

ESTIMATES OF GENETIC EFFECTS FOR PHYSIOLOGICAL AND YIELD RELATED TRAITS IN MAIZE UNDER HIGH TEMPERATURE

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ABSTRACT

Abrupt climate changes and harsh environmental conditions are basic causes of food threatening scenarios in the world. Among these, global warming is proving as a major factor in declining of cereal production especially maize all around the world. Basic aim of this research was to observe the inheritance pattern of various physiological and yield attributes in maize under stress and selection of parents for future breeding program. Six heat tolerant maize inbred lines were mated in full diallel combination. Parents along-with F₁ progeny were sown in the field using Randomized Complete Block Design with three replications. Data of seven (7) parameters like ear leaf area, leaf osmotic potential, chlorophyll contents, canopy temperature depression, net photosynthetic rate, plant height and grain yield were estimated for parents and their cross combinations. Graphical expression and dominance ratio depicted preponderance of non-additive gene action for all parameters under both environmental conditions except for leaf osmotic potential under stress environment. Due to over-dominance nature of inheritance pattern, heterosis breeding is a suitable breeding strategy for improvement of studied parameters. Inbreds NCIL-10-5 & D-135 had maximal dominant genes for most of the physiological & yield attributes under heat stress. These inbred lines have a potential of sustainable performance under adverse environment and can be used to develop heat tolerant maize hybrids with sustainable yield.

Key words: Canopy temperature depression; Hayman analysis; Leaf osmotic potential; Maize

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INTRODUCTION

Maize is a major leading crop and ranks third among cereals in Pakistan. *Zea mays* has a wider genetic variability and could be grown over a vast range of agro-ecological zones of the world. It is getting enormous popularity in over-populated countries like Pakistan due to its high productivity (Shah *et al.*, 2014). It is a versatile crop used for industry, human food and animal feed. However, direct consumption of maize as human food is decreasing while indirect consumption as wet milling and animal feed is increasing in Pakistan (Tariq and Iqbal, 2010). Climate of the globe is changing abruptly, resulting in harsh weather conditions and shifts in patterns of rain, temperature, drought and flood. Developing countries like Pakistan are more vulnerable to these climatic shifts due to short in sources of mitigation (Kurukulasuriya *et al.*, 2006, Mendlesohn, 2014).

Being a tropical crop, maize plant has a little potential to tolerate a high temperature stress at its vegetative and reproductive growth stages (Farooq *et al.*, 2009). Maize plant shows positive growth responses during day temperature 25-32 °C and 16-23 °C at night. Plant performance is highly affected with any slight changes in its optimum temperature range. Sudden

temperature escalation leads to increase in leaf temperature, lowering of photosynthesis related activities (RuBisCO activity decreased) and increase of evapotranspiration from soil and plant was triggered (Steven *et al.*, 2002, Janni *et al.*, 2020). Plant height and stem growth were adversely affected by high temperature, as under stress conditions short plant height because of retarded stem growth was observed in maize (Parsad *et al.*, 2006a).

Understanding the nature of genetic attributes for inheritance of studied parameters is essential to run a successful maize breeding programme under high temperature stress environment. It is difficult to run a breeding plan for evolution of high yielding hybrids under unfavourable environment as compared to favourable environment. Diallel is one of the best biometrical technique for estimation of genetic attributes like gene action and heritability which are helpful in selection of suitable parents for particular breeding programme (Al-Falahy, 2015).

The primary objective of this study was to find out the pattern of inheritance (gene action & heritability) for physiological traits & grain yield under normal and heat stress environment and selection of parents to develop heat resilient maize hybrids.

MATERIALS AND METHODS

Six heat tolerant inbred lines i.e., D-103, D-135, WA-3748, NCIL-10-5, NCIL-20-4 and NCIL-30-5, were obtained from NARC, Islamabad. These parents were mated in full diallel fashion during Autumn 2018. Controlled cross-pollination was done to avoid foreign contamination and to obtain desired and productive hybrids. Parents, F₁s and their reciprocal crosses were planted in the field during spring 2019 under normal and stress environment. The plant material was sown into two sets using a triplicate randomized complete block design during first fortnights of February & March, respectively. Purpose of late planting (March) was to expose the crop against high temperature at flowering and terminal growth stages. Data of the following attributes was noted from five (5) randomly selected plants under both experimental conditions. Recorded data was averaged to use for statistical analysis. Following parameters were observed;

Physiological Traits: 3rd leaf from the plant was removed and freezed below -20°C in a freezer. Cell juice was extracted by using a disposable syringe, after thawing process was completed in the tissue. Osmometer was used to measure the leaf osmotic potential (LOP) from extracted cell juice.

$$\text{Leaf osmotic potential (n)} = \text{miliosmoles} \times 0.0832 \times \text{Temp.} \left(\frac{^{\circ}\text{K}}{1}\right)$$

Chlorophyll contents (mg g⁻¹ fr. wt.) were measured from the top second intact leaf by using chlorophyll meter (SPAD 502DL Plus).

A portable Infrared gas analyzer (CI-340, CID, Inc. USA) was used to measure the net photosynthetic rate (Pn) from the second intact leaf. Data was recorded at noon between 11:00 – 14:00 pm on a clear sunny day at PAR>1150 μmol m⁻² s⁻¹.

$$P = -W \times (C_0 - C_1) = -2005.39 \times V \times P \times (C_0 - C_1) T \times A$$

Where,

C₀ (C₁): o (i) CO₂ c (ppm or μmol ÷ mol)

$$W = M f r p l e a \left(\frac{m}{m^2}\right) / s$$

$$V = V i f r \left(\frac{li}{m}\right)$$

$$P = A i h e p (b)$$

$$T = A t e (K)$$

$$A = L a (cm^2)$$

Ear leaf area was measured by using the formula as described by Mckee, (1964).

$$L a = l e l e h (c) \times \text{leaf width (cm)} \times 0.73$$

At anthesis stage, canopy temperature was measured between 12:00-3:00 pm on a sunny day with the help of a portable infrared thermometer (CHINO-IR-AHOT). While ambient air temperature was measured by using portable thermometer and canopy temperature depression (CTD) was calculated as;

$$C = A a t e (A) - C t e (C)$$

Plant height and Grain yield per plant: Data related to plant height (PH) was measured with a meter rod in cm from ground to base of flag leaf after flowering as suggested by Guzman & Lamkey, (2000).

Grain yield (GY) in grams was measured when moisture level in the seeds was reduced upto 15%.

$$G = T w . o s h e . g (a e o e h p) \div n i o p l u p p$$

Statistical analysis: To measure the extent of genetic variation in parental lines, recorded data of the studied traits was put through for ANOVA (Steal *et al.*, 1997). Fitness of additive-dominance (AD) model, nature of genetic effects and inheritance pattern was estimated by using biometrical procedures of Hayman (1954a, b) and Mather and Jinks (1982).

RESULTS

Results of analysis of variance (Table 1) revealed that all physiological attributes & grain yield were highly significant, showing high genetic variability among inbreds & their crosses under optimal and stress environments. Components of genetic variation revealed that male, female and their interactions (Table 2) for the studied parameters were significant under both environmental conditions. These results indicated the significant role of additive as well as dominance gene action for trait inheritance.

Analysis of scaling test (Table 3a, b) pursued that regression coefficients were statistically divergent from zero (0), but not from unity for studied parameters. However, magnitude of variance and covariance analysis for array means revealed that Wr+Vr components were consequential, while Wr-Vr components were insignificant under both experimental conditions. These results showed that studied parameters were fully fit to additive-dominance model and data could be used for further biometrical analysis.

Table 1: Mean squares of maize genotypes for various traits under normal and high temperature.

Traits	Mean Squares (df = 35)	
	Normal Temperature	High Temperature
Ear leaf area	1854.03 **	1967.59 **
Leaf osmotic potential	0.006 **	0.011 **
Chlorophyll contents	16.96 **	22.68 **
Net photosynthetic rate	17.10 **	26.80 **
Canopy temperature depression	1.21 **	1.18 **
Plant height	24.28 **	21.65 **
Grain yield per plant	1367.13 **	839.68 **

** = Significant at $P \leq 0.01$ **Table 2: Mean squares (male, female and their interaction) for physiological traits and grain yield in maize under normal and high temperature.**

Traits	SOV		Female		Male × Female interaction	
	Male (df = 5)		(df = 5)		(df = 25)	
	NT	HT	NT	HT	NT	HT
Ear leaf area	5064.03 **	6882.31 **	4219.49 **	2931.9 **	738.94 **	791.78 **
Leaf osmotic potential	0.022 **	0.033 **	0.005 **	0.020 **	0.003 **	0.004 **
Chlorophyll contents	44.79 **	69.81 **	17.93 **	76.44 **	11.20 **	10.50 **
Net photosynthetic rate	54.92 **	95.57 **	22.72 **	31.70 **	8.41 **	12.07 **
Canopy temperature depression	4.04 **	3.67 **	1.89 **	2.26 **	0.50 **	0.47 **
Plant height	77.09 **	64.95 **	20.44 **	22.89 **	14.43 **	12.75 **
Grain yield per plant	3085.97 **	2860.56 **	2168.02 **	1144.6 **	863.19 **	374.52 **

** = Significant at $P \leq 0.01$ NT = Normal temperature HT = High temperature**Table 3a: Tests of adequacy of additive-dominance model for physiological traits and grain yield in maize under normal temperature.**

Traits	Regression Analysis		Mean Squares		Remarks
	Ho b=0	Ho b=1	Wr+Vr	Wr-Vr	
Ear leaf area	11.64 **	0.41 NS	1305712.30 **	9826.90 NS	Fully adequate
Leaf osmotic potential	6.56 **	0.30 NS	7.66 E-06 **	1.68 E-07 NS	Fully adequate
Chlorophyll contents	7.55 **	2.08 NS	33.07 **	0.86 NS	Fully adequate
Net photosynthetic rate	6.74 **	0.27 NS	12.03 **	0.23 NS	Fully adequate
Canopy temperature depression	11.99 **	0.38 NS	0.13 **	0.001 NS	Fully adequate
Plant height	4.26 **	0.67 NS	63.44 **	3.13 NS	Fully adequate
Grain yield per plant	7.60 **	0.51 NS	390847.01 **	6697.52 NS	Fully adequate

* = Significant at $P \leq 0.05$, ** = Significant at $P \leq 0.01$, NS = Non-significant**Table 3b: Tests of adequacy of additive-dominance model for physiological traits and grain yield in maize under high temperature.**

Traits	Regression Analysis		Mean Squares		Remarks
	Ho b=0	Ho b=1	Wr+Vr	Wr-Vr	
Ear leaf area	12.56 **	0.90 NS	1417594.54 **	10140.64 NS	Fully adequate
Leaf osmotic potential	9.97 **	2.73 NS	1.59E-05 **	3.45 E-07 NS	Fully adequate
Chlorophyll contents	7.73 **	0.10 NS	55.96 **	1.04 NS	Fully adequate
Net photosynthetic rate	8.83 **	0.08 NS	184.41 **	2.91 NS	Fully adequate
Canopy temperature depression	7.10 **	0.20 NS	0.10 **	0.002 NS	Fully adequate
Plant height	5.42 **	0.83 NS	89.82 **	3.19 NS	Fully adequate
Grain yield per plant	5.33 **	0.02 NS	94057.53 **	3314.23 NS	Fully adequate

* = Significant at $P \leq 0.05$, ** = Significant at $P \leq 0.01$, NS = Non-significant

Diallel ANOVA: Existence of additive & non-additive genetic effects was remarkable for transfer of all studied traits as both 'a & b' components were found significant under both experimental conditions. Reciprocal along-with maternal genetic components were found insignificant for LOP, Chl. Contents, P_n and CTD (Table 4a) under optimal and stress temperature regimes, so retesting was not required. Maternal genetic component 'c' was consequential for ELA, PH and GYP (Table 4b)) under both temperature regimes. For these three

parameters, additive mean squares were retested against 'c' component. Retesting results showed absence of maternal effects as additive components were highly consequential. For ELA, reciprocal genetic component 'd' was found remarkable only under stress environment. Retesting of means squares of 'b' components revealed no significant role of reciprocal effects for inheritance of ELA, as dominance and its related genic components of variation were significant.

Table 4a: Mean squares (ANOVA) of 6 × 6 diallel crosses in maize for physiological traits under normal and high temperature (Hayman's approach, 1954a).

SOV	df	LOP		Chl. Contents		P_n		CTD	
		NT	HT	NT	HT	NT	HT	NT	HT
a	5	2.35E-02 **	5.13E-02 **	58.61 **	101.92 **	72.55 **	117.83 **	5.68 **	5.81 **
b1	1	2.60E-02 **	3.73E-02 **	213.51 **	183.17 **	126.56 **	195.27 **	4.97 **	5.05 **
b2	5	1.87E-03 **	1.60E-03 **	2.69 **	5.90 **	2.41 **	3.64 **	0.25 **	0.32 **
b3	9	2.74E-03 **	5.26E-03 **	4.68 **	4.03 **	6.88 **	8.73 **	0.68 **	0.56 **
b	15	3.98E-03 **	6.18E-03 **	17.94 **	16.60 **	13.37 **	19.47 **	0.82 **	0.78 **
c	5	3.60E-03 NS	1.47E-03 NS	4.11 NS	4.32 NS	5.11 NS	9.45 NS	0.26 NS	0.13 NS
d	10	2.67E-04 NS	9.00E-04 NS	1.10 NS	1.35 NS	0.98 NS	0.96 NS	0.012 NS	0.01 NS
Total	35	5.66E-03	1.04E-02	16.96	22.68	17.10	26.80	1.20	1.18
a × B	10	8.06E-05	9.22E-05	0.248	0.177	0.29	0.316	1.40E-02	3.49E-03
b1 × B	2	1.65E-04	3.74E-04	0.489	0.283	0.24	0.375	1.78E-03	1.06E-03
b2 × B	10	1.33E-04	9.03E-05	0.222	0.730	0.103	0.503	4.09E-03	8.76E-03
b3 × B	18	7.91E-05	1.93E-04	0.270	0.303	0.27	0.995	1.27E-02	7.31E-03
b × B	30	1.14E-04	1.71E-04	0.269	0.444	0.21	0.789	9.11E-03	7.37E-03
c × B	10	1.09E-03	4.83E-04	1.269	1.330	1.55	3.232	7.87E-02	4.32E-02
d × B	20	1.70E-04	4.04E-04	0.961	0.585	0.60	0.831	1.65E-02	4.58E-03
Total × B	70	2.60E-04	2.71E-04	0.606	0.573	0.52	1.083	2.19E-02	1.11E-02

SOV = source of variation; df = degree of freedom; LOP = leaf osmotic potential; Chl. Contents = chlorophyll contents; CTD = canopy temperature depression; NT = normal temperature; HT = high temperature

Variance components of additive & dominance effects 'D & H' were found highly significant for studied parameters (Table 5) under both experimental conditions. Additive genic variance 'D' was less in magnitude than dominance 'H' genic variance for all parameters except LOP under stress environment. For LOP, magnitudes of 'D & H' were equal. Values of genic components of variance due to dominance 'H₁ & H₂' were significant but different from one another for ELA, P_n and GYP under both temperature regimes. However, for LOP, Chl. Con., CTD and PH both values were of equal magnitude under both experimental conditions. Component 'F' was found negatively significant for ELA, CTD and GYP under both experimental conditions and for LOP under normal experiment only. For PH, component 'F' was positively significant, while for Chl. contents value of 'F' component was non-significant but with positive sign. Under both experimental conditions, component of genic variation 'h²' was positively significant for studied parameters. Magnitude of environmental variance 'E' was insignificant with positive sign for observed parameters except for P_n , CTD (normal temperature) and

PH (high temperature). All traits were influenced by over-dominant genetic effects as magnitude of degree of dominance was > one, except LOP (1.0) under heat stress. Proportional value of genes with positive & negative effects among parents 'H₂/4H₁' was ≈ 0.25 for ELA, LOP, Chl. Con., CTD, PH and GYP (NT). For remaining parameters, magnitude was less or higher under both experimental conditions. Extent of narrow sense heritability 'h_{ns}', was higher than 60 percent for studied parameters, except for PH under optimal and stress environment. Extant of broad sense heritability 'h_{bs}' was greater than 95 percent for observed parameters under both experimental conditions.

Graphical presentation of the data is helpful to understand the type of genetic effects exist in parents. Two dimensions illustration, presented by Hayman's graphical approach. based upon variance of parents and covariance between parents & progeny. Allocation of the array points over regression line indicated the existence of dominant alleles among parents. For all studied traits, regression line intersects the Vr-axis below origin indicating predominance of non-additive genetic effects

under both experimental conditions. Parental lines that lie near the origin indicate the presence of maximal dominant alleles for particular trait, while parents which fall on farthest position from origin possess maximal recessive alleles. For ELA (Fig. 1), parental lines D-135, NCIL-10-5 & NCIL-20-4 possess maximal dominant alleles under both experimental conditions. Parental lines D-103 and NCIL-30-5 lie at middle position on regression line, so they possess equal proportion of recessive and dominant genes. Parental line WA-3748 fall at farthest point from origin and possess maximum frequency of recessive alleles under both temperatures. For LOP (Fig. 2), WA-3748 and NCIL-30-5 contain maximal dominant alleles, while NCIL-10-5 and NCIL-20-4 possess more recessive alleles.

Parent NCIL-10-5 possess maximal frequency of dominant alleles for Chl. Contents (Fig. 3) under both experimental conditions. Under normal environment, D-135 and NCIL-20-4 fall in centre of the regression line, hence these parental lines had identical number of recessive & dominant alleles. Parental line D-103 had maximal recessive alleles than dominant as it falls near the farthest point. Under stress environment, D-103, NCIL-20-4 and NCIL-30-5 fall on centre position and had a balanced share in between recessive and dominant

genes. Parental lines WA-3748 and D-135 fall at farthest point from origin, hence possess more recessive genes.

For P_n (Fig. 4), NCIL-10-5 had maximal dominant genes, while D-135, NCIL-20-4 & NCIL-30-5 lie in the middle of regression line and hence possess balanced number of recessive & dominant genes. Parents D-103 and WA-3748 lie at farthest point from origin and hence had maximal number of recessive genes under both environmental conditions. For CTD (Fig. 5), parental lines D-135, WA-3748, NCIL-10-5, NCIL-20-4 & NCIL-30-5 lie in the middle of regression line and possess balanced ratio of recessive and dominant genes under both experimental conditions.

Inbred NCIL-30-5 lies nearest to the origin and had maximal dominant genes for PH (Fig. 6) under both experimental conditions. Parental lines NCIL-10-5 & NCIL-20-4 lie in the middle of regression line and thus possess balanced ratio of recessive and dominant genes. Parent WA-3748 fall on the farthest point from origin and contain more recessive genes under both experimental conditions. For GYP (Fig. 7), NCIL-10-5 possess maximal number of dominant alleles under both experimental conditions. Inbred lines WA-3748 and NCIL-30-5 fall on the farthest end from origin, thus possess maximal recessive genes under both temperature regimes.

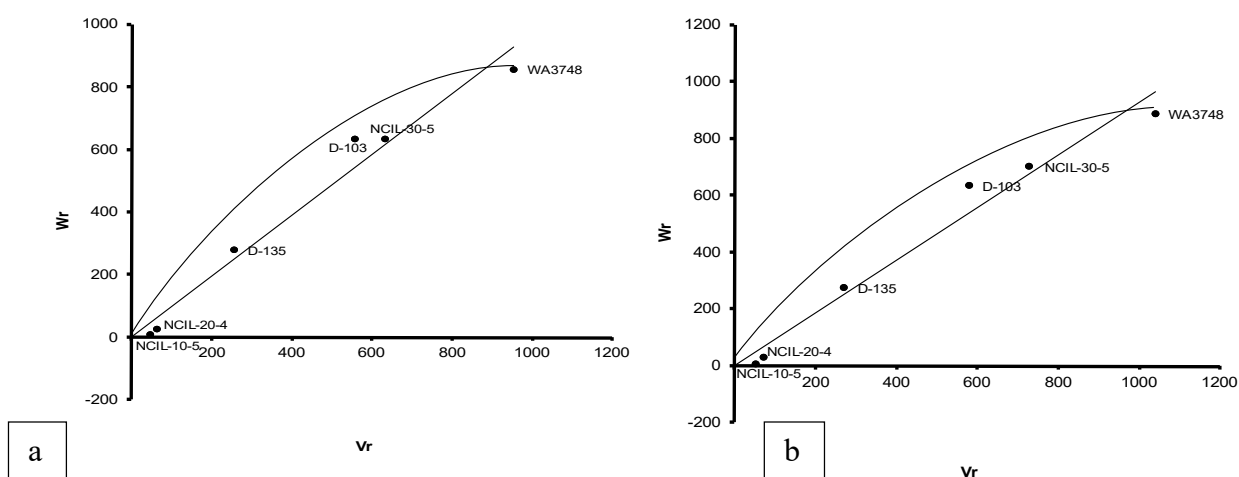


Fig. 1: W_r/V_r graph for ear leaf area; (a) normal temperature (b) high temperature

Table 4b: Mean squares (ANOVA) of 6 × 6 diallel crosses in maize for physiological and yield traits under normal and high temperature (Hayman’s approach, 1954a).

SOV	DF	ELA		Restesting of ‘a’ and ‘b’ MS against				PH		Restesting of ‘a’ and ‘b’ MS against				GY		Restesting of ‘a’ and ‘b’ MS against			
				c		d				c		d				c		d	
		NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT
a	5	9262.76**	9366.87**	110.88**	18.04**	-	-	75.44**	62.30**	19.24**	14.99**	-	-	5196.96**	3765.81**	-	102.50**	-	-
b1	1	12785.71**	11953.05**			-	1014.13**	166.45**	133.28**			-	-	17098.09**	5722.22**			-	-
b2	5	200.51**	183.87**			-	4.93*	11.44**	12.69**			-	-	195.01**	380.68**			-	-
b3	9	510.39**	740.84**			-	16.34**	10.67**	4.62**			-	-	349.12**	150.59**			-	-
b	15	1225.45**	1302.67**			-	32.21**	21.31**	15.89**			-	-	1414.35**	598.73**			-	-
c	5	20.763**	447.32**					22.34**	25.54**					57.03 ^{NS}	239.35**			-	-
d	10	9.16 ^{NS}	25.46**					4.11 ^{NS}	8.03 ^{NS}					36.45 ^{NS}	38.20 ^{NS}				
Total	35	1854.03	1967.59					24.28	21.65					1367.13	839.68				
a × B	10	4.53	4.41					0.36	0.48					10.40	8.22				
b1 × B	2	2.07	1.47					0.38	2.12					19.71	17.14				
b2 × B	10	7.71	4.66					0.64	0.39					14.40	12.40				
b3 × B	18	3.07	5.67					0.51	0.71					12.01	13.51				
b × B	30	4.55	5.05					0.54	0.70					13.32	13.38				
c × B	10	1.13	3.80					2.03	2.93					20.25	53.53				
d × B	20	4.20	3.18					1.95	3.52					16.69	18.50				
Total × B	70	3.96	4.25					1.13	1.79					14.86	19.84				

ELA = ear leaf area; PH = plant height; GY = grain yield per plant; c = maternal effects; d = reciprocal effects

Table 5: Components of genetic variation for physiological and yield traits in maize under normal and high temperature.

Components	ELA		LOP		Chl. Con.		P _n		CTD		PH		GYP	
	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT
D	788.76*	770.29*	0.001*	0.004*	6.48*	7.91*	7.23*	10.38*	0.37*	0.36*	7.11*	7.00*	479.69*	161.52*
H ₁	857.77*	905.27*	0.003*	0.004*	11.99*	11.87*	8.99*	12.84*	0.58*	0.58*	15.77*	11.80*	973.22*	465.68*
H ₂	819.71*	871.39*	0.003*	0.004*	12.38*	11.48*	9.25*	13.67*	0.56*	0.53*	14.93*	11.77*	952.38*	412.32*
F	-196.34*	-230.12*	-0.001*	-0.001 ^{NS}	0.50 ^{NS}	-2.17 ^{NS}	-0.36 ^{NS}	-2.02 ^{NS}	-0.22*	-0.21*	1.14 ^{NS}	2.70 ^{NS}	-56.04*	-174.57*
h ²	2366.94*	2212.69*	0.005*	0.007*	39.42*	33.82*	23.34*	35.96*	0.92*	0.93*	30.62*	24.34*	3163.60*	1055.91*
E	1.41 ^{NS}	1.52 ^{NS}	0.0001 ^{NS}	0.0001 ^{NS}	0.22 ^{NS}	0.19 ^{NS}	0.17*	0.36 ^{NS}	0.01*	0.004 ^{NS}	0.37 ^{NS}	0.61*	4.88 ^{NS}	6.77 ^{NS}
(H ₁ / D) ^{0.5}	1.04	1.08	1.488	1.0	1.36	1.23	1.12	1.11	1.25	1.28	1.49	1.30	1.42	1.70
(H ₂ / 4H ₁)	0.24	0.24	0.249	0.255	0.26	0.24	0.26	0.27	0.24	0.23	0.24	0.25	0.25	0.22
(√4DH ₁ + F / √4DH ₁ - F)	0.79	0.76	0.602	0.737	1.06	0.10	0.96	0.84	0.64	0.61	1.12	1.35	0.92	0.52
H _{ns}	71.26	70.22	58.70	69.31	45.81	63.35	59.60	60.53	66.99	69.96	45.33	37.92	59.0	62.45
H _{bs}	99.80	99.79	95.57	97.25	96.49	97.75	97.21	96.28	99.39	99.18	95.08	89.42	97.7	97.74

Additive variance (D), Dominance variance (H₁), Proportion of positive and negative genes in the parent (H₂), Relative frequency of dominant and recessive alleles in the parents (F), Dominance effect (over all loci in heterozygous phase) (h²), Environmental variance (E), Mean degree of dominance (H₁/D)^{0.5}, Proportion of genes with positive and negative effects in the parents (H₂/4H₁), Proportion of dominant and recessive genes in the parents (√4DH₁ + F / √4DH₁ - F), Heritability narrow sense (H_{ns}), Heritability broad sense (H_{bs}).

(Note: The value of variance is significant (*) when the value exceeds 1.9996 after dividing it with its S.E.).

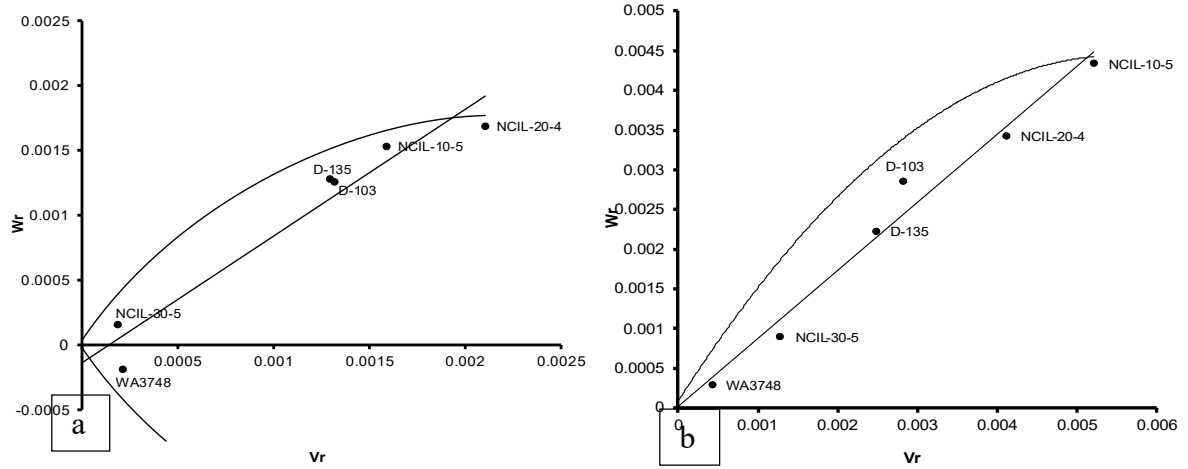


Fig. 2: W_r/V_r graph for leaf osmotic potential; (a) normal temperature (b) high temperature

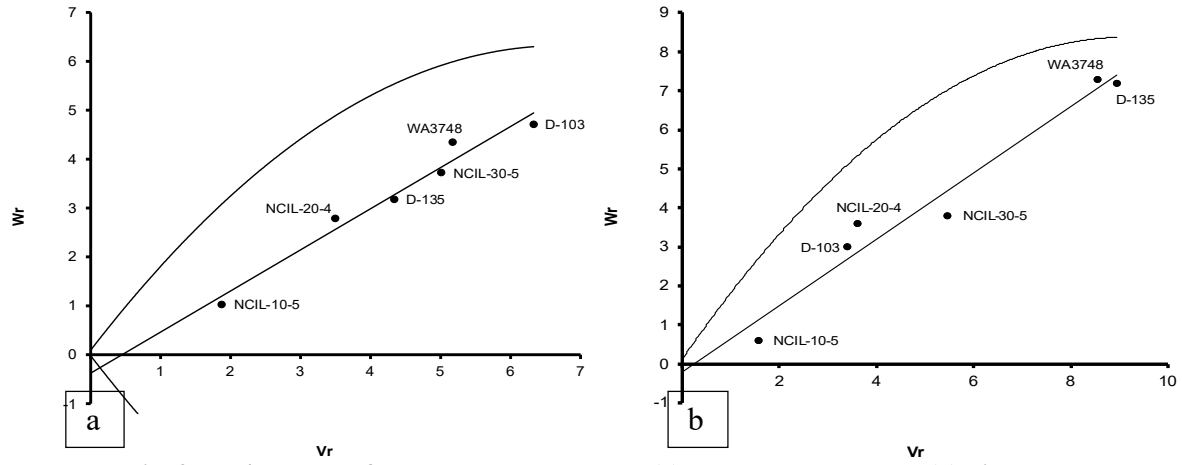


Fig. 3: W_r/V_r graph for chlorophyll contents; (a) normal temperature (b) high temperature

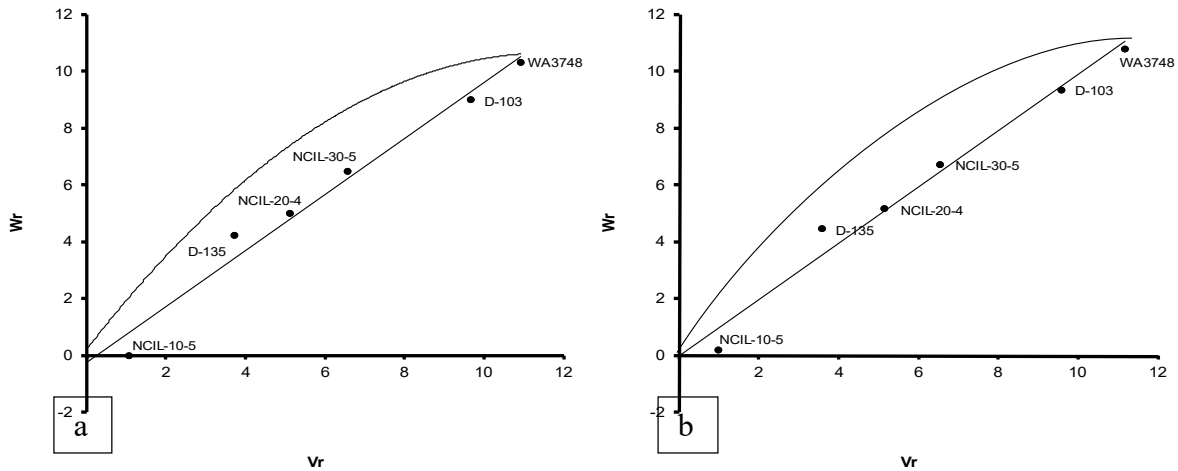


Fig. 4: W_r/V_r graph for Net Photosynthetic Rate; (a) normal temperature (b) high temperature

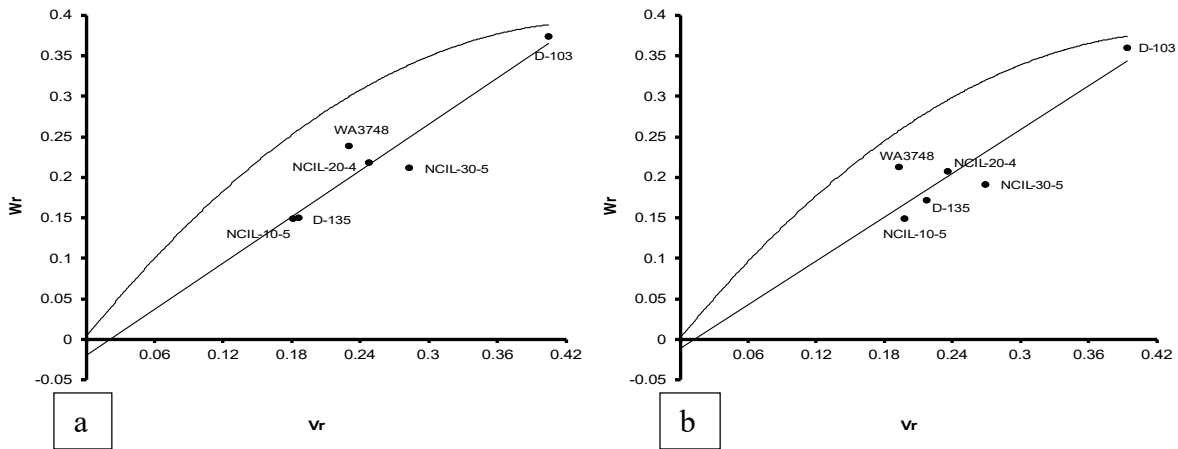


Fig. 5: W_r/V_r graph for Canopy Temperature Depression; (a) normal temperature (b) high temperature

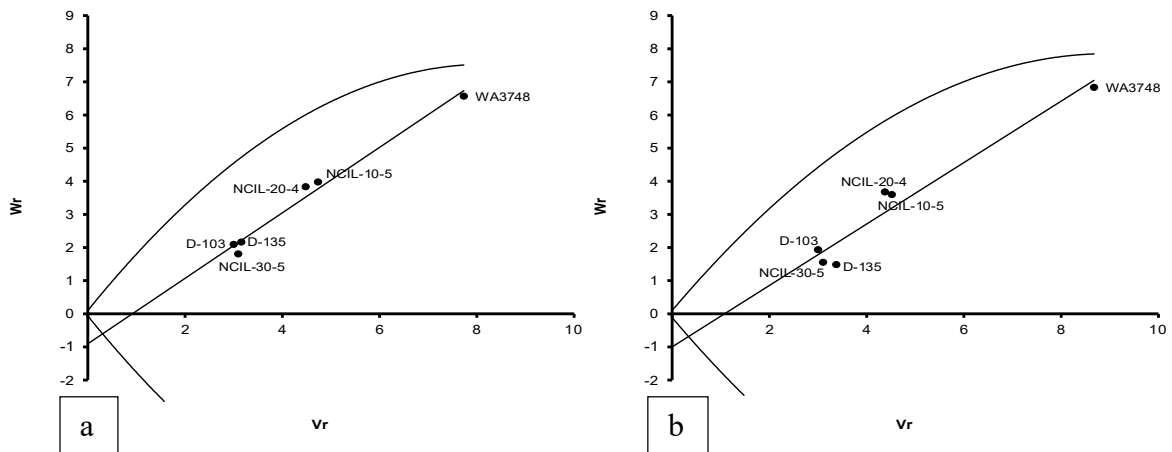


Fig. 6: W_r/V_r graph for Plant Height; (a) normal temperature (b) high temperature

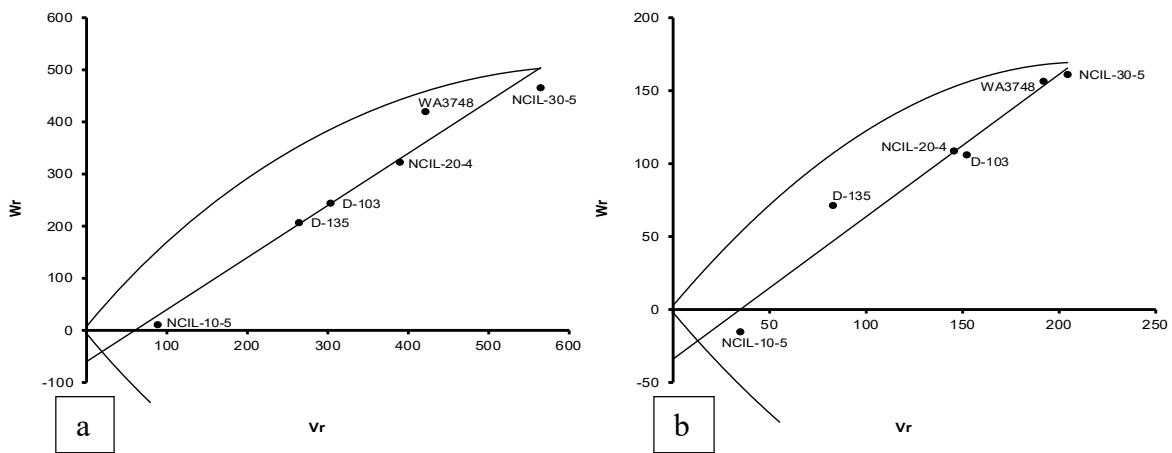


Fig. 7: W_r/V_r graph for grain yield per plant; (a) normal temperature (b) high temperature

DISCUSSION

Results of ANOVA proved the presence of high genetic variation among parents for studied traits under

optimal & stress environment. Presence of significant genetic variability among genotypes is necessary for a particular trait to continue a successful breeding program (Chohan *et al.*, 2012, Wattoo *et al.*, 2013, and Ahmad *et al.*, 2015). All parameters showed full adequacy to

additive-dominance model. Fitness of data to additive-dominance is the foremost prerequisite for advance statistical analysis. Only fully or partially adequate data could be used for estimation of genetic parameters and graph analysis (Dar *et al.*, 2017, Lay and Razdan, 2017, Rohman *et al.*, 2019). Hayman's approach was used for genetic analysis of the data. Results of components of genetic variation proved the existence of additive and non-additive genetic effects for studied traits under both environmental conditions, but overall situation revealed the predominance of non-additive gene action. Significant magnitude of 'D & H' components showed that heritability of the traits was influenced by additive & dominant genetic effects. However, PH and GY were influenced by dominant gene action (Rohman *et al.*, 2019), while, PH, ELA and GY were influenced by non-additive genetic attributes (Hussain *et al.*, 2009, Aslam *et al.*, 2015, Dar *et al.*, 2017, Lay and Razdan, 2017). PH, ELA, P_n and GYP were influenced by additive gene action under both experimental conditions (Chohan *et al.*, 2012, Wattoo *et al.*, 2013).

Values of 'F' with negative sign showed high frequency of recessive genes, while positive value expressed high frequency of dominant genes for particular traits. These results were also supported by ' $(\sqrt{4DH_1} + F) / \sqrt{4DH_1} - F$ ' value which was >1 for Chl. Contents and PH, while for remaining traits value was <1. Recessive alleles were frequent in number than dominant for PH and GY (Rohman *et al.*, 2019), ELA and P_n (Chohan *et al.*, 2012), PH, ELA, P_n & GY (Wattoo *et al.*, 2013). Extent of broad sense heritability was greater in magnitude than narrow sense heritability under both temperature regimes, due to which early selection for studied parameters is not useful and better to go for heterosis breeding. Because of $h_{ns} > h_{bs}$ early selection is useful for phenotypic improvement of traits (Aslam *et al.*, 2015).

Hayman's approach of diallel mating design is very useful to study the mode of genetic effects (either additive or non-additive) of the parent, which is part of mating scheme, and rely upon oligogenic additive model (Begum *et al.*, 2018, Rohman *et al.*, 2019). Variance and co-variance among parents and parents-offsprings is expressed in terms of bi-dimensional direction using Vr-Wr graphs. Results regarding expression behaviour of genetic effects for particular trait are confirmed by the magnitude and nature of intercept 'a'. Value of 'a' for studied parameters under normal and high temperature are; ELA (-1.244, -1.016), LOP (-0.0001, 0.00001), Chl. Contents (-0.376, -0.202), P_n (-0.346, -0.258), CTD (-0.02, -0.01), PH (-0.905, -0.998) and GY (-59.95, -33.91), which revealed that for all traits regression line intersect the Wr-axis below the origin line (Fig. 1- Fig. 7).

Conclusion: Valuable genetic variation was present in parents and their F₁ crosses. Results revealed that studied parameters were fully fit to additive-dominance model and influence of over-dominant gene action was high for transfer of parameters from parents to off-springs under optimal and stress environment. Role of maternal and reciprocal genic effects was not important for heredity of studied parameters. Parents NCIL-10-5 and D-135 performed well and possess dominant genes for grain yield and most of the physiological parameters under both experimental conditions. These parents can be used in future for hybrid breeding programme to develop high yielding heat resistant genotypes.

REFERENCES

- Ahmad, Z., E.A. Waraich, T. Ahmad, R. Ahmad and M.I. Awan (2015). Yield responses of maize as influenced by supplemental foliar applied phosphorus under drought stress. *Int. J. Food Allied Sci.*, 1(2):45-55.
- Al-Falahy, M.A. (2015). Estimation combining ability, heterosis and some genetic parameters across four environments using full diallel cross method. *Int. J. Pure Appl. Sci. Technol.*, 26(1): 34-44.
- Aslam, M., M. Ikram, M.A. Maqbool and W. Akbar (2015). Assessment of genetic components for different traits in maize (*Zea mays* L.). *J. Agric. Res.* 53(1): 1-10.
- Begum, S., S.S. Alam, S.H. Omy, M. Amiruzzaman and M. Rohman (2018). Inheritance and combining ability in maize using a 7×7 diallel cross. *J. Plant Breed. Crop Sci.*, 10(9): 239-248.
- Chohan, M.S., M. Saleem, M. Ahsan and M. Asghar (2012). Genetic analysis of water stress and various morphological traits in *Zea mays* L. using graphical approach. *Pakistan J. Nutr.*, 11(5): 489-500.
- Dar, Z.A., A.A. Lone, B.A. Elahi, S.A. Dar, G. Ali. I. Abidi, R.A. Lone, S. Gulzar and N. Yousaf (2017). Genetic variations in maize inbred lines under temperate conditions. *J. Exp. Biol. Agric. Sci.*, 5(2): 215-219.
- Farooq, M., A. Wahid, T. Aziz, D.J. Lee and K.H.M. Siddique (2009). Chilling tolerance in maize: physiological and agronomic implications. *Crop Pasture Sci.*, 60: 501-516.
- Guzman, P.S. and K.R. Lamkey (2000). Effective population size and genetic variability in the BS11 maize population. *Crop Sci.*, 40(2): 338-346.
- Hayman, B.I. (1954a). The theory and analysis of diallel cross-I. *Genetics*, 32: 789-809.
- Hayman, B.I. (1954b). The analysis of variance of diallel tables. *Biometrics*, 10(2): 235-244.

- Hussain, I., M. Ahsan, M. Saleem and A. Ahmad (2009). Gene action studies for agronomic traits in maize under normal and water stress conditions. *Pakistan J. Agri. Sci.*, 46(2): 107-112.
- Janni, M., M. Gulli, E. Maestri, M. Marmioli, B. Valliyodan, H.T. Ngyuen and N. Marmioli (2020). Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. *J. Exp. Bot.*, 71(13): 3780-3802.
- Kurukulasuriya, P., R. Mendelsohn, R. Hassan, J. Benin, T. Deressa, M. Diop, H.M. Eid, K.Y. Fosu, G. Gbetibuo, S. Jain, A. Mahamadou, R. Mano, J. K. Mariara, S.E. Marsafawy, E. Molua, S. Ouda, M. Ouedraogo, I. Séne, D. Maddison, S. N. Seo and A. Dinar (2006). Will African agriculture survive climate change? *World Bank Econ. Rev.* 20: 367–388.
- Lay, P., and A.K. Razdan (2017). Genetic analysis of grain yield and its components of maize (*Zea mays* L.) inbred lines. *Int. J. Curr. Microbiol. App. Sci.* 6(7): 1366-1372.
- Mather, K. and J.L. Jinks (1982). *Introduction to Biometrical Genetics*. Chapman & Hill Ltd. London.
- McKee, G. W. (1964). A coefficient for computing leaf area in hybrid corn. *Agron. J.* 56(2): 240-241.
- Mendelsohn, R. (2014). The impact of climate change on agriculture in Asia. *J. Integr. Agric.* 13(4): 660–665.
- Prasad, P.V.V., K.J. Boote and L.H. Allen (2006a). Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. *Agric. For. Meteorol.* 139(3): 237–251.
- Rohman, M. M., S. H. Omy, S. Begum, M. A. Rahman, M. G. Hossain, M. M. Hoque, and M. Amiruzzaman. 2019. Genetic action and potence ratio of maize in an 8× 8 diallel cross growing under saline condition. *J. Plant Breed. Crop Sci.* 11(1): 17-25.
- Shah, H., W. Akhter, N. Akmal and M.A. Khan (2014). Competitiveness of maize production in Pakistan. In: Prasanna, B.M., B.S. Vivek, A.R. Sadananda, D. Jeffrs, P.H. Zaidi, C. Boeber, O. Erenstein, R. Babu, S.K. Nair, B. Gerard, M.L. Jat, N. Palacios and K. Pixle (eds.). 12th Asian maize conference and expert consultation on maize for food, feed, nutrition and environmental security, book of extended summaries, 30 October–01 November, Bangkok (Thailand). 162-167 p
- Steel, R.G.D., J.H. Torrie and D.A. Dicky (1997). *Principles and procedures of statistics. A biometrical approach*, McGraw Hill Book Co., New York, U.S.A.
- Steven, J., C. Brandner and M. Salvucci (2002). Sensitivity of photosynthesis in C4 maize plant to heat stress. *Plant Physiol.* 129: 1773-1780.
- Tariq, M. and H. Iqbal (2010). Maize in Pakistan – an overview. *Kasetsart J. (Nat. Sci.)* 44(5): 757-763.
- Wattoo, F.M., M. Saleem, M. Ahsan and S.M.A. Basra (2013). Genetics of physio-agronomic traits in maize under water deficit conditions. *Pakistan J. Nutr.*, 12: 398-409.