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Genetic Analysis of Physiological Criteria of Drought Tolerance in Bread Wheat under Rainfed Conditions

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ABSTRACT: In this study 15 genotypes from a six-parental diallel cross, excluding reciprocals, were grown in the field using a randomized complete block design (RCBD) with three replications under rainfed condition. Significant differences were found for chlorophyll a (Ch_a), chlorophyll b (Ch_b), total chlorophyll (Total Ch) and Prolin Content (PC) indicating the presence of genotypic variability, different responses of genotypes and possibility of selection genotypes for breeding programs. Mean square of specific combining ability (SCA) was significant for Ch_b, exhibiting the involvement of non- additive gene action in its inheritance. According to general combining ability of parents for significant traits, the high amount of PC, cell membrane stability (CMS), relative chlorophyll content (RCC), total Ch, Ch_b, Ch_a and relative water content (RWC) were attributed to the parents 5, 3, 6, 3, 3, 3 and 5, while low amount were observed for parents 1, 5, 1, 1, 4, 1 and 6 respectively. The best specific combination with heterobeltiosis over the best parents for improvement of PC, CM, RCC, total Ch, Ch_b, Ch_a and RWC were the crosses 6 × 2, 5 × 3, 5 × 1, 3×2, 3 × 1, 6 × 1 and 5 × 3 respectively indicating that parents of these crosses are genetically diverse.

Keywords: Wheat, diallel analysis, physiological traits, drought stress

INTRODUCTION

Water limitation is one of the most important constraints for agriculture. More recently, global warming may be worsening this situation in most agricultural regions. Thus, it is quite relevant to understand the mechanisms that enable plants to cope with water deficit. Indeed, plants show a wide range of adaptations, at different levels, to drought stress. Several strategies used by plants to adapt to low water potential at the physiological, biochemical and molecular levels (Xoconostle-Cazares *et al.,* 2010).Water stress is a problem that affects 45% of the world's geographic area and is a major restriction in wheat production and the most important contributor to yield reduction in semiarid regions (Ali *et al.,* 2011).

Diallel cross is one of the most complex designs that have been used extensively for the genetic analysis of quantitative characters and it also frequently used in plant breeding research to obtain information about genetic properties of parental lines or estimates of general (GCA) and specific (SCA) combining abilities and heritability (Iqbal*et al.,* 2007).Information on general and specific combining ability effects is significant in breeding program. Diallel crosses method provide early information on the genetic behavior of these attributes in the first generation (Topal *et al.,* 2004). To date, several methods have been proposed for the genetic analysis of data from a diallel cross (Griffing, 1956; Hayman, 1954a; Hayman, 1954b; Jones, 1965). Among various diallel forms, the half diallel methods have certain advantages, giving maximum information about genetic architecture of a trait, parents and allelic frequency (El-Maghraby *et al.,* 2005; Farshadfar *et al.,* 2011a.). Griffing used the half diallel analysis for combining ability (Griffing, 1956).Morley-Jones (1965) extended the analysis of variance of a full diallel table to a half diallel table. Hayman developed the best-known methods for diallelic analysis, exclusively for homozygous parents (Hayman, 1954a; Hayman, 1954b).

The main reasons that justify the universal uses of the Griffin's method are its generality, since the parents can be pure lines, clones, populations of a self pollinated, inbred lines, cross-pollinated or intermediate species, the ease of analysis and interpretation (Griffing, 1956) on the other hand, the Hayman's method, may include statistical and graphical analyses of array variances and covariances and the estimation of a number of genetic parameters (Farshadfar *et al.,* 2012). Morley Jones (1965) method was carried out on the traits with high significant differences among the genotypes. In this technique, total sum of square is partitioned into various components, namely a (additive), b (non-additive). b component is further subdivided into b1, b2, and b3. Significant amount of a and b components, show the significant additive and dominance effect of genes, respectively.

Significant b1 indicates unidirectional dominance which it is in fact a comparison of F1's mean with mid-parental value. Asymmetry of gene distribution is indicated by the component b2, whereas b3 tests that part of dominance deviation which are not attributable to b1 and b2.

As the genetics of drought related characters is complex and not adequately understood, and since little information is available on the genetics of characters associated with drought, it is necessary to assess the estimates of gene effects under variable environmental stress conditions so as to ensure better prediction and gain under selection (Arraudeau, 1989).

The objectives of the present investigation were to study (i) specific and general combining abilities, as well as (ii) inheritance of physiological indicators of drought tolerance in wheat under rain-fed condition.

MATERIALS AND METHODS

A. Materials

Six bread wheat genotypes as parents [(Pishtaz (1), CHAM-4DOVN-2ICW93-0001-AP-OL-1AP-2AP-OAP (2), Zagros (3), Ns732.HER//Darab (4), TEVEE S/KARAWAN "S" ICW93-0073-1AP-OL-8AP-OL (5), URES/3//FURY//SLN/ALDAN "S"/4/NS732/HER ICW93-0531 (6)] and their 15 hybrids(1 × 2, 1 × 3, 1 × 4, 1 × 5, 1 × 6, 2 × 3, 2 × 4, 2 × 5, 2 × 6, 3 × 4, 3 × 5, 3 × 6, 4 × 5, 4 × 6, 5 × 6) were assessed in a randomized complete blocks design with three replications under rainfed condition at the Research Farm of the Campus of Agriculture and Natural Resources, Razi University, Kermanshah, Iran during 2010-2011 cropping season. Sowing was done by hand in plots with three rows, 2 m length and 0.25 m row spacing. The seeding rate was 170 seeds per m^2 for all plots. After physiological maturity, the following physiological traits were recorded.

Chlorophyll Content (Chl_a, Chl_b, Chl T): Chlorophyll content was determined in 99.5% methanol extract. After centrifugation (10000 rpm for 10 min) the absorbance was read spectro-photometrically at 665 and 650 nm. Total chlorophyll as well as chlorophyll a and b concentrations were calculated according to Hipkins and Baker (1986)formula:

Chlorophyll $_a$ (µg/ml) = 16.5 × A665 – 8.3 × A650

Chlorophyll $_b$ (µg/ml) = 33.8 × A650 – 12.5 × A665

Total Chlorophyll (µg/ml) = 25.8 × A650 + 4.0 × A665

Proline concentration (PC): Proline content was measured according to the method of Bates *et al.* (1973). During the grain filling period plant material (0.5 g) was grinded with 10 ml of 3% sulfosalicylic acid. The homogenate was filtered and 1 ml of glacial acetic acid and 1 ml acid ninhydrin reagent were added to a 1 ml of filtrate. Then the mixture was shaken by hand and incubated in boiling water bath for 1 h. After that, it was transferred to ice bath and warmed to room temperature. 2 ml toluene was added to the mixture and the upper toluene layer was measured at 520 nm using UV spectrophotometer. Proline concentration was determined using a calibration curve and expressed as µ mol.

$$\text{Proline} = \left[\frac{\text{CDV}}{\text{DM}\times 115.5\times 10^{6}}\right] 1\times 10^{5}$$

Relative chlorophyll content (RCC): The chlorophyll content in the flag leaf was determined using a chlorophyll meter (SPAD-502, MINOLTA-Japan). Five flag leaves of each genotype at all plots were measured after anthesis stage. Three measurements at random locations in the middle of the flag leaf were made for each plant, and the average sample was used for analysis.

Relative water content (RWC): The fresh weight (FW) of five flag leaves (0.5 g) was weighed. Segments were then placed in distilled water for 4h and reweighed to obtain turgor weight (TW). Thereafter, the leaf segments were oven dried for 48 h at 72°C and re-weighed to obtain dried weight (DW). RWC was calculated using the following formula (Egert and Tevini, 2002):

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

Cell membrane stability (CMS): CMS was determined according to the method described bySullivan (Sullivan, 1972). For this purpose, young leaves were selected at anthesis stage from each genotype and each replication. Twenty leaf discs (1 cm in diameter) were cut from leaves and washed with deionized water to remove the solution from the injured cells. For desiccation treatment, ten leaf discs were flooded in 10 ml of 30% PEG-6000 in test tubes for 24 h at 10 °C and for control treatment, after that leaf discs were flooded in distilled water. Then the leaf discs were washed with deionized water. Next, 10 ml of deionized water was added to tubes, and they were maintained for 24 h at 10°C. After that, the conductivity of the solutions was determined. Finally, the tubes were boiled in a water bath for 30 min, cooled to room temperature, and the conductivity of the solutions was read again. CMS of leaf tissues was calculated using the following equation:

CMS (%) = 100- [1-(1-T_1/T_2)/ (1-C_1/C_2) ×100]

T_1 and T_2 are the first and second (after boiling) measurements of the conductivity of solutions and C_1 and C_2 are the respective values for the controls.

B. Methods

(a) Biometrical genetic analysis

Griffing method: This method was calculated by following model:

$$Xij = \mu + g_i + g_i + s_{ij} + \frac{1}{b}\sum_k e_{ijk}$$

Where, µ = the population mean, g_i = the general combining ability effect of the i^{th} parent, g_j = the general combining ability effect of the j^{th} parent, s_{ij} = the specific combining ability effect of the cross between i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$ and e_{ijk} the environmental effect associated with ijk^{th} observation.

Morley-Jones model: This analysis was performed as: $Y_{ij} = m + 2 J_i – (p-1) l – (p-2) l_i$ for parents and $C_{ij} = m + J_i + J_j + l + l_i + l_j + l_{ij}$ for single cross progeny. Where m = grand mean, J_i = mean deviation from the grand mean due to the i^{th} parent = "a" component, l = mean dominance deviation = b_1, l_i = further dominance deviation due to the i^{th} parent = b_2 and l_{ij} = dominance deviation that is unique to each F1 and unexplained by above two dominance deviations = b_3. Also $b_1 + b_2 + b_3 = b$.

Hayman's graphical analysis: Hayman's graph (Vr-Wr graph) is drawn with the help of variances of arrays (Vr) and covariances (Wr) between parents and their offspring. The array refers to the crosses in which a particular parent is common. The Wri values are estimated for all the arrays by the following formula: $Wri = (Vri \times VOLO)^{1/2}$ 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 regression line on Vr-Wr graph provides information about average degree of dominance. (a) When the regression line passes through the origin, it indicates complete dominance (D = H1). (b) When it passes above the origin, cutting the Wr axis, it shows that there is partial dominance (D>H1). (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 over-dominance.

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 (Farshadfar, 2010; Singh and Chaudhary, 1979).

Statistical analysis of Morley-Jones and Hayman performed by MSTAT-C, SPSS version 17 and Dial 98 statistical packages to estimate genetic parameters.

RESULTS AND DISCUSSION

A. Analysis of variance

Analysis of variance (Table 1) revealed significant differences among treatments for Ch_a, Ch_b, total Chand PC indicating the presence of genotypic variability, different responses of genotypes and possible selection of genotypes for breeding programs. No significant difference was found for RWC, RCC and CM (Table 1), but as F-test in the analysis of variance can only detect large differences between the genotypes, therefore non-significances in the table of analysis of variance does not mean no significant difference between the genotypes for the characters RWC, RCC and CM unless mean comparisons classified these traits in the same groups (Bassiri, 1990).Generally the results showed enough variation in the accessions for most of the traits. In fact the development of any plant breeding program is dependent to the efficiency of selection, expression of heterosis in the plant population and the existence of genetic variability (Farshadfar *et al.*, 2012; Singh and Choudhary, 1995).

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

S.O.V	RWC	Ch a	Ch b	Total Ch	RCC	CM	PC
Replications	400.202	103.997	1.675	2.721	103.918	401.3525	0.0138
Treatments	81.95	55.310*	29.901**	45.807**	7.874	31.298	0.558**
Error	77.174	27.970	4.977	18.068	9.633905	32.993	0.2057
cv	12.148	25.648	25.114	21.275	6.586	5.983	23.927

** ;*significant at the 5% and 1% probability levels, respectively, ns; non significant.

B. Mean comparisons

For comparison of means Duncan multiple range test was used at 5% probability level. When the F-test of treatment is not significant in the analysis of variance table this test can be used. The results of the comparison of means (Table 2) displayed that the highest amount of PC, CM, RCC, total Ch, Ch_b, Ch_a and RWC belonged to the hybrids (6 × 2, 5 × 3, 6 × 2), parents 6, 6, 6 and 2 respectively, while the lowest amount was attributed to the parent 1 and hybrids(1 × 3,1 × 6, 1 × 5, 1 × 6, 1 × 5), parent 2, 2 and hybrids(1 × 5 and 2 × 3) respectively.

C. Griffing analysis of variance

Mean squares of combining ability effects for studied genotypes were partitioned into general and specific combining abilities (GCA and SCA) reported in Table 3. According to this table mean square of SCA was significant for Ch_b, indicating the involvement of non-additive gene action in its inheritance. As GCA was not significant for Ch_b and SCA was significant, hence Ch_b are predominantly controlled by non-additive (dominance and epistasis) gene action.

The relative importance of additive gene action showed by the ratio of MSgca/MSsca (Table 3). This ratio was no significant for all of treats. For any breeding program, the choice of parents to be used in the crossing program is of principal 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.*, 2012). According to general combining ability of parents for significant traits (Table 4), the highly amount of PC, CM, RCC, total Ch, Ch_b, Ch_a and RWC were for parents 5, 3, 6, 3, 3, 3 and 5, while the low amount was for parents 1, 5, 1, 1, 4, 1 and 6 respectively.

Table 2: Mean comparison of physiological traits under rainfed condition.

Varieties	RWC		Ch_a		Ch_b		Total Ch		SPAD		CM		PC	
1	80.743	ab	23.459	abc	12.867	defg	20.81	abcde	45.11	ab	98.78	ab	1.29	f
2	81.793	a	13.538	cd	7.747	h	13.42	e	47.03	ab	93.28	ab	1.76	bcdef
3	80.013	abc	22.96	abc	12.86	defg	20.59	abcde	46.79	ab	96.65	ab	1.40	ef
4	70.813	abc	20.504	abcd	11.704	efgh	18.58	bcde	47.37	ab	89.62	b	1.70	bcdef
5	76.957	abc	20.096	abcd	18.464	abc	26.84	ab	46.83	ab	98.65	ab	2.57	ab
6	73.853	abc	27.096	a	20.136	a	28.59	a	46.11	ab	96.69	ab	2.16	abcdef
1*2	70.423	abc	17.093	abcd	9.657	gh	14.54	de	47.16	ab	94.92	ab	2.06	abcdef
1*3	71.067	abc	23.194	abc	18.832	ab	22.97	abcd	45.00	ab	94.71	ab	1.30	f
1*4	73.91	abc	21.621	abc	12.151	defg	19.43	bcde	45.20	ab	93.69	ab	2.13	abcdef
1*5	71.09	abc	11.122	d	9.816	gh	13.27	e	46.93	ab	92.00	b	1.65	cdef
1*6	73.707	abc	24.794	ab	13.159	defg	21.61	abcde	44.47	b	95.99	ab	1.30	f
2*3	63.04	c	25.662	a	16.261	abcd	24.65	ab	47.20	ab	99.69	ab	1.79	bcdef
2*4	72.067	abc	14.716	bcd	10.689	fgh	17.35	cde	48.74	ab	95.84	ab	1.83	bcdef
2*5	74.41	abc	18.16	abcd	14.576	cdef	17.21	cde	46.82	ab	97.52	ab	2.08	abcdef
2*6	63.823	bc	23.771	abc	12.012	defg	20.04	bcde	50.99	a	93.51	ab	2.74	a
3*4	73.737	abc	23.51	abc	12.48	defg	20.49	abcde	48.47	ab	96.99	ab	1.45	edf
3*5	76.953	abc	23.874	abc	14.791	bcdef	22.64	abcd	48.30	ab	104.05	a	2.40	abc
3*6	67.047	abc	14.43	bcd	11.074	fgh	17.61	cde	48.01	ab	98.24	ab	1.55	cdef
4*5	66.67	abc	21.434	abc	12.292	defg	19.47	bcde	45.38	ab	92.84	ab	2.33	abcd
4*6	65.98	abc	20.424	abcd	13.642	defg	18.78	bcde	49.61	ab	93.26	ab	2.03	abcdef
5*6	70.573	abc	21.569	abc	15.972	bcde	20.69	abcde	48.11	ab	99.21	ab	2.28	abcde
mean	72.32		20.62		13.39		19.98		47.13		96.01		1.90	
min	63.04		11.122		7.747		13.27		44.47		89.62		1.29	
max	81.793		27.096		20.136		28.59		50.99		104.05		2.74	
cv	12.14766		25.6478		25.1143		21.28		6.59		5.98		23.93	

Means with the same letter are not significantly different at the 5% level.

Table 3: Griffing analysis of variance for significant traits in diallel crosses of wheat.

S.O.V	df	PC	CM	SPAD	Total Ch	Ch_b	Ch_a	RWC
GCA	5	0.709	35.57	15.43	27.76	14	16.74	44.02
SCA	9	0.442	40.82	6.86	28.81	22.92**	27.83	53.2
error	28	0.265	23.46	10.08	22.85	5.07	12.64	71.96**
MS_{GCA}/MS_{SCA}		1.604072	0.8714	2.2493	0.9636	0.6108	0.6015	0.8274
2 MS / 2 MS + MS		0.762366	0.6354	0.8181	0.6584	0.5499	0.5461	0.6233

** significant at 1% probability level

Table 4: General combining ability of parents for studied traits.

Parent	PC	CM	SPAD	Total Ch	Ch_b	Ch_a	RWC
1	-0.297	-1.17	-2.01	-1.28	-0.55	-1.60	2.01
2	0.215	0.01	1.03	-0.78	-0.65	0.37	-1.85
3	-0.284	3.06	0.05	2.86	1.91	1.86	0.17
4	0.032	-0.80	0.15	-0.35	-1.14	-0.38	0.05
5	0.273	-1.74	-0.31	-0.91	0.41	-0.68	2.13
6	0.061	0.65	1.10	0.45	0.01	0.44	-2.51

Specific combining ability effects are presented in Table 5. The best specific combination with heterobeltiosis over the best parents for improvement of PC, CM, RCC, total Ch, Ch_b, Ch_a and RWC were the crosses 6×2, 5×3, 5×1, 3×2, 3×1, 6×1 and 5×3 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. The worst specific combination with heterobeltiosis over the best parents for improvement of PC, CM, RCC, total Ch, Ch_b, Ch_a and RWC were the crosses 6×1, 3×1, 6×1, 6×3, 6×3, 6×3 and 5×4 respectively.

Table 5: Specific combining ability effects of the crosses for the traits investigated.

Crosses	PC	CM	SPAD	Total Ch	Ch_b	Ch_a	RWC
1×2	0.219	1.17	0.78	-2.79	-2.31	-3.39	0.03
1×3	-0.046	-4.47	-0.39	2.00	4.31	1.22	-1.34
1×4	0.468	0.08	-0.30	1.67	0.67	1.89	0.62
1×5	-0.253	-0.44	1.90	-3.93	-3.21	-3.97	-3.28
1×6	-0.387	3.66	-1.98	3.05	0.53	4.24	3.97
2×3	-0.065	-1.63	-1.23	3.19	1.84	1.71	-5.52
2×4	-0.349	1.54	0.20	-0.90	-0.68	-1.66	3.64
2×5	-0.336	2.26	-1.25	-0.48	1.66	2.09	3.90
2×6	0.532	-3.35	1.50	0.99	-0.51	1.25	-2.05
3×4	-0.224	0.41	0.91	-1.40	-1.45	0.32	3.29
3×5	0.487	5.59	1.21	1.30	-0.69	0.99	4.42
3×6	-0.153	0.10	-0.49	-5.09	-4.01	-4.25	-0.85
4×5	0.1	-4.51	-1.82	1.35	-0.14	0.79	-5.75
4×6	0.006	2.47	1.00	-0.71	1.61	-1.35	-1.79
5×6	0.003	-2.89	-0.03	1.76	2.39	0.10	0.72

D. Morley-Jones analysis of variance

Morley-Jones method considers the homozygous varieties as taken at random from some base population about which the conclusion is to be drawn and also is concerned with variances and not the estimates of genetic constants (Farshadfar *et al.*, 2011b; Singh and Paroda, 1984). If reciprocal differences are absent and only one of each pair of reciprocal crosses is raised then this half-diallel data can be analysed following Morley-Jones (1965). In this model the sum of squares corresponding to a, b1, b2 and b3 can be obtained. The general ANOVA in half-diallel analysis will take the form as given in Table 6 (Roy, 2000). According to the Table 6 highly significant differences were observed for additive (a) effect for PC, total Ch, Ch_b and Ch_a while dominance (b) item was significant for total Ch, Ch_b and Ch_a, this result reveals that the inheritance of PC, total Ch, Ch_b and Ch_a was mainly controlled by additive gene effects and total Ch, Ch_b and Ch_a controlled by both additive as well as dominance type of gene action. As the component (b1) was significant for RWC, therefore dominance effects were due to directional dominance. Significant (b2) item for total Ch, Ch_b and Ch_a indicating imbalance of gene distribution for these traits. Significant (b3) item for PC, Ch_b and Ch_a exhibited residual dominance effect (b3) resulted from additive × additive, additive × dominance and dominance × dominance interaction effects. As (b2) and (b3) were not significant for CM, RCC and RWC, therefore epistasis (interallelic interaction) is not involved in their genetics.

Table 6: Morly-Jones analysis of variance.

S.O.V	df	PC	CM	SPAD	Total Ch	Ch_b	Ch_a	RWC
a	5	1.28**	32.05	12.25	64.83**	46.83**	53.29**	58.01
b	15	0.315	37.39	6.42	39.44*	24.27**	34.9**	89.53
b1	1	0.169	10.89	8.62	56.09	8.3	0.14	653.58**
b2	5	0.117	36.48	5.16	55.25*	29.89**	54.57**	42.08
b3	9	0.442*	40.83	6.87	28.81	22.92**	27.83*	53.21
error	40	0.205	34.11	9.63	18.07	4.98	12.37	77.64

* and **: significant at 0.05 and 0.01 probability level responsively

E. Heymangenetic parameters analysis and graphical analysis of traits

According of analysis of Hayman genetic parameters (Table 7), component D was significant for Ch_b, but parameters H1 and H2 were also significant for the characters total Ch, Ch_b and Ch_a which confirms the existence of dominance in the inheritance of all the traits, thus simultaneous effect of additive and dominant gene action is involved for Ch_b. Difference between (H1-H2) was positive for CM, total Ch, Ch_b and Ch_a; hence 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 CM and Ch_a exhibiting that the distribution of alleles in the parents is unknown.

F value was negative for the PC, RCC and RWC characters, hence it can be concluded that frequency of recessive alleles are more than dominant. As the ratio of $\sqrt{(\frac{H1}{D}}$ is greater than one for PC, CM, total Ch, Ch_b and Ch_a, hence, over dominance is involved in the genetic of these traits. Direction of dominance was positive for PC, CM, RCC and Ch_a traits indicating that parents have lower additive genes. Because of the significance of the b for characters total Ch, Ch_b and Cha, Hayman graphical analysis for these characters is possible. This analysis was conducted to assess the genetic relationship among the parents.

Table 7: Hayman genetic parameters for significant traits.

Genetic parameters	PC	CM	SPAD	Total Ch	Ch_b	Ch_a	RWC
D	0.15493	1.34	-2.52	24.27	19.2762**	26.33	-6.08
H_1	0.23275	29.11	0.51	41.36**	32.1382**	43.8217*	35.33
H_2	0.2519	25.27	1.282*	29.6859**	24.4573**	30.5744*	40.75
F	-0.05187	2.77	-4.93	30.23**	21.9379*	35.39	-11.65
H^2	-0.0015	-2.56	0.24	8.81	0.96	-2.03	128.59
E	0.07452**	9.6478**	3.1809**	6.5018**	1.627**	4.0441**	24.7727**
$\sqrt{H1/D}$	1.226	4.66	0.00	1.305**	1.291**	1.29*	0.00
(kd/(kd+kr)	0.43171*	0.611**	0.00	0.7385**	0.7204**	0.7605**	0.00
h^2/H_2	-0.00716	-0.12	0.23	0.36	0.05**	-0.08	3.79
(h)	0.19091	1.53	1.37	-3.48	-1.34	0.17	-11.88
U.V	0.271**	0.217**	0.623**	0.179**	0.19**	0.174**	0.288**
D/(D+E)	0.675**	0.12	-3.81	0.789**	0.922**	0.867**	-0.33
H_b^2	0.678**	0.438**	0.27	0.613**	0.841**	0.707**	0.293*
H_n^2	0.406**	0.07	0.19	0.17	0.245**	0.15	0.00

D = Additive variance, H1 = Dominance variance, H2 = Dominance variance, F = Relative frequency of dominant and recessive allels, H2 = square of difference P vs. all, E = Environment variance, (H1/D)0.5 = Average degree of dominance, (kd/(kd+kr) = Proportion of dominance genes, (h2/H2) = Number of effective factors, (h)=Average direction of dominance, (D/(D+E)) = Heritability by parents or true sense heritablility, H2b)= Broad-sense heritability, (H2n)= Narrow-sense heritability; * and **: significant in 0.05 and 0.01 level responsively.

Graphic analysis of the mode of inheritance varied from additive to over domince for the characters investigated. The position of regression line on Vr-Wr graph provides information about the average degree of dominance (Farshadfar *et al.*, 2011b; Singh and Chaudhary,1995). Since in these three traits, the regression line cutting Y axis (Wr) in down of origin of coordinates, exists over dominance (Fig. 1,2 and 3). Distribution of parents around regression line shows that in total Ch (Fig. 3) and Cha (Fig.1) parents 2 and 5 has a maximum dominant allele respectively.

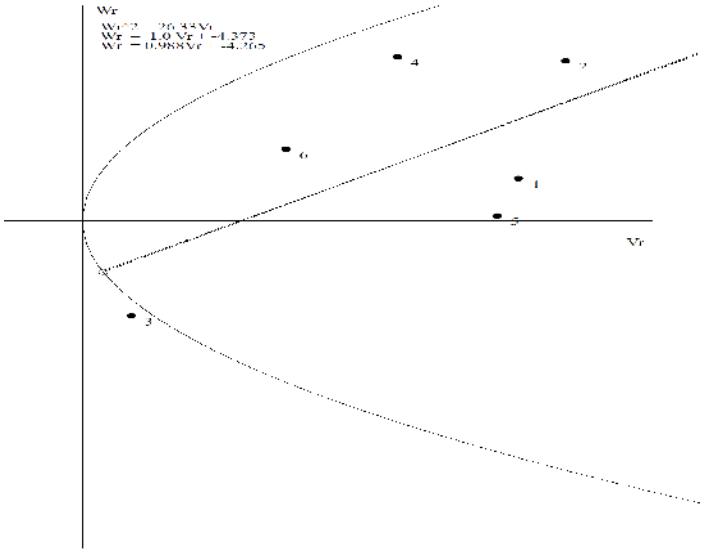

Fig. 1. Regression line and dispersion around origin for Ch_a under rainfed condition.

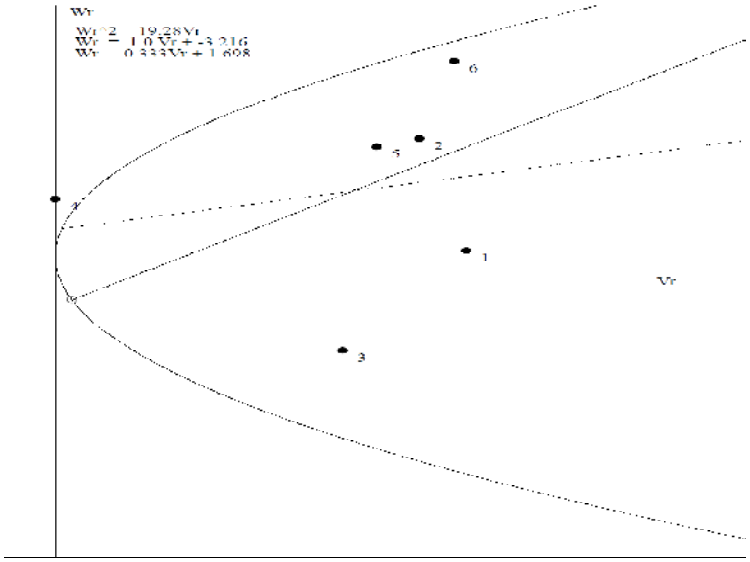

Fig. 2. Regression line and dispersion around origin for Ch_b under rainfed condition.

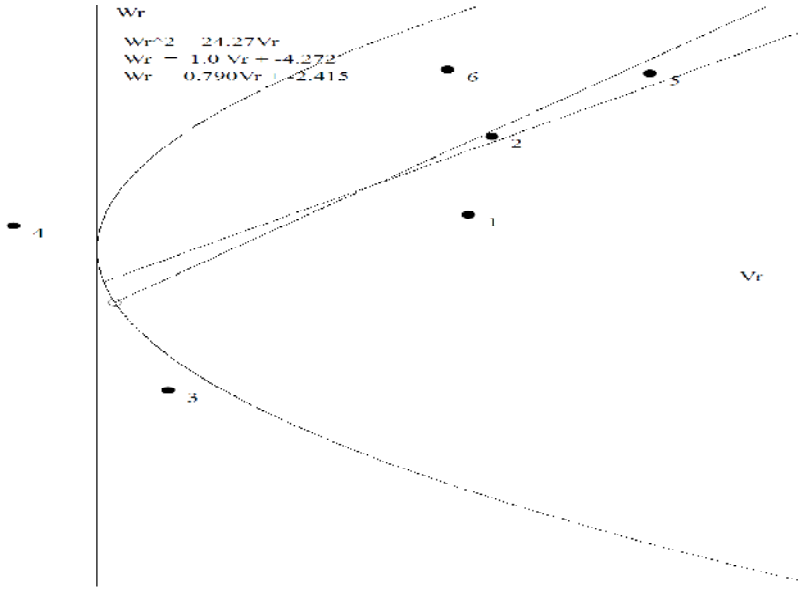

Fig. 3. Regression line and dispersion around origin for total Ch under rainfed condition.

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