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Research Article

Combining Ability and Gene Action Studies for Heat-tolerance Physio-biochemical Traits in Tomato

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Abstract

High temperature disrupts normal physiological functions of plant and affects its growth and development. A 5 × 5 diallel cross in tomato (*Lycopersicon esculentum*) showed Nagcarlan to be the best combiner for heat-tolerance traits. The crosses involving high General Combining Ability (GCA) parents also showed good Specific Combining Ability (SCA) effects. Heat-tolerance traits were governed by both additive and non-additive gene action. Total chlorophyll content and nitrate reductase activity were governed by dominant gene action and had more dominant genes than recessive genes for heat tolerance. Pollen viability, relative leaf water content and chlorophyll stability index were governed by both additive and dominant gene action. These traits could be used in the pure line selection to accumulate more additive effects. The Wr-Vr graph indicated over-dominance for heat tolerance. Moderate narrow-sense heritability h^2 (ns) was found for pollen viability (0.44) and total chlorophyll content (0.43). Heterosis breeding was appropriate to utilize the dominant gene action involved for heat tolerance.

Key words: Additive, diallel cross, dominant gene action, GCA, SCA

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Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

The growth and development of tomato are highly sensitive to increased day and night temperatures. This is because of the inability of cultivars to set fruit under such temperature stress. In tomato, high temperature (>28°C) during reproductive stage causes a significant increase in flower drop (Hanna and Hernandez, 1982; Hazra and Ansary, 2008) and a significant decrease in fruit set (Berry and Rafique Uddin, 1988) and pollen fertility (Singh and Shono, 2012), which consequently leads to a huge decrease in fruit yield. These types of stress phenotypes observed in plants are mainly attributable to alterations in physiological and biochemical functions. Some important physiological reactions to heat stress in tomato relate to crop water relations, concentration of compatible osmolytes, cell membrane thermo-stability, photosynthesis and alterations in hormones (Golam *et al.*, 2012). Studies on some of these physiological phenomena have been made, whereas, genetics of the changes in such physiological phenomena have not been well documented yet. Increase in proline content and decrease in relative leaf water content are observed during temperature stress (Claussen, 2005). High membrane thermo-stability is associated with an increase in fruit yield (Saeed *et al.*, 2007). At high-temperature, disruption of sugar metabolism and proline transport can be observed, which are responsible for physiological dysfunction (Sato *et al.*, 2006). Heat stress also has a major effect on pollen growth and development. Heat stress decreases starch concentration, which results in decreased sugar concentration of pollen, thus reducing its growth and viability (Maiti *et al.*, 2014). Furthermore, resistance to heat stress is developmentally regulated, stage-special event and resistance at one stage of crop improvement is sometimes not related to resistance at other growth stages. Therefore, to produce tomato under heat stress successfully, resistance may be required at whole imperative stages of crop growth and development (Golam *et al.*, 2012). Studies on the genetics of physiological aspects occurring in plants during heat stress could provide an overall picture regardless of the growth stages.

Combining ability studies of parents and crosses are helpful to select appropriate parents and hybrids and to use them in a breeding program. It helps to find the gene action and the type of genetic interactions involved in governing the traits. General Combining Ability (GCA) is used to find a variety showing good performance in a series of crosses, whereas, Specific Combining Ability (SCA) can be used to find any specific cross combination that shows the best performance (Sprague and Tatum, 1942). The GCA gives the estimation of

additive genetic effects and SCA estimates the non-additive genetic effects (Falconer and Mackay, 1996). Heat tolerance is a complex trait and unraveling the genetics of heat tolerance is difficult. Additive gene action is found to govern heat tolerance in tomato considering some of the phenotypic traits (Dane *et al.*, 1991). Non-additive gene action was predominant in controlling yield and yield attributing traits (El-Gabry *et al.*, 2014; Saleem *et al.*, 2009). Yield being a complex trait is determined by various yield-attributing traits; it is conditioned by both additive and non-additive gene actions (El-Gabry *et al.*, 2014). As phenotype is a cumulative exposure of many physiological events, study on the genetics of physiological traits will be useful to improve those phenotypic traits. This experiment was conducted to study the genetics of some of the individual physiological traits which are considered as a good indicator of heat tolerance. Study on the genetics of the physiological traits will be helpful to design a suitable breeding program to improve heat tolerance in tomato.

MATERIALS AND METHODS

The experimental material consisted of genetically diverse five parental lines, viz., BL1173, H7997, CLN1621E, BL1176 and Nagcarlan. Among them, Nagcarlan is heat tolerant; BL1173, CLN1621E and BL1176 are moderately heat tolerant, whereas, H7997 is susceptible to heat stress. These were crossed to generate 10 one-way F₁ hybrids. All the F₁s and parents were planted in a completely randomized design with three replications inside a greenhouse of Department of Plant Breeding and Genetics, Assam Agricultural University during April-August, 2012. The plants were exposed to a temperature of 38-40°C inside the greenhouse which was 10-12°C greater than the optimum growing temperature of tomato (28°C). Data were recorded for pollen viability, chlorophyll content, chlorophyll stability index, relative leaf water content, membrane thermo-stability, nitrate reductase activity and proline content. The data were analyzed using Agronomix Software Inc. (2013).

Estimation of pollen viability was done using Triphenyl Tetrazolium Chloride (TTC) test as described in Norton (1966). Viable pollens are stained as bold red colored. Pollen viability percentage was calculated as the number of viable pollens among a hundred pollens randomly counted under a microscope. Leaf chlorophyll was estimated by acetone extraction method and chlorophyll content was determined using the equation as in Hiscox and Israelsan (1979) and expressed as mg g⁻¹ leaf fresh weight. Chlorophyll stability index was estimated following the method mentioned in

Chetry *et al.* (2003) which is the ratio of chlorophyll content of heated samples to normal samples expressed in percentage. Estimation of Relative Leaf Water Content (RLWC) was done using the formulae of Barrs and Weatherley (1962). Membrane thermo-stability was estimated by measuring the conductivity of leaf in normal condition and boiling water bath and calculated using the formula mentioned in Premachandra *et al.* (1989). *In vitro* nitrate reductase assay was done following the method of Thimmaiah (1999) and expressed as $\mu\text{mol NO}_2$ formed per gram tissue per hour. Proline content was estimated by the method proposed by Bates *et al.* (1973). The protocol was based on the formation of the red colored formazon by the protein with ninhydrin in acid medium, which is soluble in organic solvent like toluene.

Mean values for each plot were used in statistical analyses. The combining ability effects of parents and hybrids were estimated following fixed effect model of Griffing (1956a, b). Method II and variance components following Hayman (1954). The components of variation and the genetic ratios derived from them, were defined by Hayman as: D = component of variation due to the additive effects of genes, H_1 = component of variation due to dominance effects of genes over all segregating loci, H_2 = component of variation due to non-additive effects corrected for gene distribution, F = covariance of additive and non-additive gene effects in all the arrays, E = environmental or non-heritable variation and h^2 = overall dominance effects of the heterozygous loci. Some genetic proportions estimated were H_1/D = measure of average degree of dominance over loci, proportion of genes

with positive and negative effects in the parents ($H_2/4H_1$), proportion of dominant and recessive genes in the parents (KD/KR), number of gene groups controlling the characters (h^2/H_2), the coefficient of correlation (r) between the parental order of dominance (W_r+V_r) and parental measurement Y_r and heritability in narrow sense (h^{2ns}). The W_r-V_r graph was used to find the degree of dominance.

RESULTS

Combining ability analysis: Analysis of variance for combining ability (Table 1) showed GCA was higher than SCA for pollen viability, relative leaf water content, membrane thermo-stability and total chlorophyll content. These traits were governed by additive gene action. The SCA effects of chlorophyll stability index, nitrate reductase activity and proline content were more than GCA effects, so these traits were governed by non-additive gene action. General combining ability effects of parents (Table 2) showed Nagcarlan to be the best general combiner for relative leaf water content, membrane thermo-stability, total chlorophyll content and chlorophyll stability index. Besides these, H7997 was found to be the best general combiner for pollen viability, BL1176 for nitrate reductase activity and CLN1621E for proline content. A high and significant SCA effects were shown by most of the crosses (Table 3). The best SCA effect for pollen viability was shown by cross BL1173 \times Nagcarlan. The cross BL1173 \times BL1176 exhibited best SCA for nitrate reductase activity and H7997 \times BL1176 for chlorophyll stability

Table 1: Analysis of variance for combining ability

Source of variation	DF	Mean sum of squares						
		† PV	RLWC	MT	TCC	CSI	NR	PC
GCA	4	101.56**	32.16**	46.52**	0.32**	22.60**	0.51**	1.09**
SCA	10	36.71**	20.09*	43.42**	0.23**	37.11**	0.80**	1.60**
Error	30	12.66	4.66	7.21	0.05	5.47	0.09	0.20

***Significant at 5 and 1% probability levels, respectively, † PV: Pollen viability (%), RLWC: Relative leaf water content (%), MT: Membrane thermo-stability (%), TCC: Total chlorophyll content (mg g^{-1} FW), CSI: Chlorophyll stability index (%), NR: Nitrate reductase activity ($\mu\text{m g}^{-1} \text{h}^{-1}$) and PC: Proline content ($\mu\text{m g}^{-1}$)

Table 2: General combining ability effects of parents

Parent	Traits †						
	PV	RLWC	MT	TCC	CSI	NR	PC
BL 1173	-1.82	-1.03	-1.93*	-0.31**	-0.59	-0.30**	-0.50**
H 7997	5.28**	1.00	1.71	0.16*	1.15	-0.21*	0.14
CLN 1621E	0.11	0.71	-0.92	-0.02	0.61	-0.04	0.51**
BL 1176	-4.98**	-3.13**	-2.46*	-0.06	-2.84**	0.31**	-0.28
Nagcarlan	1.41	2.45**	3.61**	0.23**	1.67*	0.24*	0.12
SE (g)	1.20	0.73	0.91	0.07	0.79	0.10	0.15
SE (g _i -g _j)	1.90	1.15	1.44	0.12	1.25	0.16	0.24

***Significant at 5 and 1% probability levels, respectively, † PV: Pollen viability (%), RLWC: Relative leaf water content (%), MT: Membrane thermo-stability (%), TCC: Total chlorophyll content (mg g^{-1} FW), CSI: Chlorophyll stability index (%), NR: Nitrate reductase activity ($\mu\text{m g}^{-1} \text{h}^{-1}$), PC: Proline content ($\mu\text{m g}^{-1}$), SE (g): Standard error of GCA effect and SE (g_i-g_j): Standard error of the difference between two GCA estimates

Table 3: Specific combining ability effects of crosses

Cross	Traits †						
	PV	RLWC	MT	TCC	CSI	NR	PC
BL1173×H7997	-9.62**	-1.97	-2.50	-0.01	-4.33*	0.69**	2.18**
BL1173×CLN1621E	-2.55	-1.39	2.46	-0.08	2.29	0.01	0.46
BL1173×BL1176	0.04	4.10**	7.45**	0.09	5.98**	0.82**	-1.14**
BL1173×Nagcarlan	11.71**	4.02*	-5.27**	0.33*	2.97	0.09	-0.55
H7997×CLN1621E	7.41**	3.66*	8.07**	0.11	7.07**	-0.32	0.56
H7997×BL1176	2.18	-3.07*	-5.74**	0.53**	7.41**	1.11**	0.60
H7997×Nagcarlan	-2.22	0.21	10.58**	0.55**	-6.85**	-0.51*	-1.01**
CLN1621E×BL1176	2.10	3.25*	-1.09	0.18	2.65	0.61**	1.07**
CLN1621E×Nagcarlan	2.29	-8.13**	-0.12	-0.22	2.08	0.80**	0.67*
BL1176×Nagcarlan	-0.78	5.51**	5.96**	0.55**	1.09	0.60**	1.34**
SE (g _i)	2.46	1.49	1.85	0.15	1.61	0.21	0.31
SE (g _i -g _j)	4.23	2.58	3.21	0.26	2.79	0.36	0.53

***Significant at 5 and 1% probability levels, respectively, † PV: Pollen viability (%), RLWC: Relative leaf water content (%), MT: Membrane thermo-stability (%), TCC: Total chlorophyll content (mg g⁻¹ FW), CSI: Chlorophyll Stability Index (%), NR: Nitrate reductase activity (μm g⁻¹ h⁻¹), PC: Proline content (μm g⁻¹), SE (g_i): Standard error of SCA effect, SE (g_i-g_j): Standard error of the difference between two SCA estimates

Table 4: Genetic components of variation and genetic proportions

Components of variation	Traits †						
	PV	RLWC	MT	TCC	CSI	NR	PC
D	59.90**	37.18**	8.19	0.08	41.96**	0.18	0.25
H ₁	125.80*	75.29*	144.70**	0.71**	130.18**	2.49**	5.40**
H ₂	106.69*	62.29*	136.66**	0.52*	102.19**	2.05**	4.91**
F	16.99	35.88	-19.58	0.01	60.97	0.16	-0.17
E	12.66	4.66	7.21	0.05	5.47	0.09	0.20
h ²	9.71	3.14	58.07*	0.62**	62.99*	2.37**	2.66**
Genetic proportions							
(H ₁ /D) ^{1/2}	1.44	1.42	4.20	2.90	1.76	3.72	4.67
H ₂ /4H ₁	0.21	0.21	0.24	0.18	0.20	0.21	0.23
KD/KR	1.22	2.02	0.56	1.02	2.40	1.27	0.87
h ² /H ₂	0.09	0.05	0.42	1.19	0.62	1.15	0.54
r(W _r +V _r), Y _r	0.26	-0.72	0.26	-0.70	-0.90	-0.59	-0.83
h ² (ns)	0.44	0.26	0.30	0.43	0.13	0.27	0.24

***Significant at 5 and 1% probability levels, respectively, † PV: Pollen viability (%), RLWC: Relative leaf water content (%), MT: Membrane thermo-stability (%), TCC: Total chlorophyll content (mg g⁻¹ FW), CSI: Chlorophyll stability index (%), NR: Nitrate reductase activity (μm g⁻¹ h⁻¹), PC: Proline content (μm g⁻¹), D: Component of variation due to additive effects of genes, H₁: Component of variation due to dominance effects of genes over all segregating loci, H₂: Component of variation due to non-additive effects corrected for gene distribution, F: Covariance of additive and non-additive gene effects in all arrays, E: Environmental or non-heritable variation, h²: Overall dominance effects of heterozygous loci, (H₁/D)^{1/2}: Measure of average degree of dominance over loci, H₂/4H₁: Proportion of genes with positive and Negative effects in the parents, KD/KR: Proportion of dominant and recessive genes in parents, h²/H₂: No of gene groups controlling character, r(W_r+V_r), Y_r: The coefficient of correlation(r) between parental order of dominance (W_r+V_r) and parental measurement (Y_r) and h²(ns): Narrow sense heritability

index. H7997×Nagcarlan showed the best SCA effect for membrane thermo-stability and total chlorophyll content, BL1176×Nagcarlan showed the best SCA effect for relative leaf water content, total chlorophyll content and proline content.

Gene action: The different genetic parameters and proportions are presented in Table 4. Both additive (D) and dominance (H₁ and H₂) gene action were involved in controlling most of the characters. A predominant role of non-additive gene action was observed from a relatively higher magnitude of dominance components H₁, H₂ and h². The characters membrane thermo-stability, total chlorophyll content, nitrate reductase activity and proline content were found to be predominantly controlled by dominant

component. On the other hand, the dominant component h² was significant for membrane thermo-stability, total chlorophyll content, chlorophyll stability index, nitrate reductase activity and proline content. A negative F-value indicated having more of recessive genes to control membrane thermo-stability and proline content. Pollen viability, relative leaf water content, total chlorophyll content, chlorophyll stability index and nitrate reductase activity were controlled by dominant genes. Dominant genes and non-additive gene actions controlled heat-tolerance physiological traits. So, heterosis breeding was most recommended to improve such traits.

The estimates of the degree of dominance were found to be more than unity for all the characters indicating the prevalence of over-dominance. The proportion of alleles in the

parents with positive and negative effects ($H_2/4H_1$) was less than the expected value of 0.25 for all the characters. This indicated unequal allelic frequencies for all the characters. From KD/KR value, it can be inferred that the parents might contain more number of dominant genes than recessive genes for pollen viability, relative leaf water content, total chlorophyll content, chlorophyll stability index and nitrate reductase activity. The value of h^2/H_2 indicated that nearly one group of genes might be involved in the control of total chlorophyll content, chlorophyll stability index, nitrate reductase activity and proline content. The characters controlled by a single group of genes having more of dominant genes are good to be used in improving the heat-tolerance trait. The negative correlation between the mean value of the parents Y_r and the parental order of dominance (W_r+V_r) for the characters indicated that the dominant genes were associated with higher mean expression, which was found in relative leaf water content, total chlorophyll content, chlorophyll stability index, nitrate reductase activity and proline content. A moderate narrow sense heritability $h^2(ns)$ was found for pollen viability and total chlorophyll content. Physiological traits showing higher narrow sense heritability explained more of the additive variance. These traits could be well used in selection program to improve heat-tolerance traits in tomato.

Wr-Vr Graphical analysis: Graphical analysis of a diallel cross provided information on the average degree of dominance, dominance order of the parents and relationship among the parents. The regression of W_r on V_r did not deviate significantly for all the characters under study except membrane thermo-stability indicating the absence of epistasis for those characters (Fig. 1a-g). The regression line intercepted W_r -axis below origin for all the characters under study conclude over-dominance for those characters. The parents well scattered in the regression line indicated their divergence. The parent being close to origin was supposed to possessed more dominant genes and that lying away from origin possessed more of recessive genes. The parent lie near about the center of W_r - V_r graph possessed almost equal proportion of dominant and recessive genes. The BL1173 was found to possess a more dominant gene than recessive genes for membrane thermo-stability and chlorophyll stability index. The CLN1621E had dominant genes for total chlorophyll content and proline content. Nagcarlan had dominant genes for chlorophyll stability index. Parents having more dominant genes are good to be used in a breeding program, as it is easier in further selection.

DISCUSSION

Nagcarlan showed the best GCA for many of physio-biochemical traits, it can be used as the best combiner to develop heat-tolerant tomato lines. Further, most of the crosses involving Nagcarlan showed better SCA. The cross BL1176×Nagcarlan showed higher and positive SCA for most of the traits. This particular cross is controlled by more of non-additive gene action and can be improved using heterosis breeding. The SCA effects of the crosses, where at least one of the high GCA parents are involved, showed better results. The F_1 hybrids having higher SCA for one or few traits can be used as parents in breeding programs (El-Gabry *et al.*, 2014). The crosses having high SCA were due to high×high or high×low combining parents and showed additive×additive or additive×dominance type of gene action. Additive gene action was seen as more important in governing heat-tolerance traits in tomato (Dane *et al.*, 1991); however, the role non-additive gene action cannot be ignored (Saleem *et al.*, 2009; Hazra and Ansary, 2008). If the traits are governed by non-additive gene action, they may produce transgressive segregants in subsequent generations (because of dominance and epistatic interactions) (Salimath and Bahl, 1985). So, bi-parental mating at early segregating generations was recommended to utilize non additive gene action which was followed by selection in subsequent generations to utilize additive gene action.

Total chlorophyll content and nitrate reductase activity were governed by dominant gene action and also had more of dominant genes in them. These traits having more dominant genes could be improved using heterosis breeding, which was expected to bring more of hybrid vigor due to more number of dominant genes (Biswas *et al.*, 2011). Pollen viability (Dane *et al.*, 1991) relative leaf water content and chlorophyll stability index could be used as selection traits in segregating generations. These traits were governed by both additive and non-additive gene action but had more number of dominant genes. Selection in those traits would accumulate dominant genes due to additive effects in the segregating population. The traits with high narrow sense heritability can be improved faster through selection (Falconer and Mackay, 1996). The CLN1621E had more of the dominant genes for proline content as shown by W_r - V_r graph and their general combining ability was also high. So, proline content was a good trait to select the cross involving CLN1621E. Similarly, chlorophyll stability index could be used to select the crosses involving Nagcarlan and BL1173.

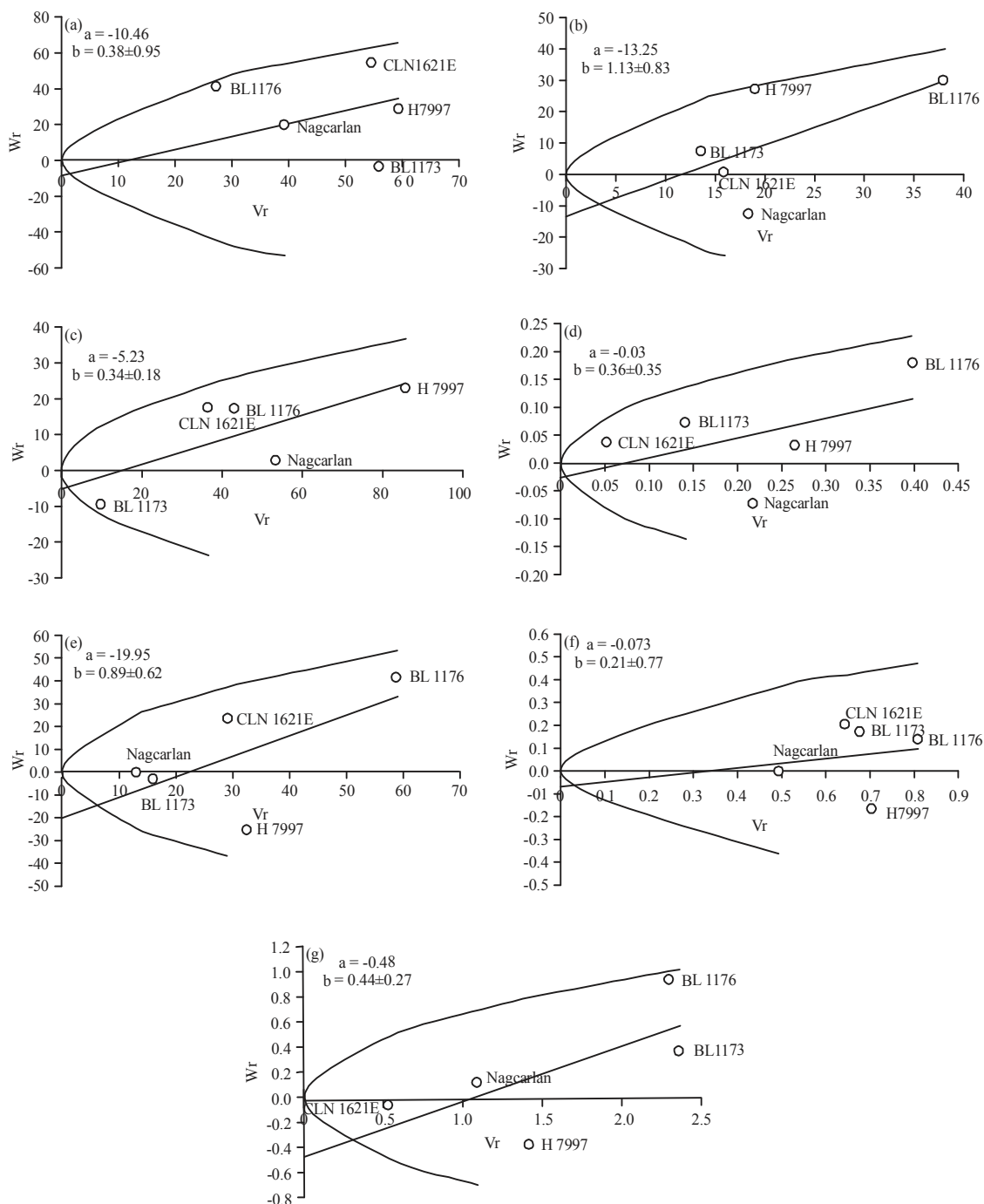


Fig. 1(a-g): Wr-Vr graphs for, (a) Pollen viability, (b) Relative leaf water content, (c) Membrane thermo-stability, (d) Total chlorophyll content, (e) Chlorophyll stability index, (f) Nitrate reductase activity and (g) Proline content. The parents closer to the origin have more dominant genes and the parents far from origin have more recessive genes for the respective traits

Most of the heat-tolerant traits were governed by non-additive gene action. Heterosis breeding was the most appropriate strategy to breed tomato for heat-tolerance

(Biswas *et al.*, 2011). Use of parents with high GCA effects was better as their crosses produced better SCA effects. Total chlorophyll content and nitrate reductase activity were the

best traits to be used as markers in the heterosis breeding program as they were governed solely by dominant gene action, had more number of dominant genes and showed good heritability. Breeding programs formulated using physiological and biochemical traits have been faster since selection can be done in early stages of plant growth.

CONCLUSION

Nagcarlan showed the best GCA for most of the physio-biochemical characters studied followed by H7997. Nagcarlan is a heat tolerant variety whereas H7997 is heat susceptible one. Nagcarlan can thus be used in further breeding program. The SCA effects of the crosses involving Nagcarlan is the best when crossed with other low GCA parents. This suggests that the genes for biochemical traits are governed by additive x dominance type of interaction. To utilize both additive and dominance type of gene action bi-parental mating is appropriate for such type of crosses. Graphical analysis showed that the physio-biochemical traits are governed by over-dominance gene action. The genetic analysis (D, H₁, H₂, F) also suggests that the traits governed by dominance component. Thus, it can be concluded that physio-biochemical traits under study are mostly governed by non-additive gene action, so heterosis breeding is recommended using Nagcarlan as a combiner to develop heat tolerant tomato variety for off-season production.

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