



Full Length Article

Genetic Basis of Physiological Traits and Grain Yield in Maize under Normal and High Temperature

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Abstract

High temperature is a big reason of reducing global cereal productivity especially in maize. To cope with this threat, breeding for heat resilient maize hybrids is important to sustain high yield. Six heat tolerant inbred lines were crossed in diallel fashion to develop F₁ generations. Data of five agro-physiological traits *viz.*, leaf temperature, cell membrane thermostability, stomatal conductance, transpiration rate and grain yield per plant were measured for inbred lines and F₁ crosses including reciprocals under normal and high temperature environment. Scaling tests proved the fitness of data to additive-dominance model for all traits under both temperature regimes. Dominance ratio and graphical expression of data showed significant role of non-additive gene action for all traits under both environments. High broad sense heritability for these traits showed importance of high genetic variance than environmental variance for inheritance of these traits. Heterosis breeding is an efficient strategy due to over-dominant nature of gene action for all traits under both temperatures. Moderate to high narrow sense heritability suggested that direct selection of studied physiological traits for yield improvement under high temperature can be fruitful. Inbred lines NCIL-10-5, NCIL-20-4 and NCIL-30-5 showed maximum dominant genes for grain yield under both temperatures. These parental lines can be used for development of heat resilient maize hybrids, having potential of high yield under unfavourable environment. © 2019 Friends Science Publishers

Keywords: Broad-sense heritability; Cell membrane thermostability; Diallel; Hayman's approach; Stomatal conductance; Maize

Introduction

Maize (*Zea mays* L.), one of the leading cereal worldwide and staple food of some countries. Because of large genetic diversity, it is adaptable to grow throughout the world under different agro-ecological zones. Maize ranks third among cereals after wheat and rice and provides 30% calories to poor peoples of the developing world (Shiferaw *et al.*, 2011).

Maize is a tropical crop but it can tolerate only brief exposures to adverse temperatures. Optimum day and night temperature at germination and growth ranged between 17–23°C and 25–33°C, respectively (Medany *et al.*, 2007; Farooq *et al.*, 2009). The average yield of maize in Pakistan is low and the country ranks 68th among maize growing countries of the world, which is because of abrupt climatic changes (Shah *et al.*, 2014). High temperature at anthesis, severely effect pollen viability, silk receptiveness and eventually grain yield of spring maize. Maize is more susceptible to high temperatures at reproductive stage compared to early growth stages (Chen *et al.*, 2010).

In plants, heat resistance is a complicated event and controlled by many genes. High temperature is a critical stress factor with dominated impact on crop yield. Plant responses to stress are complex, and one cannot be successful by improving merely few agronomic or physiological traits. Breeder must know the changes in structure and function of a plant under specific environment, to study the plant response against stress. Study of these responses carried out at different growth stages of plant including cellular, molecular and organism level (Barnabas *et al.*, 2008). Few reports available to know the impact of high temperature on maize than other abiotic stresses (Salinity and water stress). Previous research mostly based on study of molecular and biochemical responses of maize plant at specific temperature under lab conditions using few genotypes, rather to study these effects under natural environment (Cairns *et al.*, 2013). Diallel is well established biometrical technique, used to evaluate the genetic features like heritability, combining ability and gene action, to recognize and choose the best parents and cross-combinations in breeding programs (Al-Falahy, 2015).

The basic objective of present research was to estimate nature of gene action and heritability pattern of physiological traits and grain yield under normal and high temperature environment for identification of inbred lines to develop heat resilient maize hybrids.

Materials and Methods

The present research was conducted in the Department of Plant Breeding & Genetics, University of Agriculture Faisalabad during 2014–2015. Six heat tolerant inbred lines *i.e.*, D-103, NCIL-20-4, D-135, NCIL-10-5, WA3748 and NCIL-30-5, obtained from NARC, Islamabad were crossed using full diallel mating design in the field during autumn 2014. Controlled pollination was done to avoid foreign contamination. Parental lines and F₁ crosses including reciprocals were planted in the field using triplicate Randomized Complete Block Design (RCBD), during spring 2015 under normal and stress environment. First set was planted in the field during first fortnight of February under normal spring season, while second set was planted during first fortnight of March, for exposure of high temperature stress at reproductive and grain filling stage. Each genotype was planted in two rows of 5.3 m each, with row × row distances of 75 cm and plant × plant spacing of 23 cm. To ensure good plant population, two seeds per hill were dibbled followed by thinning after 7 days of emergence to keep one healthy plant per hill. All agronomic and plant protection practices were kept uniform for each treatment. Optimum irrigations were applied to both normal and late sowing trials to avoid drought stress. Maximum temperature at time of data recording was 35.9°C and 40.4°C for normal and heat stress treatments, respectively. Ten randomly earmarked plants used for data recording of physiological traits at dough stage.

Physiological Traits

Leaf temperature (LT) was measured from three fully expanded leaves per plant of ten randomly earmarked plants on a sunny day at 13.00–15.00 P.M. by using infrared thermometer (RAYPRM 30 CFRJ, RAYTEK, USA) and averaged.

For cell membrane thermostability, fully expanded leaves were used to cut 0.75 cm diameter round discs with sharp punch machine. The discs were washed gently with three changes of de-ionized distilled water in 50 mL glass tube to remove surface adhered electrolytes. After washing, immerse the leaf discs in 10 mL of distilled water in glass tubes. One set of the tubes was placed in water bath for one hour at 45°C and then transfer both the sets in air-conditioned room at 22°C overnight. After shaking well each test tube, electrical conductivity of each sample was measured by EC meter (LF 538). The samples were autoclaved for 15 min at 15 lbs. pressure and 121°C temperature to kill the leaf tissues and then allowed to cool

down up to 22°C overnight. After autoclaving, electrical conductivity was noted for the second time. Recorded electrolyte leakage, under both normal and stress environments, was used to estimate the percentage stability of leaf tissues by using the formulae of Sullivan (1972).

Normal Temperature: Cell membrane thermostability = $(1 - C1/C2) \times 100$

High Temperature: Cell membrane thermostability = $(1 - T1/T2) \times 100$

Where C1 & C2 are 1st and 2nd conductivity measurement at room temperature (22°C) before and after autoclave, respectively.

T1 & T2 are 1st and 2nd conductivity measurement of plant sample treated at 45°C before and after autoclave, respectively.

Stomatal conductance (g_s) and transpiration rate (T_r) were measured from the second intact leaf from top of each plant using a CI-340 Hand-held Photosynthesis System (CID, Inc. USA). Measurements performed at noon between 11:00–14:00 p.m., with PAR > 1150 μmol m⁻² s⁻¹ on clear cloudless days.

Agronomic Trait

For grain yield per plant (GYP), total weight of shelled grains from all ears of each plot was divided by the number of plants in that plot at 15% moisture level.

Statistical Analysis

To estimate the genetic variability among genotypes, data about various physiological and yield traits was subjected to analysis of variance (Steel *et al.*, 1997). The data were then subjected to analyse gene action and inheritance pattern from parents to offsprings, using Hayman's approach (1954a, b). Appraisal of adequacy of diallel data for additive-dominance model is necessary before running Hayman's approach.

Diallel analysis technique provided complete information about genetic behaviour of quantitative traits in early F₁. At first, the lineage effects of diallel table were separated into 'a' (additive) and 'b' (dominance) genetic components. The 'b' component is partitioned into 'b₁' (directional dominance effect), 'b₂' (effects due to unequal distribution of dominance) and 'b₃' (effects due to dominance deviation unique to F₁). Component "c" explained the average maternal effects of each parental line and 'd' the reciprocal differences not ascribable to "c" (Hayman, 1954a).

Second step estimates the variance components of each array, variance of paternal means and covariance of all the offspring included in each parental array with the non-recurrent parents. These variances were helpful for estimation of four genetic components *viz.*, D (variance due

to additive effects), H_1 & H_2 (variance due to dominant effects) and F (relative frequency of dominant and recessive alleles in the parental lines) (Hayman, 1954b; Mather and Jinks, 1982).

To estimate the broad-sense and narrow-sense heritability for each trait, we used the formula of Mather and Jinks (1982).

Heritability

(NS) = $0.5D +$

$$0.5H_1 - 0.5H_2 - 0.5F / 0.5D + 0.5H_1 - 0.25H_2 - 0.5F + E$$

Heritability

(BS) =

$$0.5D + 0.5H_1 - 0.25H_2 - 0.5F / 0.5D + 0.5H_1 - 0.25H_2 - 0.5F + E$$

Results

The results of ANOVA showed significant genetic variability ($P \leq 0.01$) among the parents and crosses for all the traits under normal and heat stress conditions (Table 1). Mean squares for male, female and male \times female interaction were significant ($P \leq 0.01$) as genotypic components of ANOVA under normal and high temperature for studied traits (Table 2). These results manifested the importance of both additive and non-additive genetic attributes for trait inheritance in maize under normal and stress environments.

Scaling Test

All plant traits were fully fit to additive-dominance model as they passed both scaling tests under normal and high temperature (Table 3a and b). Results revealed that for all traits, regression coefficient (b) was statistically different from zero but not from unity. For analysis of variance and covariance of array means, significant results for W_r+V_r analysis but non-significant results for W_r-V_r . Because of adequacy to additive dominance model, the data for all traits were good for further biometrical analysis.

Diallel ANOVA

Hayman's ANOVA displayed that both 'a & b' genetic components were significant for all traits (Table 4). Results revealed that both additive and non-additive genetic effects played a significant role for trait inheritance under normal and stress environment. All traits except transpiration rate displayed highly significant values for genetic components of 'b' (b_1 , b_2 & b_3) under normal and high temperature environments. Highly significant values of ' b_1 ' justified directional dominance. Significant ' b_2 ' showed that each parent had disproportional balance of genes and dominance effects, which controlled the trait under both temperature regime. High significant value of ' b_3 ' revealed presence of particular genetic interactions among crosses because of dominance deviation distinctive to F_1 crosses. For

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

Traits	Mean squares (df = 35)	
	Normal Temperature	High Temperature
Leaf temperature	3.524**	2.46**
Cell membrane thermostability	43.075**	63.130**
Stomatal conductance	0.029**	0.013**
Transpiration rate	0.803**	0.711**
Grain yield per plant	1367.13**	839.68**

** = Significant at $P \leq 0.01$

transpiration rate, value of ' b_2 ' was non-significant, showing symmetrical proportion of genes and dominance effects in particular parent for trait inheritance under normal temperature. Maternal and reciprocal components 'c and d' were non-significant for studied traits under normal and stress conditions except grain yield. So retesting of additive and dominance mean squares against 'c and d' mean square was not useful. However, maternal component 'c' was significant for grain yield per plant under high temperature. So retesting of additive mean squares was necessary against mean square of 'c' component. Retesting result showed absence of maternal effects for grain yield as value of additive component was (102.5**) highly significant after retesting under high temperature.

Components of Genetic Variation

Both 'D & H' variance components were highly significant and revealed that additive and non-additive genetic variances played a significant role for all traits under both temperature regimes (Table 5). However, dominance variance was greater than additive variance and results revealed importance of dominance effects for all traits under normal and stress environment.

Magnitudes of ' H_1 & H_2 ' were almost equal and significant for all traits under both temperature regimes. Result displayed equal proportion of positive and negative genes in parents. Value of 'F' was negative for all studied traits under both environments, except leaf temperature. These results showed imbalanced proportion of dominant and recessive alleles among the parents. Recessive alleles were dominant in parents for these traits under both temperature environments. For leaf temperature (normal environment), value of 'F' was positive, showing predominance of dominant alleles in parents for this traits. Positive and significant value of ' h^2 ' for all traits depicted dominance impact of heterozygous loci under normal and high temperature.

Positive and non-significant values of environmental variance (E) depicted little influence of environment on all traits under both temperature regimes. Values of dominance ratio were greater than unity and revealed importance of over-dominant genetic effects for all traits under normal and high temperature environments.

Value of ' $H_2/4H_1$ ' was ≈ 0.25 for all traits under both

Table 2: Mean squares (male, female and their interaction) for physiological and yield traits in maize under normal and high temperature

SOV Traits	Male(df = 5)		Female (df = 5)		Male × Female interaction (df = 25)	
	NT	HT	NT	HT	NT	HT
Leaf temperature	7.33**	8.39**	3.27**	3.53**	1.30**	1.06**
Cell membrane thermostability	8.75**	187.21**	5.68**	111.38**	2.05**	28.65**
Stomatal conductance	0.077**	0.033**	0.056**	0.029**	0.02**	0.006**
Transpiration rate	2.11**	1.57**	1.66**	1.54**	0.37**	0.37**
Grain yield/ 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 and yield traits in maize under normal temperature

Traits	Regression Analysis		Mean Squares Wr+Vr	Mean Squares Wr-Vr	Remarks
	H ₀ b=0	H ₀ b=1			
Leaf temperature	7.89 ^{NS}	0.60 ^{NS}	4.35**	0.07 ^{NS}	Fully adequate
Cell membrane thermostability	6.53**	0.002 ^{NS}	255.28**	5.91 ^{NS}	Fully adequate
Stomatal conductance	10.99**	0.43 ^{NS}	1.8E-04**	1.54E-06 ^{NS}	Fully adequate
Transpiration rate	8.03**	0.07 ^{NS}	0.03**	3.7E-04 ^{NS}	Fully adequate
Grain yield/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 and yield traits in maize under high temperature

Traits	Regression Analysis		Mean Squares Wr+Vr	Mean Squares Wr-Vr	Remarks
	H ₀ b=0	H ₀ b=1			
Leaf temperature	4.84**	0.17 ^{NS}	0.97**	0.04 ^{NS}	Fully adequate
Cell membrane thermostability	5.45**	0.34 ^{NS}	439.58**	14.34 ^{NS}	Fully adequate
Stomatal conductance	3.25**	0.82 ^{NS}	1.48E-05**	1.32E-06 ^{NS}	Fully adequate
Transpiration rate	4.12**	0.74 ^{NS}	0.07**	0.004 ^{NS}	Fully adequate
Grain yield/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

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

SOV	df	Mean Squares									
		LT		CMT		g _s		T _r		GYP	
		NT	HT	NT	HT	NT	HT	NT	HT	NT	HT
a	5	14.16**	11.31**	200.87**	292.91**	1.3E-01**	6.2E-02**	3.68**	3.08**	5196.96**	3765.81**
b1	1	31.63**	11.07**	297.97**	611.8**	2.4E-01**	1.1E-01**	6.00**	6.85**	17098.09**	5722.22**
b2	5	1.09**	1.15**	9.83**	8.24**	3.4E-03**	2.5E-03**	0.04 ^{NS}	0.17**	195.01**	380.68**
b3	9	1.40**	0.94**	8.89**	6.24**	8.0E-03**	3.0E-03**	0.28**	0.13**	349.12**	150.59**
b	15	3.36**	1.68**	28.48**	47.28**	2.2E-02**	9.9E-03**	0.58**	0.59**	1414.35**	598.73**
c	5	0.27 ^{NS}	0.61 ^{NS}	12.51 ^{NS}	5.68 ^{NS}	1.7E-03 ^{NS}	4.7E-04 ^{NS}	0.09 ^{NS}	0.03 ^{NS}	57.03 ^{NS}	239.35**
d	10	0.08 ^{NS}	0.13 ^{NS}	1.39 ^{NS}	0.72 ^{NS}	2.9E-03 ^{NS}	8.3E-04 ^{NS}	0.06 ^{NS}	0.05 ^{NS}	36.45 ^{NS}	38.20 ^{NS}
Total	35	3.52	2.46	43.08	63.12	2.9E-02	1.4E-02	0.80	0.71	1367.13	839.68
a × B	10	0.01	0.04	0.33	0.24	1.4E-04	2.0E-04	8.0E-03	1.1E-02	10.40	8.22
b1 × B	2	0.01	0.01	1.29	0.53	7.3E-04	1.1E-04	2.0E-02	5.1E-03	19.71	17.14
b2 × B	10	0.04	0.04	0.27	0.72	2.6E-04	2.2E-04	1.2E-02	1.7E-02	14.40	12.40
b3 × B	18	0.02	0.05	0.29	0.26	2.4E-04	9.4E-05	1.1E-02	1.0E-02	12.01	13.51
b × B	30	0.03	0.05	0.35	0.43	2.8E-04	1.4E-04	1.2E-02	1.2E-02	13.32	13.38
c × B	10	0.09	0.2	3.98	2.15	5.3E-04	2.6E-04	2.6E-02	1.1E-02	20.25	53.53
d × B	20	0.04	0.06	0.65	0.44	1.3E-03	4.3E-04	3.8E-02	2.2E-02	16.69	18.50
Total × B	70	0.04	0.07	0.95	0.65	5.8E-04	2.5E-04	2.1E-02	1.5E-02	14.86	19.84

leaf temperature (LT), cell membrane thermostability (CMT), stomatal conductance (g_s), transpiration rate (T_r), grain yield per plant (GYP), additive component (a), dominance component (b), directional dominance effect (b₁), effects due to unequal distribution of dominance (b₂), dominance deviation particular to each F₁ (b₃), average maternal effects (c), reciprocal differences not ascribable to "c" (d), * = Significant at $P \leq 0.05$, ** = Significant at $P \leq 0.01$, Each item is tested against its own block interaction

temperatures. These results showed that dominant genes with positive and negative impact on trait inheritance, were in balanced proportion. Value of $(\sqrt{4DH_1 + F} / \sqrt{4DH_1 - F})$ was less than unity for all traits under both temperature environments, except leaf temperature under normal

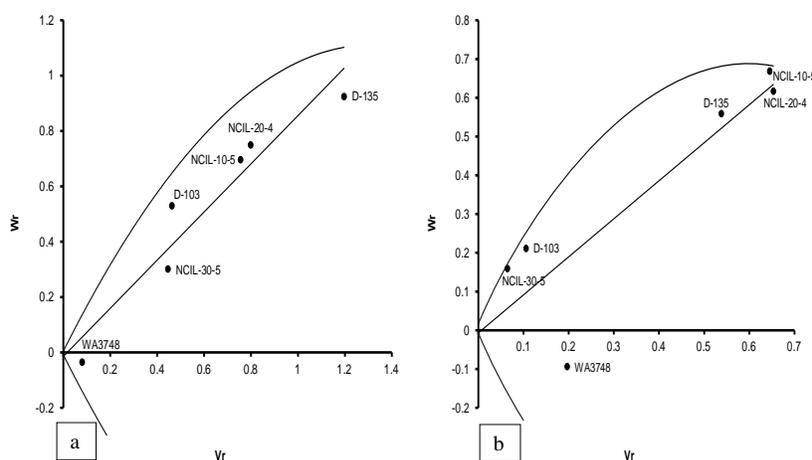
temperature. These results showed minority of dominant alleles and majority of recessive alleles for trait inheritance. However, for leaf temperature under normal temperature this value was higher than unity revealing majority of dominant genes over minor genes.

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

Components	LT		CMT		g_s		T_r		GYP	
	NT	HT	NT	HT	NT	HT	NT	HT	NT	HT
D	2.01*	0.67*	16.81*	27.71*	0.011*	0.004*	0.348*	0.218*	479.69*	161.52*
H_1	2.45*	1.31*	20.31*	32.78*	0.015*	0.007*	0.376*	0.419*	973.22*	465.68*
H_2	2.26*	1.18*	19.61*	31.93*	0.015*	0.007*	0.396*	0.404*	952.38*	412.32*
F	0.68*	-0.34 ^{NS}	-3.43 ^{NS}	-3.07 ^{NS}	-0.003*	-0.002*	-0.06*	-0.09 ^{NS}	-56.04 ^{NS}	-174.57*
h^2	5.85*	2.034	55.00*	113.18*	0.044*	0.020*	1.107*	1.265*	3163.60*	1055.91*
E	0.01 ^{NS}	0.02 ^{NS}	0.32 ^{NS}	0.215 ^{NS}	0.0002 ^{NS}	0.0001 ^{NS}	0.007*	0.005 ^{NS}	4.88 ^{NS}	6.77 ^{NS}
$(H_1/D)^{0.5}$	1.10	1.39	1.10	1.09	1.17	1.33	1.04	1.39	1.42	1.70
$(H_2/4H_1)$	0.23	0.23	0.24	0.24	0.25	0.25	0.26	0.24	0.25	0.22
$(\sqrt{4DH_1} + F)/\sqrt{4DH_1} - F)$	1.36	0.69	0.83	0.903	0.780	0.623	0.858	0.748	0.92	0.52
$H_{n.s.}$	56.88	64.72	66.7	65.86	63.75	64.87	64.13	60.10	59.0	62.45
$H_{b.s.}$	99.11	97.39	97.95	99.11	98.23	98.38	97.72	98.07	97.7	97.74

Additive variance (D), Dominance variance (H_1), Proportion of positive and negative genes in the parent (H_2), Relative frequency of dominant and recessive alleles in the parents (F), Dominance effect (over all loci in heterozygous phase) (h^2), Environmental variance (E), Dominance ratio $(H_1/D)^{0.5}$, Proportion of genes with positive and negative effects in the parents ($H_2/4H_1$), Proportion of dominant and recessive genes in the parents $(\sqrt{4DH_1} + F)/\sqrt{4DH_1} - F)$, Heritability narrow sense ($H_{n.s.}$), Heritability broad sense ($H_{b.s.}$)

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

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

Extent of broad sense heritability was higher than 90% for all traits under normal and stress environment. These result proved higher genetic variability compared to environmental variability for these traits among maize parental lines. Narrow sense heritability was $\geq 60\%$ for physiological traits and grain yield per plant under both temperatures.

W_r/V_r Analysis

Graphical presentation of the results displayed the important role of over-dominant gene action for all traits under both temperature regimes, except osmotic potential (Fig. 1, 2, 3, 4 and 5). Value of intercept (a) was negative for LT (-0.015, -0.01), CMT (-0.26, -0.11), g_s (-0.0004, -0.0003), T_r (-0.01, -0.04) and GYP (-59.95, -33.91) under both experimental conditions and regression line passed below the origin. Distribution of array points along regression line revealed that inbred lines close to the point of origin contain highest dominant genes for specific trait. However, inbreds lines

having farthest position on regression line contain maximum recessive genes for studied traits.

For leaf temperature (Fig. 1a and b), inbred lines WA3748 & NCIL-30-5 had highest dominant genes and D-135, NCIL-20-4 & NCIL-10-5 have maximum recessive genes under normal and high temperature, respectively. For cell membrane thermostability (Fig. 2a and b), parents NCIL-20-4, D-103 and NCIL-10-5 had highest dominant genes under both environments. However, inbreds WA3748, D-135 and NCIL-30-5 carried maximum recessive genes for CMT under normal and high temperature, respectively. For stomatal conductance (Fig. 3a and b), NCIL-10-5 and NCIL-20-4 had highest dominant genes under both temperatures. Inbred lines WA3748, NCIL-30-5 and D-103 had maximum recessive genes for stomatal conductance under normal and high temperature, respectively. For transpiration rate (Fig. 4a) under normal temperature, parents D-103 and NCIL-30-5 had highest dominant and recessive genes, respectively.

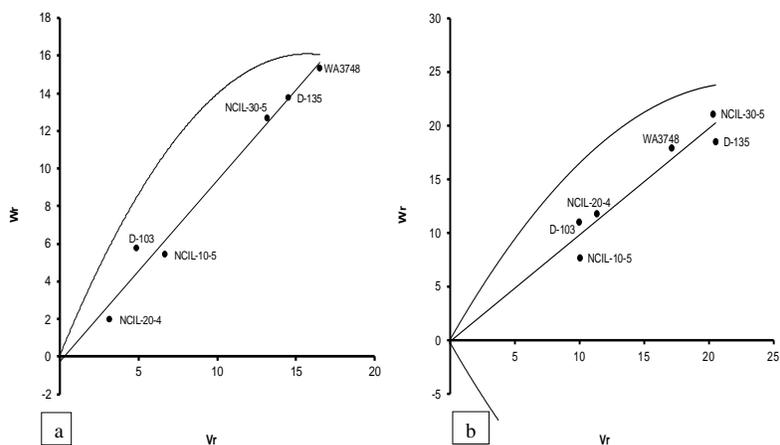


Fig. 2: W_t/V_r graph for cell membrane thermostability; (a) normal temperature (b) high temperature

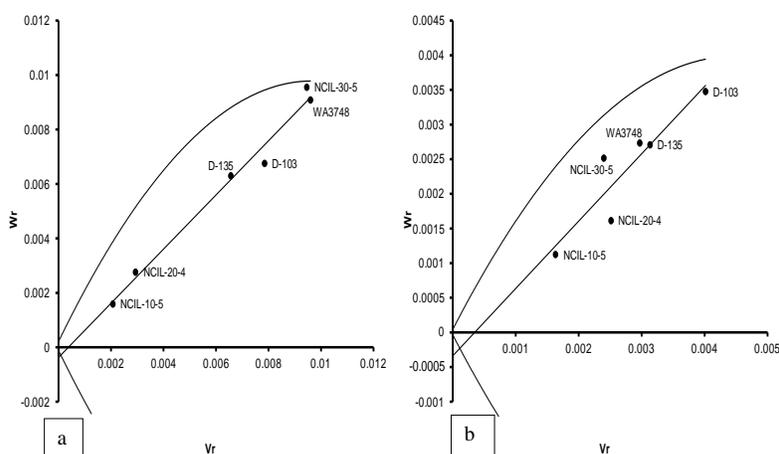


Fig. 3: W_t/V_r graph for stomatal conductance; (a) normal temperature (b) high temperature

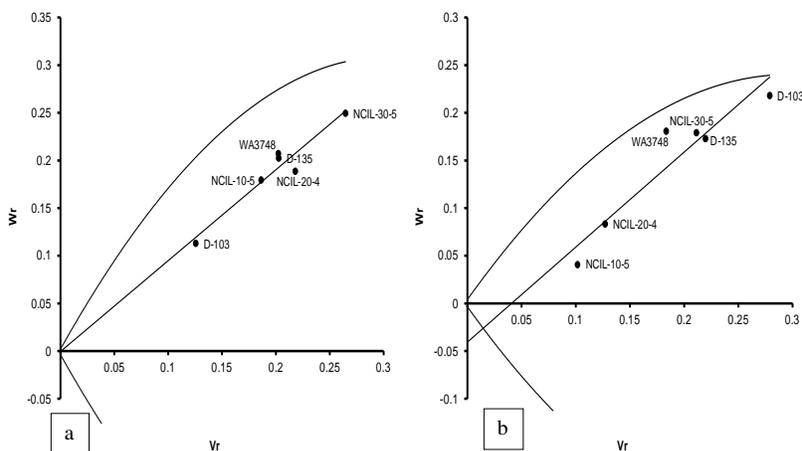


Fig. 4: W_t/V_r graph for transpiration rate; (a) normal temperature (b) high temperature

However under high temperature (Fig. 4b), inbreds NCIL-10-5, NCIL-20-4 had maximum dominant while D-103 possessed maximum recessive genes. For grain

yield per plant (Fig. 5a and b), inbred lines NCIL-10-5 and NCIL-30-5 had maximum dominant & recessive genes under both environments, respectively.

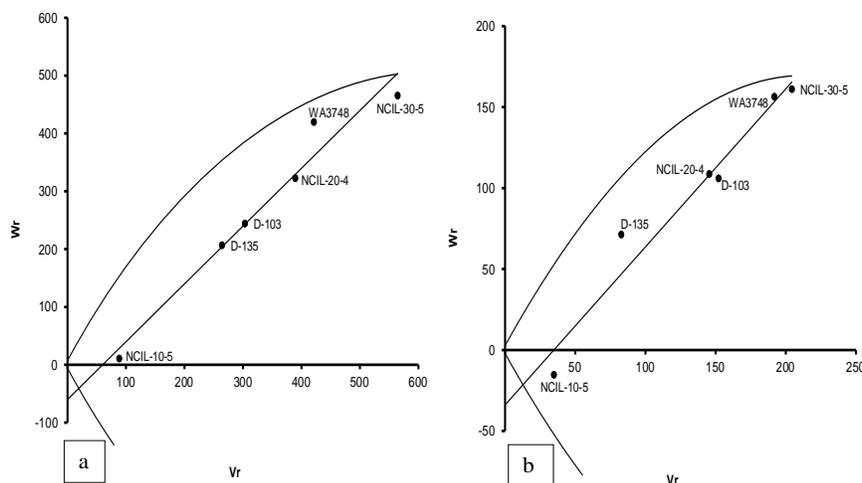


Fig. 5: Wt/Vr graph for grain yield per plant; (a) normal temperature (b) high temperature

Discussion

Diallel is most common method for estimation of genetic characters, to study inheritance pattern for yield and associated agro-physiological characters (Bocanski *et al.*, 2011). Results of ANOVA revealed the existence of genetic variability in the genetic material under both environments (Table 1). Data for all traits were fully fit to additive dominance model (scaling test) in maize under normal and high temperature environment (Table 3a and b). Cell membrane thermostability and grain yield were fully fit under normal and water deficit environment (Chohan *et al.*, 2012). Leaf temperature and grain yield per plant were fully fit, while CMT and stomatal conductance were partially fit to additive dominance model under normal and water deficit environment (Wattoo *et al.*, 2013). Transpiration rate was partially fit to additive dominance model under normal and high temperature (Akbar *et al.*, 2017). Significant 'a' and 'b' statistics depicted that both additive and non-additive genetic effects played a significant role for inheritance of all traits under normal and high temperature (Table 4). Significant additive and non-additive genetic effects were observed for leaf temperature, CMT & stomatal conductance (Chohan *et al.*, 2012; Wattoo *et al.*, 2013), transpiration rate and grain yield under normal and stress environments (Khodarahmpour *et al.*, 2011; Akbar *et al.*, 2017).

Dominance ratio was greater than unity for all traits under normal and high temperature, showing that non-additive genetic effects were important for trait inheritance (Table 5). These results were corroborated by graphical presentation of data (Fig. 1, 2, 3, 4 and 5), which revealed that value of intercept was negative and regression line cut the Wt -axis below origin for each trait under normal and high temperature. For stomatal conductance, over-dominance genetic effects played significant role as confirmed by $(H_1/D)^{0.5}$ under normal and high temperature, respectively (Mohamad *et al.*, 2007).

Transpiration rate was controlled by additive and over-dominance genetic effects under normal and high temperature, respectively (Akbar *et al.*, 2017). Average degree of dominance was higher than one for grain yield. These results revealed the importance of over-dominant gene action for trait inheritance (Hussain *et al.*, 2014; Moradi, 2014; Akbar *et al.*, 2017; Dar *et al.*, 2017).

Due to over-dominance nature of gene action, early selection for trait improvement is not possible. Hybrid breeding is the best strategy to improve these traits among inbreds and to develop heat resilient hybrids (Shams *et al.*, 2010; Amiruzzaman *et al.*, 2013; Badu-Apraku *et al.*, 2016; Murtadha *et al.*, 2016).

However, findings of some other scientists opposed these results and declared that leaf temperature, CMT, stomatal conductance and grain yield were influenced by additive genetic effects under normal and stress environment. As trait was controlled by additive genetic effects, early selection was suggested to get maximum genetic gain (Chohan *et al.*, 2012; Wattoo *et al.*, 2013; Khan *et al.*, 2014).

Conclusion

Data of all traits passed both the scaling tests to fulfil the adequacy of additive-dominance model under normal and high temperature. Hayman's NOVA revealed that both additive and non-additive genetic effects were important for trait inheritance under both environments. Components of genetic variation and graphical presentation of data revealed preponderance of over-dominant gene action for all traits under both environments. Development of (heat resilient) hybrids is an efficient breeding strategy for improvement of studied traits in maize that are governed by over-dominant gene action. Inbred lines NCIL-10-5 and NCIL-20-4 possessed maximum dominant genes for physiological traits. For yield traits, NCIL-10-5 and NCIL-30-5 possessed maximum dominant genes under both temperature regimes.

Exploitation of these three inbreds in future hybrid breeding program will give positive outcomes and can be a good source for development of heat resilient maize hybrids.

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