of gene action at high temperature stress regime (Figure 1B). The inbred line R2304-2 followed by 935006, R2205-4, and F113-1-1-1 had maximum dominant genes while F101-7-2-6 followed by F165-2-4 had maximum recessive genes for osmotic potential at normal temperature regime while the inbred line R2205-4 had maximum dominant genes while F101-7-2-6, 935006, and F165-2-4 had intermediate position and R 2304-2 and F113-1-1-1 had maximum recessive genes for osmotic potential at high temperature stress regime.

Genetic analysis for transpiration rate was proved partially adequate at normal temperature regime due to adequacy in regression analysis and completely adequate by both the tests for additive dominant model at high temperature regime (Table 3). Genetic components of variation were estimated (Hayman, 1954b). Significant values of **D** at normal and high temperature regimes were assessed. The magnitude of $\mathbf{H_1}$ and $\mathbf{H_2}$ were non-significant at normal temperature regime but the magnitude of $\mathbf{H_1}$ was much higher than that of **D** value for this trait at high temperature regime. Dominant variation was also indicated by **H** components ($\mathbf{H_1}$ and $\mathbf{H_2}$). $\mathbf{H_1}$ was non-significant at normal temperature which turned highly significant at high temperature regime. However, $\mathbf{H_2}$ values were non-significant at both the temperature regimes. Un-

Table 2 - Genotypic mean squares for different traits in a complete 6×6 diallel cross under normal and high temperature regimes.

Traits	MEAN SQUARES	
	Normal temperature	High temperature stress
Transpiration rate	1.0997**	0.0538**
Osmotic potential	0.0206*	0.093**
GDDS to 50% tasseling	11,465.79**	10,223.29**
Number of grains plant^{-1}	64,851.37**	28,271.55**
kernel yield plant^{-1}	1,350.58**	1,523.509**

* = Significant at 0.05 and **= 0.01 probability levels

Table 3 - Summary of tests of adequacy of additive-dominance model (regression and arrays analyses of variance) for the physiological traits.

Trait	Temp	Regression analysis		Analysis of variance of arrays		Remarks
		H_o: b = 0	H_o: b = 1	$W_r + v_r$	$W_r - v_r$	
Osmotic Potential	NT	3.977*	-0.545^{NS}	0.0002^{NS}	0.00008^{NS}	Adequate by regression analysis
	HTS	3.4435*	0.2374^{N}	0.0003^{NS}	0.000026^{NS}	Adequate by regression analysis
Transpiration rate	NT	2.8217*	1.2085^{NS}	0.1957**	0.0213**	Adequate by regression analysis
	HTS	3.4276*	-0.7424^{NS}	2.4482**	0.3754^{NS}	Adequate by both the tests
GDDs to 50% tasseling	NT	6.3738**	1.7216^{NS}	8,109,174 **	2497,413**	Adequate by regression analysis.
	HTS	6.8272**	1.3168^{NS}	69,032,500**	1,009,890^{NS}	Adequate by both the tests
No. of kernels plant^{-1}	NT	3.0078*	1.07445^{NS}	360,308,900**	340654100^{NS}	Adequate by both the tests
	HTS	3.2512*	2.5851^{NS}	22.7471**	3.0572**	Adequate by regression analysis
Grain yield plant^{-1}	NT	3.03111*	1.5877^{NS}	57,743.6*	7684.1^{NS}	Adequate by both the tests
	HTS	2.7928*	1.7104^{NS}	5.9542 **	1.0414**	Adequate by regression analysis

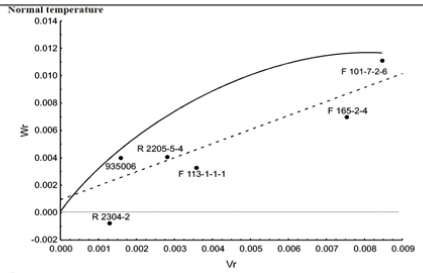
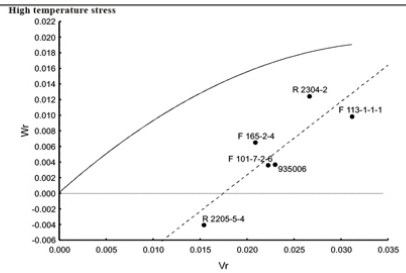
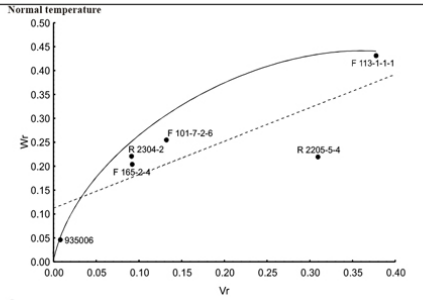
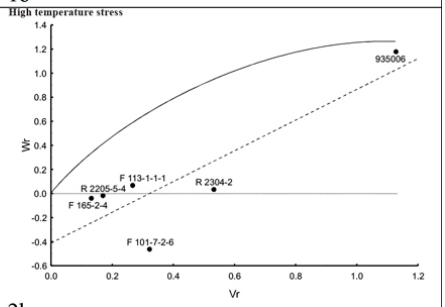
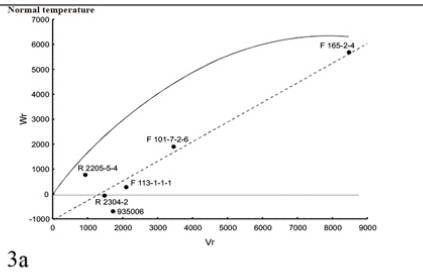
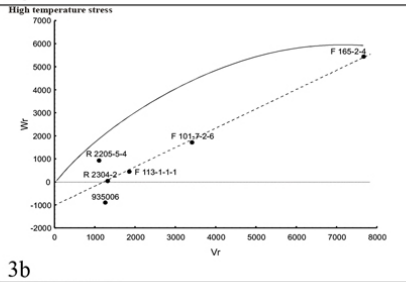
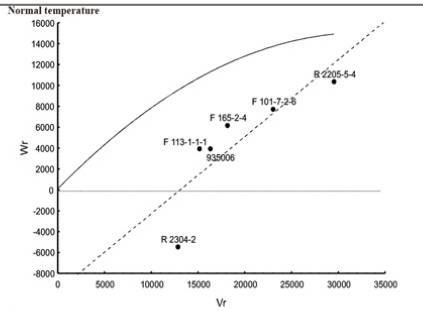
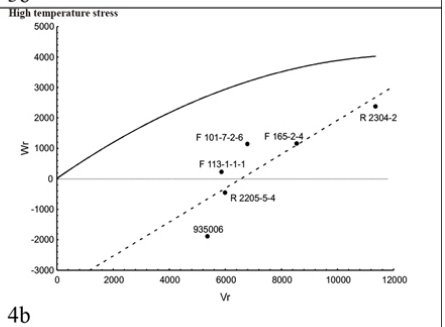
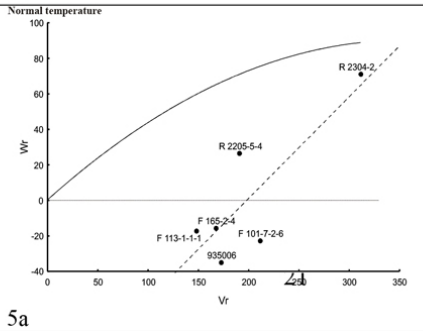
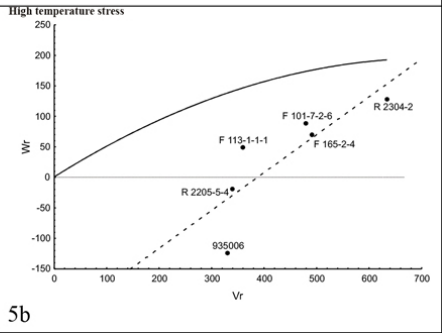
equal values of H_1 and H_2 at both the regimes for this trait were found. A positive and non significant value of **F** at normal temperature regime was assessed but at high temperature stress, positive genes became significantly frequent. The non-significance of values of h^2 indicated that effect of heterozygous loci was not important for transpiration rate. Mean degree of dominance $(H_1/D)^{0.5}$ at normal temperature regime was much less than one (0.7174) the position of intercept above origin estimated was more than one (1.2438) at high temperature stress regime.

Heritability in broad sense was 96.95% at normal temperature regime that was reduced to 38.54% at high temperature regime. Because high temperature stress significantly influenced the trait and reduced genetic variation to a larger extent. Narrow sense heritability was higher at normal temperature regime (76.49%) that was reduced to negative influenced with high temperature. Environmental variation (**E**) was non significant at normal temperature but it was highly significant at high temperature stress.

Graphical presentation of the data (Figure 2A) also displayed significant additive variation at normal temperature regime because the intercept of the regression line was passing through origin but over dominant type of gene action for transpiration rate at high temperature regime because the intercept of the regression line was passing bellow origin at high temperature regime. Distribution of array points in the graphs depicted that at normal regime, parent 935006 had the most dominant genes for transpiration rate followed by F165-2-4 and R2304-2 while F113-1-1-1 had the most recessive genes for this trait. R2205-5-4 was of intermediate constitution (Figure 2A). In case of high temperature stress regime, the array points revealed that the parent F165-2-4 had the most dominant genes being in close vicinity to the origin followed R2205-5-4, F101-7.2-6, and F113-1-1-1 while the parent by 935006 had the most recessive genes for transpiration rate having farthest position from the origin. The line F165-2-4 proved most stable at both temperature regime in expression of dominant genetic behavior (Figures 2A,B).

Genetic analysis for growing degree days to 50% tasseling was partially adequate at normal temperature regime due to adequacy in regression analysis and completely adequate by both the tests for additive dominant model at high temperature regime (Table 3). Genetic components of variation were estimated (Hayman, 1954b) and presented in Tables 4 and 5 at normal and high temperature regimes respectively. Significant value of **D** and H_1 and H_2 at both temperature regimes for control of this trait was calculated. The magnitude of H_1 and H_2 were much higher than that of **D** values for this trait at both temperature regimes. Unequal values of H_1 and H_2 at both environmental regimes were estimated. A positive and significant value of **F** was found at both temperature regimes. Significant values of h^2 for growing degree days to 50% tasseling at both temperature regimes were also assessed. Environmental portion of variation (**E**) was found non-significant. Heritability in broad sense was medium at normal temperature regime (44.91%) that increased up to 89.77% at high temperature regimes. Lower values of narrow sense heritability revealed that genetic variation relevant to additive genes was comparatively low (40.35% and 17.6%, respectively).

Graphical presentation of the data (Figures 3A,B) also displayed the over dominant type of gene action for growing degree days to 50% tasseling under both temperature conditions. Distribution of array points depicted that at normal regime, parents R2304-2, R2205-5-4, 935006, and F113-1-1-1 had the most dominant while F165-2-4 had the most recessive genes for this trait. The F101-7-2-6 had intermediate constitution (Figure 4A). At high temperature stress, the parents R2304-2, R2205-5-4, and F113-1-1-1 had the most dominant genes for growing degree days to 50% tasseling while F165-2-4 had the most recessive genes for this trait having farthest position from the origin (Figure 4B).

Trait	At normal temperature regime	At high temperature regime
Osmotic potential	 1a	 1b
Transpiration rate	 2a	 2b
Growing degree days to 50% tasseling	 3a	 3b
No. of kernels plant^{-1}	 4a	 4b
Kernel yield plant^{-1}	 5a	 5b

Figures 1~5 - W_r/V_r graphs for various physio-agronomic traits studied in maize.

Table 4 - Estimation of the components of genetic variation at normal temperature regime.

Genetic components	Osmotic potential	Genetic components	Osmotic potential	Genetic components	Osmotic potential
D	0.0129* ± 0. 001412	0.5388* ± 0.0635	7651.73 *± 697.41	7274.9* ± 2602.1	133.29* ± 36.01
H_1	0.00387^{NS} ± 0.000359	0.2773^{NS} ± 0.1611	11238.66* ± 1770.44	65219.97* ± 6605.76	1470.36* ± 91.40
H_2	0.001351^{NS} ± 0.00320	0.2274^{NS} ± 0.1439	8317.4* ± 1581.59	63203.65* ± 5901.1	1455.36* ± 81.65
F	0.00945* ± 0.00345	0.1637^{NS} ± 0.1551	4086.03* ± 1703.8	-3021.9^{NS} ± 6357.02	-30.42^{NS} ± 87.96
h^2	-0.00215^{NS} ± 0.00216	0.02527^{NS} ± 0.0969	18043.56* ±1064.51	202560.3* ± 3971.82	4705.85*± 54.96
E	0.00408* ± 0.000534	0.00848^{NS} ± 0.0240	123.6100^{NS} ± 263.60	479.46^{NS} ± 983.51	11.351^{NS}± 13.61
$(H_1/D)^{0.5}$	0.5477	0.7174	1.5544	2.9942	3.3214
$h^{2\,(n.s)}$	40.35%	76.49%	44.18%	27.43%	19.24%
$h^{2\,(b.s)}$	44.91%	96.95%	96.87%	97.86%	97.56%

* = P < 0.05; NS = Not Significant

Genetic analysis for number of kernels plant^{-1} was completely adequate by both the tests for additive dominant model at normal temperature regime and partially adequate due to adequacy by regression analysis at high temperature regime (Tables 4 and 5). However, specific genes effects for additive variance (**D**) was significant at normal temperature regime for number of kernels plant^{-1} while at high temperature stress significant **D** turned-non significant. The magnitude of H_1 was much higher than that of **D** value for this trait at high temperature regime. Dominant variations (**H**) were significant at both temperature regimes. H_1 and H_2 components were found unequal distribution at both temperature regimes (Tables 4 and 5). Non-significant values of **F** were evaluated at both temperature stress regimes. The values of h^2 were found significant at both temperature regimes. However, environmental variance (**E**) was non-significant in both temperature regimes for kernels plant^{-1}. Over dominance type of gene action for the trait was previously reported (Shakil, 1992). Mean degree of dominance $(H_1/D)^{0.5}$ at normal (2.9942) and high temperature (4.7565) regime was greater than one. The regression line intercepted the W_r-axis below the point of origin, for number of kernels plant^{-1} at both temperature regimes (Figures 4A,B). Distribution of array points (Figure 4A) depicted that the parental inbred line R2304-2 were located nearest to the origin while R2205-5-4 farthest from the origin at normal regime. At high temperature stress regime 935006 were computed closest to the origin while 2304-2 farthest to the origin for number of kernels plant^{-1}. The broad sense heritability was highest for number of kernels plant^{-1} **T** trait was least influenced with environment. Narrow sense heritability was less than 38% at both temperature regimes.

Genetic analysis for kernel yield plant^{-1} was completely adequate by both the tests for additive dominant model at normal temperature regime and partially adequate due to adequacy by regression analysis at high temperature regime (Table 5). Dominant components were more prominent than additive at normal temperature regime. The significant values of **D** and **H** components at normal temperature regime displayed the importance of additive as well dominance effects for the control of kernel yield plant^{-1} but dominant effect was significant compared to non significant additive effect at high temperature stress (Table 5). The magnitude of H_1 and H_2 was much higher than that of **D** value which indicated preponderance of dominant component of variation for this trait at high temperature regime. Similar values of H_1 and H_2 were recorded. Values of **F** were negative but non-significant. Components h^2 were also significant in the expression of kernel yield plant^{-1}. Environmental variation (**E**) was also non significant at both temperature regimes. Broad sense heritability was highest at both temperature regimes. Narrow sense heritability was recorded as 19.24% and 36.75%, respectively. Mean degree of dominance $(H_1/D)^{0.5}$ at normal (3.3214) and high temperature (5.906) regimes was greater than one for this trait.

Graphical presentation of the data (Figures 5A,B) also depicted over dominance for kernel yield plant^{-1} at both temperature regimes. Distribution of array points on regressions that showed that Inbred lines 935006, F165-2-4, F113-1-1-1, and F101-7-2-6 were in close proximity to the point of origin and the line R2304-2 contained the most recessive genes for kernel yield plant^{-1} at normal temperature regime. R2205-5-4 contained dominant and recessive genes in equal frequencies. At high temperature regime the inbred line 935006 followed by R2205-5-4 contained the most dominant genes while R2304-2 had the least dominant genes at normal and high temperature stress regimes, respectively. The remaining inbred lines were of intermediate constitution. The inbred lines 935006 (with frequent dominant genes) and R2304-2 (with frequent recessive genes) maintained their genetic behavior in expression of this trait.

Discussion

Genetic variation is partitioned into various components for exploiting it for crop improvement by changing traits architecture in hybrids enabling them well adopted in high temperature zones in the world. Graphical presentation over W_r/V_r not only confirm mode of gene action but also mark parents with frequent dominant close to the origin and recessive genes farther from origin on regression which is helpful in choice of parents for hybridization. Inbred lines 935006 and R2205-5-4 had maximum dominant genes for maintaining osmotic potential at high temperature stress condition

Estimation of genetic components of variation for osmotic potential displayed significant additive

Table 5 - Estimation of the components of genetic variation at high temperature stress regime.

Genetic components	Traits				
	Osmotic potential	Transpiration rate	GDDS to 50% tasseling	N° Kernels Plant^{-1}	Kernel yield Plant^{-1}
D	0.00929* ± 0.0022	1.1041* ± 0.2259	4,380.64* ± 571.84	1,258.92^{NS} ±972.17	47.409^{NS} ± 52. 97
H_1	0.0761* ± 0.00567	1.7079* ± 0.5734	9,756.64*± 1,451.64	28,481.99*± 2,467.95	1,653.58*± 134.47
H_2	0.077* ± 0.00506	0.9224^{NS} ± 0.5122	7,461.6* ± 1,296.79	21,952.22*± 2,204.68	1,326.08*± 120.13
F	-0.00105^{NS} ± 0.0055	1.9201* ± 0.5518	3,795.76* ± 1,396.98	940.42^{NS} ± 2,375.02	-25.30^{NS} ± 129.41
h^2	0.0678* ± 0.00341	-0.1715^{NS} ± 0.3448	15,303.51* ± 872.84	51,789.18*± 1,483.89	3,391.40 *± 80.85
E	0.00273* ± 0.3084	0.34* ± 0.0854	301.00^{NS} ± 216.13	198.75^{NS} ± 367.45	12.856^{NS} ± 20.02
$(H_1/D)^{0.5}$	2.8609	1.2438	1.4924	4.7565	5.906
$h^{2\,(n.s)}$	17.60%	-0.0273 %	39.93 %	37.58%	36.75 %
$h^{2\,(b.s)}$	89.77%	38.54 %	91.65 %	97.82 %	97. 64 %

* = P < 0.05; NS = Not Significant

variation (**D**) only for osmotic potential at normal temperature regime (Table 4) while the significant dominant variation (**H_1** and **H_2**) at high temperature regime (Table 5). Equal values of **H_1** and **H_2** at high temperature regime were calculated. Value of **F** was significant and positive indicating dominant alleles were more frequent than recessive alleles at normal temperature regime but the value of **F** turned negative and non-significant depicting that dominant gene frequency was decreased under high temperature stress. **h^2** was non-significantly negative which also confirmed decreasing dominant genes. Heritability in broad sense was low under normal temperature regime (44.91%) that increased up to 89.77% at high temperature regime depicting higher genetic variation or least influence of environment at high temperature stress. Lower values of narrow sense heritability revealed that genetic variation relevant to additive genes was comparatively low (40.35 and 17.6%). Low heritability in narrow sense at high temperature stress also depicted the trait was less contribution of additive genetic component.

Graphical presentation of the data (Figure 1A) also displayed significant additive gene action for osmotic potential at normal temperature regime while over dominant type of gene action at high temperature stress regime (Figure 1B). It seems that some silent genes were triggered on at high temperature stress to enable plant tolerant to high temperature due to phenomena of homoeostasis. Distribution of array points closed to origin displayed the dominant gene distribution among the parents. The inbred line R2304-2 followed by 935006, R2205-4, and F113-1-1-1 had maximum dominant genes while F101-7-2-6 followed by F165-2-4 had maximum recessive genes for osmotic potential at normal temperature regime while the inbred line R2205-4 had maximum dominant genes while F101-7-2-6, 935006, and F165-2-4 had intermediate position and R2304-2 and F113-1-1-1 had maximum recessive genes for osmotic potential at high temperature stress regime This line can be utilized in hybridization program for maintaining osmotic potential under high temperature stress. The inbred line R2205-4 showed stability in genetic behavior at both temperature regimes. Over-dominant type of gene action was assessed in drought stress regime for this trait (Malik et al, 2004; Tabassum, 2004).

Genetic analysis for transpiration rate was proved partially adequate at normal temperature regime due to adequacy in regression analysis and completely adequate by both the tests for additive dominant model at high temperature regime (Table 3). Genetic components of variation were estimated (Hayman, 1954b). Significant value of **D** at normal and high temperature regimes indicated the importance of additive genetic effects. The magnitude of **H_1** and **H_2**were non-significant at normal temperature regime indicated preponderance of additive mode of gene action for this trait at normal temperature regime but the magnitude of **H_1** was much higher than that of **D** value which indicated preponderance of over dominant mode of gene action for this trait at high temperature regime. Dominant variation was also indicated by **H** components (**H_1** and **H_2**).

H_1 was non-significant at normal temperature which turned highly significant at high temperature regime. However, **H_2** values were non-significant at both the temperature regimes.

Unequal values of **H_1** and **H_2** at both environmental regimes displayed the dissimilar distribution of dominant genes in parents for this trait. A positive and non significant value of **F** indicated that positive genes were not significantly frequent at normal temperature regime but at high temperature stress positive genes became significantly frequent. The non-significance of values of **h^2** indicated that effect of heterozygous loci was not important for transpiration rate. Mean degree of dominance **$(H_1/D)^{0.5}$** at normal temperature regime much less than one (0.7174) the position of intercept above origin depicted prevalence of additive gene effect and mean degree of dominance **$(H_1/D)^{0.5}$** at high temperature stress regime was more than one (1.2438) indicating the over dominant type of gene action. Heritability in broad sense was 96.95% at normal temperature regime depicting higher genetic variation that was reduced to 38.54 % at high temperature regime. Because high temperature stress highly influenced the trait and reduced genetic variation to a larger extent. Narrow sense heritability revealed that genetic variation related to additive genes was higher at normal temperature regime (76.49%) that was reduced to negative at influence of high temperature. Environmental variation (**E**) was non-significant at normal temperature but it was highly significant at high temperature stress.

Graphical presentation of the data (Figure 2A)

also displayed significant additive variation at normal temperature regime because the intercept of the regression line was passing through origin but over dominant type of gene action for transpiration rate at high temperature regime because the intercept of the regression line was passing bellow origin at high temperature regime. Over dominance type of gene action for transpiration rate was reported by Siddiqui (1988) and Zia and Chaudhry (1980), while it was reported in control of partially dominant genes effect. Khalid et al (1979) claimed transpiration rate at control of additive type of gene action While Bukhari (1986), Tabassum (1989), and Setty (1975) reported additive gene action for this trait. Sharma and Bhalla (1990) reported dominance type of gene action for transpiration rate. Distribution of array points in the graphs depicted that at normal regime, parent 935006 had the most dominant genes for transpiration rate followed by F165-2-4 and R2304-2 while F113-1-1-1 had the most recessive genes for this trait. R2205-5-4 was of intermediate constitution (Figure 5A). In case of high temperature stress regime, the array points revealed that the parent F165-2-4 had the most dominant genes being in close vicinity to the origin followed R2205-5-4, F101-7.2-6, and F113-1-1-1 while the parent by 935006 had the most recessive genes for transpiration rate having farthest position from the origin. The line F165-2-4 proved most stable at both temperature regime in expression of dominant genetic behavior (Figures 2A,B).

Genetic analysis for growing degree days to 50% tasseling was partially adequate at normal temperature regime due to adequacy in regression analysis and completely adequate by both the tests for additive dominant model at high temperature regime (Table 3). Genetic components of variation were estimated (Hayman, 1954b) and presented in Tables 4 and 5. Significant value of **D**, $\mathbf{H_1}$, and $\mathbf{H_2}$ at both temperature regimes indicated the significance of additive and dominant genetic effects for control of this trait. The magnitude of $\mathbf{H_1}$ and $\mathbf{H_2}$ were much higher than that of **D** values which indicated preponderance of dominant of gene action for this trait at both temperature regimes. Unequal values of $\mathbf{H_1}$ and $\mathbf{H_2}$ at both environmental regimes displayed the different distribution of dominant genes in parental inbred lines. A positive and significant value of **F** indicated that positive genes were frequent at both temperature regimes. The significance of value of $\mathbf{h^2}$ indicated the important effect of heterozygous loci for growing degree days to 50% tasseling at both temperature regimes. $\mathbf{h^2}$ was significantly positive which also confirmed significance of dominance. This trait was least influenced with environment. Heritability in broad sense was low at normal temperature regime (44.91%) that increased up to 89.77% at high temperature regime depicting higher genetic variation at high temperature stress. Lower values of narrow sense heritability revealed that genetic variation relevant to additive genes was comparatively low (40.35 and 17.6%). Heritability in narrow sense at both temperature regimes also depicted that the trait was predominantly in control of dominant/over dominant type of gene action. Number of days to 50% tasseling was reported in control of additive gene action (Prakash et al, 2004). Contradictory results may be due to different genetic background of the cultivars used and different environmental regimes.

Graphical presentation of the data (Figures 3A,B) also displayed the over dominant type of gene action for growing degree days to 50% tasseling under both temperature conditions. The results are in accordance with those of an over dominance type of gene action for growing degree days to 50% tasseling as reported by Saleem et al (2002) and Siddiqui (1988), while Zia and Chaudhry (1980) found growing degree days to 50% tasseling in control of partially dominant gene effect. Bukhari (1986) and Tabassum (1989) evaluated growing degree days to 50% tasseling under control of additive type of gene action. Sharma and Bhalla (1990) reported dominant type of gene action for growing degree days to 50% tasseling. The genetic control for growing degree days to 50% tasseling may vary from breeding material to material due to genes modification, difference in environment or interaction of genes with the environment.

Distribution of array points depicted that at normal regime, parents R2304-2, R2205-5-4, 935006, and F113-1-1-1 had the most dominant while F165-2-4 had the most recessive genes for this trait. The F101-7-2-6 had intermediate constitution (Figure 4A). At high temperature stress, the parents R2304-2, R2205-5-4 and F113-1-1-1 had the most dominant genes for growing degree days to 50% tasseling while F165-2-4 had the most recessive genes for this trait having farthest position from the origin (Figure 4B).

Genetic analysis for number of kernels plant^{-1} was completely adequate by both the tests for additive dominant model at normal temperature regime and partially adequate due to adequacy by regression analysis at high temperature regime (Tables 4 and 5). However, specific genes effects changed the additive variance (**D**) was significant at normal regime which indicated that the additive genetic effects for number of kernels plant^{-1} were important; while at high temperature stress significant **D** turned-non significant. The magnitude of $\mathbf{H_1}$ was much higher than that of **D** value which indicated preponderance of dominant mode of gene action for this trait at high temperature regime. Dominant variations (**H**) were significant at both temperature regimes. $\mathbf{H_1}$ and $\mathbf{H_2}$ components were unequal, depicting a different gene distribution at both temperature regimes (Tables 4 and 5). Negative but non-significant value of **F** expressed that negative genes were present in lesser number at normal temperature regime whereas at high temperature stress regime, positive genes were present in lesser

number as indicated by a non significant positive value of **F**. The values of h^2 were significant at both temperature regimes, depicting important effects of heterozygous loci. However, environmental variance (**E**) was non-significant in both regimes, indicating negligible effects of environment in the determination of number of kernels plant^{-1}. Over dominance type of gene action for the trait was previously reported (Shakil, 1992). Mean degree of dominance $(H_1/D)^{0.5}$ at normal (2.9942) and high temperature (4.7565) regime was greater than one indicating the over dominance type of gene action.

The regression line intercepted the W_r-axis below the point of origin, showing the presence of over dominance in the expression of number of kernels plant^{-1} at both temperature regimes (Figures 4A,B). Saleem et al (2002), Malik et al (2004), and Tabassum (2004) reported over dominance type of gene action for numbers of kernel rows/ear and numbers of kernels per row. Distribution of array points (Figure 4A) depicted that the parental inbred line R2304-2 being located nearest to the origin, carried the most dominant genes while R2205-5-4 being farthest from the origin contained the least dominant genes at normal regime. At high temperature stress regime 935006 had maximum dominant genes being closest to the origin while 2304-2 contained the least dominant genes being farthest to the origin for number of kernels plant^{-1}. The change in genes expression for a trait at different environments was also reported by Jana (1975). The broad sense heritability revealed that number of kernels plant^{-1} was least influenced by environment. Narrow sense heritability depicted that the trait was predominantly in control of non additive genes as narrow sense heritability was less than 38% at both temperature regimes.

Genetic analysis for kernel yield plant^{-1} was completely adequate by both the tests for additive dominant model at normal temperature regime and partially adequate due to adequacy by regression analysis at high temperature regime (Table 5). Dominant components were more prominent than additive at normal temperature regime. Kernel yield was previously reported over dominant type of gene action (Munir et al,1977; Zia and Chaudhry, 1980; Bukhari, 1986; Chen et al, 1996; Malik et al, 2004; Tabassum, 2004; Singh et al, 2001) in maize, while Hussain et al (2008) reported over dominant gene action in wheat. The significant values of **D** and **H** components at normal temperature regime displayed the importance of additive as well dominance effects for the control of kernel yield plant^{-1} but dominant effect was significant compared to non significant additive effect at high temperature stress (Table 5). The magnitude of H_1 and H_2 was much higher than that of **D** value which indicated preponderance of dominant component of variation for this trait at high temperature regime. Similar values of H_1 and H_2 indicated the approximately equal distribution of dominant genes among the parents. Values of **F** were negative but non significant displaying the frequency of dominant and recessive genes at both environments were non-significantly. Components h^2 were also significant displaying the idea that heterozygous loci had an important role in the expression of kernel yield plant^{-1}. Environmental variation (**E**) was also non significant at both temperature regimes. Broad sense heritability exhibited the highest genetic variability at both temperature regimes. Narrow sense heritability was recorded as 19.24% and 36.75%, respectively, depicting the smaller portion of genetic variability in additive genes control. Mean degree of dominance $(H_1/D)^{0.5}$ at normal (3.3214) and high temperature (5.906) regimes was greater than one indicating the over dominance type of gene action for the control of this trait.

Graphical presentation of the data (Figures 5A,B) also depicted over dominance for kernel yield plant^{-1} at both temperature regimes. Bukhari (1986), Siddiqui (1988), Naveed (1989), and Yousaf (1992) claimed over dominance type of gene action. Tabassum (1989) and Mani et al (2000), on the other hand, reported additive gene action. Distribution of array points indicated that inbred lines 935006, F165-2-4, F113-1-1-1, and F101-7-2-6 contained maximum dominant genes and the line R2304-2 contained the most recessive genes for kernel yield plant^{-1} at normal temperature regime. R2205-5-4 contained dominant and recessive genes in equal frequencies. At high temperature regime the inbred line 935006 followed by R2205-5-4 contained the most dominant genes while R2304-2 had the least dominant genes at normal and high temperature stress regimes, respectively. The remaining inbred lines were of intermediate constitution in expression of this trait. The inbred lines 935006 (with frequent dominant genes) and R2304-2 (with frequent recessive genes) maintained their genetic behavior in expression of this trait.

Conclusion

Osmotic potential and transpiration rate showed additive and partial dominance, respectively while growing degree days to 50% tasseling showed over dominance at normal temperature regime but all traits depicted over dominance at high temperature stress regime. The inbred line R2205-5-4 and 935006 kept their consistency at both the temperature regimes in their mode of genetic expression for osmotic potential. 935006 had maximum dominant genes for transpiration rate but these became recessive in their expression at high temperature stress to minimized water losses at high temperature stress. F165-2-4, 935006 followed by R2304-2 also showed consistency in their genetic mode of expression for this trait to transpire more to keep the internal plant body temperature cool. 935006 and F113-1-1-1 expressed their maximum dominant genes for growing degree days to 50% tasseling. 935006 also expressed maximum dominant genes for number of kernels plant^{-1} and kernel yield plant^{-1}. The hybrids 935006

× R2304-2, F165-2-4 × 935006 and 935006 × F101-7-2-6 involving inbred line 935006 may promise for higher yield potential at both temperature regimes for improvement in kernel yield plant^{-1} and other physiological traits.

Acknowledgements

Highly gratified to the Government of Punjab, Department of Agriculture for according permission for PhD studies and highly thank a lot to Dr M Miezzalama, Head of Seed Inspection and Distribution Unit, CIMMYT, Mexico, for addition in maize germplasm for this research.

References

Gruis DF, Guo H, Selinger D, Tian Q, Olsen OA, 2006. Surface position, not signaling from surrounding maternal tissues, specifies aleurone epidermal cell fate in maize. Plant Physiol 141: 898-909

Anonymous, 2005-2006. Agricultural Statistics of Pakistan, Government of Pakistan. Ministry of Food, Agriculture and Livestock, Food, Agriculture and Livestock division

Azhar FM, McNeilly T, 1988. The genetic basis of variation for salt tolerance in *Sorghum bicolor* L. Moench seedlings. Pl Breed 1010: 114-121

Bukhari SH, 1986. Diallel analysis of yield and yield components in maize. MSc thesis, Dept Pl Br Genet, Univ Agri Faisalabad, Pakistan

Chen L, Cui SP, Sun YB, 1996. Analysis of the gene effect on ear characters in maize. Acta Agri Boreali Sinica 11(2): 28-32

Hayman BI, 1954a. The theory and analysis of diallel crosses. Genetics 39: 379-308

Hayman BI, 1954b. The analysis of variance of diallel tables. Biometrics 10: 235-244

Herrero MP, Johnson RR, 1980. High temperature stress and pollen viability of maize. Crop Sci 20: 796-800

Hussain F, Sial RA, Ashraf M, 2008. Genetic Studies for Yield and Yield Related Traits in Wheat under Leaf Rust Attack. Int J Agri Biol 10(5): 531–535

Hussain T, Khan IA, Malik MA, Ali Z, 2006. Breeding potential for high temperature tolerance in corn. Pak J Bot 38(4): 1185-1196

Jana S, 1975. Genetic analysis by means of diallel graph. Heredity 35: 1-19

Johnson LVP, Aksel R, 1964. Inheritance of malting quality and agronomic characters in diallel cross of barley. Can J Genetic Cytol 6: 178-200

Kruvadi S, 1991. Diallel analysis and heterosis for yield and associated characters in maize in upland regime. Turrialba Publ 41(3): 335-338

Mahmood IM, Rashed MA, Fahmy EM, Dheaf MFA, 1990. Heterosis, combining ability and type of gene action in a 6x6 diallel of maize. Proceedings of the 3rd conference of Agric Development Res. Annal Agric Sci Cairo Special Issue 307.

Malik SI, Malik HN, Minhas NM Munir M, 2004. General and specific combining ability studies in maize diallel crosses. Int J Agri Biol 6(5): 856–859

Mani VP, Gupta NP, Bisht GS, Singh R, Singh R, 2000. Genetic variance and heritability of some ear traits in prolific maize (*Zea mays* L.). Crop Res Hisar (India) 20(2): 217-220

Munir MSD, Shah, Aslam M, 1977. Gene action controlling yield and its components in maize. Pak J Agic Sci 14(1): 63-68

Naved A, 1979. Genetic analysis of yield ant its economic characters in maize. MSc thesis, Dept Pl Br Genet Univ Agri Faisalabad, Pakistan

Saleem M, Shahzad K, Javed M, Ahmed A, 2002. Genetic analysis for various quantitative traits in maize (*Zea mays* L.) inbred lines. Int J Agric Biol 4(3): 379-382.

Sharma JK, Bhalla SK, 1990. Combining ability for drought tolerant traits in maize. Crop Improvement 1792: 144-149

Siddiqui NA, 1988. Genetic analysis of yield its components in maize diallel crosses. MSc thesis, Dept Pl Br Genet Univ Agri Faisalabad, Pakistan

Singh AK, Shahi JP, Singh JK, Singh RN, 2001. Genetic control of some traits in maize (*Zea mays* L.). Crop Improvement 28(1): 56-61

Singh RK, Chaudhry BD, 1985. Biometrical methods in quantitative genetics analysis. Kalyani Publishers, New Delhi, India

Sinsawat V, Pandy J, Leipner P, Stamp P, Fracheboud Y, 2004. Effect of heat stress on the Photosynthetic apparatus in maize (*Zea mays* L.) grown at control and high temperature. Environ Exp Bot 52: 123-129.

Smith KL, 1996. Ohio Agron. Guide, Corn production. Ohio state Univ, USA, bulletin: 472

Steel RGD, Torrie JH, 1984. Principles and Procedures of Statistics. A biometrical Approach. 2nd Ed. McGraw Hill Book Co, New York

Steven J, Brandner C, Salvucci M, 2002. Sensitivity of photosynthesis in C4 maize plant to heat stress. Plant Physiol 129: 1773-1780

Sullivan CY, 1972. Mechanisms of heat and drought resistance in grain sorghum and methods of measurement. In: Sorghum in the seventies. Rao NGP, House LR eds. Oxford and IPH publishing Co, New Delhi

Tabassum MI, 1989. A study of gene action for economic characters in maize (*Zea mays* L.). MSc (Hons.) thesis, Dept Pl Breed Genet Univ Agri Faisalabad, Pakistan

Yousaf M, 1992. Genetic analysis of yield and yield components in maize diallel crosses. MSc thesis, Dept Pl Br Genet Univ Agri Faisalabad

Zia MK, Chaudhry AR, 1980. Gene action for yield and its components in maize. Pak J Agric Sci 17(2): 87-92