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Full Length Research Paper

Genetic analysis of field and physiological indicators of drought tolerance in bread wheat (*Triticum aestivum* L.) using diallel mating design

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In order to study the inheritance of field, physiological and metabolite indicators of drought tolerance in wheat, an eight-parental diallel cross, excluding reciprocals, was grown in a randomized complete block design (RCBD) with three replications under two different water regimes (irrigated and rainfed). Significant differences were found for yield potential (Y_p), stress yield (Y_s), stress tolerance index (STI), leaf water potential (LWP), relative water content (RWC), water use efficiency (WUE) and evapotranspiration efficiency (ETE). Y_p, RWC and evapotranspiration efficiency ETE showed highly significant differences for both general combining ability (GCA) and specific combining ability (SCA), indicating the involvement of both additive and non-additive gene action in their inheritance. Y_s, STI and WUE revealed highly significant differences for SCA, hence non-additive gene action was predominant for these traits. The best general combiners with positive effects, for improvement of Y_p, Y_s, STI, LWP, RWC, WUE and ETE under drought conditions were parents 5, 1, 6, 2, 7, 1 and 2, respectively. The best specific combination with heterobeltiosis over the best parents for improvement of Y_p, Y_s, STI, LWP, RWC, WUE and ETE were crosses 3 × 6, 2 × 4, 2 × 6, 5 × 8, 2 × 6, 2 × 4 and 1 × 7, respectively indicating that parents of these crosses are genetically diverse. High broad-sense heritability observed for all the traits confirmed that all the traits are more genetic, but because of low narrow-sense heritability the rule of additive part was low.

Key words: Drought tolerance, physiological indicators, diallel mating design, genetic analysis.

INTRODUCTION

Wheat crops growing in both irrigated and rainfed environments commonly experience water deficit during some stages of the crop growth cycle. However, changing weather pattern and worldwide water shortages will likely result in irrigated wheat being grown with less applied water, increasing the likelihood of soil water deficit (Rebetzke et al., 2006). Improving drought resistance is, therefore, a major objective in plant breeding programs for rainfed conditions. To formulate an efficient breeding program for developing drought-tolerant varieties, it is essential to understand the mode of inheritance and genes or gene products which are responsible for desired characteristics of drought resistance at different stages of plant growth. Since drought is a complex physiological reaction, its genetic basis has therefore received limited attention; hence, little information is available on genetic architecture of drought related physiological characters, which may provide practical information to breeders during the development of drought tolerant wheat varieties (Farshadfar et al., 2000, 2001; Zarei et al., 2007; Farshadfar et al., 2008a; Dhanda et al., 2002).

Diallel cross designs are frequently used in plant breeding research to obtain information about genetic properties of parental lines or estimates of general and specific combining abilities and heritability (El-Maghraby et al., 2005; Iqbal et al., 2007). In addition, diallel cross provides early information on the genetic behavior of attributes in the first generation (Griffing, 1956a). Up to

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now, several methods have been proposed for the genetic analysis of data from a diallel cross (Griffing, 1956b; Hayman, 1954a; Hayman, 1954b). The approaches of Griffing (1956b) and Hayman (1954b) are statistically similar in their analyses of variance (Eric et al., 2005). The Griffing's general and specific combining abilities are mathematically identical to Hayman's additive and dominance components. They differ, however, in the genetic assumptions, information and interpretation. In general, the Hayman's method appears to extract more genetic information than the Griffing's method does from the same data set. The Griffing's method involves only analysis of variance and estimation of GCA and SCA effects, while Hayman's method includes statistical and graphical analyses of array variances and covariances, and estimation of a number of genetic parameters. The objectives of this investigation were to study (i) specific and general combining ability as well as (ii) the genetic properties of drought tolerance indicators in wheat under rainfed conditions.

MATERIALS AND METHODS

An eight - parent diallel cross excluding reciprocals, was carried out in the Agricultural Research Institute of Sararood, Kermanshah, Iran during year 2004 to 2005 (47° 20´ N latitude, 34° 20´ E longitude and 1351.6 m altitudes). Climate in this region is classified as semi-arid with mean rainfall of 478 mm. Minimum and maximum temperature in the research station was -27 and 44°C, respectively. The cultivars used were Plainsman (1), Regina (2), Capelle desprez (3), Chinese spring (4), Shakha (5), Saberbeg (6), Karchia(7) and Kobomugi (8). The plant genetic materials (parents and $F_{1s)}$ were arranged in a randomized complete block design with three replications under irrigated and rainfed conditions. Single seeds were sown in 3 m rows and at 3 × 15 cm plant to plant and row to row distances, respectively. From each entry (parents and F_1s), five competitive plants were randomly selected from each replication for recording observations on the following characters:

Grain yield: Grain yield of genotype was measured under normal (Y_p) and stress (Y_s) conditions.

Relative water content (RWC)

Five flag leaves (0.5 g) were taken and weighed for fresh weight (FW). Then, segments were placed in distilled water for 24 h and reweighed to obtain turgor weight (TW). Thereafter the leaf segments were oven dried for 48 h in 72°C and weighed (dried weight, DW). RWC was calculated using the following formula (Eric et al., 2005):

$$RWC(\%) = \left[\frac{FW - DW}{TW - DW}\right] \times 100$$

Relative water loss (RWL)

A sample of five flag leaves were taken from each genotype and fresh weight was measured (FW). The leaves were then wilted at 35°C for 5 h and reweighed (W5H). Then the samples were oven dried for 70°C and weighed again (DW). RWL was calculated by the following formula (Farshadfar et al., 2000):

$$RWL = \frac{FW - W5H}{FW - DW} \times 100$$

Chlorophyll fluorescence (CHF)

From each line in each replication, five flag leaves were selected and the quantum yield was recorded after dark adaptation using a MINI-PAM instrument as:

Quantum yield = F_v / F_m

Where, F_v and F_m are variable and maximum fluorescence, respectively (Genty et al., 1989).

Leaf water potential (LWP)

Leaf water potential was measured on flag leaves of each replication using a pressure chamber (model PMS instrument CO.)

Water use efficiency (WUE)

Three seeds from each line were sown in the greenhouse, two of which were eliminated 10 days after germination. To calculate the amount of evaporation, one empty pot was used in each replication. The pots were irrigated with the measured amount of water. The run-off water in each pot was subtracted from the water applied to each pot. After 39 days, the dry matter (after drying at 70°C for 24 h) and the amount of water applied were used to calculate WUE using the formula suggested by Ehdaie and Waines (1993):

ETE = TDM / TWU
WUE = GY / TWU

Where, ETE = evapotranspiration efficiency; TDM = total dry mater; TWU = total water used and GY= grain yield. Using Y_s and Y_p, the following stress tolerance index was calculated:

Stress tolerance index (STI) = $(Y_s \times Y_p) / (\overline{Y}_p)^2$ (Fernandez, 1992).

Statistical analysis was performed by MSTAT-C ver 1.42 (analysis of variance; ANOVA), SPSS ver 17 and Dial 98 (combining ability analysis, estimate of variance components, genetic parameters and graphical analysis) softwares.

RESULTS AND DISCUSSION

Analysis of variance (Table 1) revealed significant differences among parents and hybrids for Y_p, Y_s, STI, LWP, RWC, WUE and ETE indicating the presence of genotypic variability, different responses of genotypes to water deficit and possible selection of drought tolerant genotypes. No significant difference was found for CHF, RWL and TWU (Table 1). Genetic variability was found for GY and RWC in wheat (Farshadfar et al., 2008a). RWC, RWL, STI, LWP and WUE were shown as screening techniques for discrimination of drought tolerance genotypes in wheat, barley, maize and chickpea

Table 1. Analysis of variance for the characters under investigation.

S.O.V	df	Mean square									
		Y_p	Y_s	STI	CHF	LWP	RWL	RWC	WUE	ETE	TWU
Replications	2	24.87**	0.47^{ns}	0.01^{ns}	0.002^{ns}	698.84**	0.17**	38.05^{ns}	0.008^{ns}	0.007^{ns}	0.02^{ns}
Genotypes	35	21.05**	1.85**	0.07**	0.007^{ns}	119.86*	0.02^{ns}	62.63**	0.029**	0.316**	0.011^{ns}
Error	70	2.15	0.71	0.02	0.005	71.07	0.01	12.29	0.011	0.052	0.010
CV%	-	15.9	12.3	12.3	7.9	18.7	11.6	4.1	12.3	10.1	1.2

*; ** Significant at the 0.05 and 0.01 probability levels, respectively; ns, non significant.

Table 2. Griffing analysis of variance for significant traits in the eight-parent diallel crosses of wheat.

SOV	df	Mean square						
		Y_p	Y_s	STI	LWP	RWC	WUE	ETE
Rep	2	31.73**	1.09^{ns}	0.04^{ns}	696.47**	26.33^{ns}	0.02^{ns}	0.01^{ns}
GCA	7	19.38**	1.58^{ns}	0.03^{ns}	211.36*	88.10**	0.02^{ns}	0.44**
SCA	20	22.07**	1.69**	0.07**	63.96^{ns}	35.65**	0.03**	0.22**
Error	54	1.89	0.64	0.02	76.53	12.41	0.01	0.05
Msgca / Mssca	-	0.88	0.93	0.43	3.30	2.47	0.67	2.0

*; ** Significant at the 0.05 and 0.01 probability levels, respectively; ns; non significant.

(Farshadfar and Sutka, 2002; Bayoumi et al., 2008; Ossani et al., 2009; Farshadfar et al., 2008b; Geravandi et al., 2011). In fact the development of any plant breeding program is dependent upon the existence of genetic variability, the efficiency of selection and expression of heterosis in the plant population (Singh and Narayanan, 1993; Singh and Chaudhary, 1995).

Combining ability analysis

The concept of combining ability as a measure of gene action refers to the capacity or ability of a genotype to transmit superior performance to its crosses. The value of an inbred line depends on its ability to produce superior hybrids in combination with other inbreds. Combining ability analysis helps in the evaluation of inbreds in terms of their genetic value and in the selection of suitable parents for hybridization (Singh and Narayanan, 1993; Singh and Chaudhary, 1995; Ghasemi et al., 2008). Combining ability analysis (Table 2) revealed highly significant GCA and SCA for the characters Y_p, RWC and ETE indicating the involvement of additive and non-additive type of gene action in their inheritance. The improvements of such characters warrant a breeding methodology which capitalizes on additive as well as non-additive genetic variance. In this situation, biparental mating offers good prospects for increasing the frequency of genetic recombinants hastening the rate of genetic improvement. Population breeding is also suggested in the form of biparental mating between selected recombinants to exploit the additive and non- additive effects. Highly significant SCA was observed for Y_s, STI and WUE indicating the role of dominant gene action in their genetics; hence it may be necessary to resort to heterosis breeding (Iqbal et al., 2007).

LWP showed highly significant differences for additive gene effects (GCA) indicating additive type of gene action controls inheritance of this trait. Accordingly direct selection is useful for its improvement (Table 2). Selection of parental lines with high GCA effects increases the probability of getting heterotic hybrids in crop plants. The best general combiners with positive effects, for improvement of Y_p, Y_s, STI, LWP, RWC, WUE and ETE under drought conditions were parents 5, 1, 6, 2, 7, 1and 2, respectively (Table 3). The best specific combination with heterobeltiosis over the best parents for improvement of Y_p, Y_s, STI, LWP, RWC, WUE and ETE were crosses 3 × 6, 2 × 4, 2 × 6, 5 × 8, 2 × 6, 2 × 4 and 1 × 7, respectively indicating that parents of these crosses are genetically diverse (Table 4). The expression of positive heterosis in these hybrids reveals the preponderance of additive gene action. According to Topal et al. (2004), compared to other type of gene effects, high additive gene effects for a specific trait will increase success in selection for that trait.

Analysis of variance components

An important advantage of analysis of variance components is that it is free of the assumptions of whether maternal or reciprocal effects are present or not and whether the parental lines are a fixed sample or a random sample of a population of inbred lines (Mather and Jinks, 1982). Highly significant differences were

Table 3. General combining ability of parents in an 8 × 8 diallel design for significant traits.

Parent	Character						
	Y_p	Y_s	STI	LWP	RWC	WUE	ETE
1	1.80	0.48**	-0.04	1.35	-2.71**	0.06	0.08**
2	0.45**	-0.19	-0.10**	5.13**	-1.57**	-0.02	0.21**
3	-0.23	0.17	0.02	0.01	1.72**	0.02	0.20**
4	0.12	-0.12	-0.06	0.18	-1.97**	-0.03	-0.19**
5	0.49**	0.27**	-0.01	-1.60	-1.87**	0.03	-0.06
6	-1.40**	-1.29	0.07	-5.38**	1.69**	-0.04	-0.12**
7	-1.34**	-0.32**	0.01	-3.21**	2.54**	-0.04	-0.16**
8	0.12	0.10	0.02	3.51**	2.19**	0.02	0.04
SE	0.43	0.25	0.04	2.49	1.04	0.09	0.07

*; ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 4. Specific combining ability effects of the crosses for significant traits.

Cross	Character						
	Y_p	Y_s	STI	LWP	RWC	WUE	ETE
1 × 2	0.43	-0.47	-0.08	-5.08	2.47	-0.06	-0.31**
1 × 3	-1.79**	0.60	0.13**	-0.63	-0.75	0.08	-0.21**
1 × 4	-3.23**	-0.63	0.10	-1.47	-1.29	-0.08	0.10
1 × 5	-2.12**	0.23	0.12**	2.64	2.54	0.03	-0.08
1 × 6	2.75**	0.51	-0.10	5.75	-6.06**	0.06	-0.08
1 × 7	0.99	0.08	-0.04	-1.75	2.53	0.01	0.50**
1 × 8	2.97**	-0.32	-0.13**	0.53	0.58	-0.04	0.08
2 × 3	-1.00	-0.12	-0.02	4.25	1.67	-0.01	-0.54**
2 × 4	-0.25	1.65**	0.14**	6.42	-2.33	0.21	0.15
2 × 5	2.11**	0.75**	-0.05	-1.80	-1.44	0.09	0.11
2 × 6	-5.19**	-0.54	0.36**	-6.69**	5.83**	-0.07	0.19**
2 × 7	0.26	-0.75**	-0.13**	3.48	-2.73	-0.09	0.27**
2 × 8	3.63**	-0.52	-0.21**	-0.58	-3.41**	-0.07	0.14
3 × 4	-0.94	-1.39**	-0.10	-4.80	-2.56	-0.17	-0.02
3 × 5	1.59**	0.67**	-0.01	2.31	0.44	0.08	0.10
3 × 6	5.71**	-0.02	-0.25**	1.75	-4.99**	0.00	0.15
3 × 7	-0.36	0.05	0.03	4.25	1.72	0.00	0.40**
3 × 8	-3.22**	0.21	0.22**	-7.13**	4.48**	0.02	0.12
4 × 5	2.24**	-0.84**	-0.13**	-3.86	3.13**	-0.10	0.00
4 × 6	-0.29	0.53	0.04	3.25	5.87**	0.06	-0.04
4 × 7	2.27**	0.78**	0.00	0.42	-2.11	0.09	-0.13
4 × 8	0.20	-0.11	-0.05	0.03	-0.69	-0.01	-0.07
5 × 6	-1.71**	-0.75**	-0.04	-4.30	-0.90	-0.10	0.15
5 × 7	-0.90	0.11	0.09	-3.47	-0.91	0.02	-0.26**
5 × 8	-1.22**	-0.18	0.01	8.48**	-2.82**	-0.02	-0.02
6 × 7	-0.59	-0.47	-0.06	-0.69	-0.05	-0.05	-0.44**
6 × 8	-0.69	0.73**	0.06	0.92	0.31	0.10	0.07
7 × 8	-1.68**	0.19	0.11	-2.25	1.56	0.03	-0.33**
SE	1.16	0.66	0.11	6.65	2.76	0.26	0.18

observed for additive (“a”) and dominance (“b”) gene effects for Y_p, Y_s, STI, RWC, WUE and ETE in Hayman´s method (Table 5). Only highly significant differences was observed for additive gene effects (“a”) for LWP

Table 5. Hayman analysis of variance and genetic properties for significant traits in an eight-parent diallel cross.

S.O.V	df	Mean square						
		Y_p	Y_s	STI	LWP	RWC	WUE	ETE
Rep	2	24.81**	0.45^{ns}	0.01^{ns}	698.84**	36.91^{ns}	0.01^{ns}	0.01^{ns}
a	7	10.16**	2.84**	0.08**	193.80*	90.68**	0.04**	0.40**
b	28	23.77**	1.61**	0.06**	101.37^{ns}	55.94**	0.02**	0.30**
b_1	1	88.59**	0.37^{ns}	0.15**	79.64^{ns}	236.53**	0.01^{ns}	0.71**
b_2	7	5.97*	1.61*	0.06*	61.03^{ns}	77.19**	0.02*	0.11^{ns}
b_3	20	26.76**	1.68**	0.06**	116.58^{ns}	39.47**	0.03**	0.34**
Error	70	2.16	0.71	0.02	71.07	12.34	0.01	0.05
D	-	2.71 ± 1.18	0.72 ± 0.37	0.02 ± 0.01	40.45 ± 31.34	26.17 ± 8.94	0.01 ± 0.01	0.12 ± 0.04
H_1	-	24.64 ± 2.62	1.84 ± 0.53	0.08 ± 0.02	28.42 ± 37.98	69.33 ± 13.50	0.03 ± 0.01	0.24 ± 0.05
H_2	-	23.30 ± 2.29	1.51 ± 0.38	0.07 ± 0.01	28.21 ± 27.32	48.38 ± 8.53	0.02 ± 0.01	0.22 ± 0.04
F	-	0.79 ± 1.61	0.78 ± 0.54	0.03 ± 0.02	2.43 ± 40.69	34.06 ± 14.22	0.01 ± 0.01	0.05 ± 0.04
$(H_1/D)^{0.5}$	-	3.02 ± 0.60	1.59 ± 0.37	2.03 ± 0.51	0.84 ± 0.44	1.63 ± 0.22	1.60 ± 0.37	1.45 ± 0.23
H^2b)	-	0.92 ± 0.01	0.69 ± 0.04	0.76 ± 0.03	0.52 ± 0.07	0.82 ± 0.03	0.69 ± 0.04	0.86 ± 0.02
(H^2n)	-	0.20 ± 0.03	0.18 ± 0.05	0.70 ± 0.04	0.38 ± 0.08	0.29 ± 0.05	0.18 ± 0.05	0.38 ± 0.05

*; ** Significant at the 0.05 and 0.01 probability levels, respectively; ns; non significant.

indicating that the inheritance of this trait was mainly controlled by additive gene effects. According to Mather and Jinks (1982), the "a" item primarily tests the significance of the additive effects of the gene, and the "b" item the dominance effects. As (b_2) and (b_3) were not significant for LWP, accordingly interallelic interaction (epistasis) is not involved in its genetics. The "b_1" item tests the mean deviation of the F_1s from their mid-parental value. It is significant only if the dominance deviations of the genes in the various entries used are predominantly in one direction. That is, there is a directional dominance effect. A significant "b_2" implies asymmetry of the gene distribution in the parents at the loci exhibiting dominance. That is, some parents contain considerably more dominant alleles than others.

The "b_3" item tests residual dominance interaction coming from additive × additive, additive × dominance and dominance × dominance interaction effects that are not attributed to b_1 and b_2 and is unique to each F_1. As the components (b_1), (b_2) and (b_3) were significant for Y_p, STI and RWC (Table 5), therefore significant dominance effects were due to directional dominance (b_1), imbalance of gene distribution (b_2) and residual dominance effect (b_3) resulted from additive × additive, additive × dominance and dominance × dominance interaction effects (Table 5) (Roy, 2000; Farshadfar et al., 2011c). The directional dominance effect (b_1) was not significant for Y_s and WUE and the component of b_2 was not significant for ETE, hence some parents contained considerably more dominant alleles than others for this trait.

Genetic properties

Difference between H_1 - H_2 was positive for all of the characters (Table 5), accordingly the frequency of dominant and recessive alleles over all the loci was not equal for these traits. The component F was not significant but positive for all traits which show that the distribution of alleles in the parents was unknown, while it was significant for RWC displaying that distribution of alleles in the parents was not symmetric and the frequency of dominant alleles was more than that of recessive alleles. As the ratio of $\sqrt{H_1/D}$ was greater than one for all traits except LWP (Table 5), over-dominance was involved in the genetic of these traits, but this ratio was zero for LWP which implies that the type of dominance was unknown. The variation observed between the genotypes for the characters studied revealed that selection may be effective for the improvement of drought tolerance, however selection efficiency is related to the magnitude of heritability (Manal, 2009; Farshadfar et al., 2011d). High broad-sense heritability observed for all the traits confirmed that all the traits are more genetic, but because of low narrow-sense heritability, the rule of additive part was low. Solomon and Labuschagne (2004) reported that high estimate of heritability (greater than 0.5; Stansfield, 2005) for all the traits studied may be probably due to the involvement of few major genes in the control of inheritance of these traits.

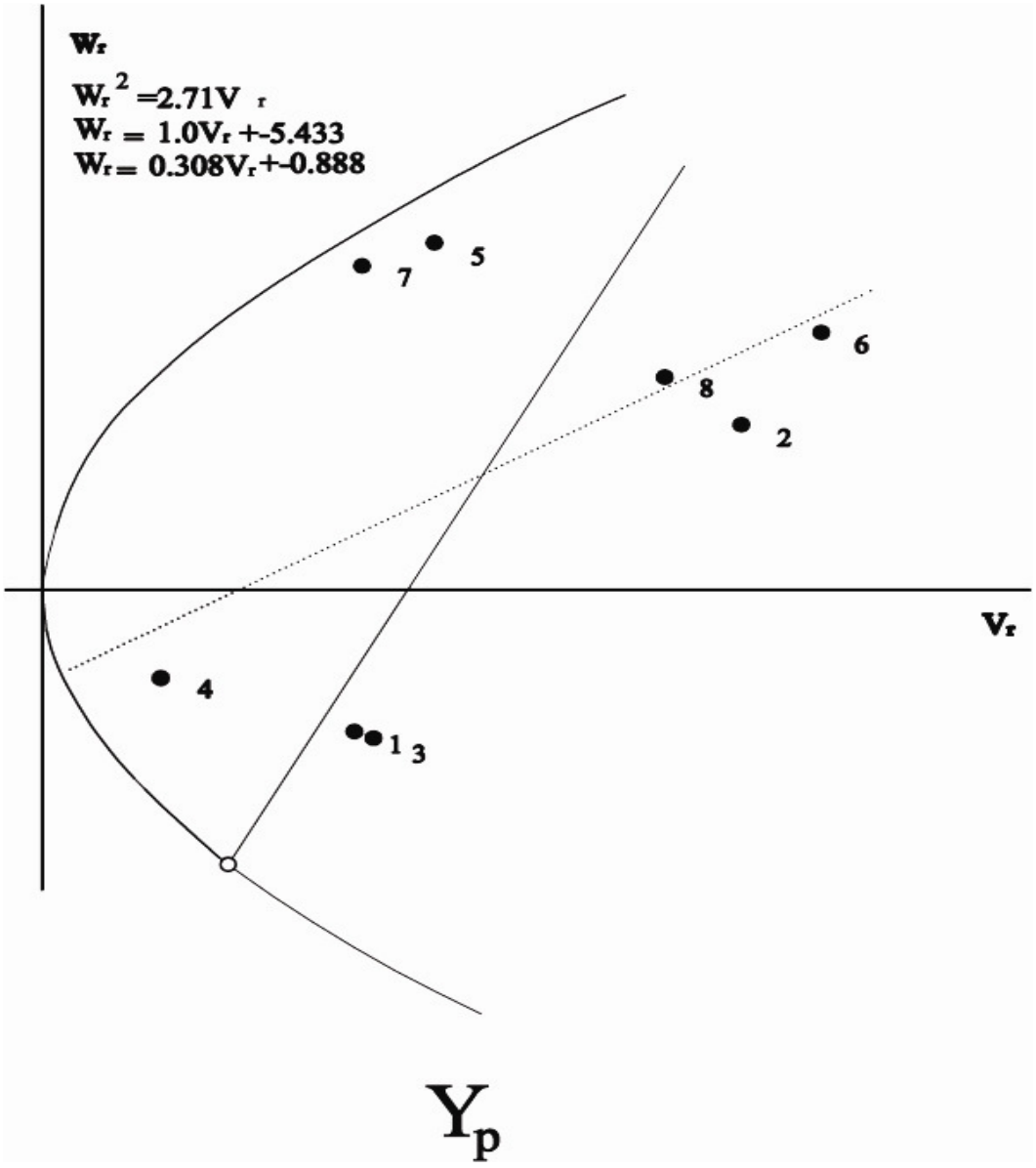

Figure 1. Regression line and dispersion of parents around origin for Yp under stress conditions.

Graphical analysis

Hayman graphical analysis was conducted to evaluate the genetic relationship among the parents. Graphic analysis of the mode of inheritance varied from additive to overdominance for the characters investigated. The position of regression line on Vr-Wr graph provides information about the average degree of dominance (Singh and Chaudhary, 1995). Regression line passed below the origin cutting Wr- axis in the negative region [intercept = a<0 (negative)] for GY (in both normal and stress conditions), STI, LWP, RWC, WUE and ETE (Figures 3 to 7) indicating the presence of over-dominance. Dispersion of parents around the regression line for Y_p (Figure 1) showed that parents 1, 3 and 4 were close to the origin of coordinate, and accordingly had more than 75% of dominant genes, while parents 2, 5, 6, 7 and 8 were far from the origin, therefore they had less than 25% of dominant genes. Dispersion of parents around regression line for Y_s (Figure 2) showed that parents 1, 4, 6, 7 and 8 had 50 to 75% of dominant genes, while parents 2, 3 and 5 were far from the origin; therefore they had less than 25% of dominant genes. Dispersion of parents around regression line for STI (Figure 3) showed that parents 1, 3, 4 and 7 had more than 75% of dominant genes, while parents 5 and 6 had 50 to 75% of dominant genes, and parents 2 and 5 were far from the origin, therefore they had less than 25% of dominant genes.

Furthermore, dispersion of parents around regression

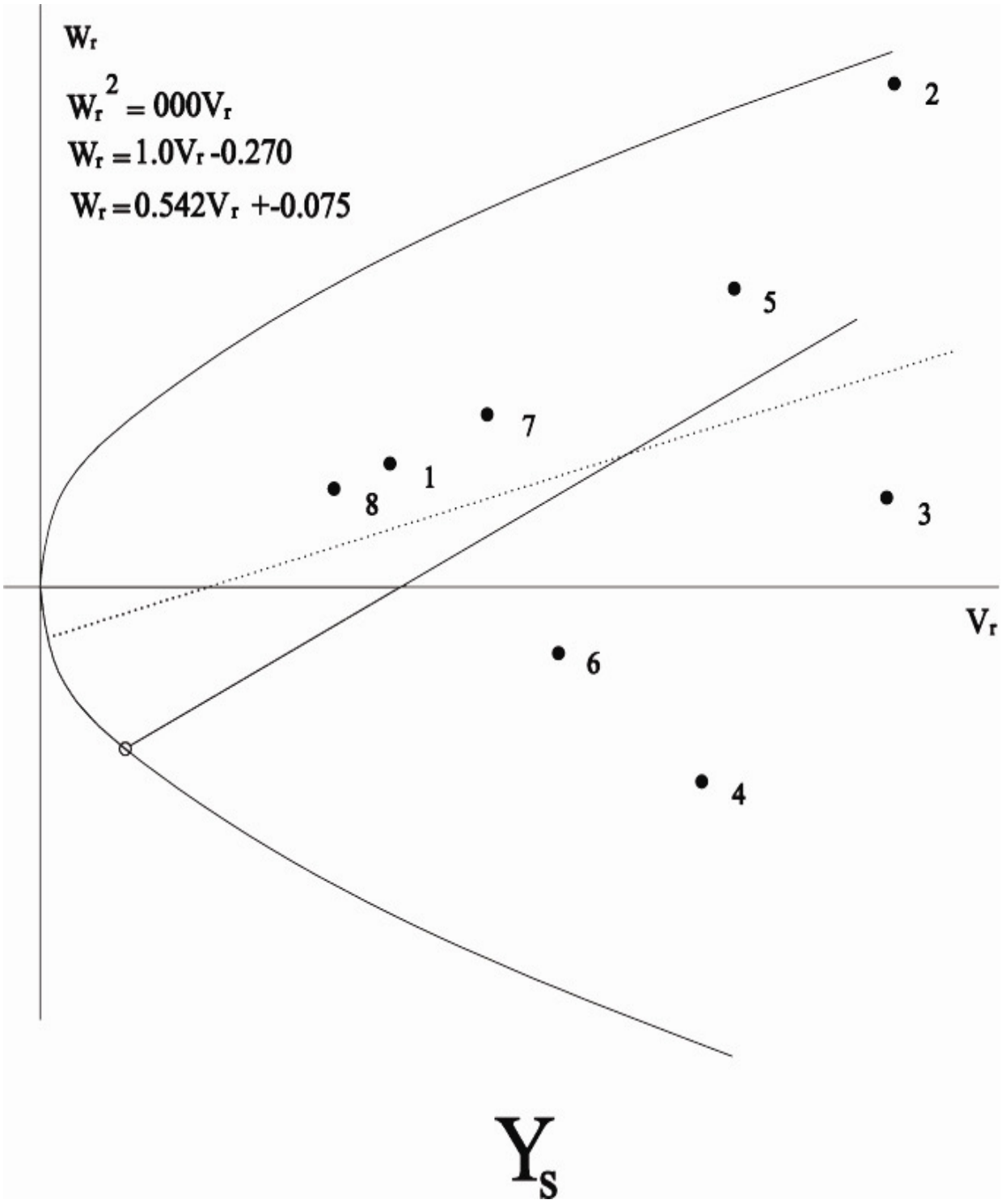

Figure 2. Regression line and dispersion of parents around origin for Ys under stress conditions.

line for LWP (Fig 4) exhibited that parents 6 and 8 had more than 75% of dominant genes, while parents 1 and 3 had 50 to 75% of dominant genes, and parents 2, 4, 5 and 7 were far from the origin, therefore they had less than 25% of dominant genes. Dispersion of parents around regression line for RWC (Figure 5) showed that parents 1, 2, 3, 4, 7 and 8 had 50 to 75% of dominant genes, while parents 5 and 6 were far from the origin; therefore they have less than 25% of dominant genes.

Dispersion of parents around regression line for WUE

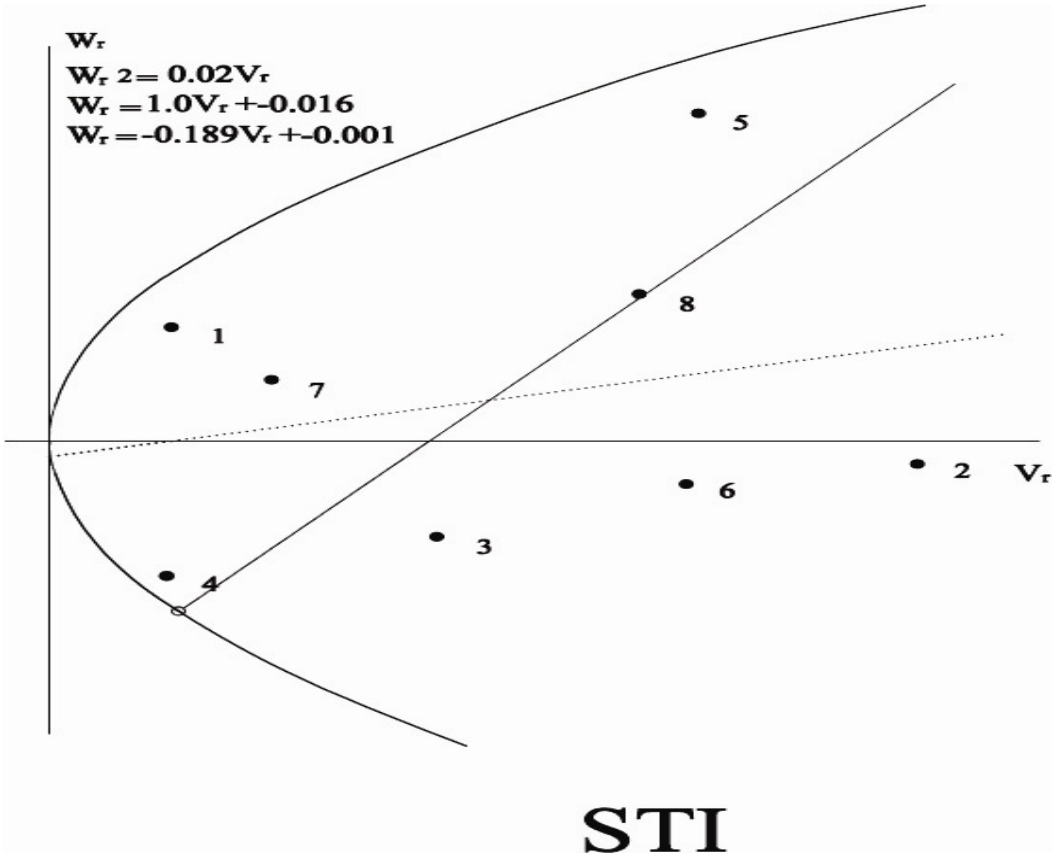

Figure 3. Regression line and dispersion of parents around origin for STI under stress conditions.

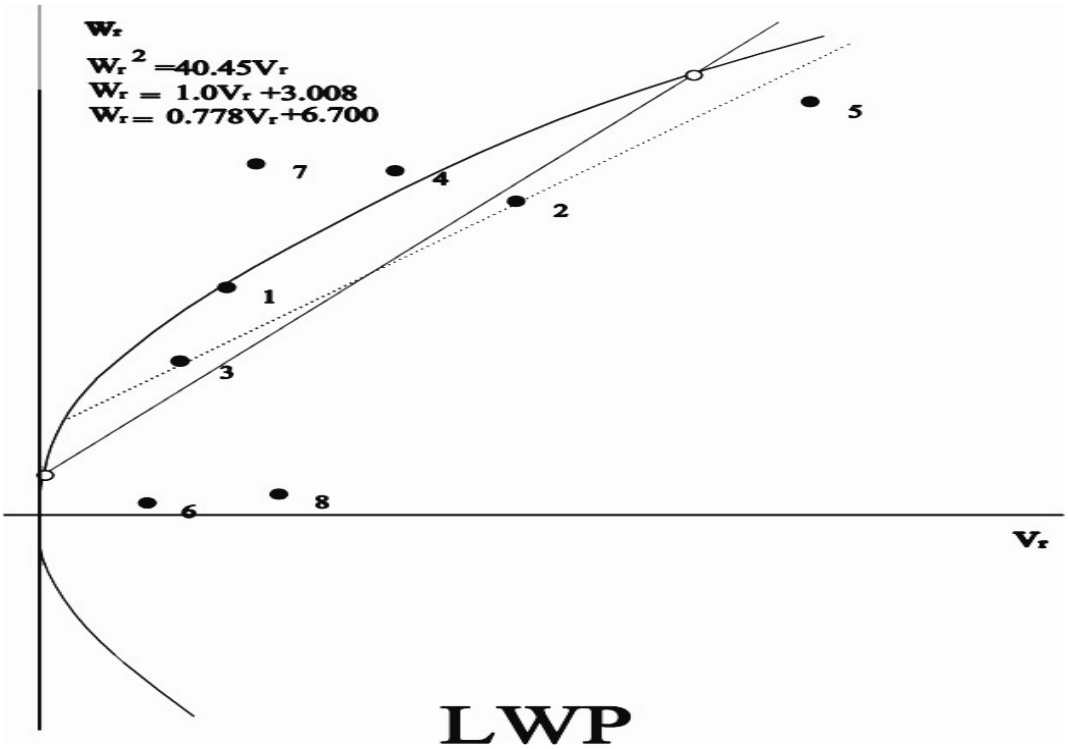

Figure 4. Regression line and dispersion of parents around origin for LWP under stress conditions.

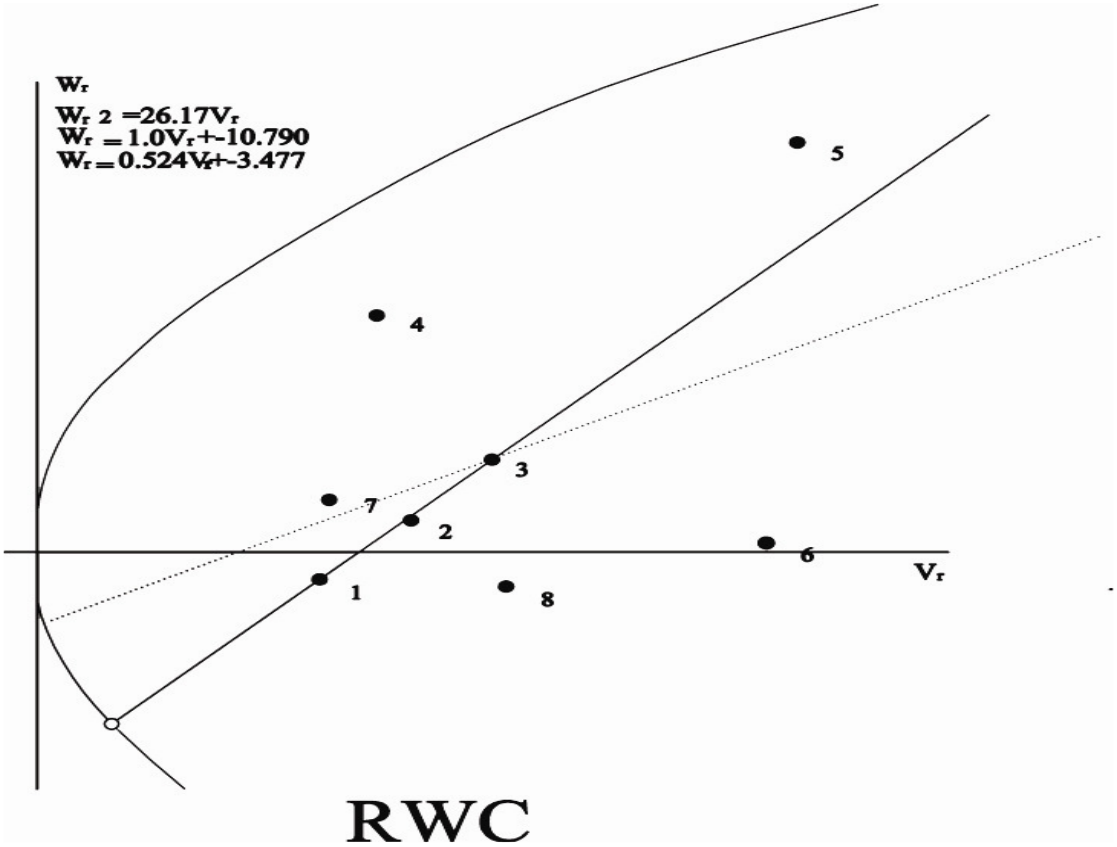

Figure 5. Regression line and dispersion of parents around origin for RWC under stress conditions.

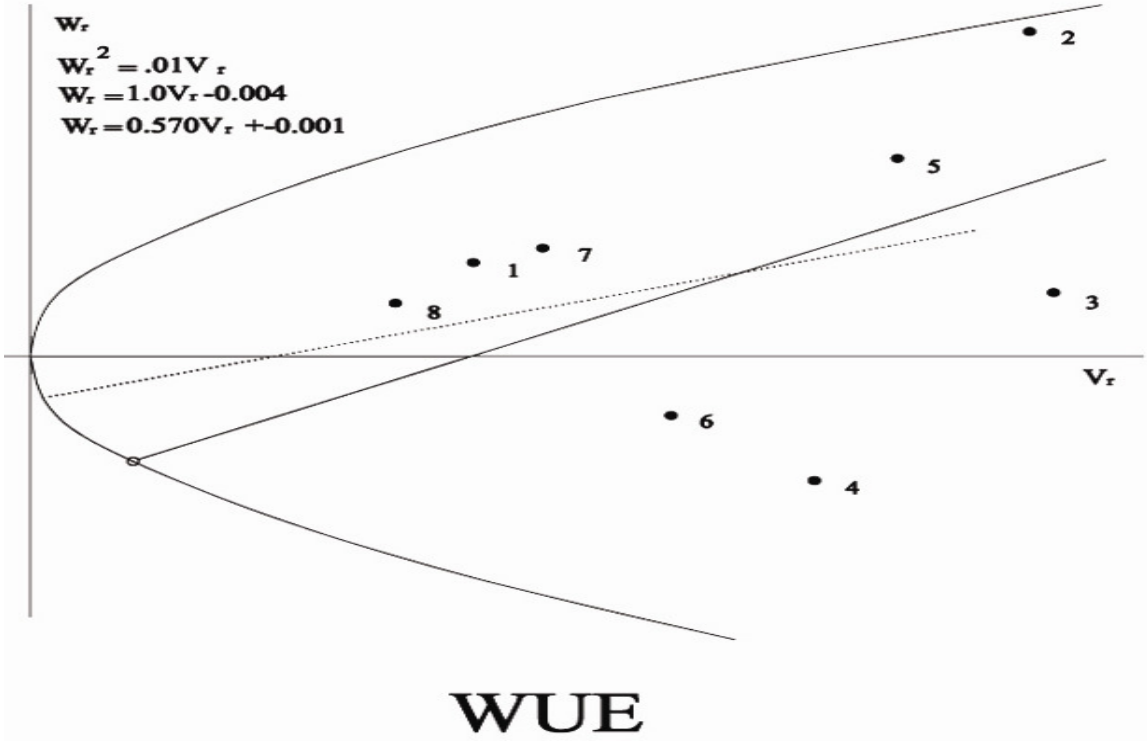

Figure 6. Regression line and dispersion of parents around origin for WUE under stress conditions.

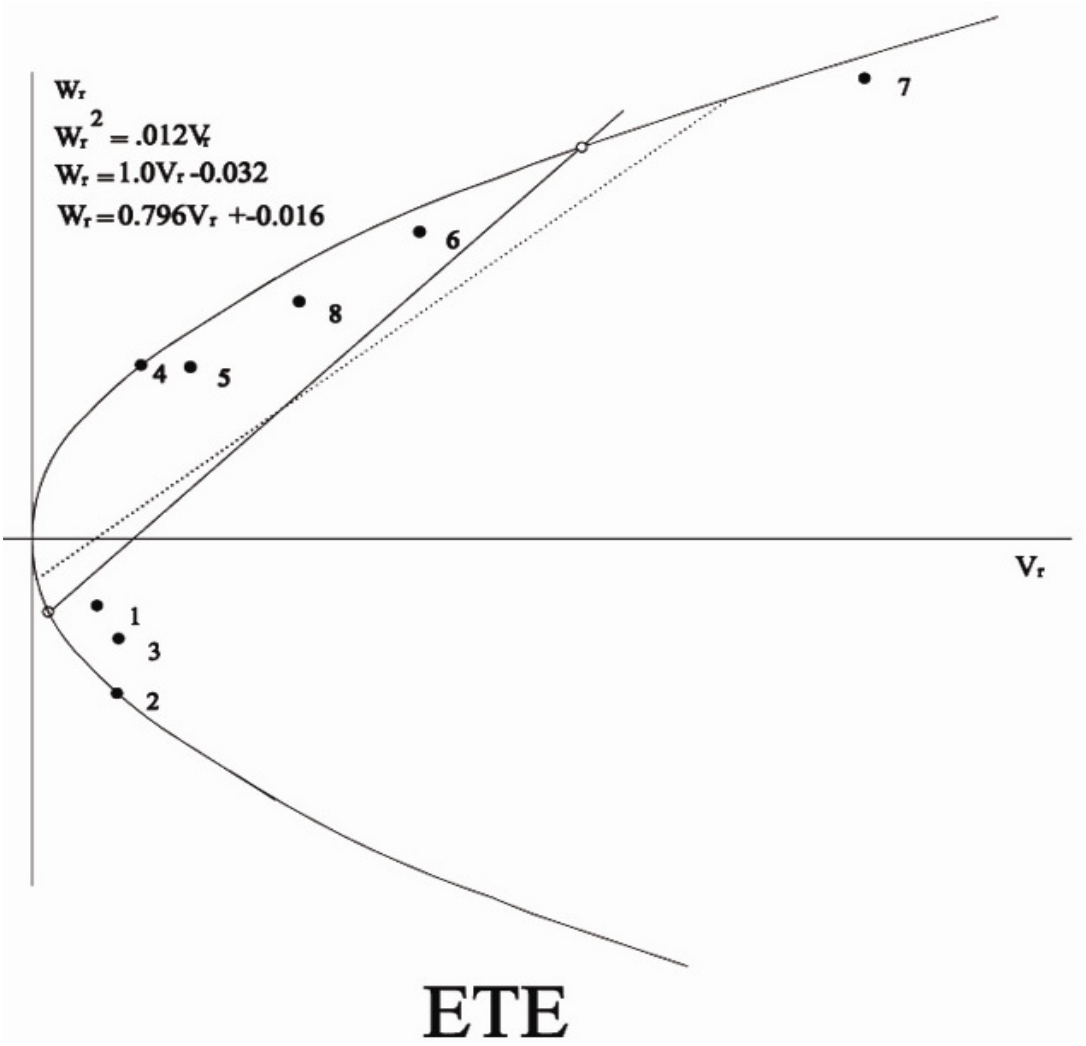

Figure 7. Regression line and dispersion of parents around origin for ETE under stress conditions.

(Figure 6) showed that parents 1, 4, 6, 7 and 8 had 50 to 75% of dominant genes, while parents 2, 3 and 5 were far from the origin; therefore they had less than 25% of dominant genes. Dispersion of parents around regression line for ETE (Figure 7) showed that parents 1, 2, 3, 4 and 5 had more than 75% of dominant genes, while parents 6 and 8 had 50 to 75% of therefore it had less than 25% of dominant genes.

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