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Diallel Analysis of Agronomic, Physiological and Metabolite Indicators of Drought Tolerance in Bread Wheat (*Triticum aestivum* L.)

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ABSTRACT

Inheritance of grain yield, physiological and metabolite indicators of drought tolerance was studied in diallel F_1 hybrids from 8 cultivars of *Triticum aestivum*, selected for their different responses to drought stress. Significant differences were found for grain yield (GY), relative water content (RWC), cell membrane stability (CMS), proline content (PC) and leaf chlorophyll content (LCC). Combining ability analysis indicated the involvement of additive and non-additive gene action in their inheritance. Parents 5 and 7 were the best general combiner for improvement of drought tolerance. The best specific combination with heterobeltiosis over the best parents for improvement of GY, RWC, CMC, PC and LCC were crosses 4×6, 1×6, 6×8, 3×8 and 2×3, respectively. High broad sense heritability observed for all the traits, but the rule of additive part was low. Graphic analysis showed that inheritance varied from dominance to overdominance, but presence of overdominance was exhibited for GY, RWC, PC and LCC. Non- allelic interaction was also found for PC and LCC, therefore selection through selfing is not effective for improvement of PC and LCC.

Keywords: combining ability, diallel mating design, genetic analysis, water stress

INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is an important crop worldwide and is grown on about 200 million ha in a range of environments, with annual production of more than 600 million metric tons. Global wheat production must continue to increase 2% annually until 2020 to meet future demands imposed by population and prosperity growth (Singh *et al.* 2007).

Wheat crops growing in both irrigated and rain-fed environments commonly experience water deficit during some stages of the crop growth cycle. The frequency and severity of soil water deficit is generally greater for rain-fed wheat crops. However, changing weather pattern and worldwide water shortages will likely result in irrigated wheats being grown with loss applied water, increasing the likelihood of soil water deficit (Rebetzke *et al.* 2006).

In turn, genetic improvement of grain yield under water limitation is a key objective for wheat breeders (Richards *et al*. 2002). Emphasis on selection for higher grain yield and improved performance under drought is not always successful (Cooper *et al*. 1997). Genetic progress is slowed owing to a large genotype × environment interaction arising from seasonal differences in rainfall and drought severity. This interaction reduces heritability, there by restricting effectiveness of empirical selection and subsequent genetic gain for yield (Calhoun *et al.* 1994; Farshadfar *et al.* 2000).

An understanding of physiological adaptation to water-limited environments has identified a number of drought tolerance characteristics with potential for genetic improvement of grain yield under drought (Zarei *et al.* 2007). However, only very few of the nominated traits have been rigorously evaluated in a breeding frame work (Rebetzke *et al.* 2006).

To formulate an efficient breeding program for developing drought-tolerant varieties, it is essential to understand the mode of inheritance. As drought is a complex physiological reaction, thus its genetic basis has received limited attention; therefore, little information is available on genetic architecture of drought related characters, which may provide practical information to breeders during the development of drought-tolerant wheat varieties (Farshadfar *et al.* 2000, 2001; Solomon and Labuschagne 2004; Farshadfar *et al.* 2008a). It is clear that the potential for the improvement of crop performance under drought stress cannot be realized until we have identified genes or gene products which are responsible for desired characteristics of drought resistance at different stages of plant growth (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 crosses reportedly provided early information on the genetic behaviour of these attributes in the first generation (Chowdhry *et al.* 1992; Topal *et al.* 2004). The objectives of the present investigation were to study (i) specific and general combining ability as well as (ii) the genetic properties of drought tolerance indicators in wheat under rain-fed condition.

MATERIALS AND METHODS

An eight-parent diallel cross, excluding reciprocals, was carried out at the Agricultural Research Institute of Sararood, Kermanshah, Iran (47° 20′ N latitude, 34° 20′ E longitude and 1351. 6 m altitude) during 2004-2005. Climate in this region is classified as semi-arid with mean rainfall of 478 mm. Minimum and maximum temperatures at the research station were -27 and 44°C, respectively. The cultivars used were ‘Sabalan’, ‘T163’, ‘T189’, ‘914GBM’, ‘4848Mashhad’, ‘72YRRGP’, ‘Chenab’ and ‘Sardari’. In the first year (2004), the genotypes were crossed and in the sec-

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ond year (2005) each of the 28 F_1 families and parental genotypes with different levels of drought resistance were used for the genetic analysis of drought tolerance.

The plant genetic materials were arranged in a randomized complete block design with three replications in two different environments (irrigated and rain-fed). Single seeds were sown in 3 m rows and at 3 × 15 cm inter-plant and inter-row distances, respectively. From each entry (parents and F_{1S}) five competitive plants were randomly selected from each replication to record observations of the following characters:

Grain yield (GY): grain yield of genotype was measured under stress condition.

Excised leaf water retention (ELWR): 5 young leaves per plot were collected and weighed, left for 5 hrs, then wilted at 20°C and reweighed. ELWR was calculated using the following formula (Farshadfar *et al.* 2001).

$$ELWR = \left[1 - \left(FW - W5H\right)/FW\right] \times 100$$

where FW = fresh weight and W5H = weight of leaves after 5 hrs.

Relative water content (RWC): 5 flag leaves (0.5 g) were taken per plot and weighed (FW). Then 3 segments from each leaf were placed in distilled water for 24 hrs and reweighed to obtain turgor weight (TW). Thereafter, the leaf segments were oven dried for 48 hrs at 72°C and weighed (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 5 flag leaves were taken from each genotype and FW was measured. The leaves were then wilted at 35°C for 5 hrs and reweighed (W5H). Then the samples were oven-dried at 70°C and weighed again (DW). RWL was calculated by the following formula (Farshadfar *et al.* 2001).

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

Cell membrane damage (CMD): CMD of leaf tissues was calculated using the following equation (Zarei *et al.* 2007).

$$CMD(\%) = \left[1 - \left[\frac{1 - \frac{t_1}{t_2}}{1 - \frac{C_1}{C_2}}\right]\right] \times 100$$

where t_1 and t_2 are first and second electrical conductivity measurement of desiccation treatment. C_1 and C_2 are first and second electrical conductivity of control.

Proline content (PC): proline of leaves was determined by Bates *et al.* (1973) method. Data were measured on 5 flag leaves at 520 nm by a Bausch and Lomb Spectrophotometer 70. A standard curve, 12.5, 31.25, 15.62, 7.8 and 1.9 mg of proline (Merck, Darmstadt, Germany) was prepared. Proline content of treated extracts was calculated using the standard curve and following formula.

$$\text{Proline} = \left[\frac{CDV}{DM \times 11.5 \times 10^6}\right] 1 \times 10^{-7}$$

where C = content of proline absorption, D = precision degree, V = toluene volume and DM = dry mass of leaf sample.

Leaf chlorophyll content (LCC): using a chlorophyll meter (SPAD-502, Minolta, Japan) five flag leaves (0.1 g) were selected and LCC was measured during heading date (Yavad 1986).

Statistical analysis

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

Graphical analysis

A Hayman's graph (Vr-Wr graph) was drawn with the help of variances of arrays (Vr) and covariances (Wr) between parents and their offspring (Wr). The array refers to the crosses in which a particular parent is common. The Wri values were estimated for all the arrays by the formula:

$$\text{Wri} = (\text{Vri} \times \text{VOLO})^{1/2}$$

where Vri is the variance of r^{th} array and VOLO is the variance of parents. The Wri values are plotted against Vr values to draw the limiting parabola. The Wrei values are obtained by the formula: Wrei = Wr – bVr + bVri for drawing regression line, where, Wr is array mean of variances, Vr array mean of covariances and b = regression coefficient. The position of the regression line on Vr-Wr graph provides information about the average degree of dominance. (a) When the regression line passes through the origin, it indicates complete dominance ($D=H_1$). (b) When it passes above the origin, cutting the Wr axis, it shows that there is partial dominance ($D>H_1$). (c) When it passes above the origin, cutting Wr axis and touching the limiting parabola it suggests the absence of dominance. (d) But when it passes below the origin, cutting the Wr axis, it denotes the presence of overdominance.

The position of parental point along the regression line indicates the dominance order of parents. The parents with more dominant genes are located closer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy the intermediate position (Singh and Narayanan 1993; Singh and Chaudhary 1995; Sharma 1998).

RESULTS AND DISCUSSION

The results of ANOVA (**Table 1**) showed significant differences for all the characters investigated except for RWL and ELWR, indicating the presence of genetic variation, genetic effects and the possibility of selection for parents and hybrids under drought condition (Farshadfar *et al.* 2008b).

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, also largely upon the magnitude of genetic variability present in the plant population (Singh and Narayanan 1993; Singh and Chaudhary 1995).

Genetic variability was found for GY, RWC, PC and LCC in wheat-barley disomic addition lines (Kocheva *et al.* 2004; Farshadfar *et al.* 2008a, 2008b).

CMS, RWC, RWL, ELWR and PC were shown as screening techniques for discrimination of drought tolerance genotypes in wheat, barley and chickpea (Suprunova *et al.* 2004; Zarei *et al.* 2007; Bayoumi *et al.* 2008; Farshadfar *et al.* 2008a, 2008b, 2008c, 2008d; Cossani *et al.* 2009).

Analysis of combining ability

Knowledge of the relative importance of additive and non-additive gene action is essential to a plant breeder for the development of an efficient hybridization program. 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 Chaudhry 1995).

Mean square of the genotypes was partitioned into general and specific combining abilities (GCA and SCA) (**Table *2***).

Table 1 Analysis of variance for different characters investigated.

Source	df	Mean square of characters						
		GY[a]	**ELWR**[b]	**RWC**[c]	**RWL**[d]	**CMS**[e]	**PC**[f]	**LCC**[g]
Replications	2	49236^{ns}	360*	378**	684**	125^{ns}	14**	760.7**
Genotypes	35	117673**	75.3^{ns}	91.0**	99.6^{ns}	590.2**	7.4**	35.9**
Error	70	79786	93	40	125.4	252	1.9	14.65
CV (%)[h]	-	14	1304	9	30	27	26.7	23.5

[a] grain yield; [b] excised leaf water retention; [c] relative water content; [d] relative water loss; [e] cell membrane stability; [f] proline content; [g] leaf chlorophyll content; [h] coefficient of variation

ns nonsignificant; * significant at 5% probability level; ** significant at 1% probability level

Table 2 Combining ability analysis of significant traits studied.

Source	df	Mean square of GCA and SCA				
		GY[a]	**RWC**[b]	**CMS**[c]	**PC**[d]	**LCC**[e]
GCA[f]	7	3565130**	86^{ns}	1193**	19.63**	51.9*
SCA[g]	20	373998**	78.3*	564*	4.80**	35.9**
Error	54	79053	41.70	256	1.98	15.90
MSgca/MSsca		9.53**	1.10^{ns}	2.11	4.09**	1.44

[a] grain yield; [b] relative water content; [c] cell membrane stability; [d] proline content; [e] leaf chlorophyll content; [f] general combining ability; [g] specific combining ability

ns nonsignificant; * significant at 5% probability level; ** significant at 1% probability level

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

Parents	Characters				
	GY[a]	**RWC**[b]	**CMS**[c]	**PC**[d]	**LCC**[e]
1	-445.60	-2.15	-2.23	-0.49	1.31
2	-301.60	1.01	6.41	-1.71	1.47
3	37.47	0.97	-8.52	1.26	-2.11
4	-438.1	-3.30	-6.64	0.61	-2.58
5	723.70	-0.89	2.82	1.40	-0.41
6	-458.1	1.18	-10.64	-0.68	2.24
7	546.80	3.66	8.01	-0.29	0.03
8	335.50	-0.44	10.78	-0.09	0.05

[a] grain yield; [b] relative water content; [c] cell membrane stability; [d] proline content; [e] leaf chlorophyll content

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

	Characters				
Crosses	**GY**[a]	**RWC**[b]	**CMS**[c]	**PC**[d]	**LCC**[e]
1×2	121.2	-11.37	-6.30	0.85	1.39
1×3	31.5	0.05	14.96	-0.42	-4.85
1×4	-232.8	2.30	2.32	0.39	-4.48
1×5	-476.1	1.78	2.71	-0.25	2.31
1×6	511.9	9.54	-30.35	-0.59	0.53
1×7	-266.8	-1.90	17.53	-0.59	2.34
1×8	311.1	-0.41	-0.87	0.62	2.75
2×3	247.4	2.97	4.12	-0.30	4.87
2×4	-52.4	2.30	14.30	-0.77	-2.49
2×5	-180.3	1.63	-2.49	-0.90	0.44
2×6	-238.3	-0.83	-4.25	0.15	-4.48
2×7	352.9	6.36	-2.62	0.91	2.01
2×8	-250.4	-1.07	-2.73	0.07	-1.73
3×4	-316.1	-0.73	-3.37	0.09	3.86
3×5	131.4	-1.01	0.07	0.91	-2.36
3×6	-194.6	-2.99	-9.82	-0.47	-2.43
3×7	-25.4	7.56	-12.69	-2.48	-1.41
3×8	125.9	-5.85	6.75	2.67	2.32
4×5	163.5	-1.82	13.36	0.31	3.37
4×6	803.5	-3.47	-4.84	0.11	4.52
4×7	-264.5	-6.19	-10.56	0.29	-1.61
4×8	-101.2	7.62	-11.20	-0.42	-3.17
5×6	-273.6	-1.01	10.51	0.64	-3.54
5×7					
5×8					
6×7					
6×8					
7×8					

[a] grain yield; [b] relative water content; [c] cell membrane stability; [d] proline content; [e] leaf chlorophyll content

Mean squares of GCA and SCA were significant for GY, CMS, PC and LCC, indicating the involvement of additive and non- additive gene action in their inheritance. As GCA was not significant for RWC and SCA was significant, hence RWC is predominantly controlled by non-additive (dominance and epistasis) gene action. The improvement of such characters warrants 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. In the case of non-additive gene action (RWC), it may be necessary to resort to heterosis breeding (Dhanda *et al.* 1998; Iqbal *et al.* 2007).

The ratio of MSgca/MSsca (**Table 2**) displays the relative importance of additive gene action. This ratio was significant for GY and PC, therefore they are predominantly controlled by additive gene effects; hence, the pedigree method of selection can be used for their improvement. For any breeding program, the choice of parents to be used in the crossing program is of paramount importance and constitutes the basis for the success of the breeding program. Combining ability analysis helps in identifying superior parents and cross combination used in the breeding program (Farshadfar *et al.* 2002). The best general combiners with positive effects, for GY, RWC, CMS, PC and LCC were parents 5, 7, 5, 7 and 6 (**Table 3**).

Accordingly, parents 5 and 7 are the best general combiners for improvement of drought tolerance. Specific combining ability effects are presented in **Table 4**. The best specific combination with heterobeltiosis over the best parents for improvement of GY, RWC, CMS, PC and LCC were crosses 4×6, 1×6, 6×8, 3×8 and 2×3, respectively indicating that parents of these crosses are genetically diverse. The expression of positive heterosis in these hybrids reveals the preponderance of additive gene action (except RWC). According to Topall *et al.* (2004), compared to other types of gene effects, high additive gene effects for a specific trait will increase success in selection for that trait.

Genetic properties

Estimation of variance components and genetic parameters are presented in **Table 5**.

ANOVA components for significant traits (**Table 5**) showed that the b component is significant for all the characters investigated; hence, we can proceed and estimate the genetic parameters. The advantage of ANOVA components (**Table 5**) is their validity, irrespective of whether there are maternal or reciprocal differences among the progeny families and whether the parental lines are a fixed sample or a random sample of a population of inbred lines (Mather and

Table 5 Estimation of variance components for significant characters.

Source	df	Mean square of significant traits				
		GY^{a}	**RWC^{b}**	**CMS^{c}**	**PC^{d}**	**LCC^{e}**
a	7	2857500**	146.4**	495.07^{ns}	15.06**	39.20*
b:	28	756534**	77.59*	614.05**	5.47**	35.24**
b_1	1	1863840**	27.92^{ns}	6.52^{ns}	0.035^{ns}	11.85^{ns}
b_2	7	1691303**	82.60^{ns}	841.97**	8.16**	36.45*
b_3	20	373999**	78.33*	564.65**	4.79**	35.99**
error	70	79786	39.83	252.02	1.86	14.72

^{a} grain yield; ^{b} relative water content; ^{c} cell membrane stability; ^{d} proline content; ^{e} leaf chlorophyll content

Table 6 Estimation of genetic parameters for the characters studied.

Genetic parameters	Traits				
	GY^{a}	**RWC^{b}**	**CMS^{c}**	**PC^{d}**	**LCC^{e}**
D	301789.9**	34.27^{ns}	-35.64	0.57^{ns}	2.92^{ns}
H_1	1215215**	81.56*	747*	7.09**	39.8*
H_2	707076**	66.5*	549**	5.04**	32.33**
F	317283*	37.75^{ns}	62.6^{ns}	0.086^{ns}	4.97^{ns}
H^2	295079^{ns}	-0.908^{ns}	-33.14^{ns}	-0.252^{ns}	-0.107^{ns}
E	26103^{ns}	13.38**	83.4**	0.63**	5.003**
$(H_1/D)^{1/2}$	2.007**	1.54*	0.0	3.53^{ns}	3.69^{ns}
Dominance to recessive	0.631**	0.67**	0.0	0.51*	0.62**
h^2/H_2	0.48*	-0.016^{ns}	-0.07^{ns}	-0.57^{ns}	-0.004^{ns}
Dominance direction	-552.98**	2.14^{ns}	1.034^{ns}	0.076^{ns}	-1.39^{ns}
$U.V$	0.145**	0.203**	0.184**	0.177**	0.203**
$D/D+E$	0.920**	0.72**	-0.75^{ns}	0.476^{ns}	0.368^{ns}
H_b^2	0.94**	0.64**	0.69**	0.801**	0.68**
H_n^2	0.54**	0.19*	0.184**	0.403**	0.17*

^{a} grain yield; ^{b} relative water content; ^{c} cell membrane stability; ^{d} proline content; ^{e} leaf chlorophyll content

Jinks 1982). As components *a* (additive) and *b* are significant (**Table 5**) for GY, RWC, PC and LCC, therefore additive and dominance gene actions are involved in the genetics of these traits. The significance of *b* shows that non-additive gene action is outstanding for all of the characters. The significance of the *b* component for all the traits also indicates that it is possible to proceed and do the graphical analysis. There was significant evidence of directional dominance (b_1) reflecting the earlier observation that F_1 progenies were on average higher for GY than the mean of all parents. A significant b_2 for GY, CMS, PC and LCC indicates that the extent of directional dominance and therefore the number of dominant alleles varies between the 8 parents. There was large significant evidence for dominance effects specific to particular crosses (b_3) for all the traits, consistent with the smaller estimated SCA (Rebetzke *et al.* 2006).

The parameters H_1 and H_2 are significant for all the characters, which confirms the existence of dominance in the inheritance of all the traits; however, as component D is also significant for GY, a simultaneous effect of additive and dominant gene action is involved for GY (**Table 6**). The difference between (H_1-H_2) is positive for GY, RWC, CMS, PC and LCC; accordingly, the frequency of dominant and recessive alleles over all the loci is not equal for these traits (**Table 6**).

The component *F* is not significant but positive for RWC, CMS, PC and LCC indicating that the distribution of alleles in the parents is unknown, while it is significant for GY indicating that the distribution of alleles in the parents is not symmetric and the frequency of dominant alleles is more than that of recessive alleles (**Table 6**).

As the ratio of $(H_1/D)^{1/2}$ is >1 for GY, RWC, PC and LCC, overdominance is involved in the genetics of these traits, but this ratio is zero for CMS which implies that the type of dominance is 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 (Eid 2009).

Salomon and Labuschagne (2004) reported that a high estimate of heritability (> 0.5; Stanfield 2002) for all the traits studied may probably involve a few major genes in the control of inheritance of these traits.

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 the additive part is low (except for GY which is moderate). This implies that the rule of non-additive part is more than additive part, therefore, hybrid production and heterosis breeding is recommended for the improvement f these traits (Dhanda and Sethi 1998; Farshadfar *et al.* 2000).

Graphical analysis

Hayman graphical analysis was conducted to assess 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 the regression line on the Vr-Wr graph provides information about the average degree of dominance (Singh and Narayanan 1993). The regression line passes below the origin cutting the Wr-axis in the negative region (intercept = a < 0 (negative)) for GY, RWC, PC and LCC (**Figs. 1-4**), indicating the presence of overdominance. Dispersion of parents around the regression line for GY showed that parents 1 and 6 are close to the origin of coordinate; accordingly, they have > 75% of dominant genes, while parents 3, 4, 5, 7 and 8 have 50-70% of dominant genes. As parent 2 is far from the origin, it therefore has < 25% of dominant genes. Dispersion of parents around the regression line for RWC indicated that parents 4, 5, 6 and 8 have > 75% of dominant genes.

Dispersion of parents around the parabola revealed the presence of variation among the parents for PC. Large differences between the regression line and the regression line with a slope of one confirmed the existence of a non-allelic interaction for PC and LCC, therefore selection through selfing is not effective for improvement of PC and LCC (Farshadfar *et al.* 2008a). Using a triple test cross analysis, non-allelic interaction (epistasis) was reported in wheat for PC and CMS (Farshadfar *et al.* 2008b).

The non-allelic interaction related to a number of interacting genes leads to inefficient selection, but if the number of interacting genes is reduced, selection will be efficient. The difference between regression line and the regression

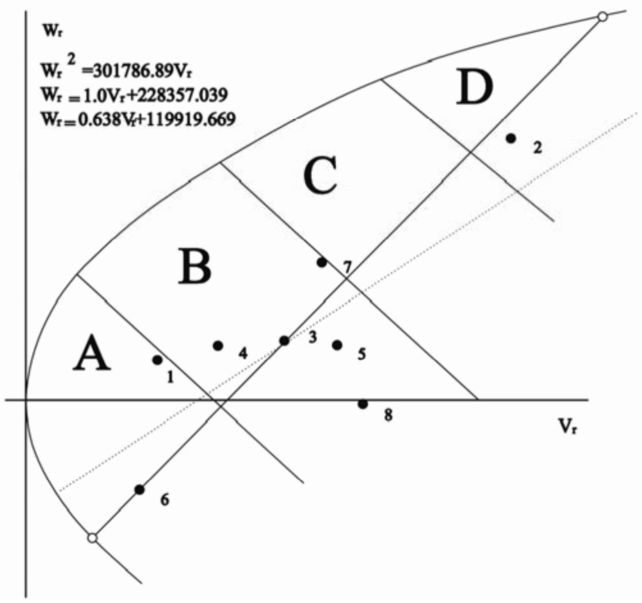

Fig. 1 Regression line and dispersion of parents around origin for GY under stress condition.

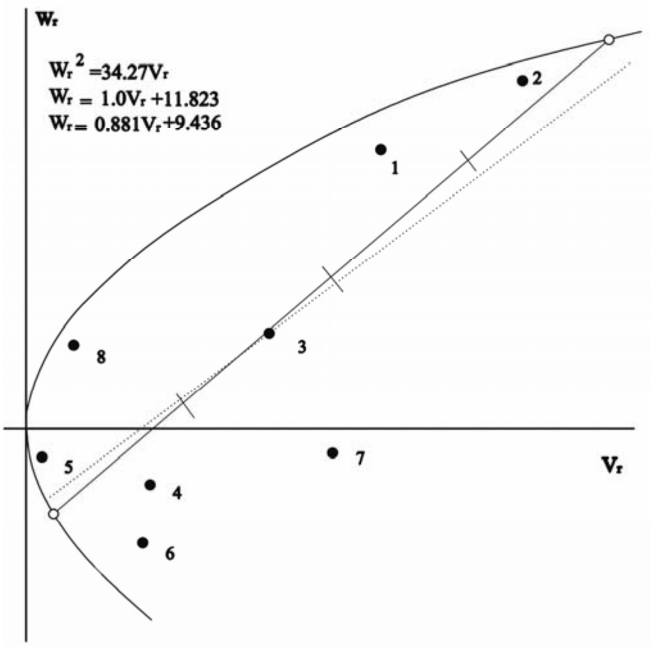

Fig. 2 Regression line and dispersion of parents around origin for RWC under stress condition.

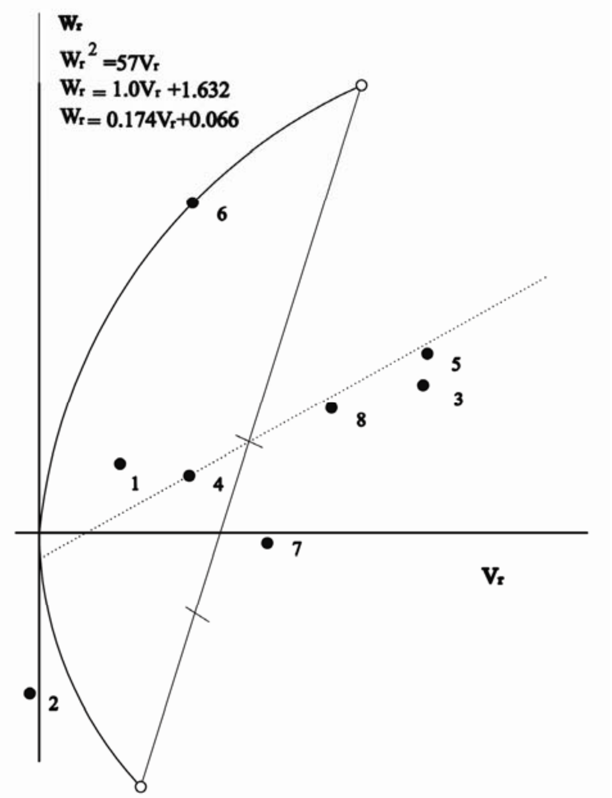

Fig. 3 Regression line and dispersion of parents around origin for PC under stress condition.

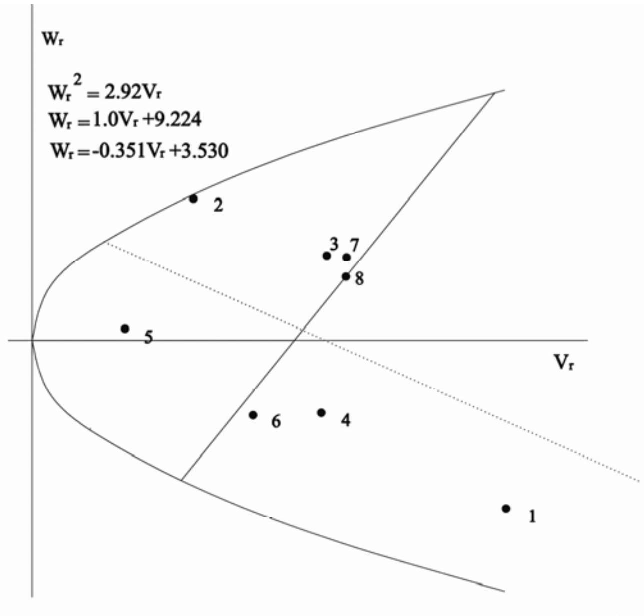

Fig. 4 Regression line and dispersion of parents around origin for LCC under stress condition.

line with slope of one ($b = 1$) indicates the role of non-allelic interaction (epistasis) controlling PC and LCC. Detection of epistasis suggested that variation for PC and LCC was higher under oligo-or polygenic control. Thus, it is conceivable that independent alleles at two or more loci could be pyramided into a single family for increasing or decreasing PC and LCC (Rebetzke *et al.* 2006).

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