

Evaluation of genetic parameters of agronomic and morpho-physiological indicators of drought tolerance in bread wheat (*Triticum aestivum* L.) using diallel mating design

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Abstract

Drought is one of the major environmental factors which threaten wheat production worldwide. In order to study the genetic parameters of field and morpho-physiological indicators of drought tolerance in bread wheat, a 6×6 diallel cross, excluding reciprocals, was grown in a randomized complete block design (RCBD) with three replications under rainfed condition. The results of analysis of variance under stress condition showed significant differences between the genotypes for plant height (PH), peduncle length (PL), number of tillers per plant (NTP), thousand seed weight (TSW), relative water content (RWC), stomatal conductance (SC), chlorophyll fluorescence (CHF), days to flowering (DTF) and stress yield (Ys). PH and PL exhibited 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. RWC and SC revealed significant differences for SCA, therefore non-additive gene action was predominant in their inheritance. The best GCA with positive effects, for improvement of PH, PL, NTP, TSW, RWC, SC, CHE, DTE and Ys under drought conditions were parents 5, 1, 6, 1, 2, 1, 1, 2 and 2, respectively. Also the best SCA with heterobeltiosis over the best parents for improvement of these traits were crosses 1 × 3, 5 × 6, 2 × 6, 1 × 6, 1 × 4, 1 × 3, 3 × 4, 2 × 3 and 1 × 2, respectively indicating that parents of these crosses are genetically diverse. Hayman and Morley-Jones analysis of variance revealed that PL, DTF and RWC were controlled by additive and non-additive, NTP by dominance and PH, TSW and SC were controlled by additive types of gene action. A high narrow-sense heritability estimate was observed for all morpho-physiological characters measured.

Keywords: wheat, drought tolerance, genetic analysis, diallel, morpho-physiological traits.

Abbreviations: CHF- chlorophyll fluorescence; DTF- days to flowering; GCA- general combining ability; GY- grain yield; NTP- number of tillers per plant; PH- plant height; PL- peduncle length; RCBD- randomized complete block design; RWC- relative water content; SC- stomatal conductance; SCA- specific combining ability; TSW- thousand seed weight; Ys- stress yield.

Introduction

Drought is one of the most important abiotic stress factors, which affects almost every aspect of plant growth (Ludlow and Muchow, 1990; Shiri et al., 2010). Genetic improvement of grain yield under water limitation is a key objective for wheat breeders. But emphasis on selection for higher grain yield and improved performance under drought is not always successful. Genetic progress is slowed owing to 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 (Farshadfar et al., 2011a). Understanding physiological adaptation to water-limited environments has identified a number of drought tolerance characteristics with potential for genetic improvement of grain yield under drought (Ludlow and Muchow, 1990). However, only very few of the nominated traits have been rigorously evaluated in a breeding framework (Farshadfar et al., 2012). The use of chlorophyll fluorescence from intact, attached leaves proved to be a reliable, noninvasive method for monitoring photosynthetic events and for judging the physiological status of plant (Rizsa et al., 2001). Fluorescence induction patterns and derived indices have been used as empirical diagnostic tools in stress physiology (Strasser et al., 2000). Thus, PSII fluorescence can be regarded as a bio-sensing device for stress detection in plants. The Fv/Fm ratio represents the maximum quantum

yield of the primary photochemical reaction of PSII. It is an important parameter of the physiological state of the photosynthetic apparatus. Environmental stresses that affect PSII efficiency lead to a characteristic decrease in the Fv/Fm ratio (Krause and Weis, 1991). Leaf water potential is considered to be a reliable parameter for quantifying plant water stress response. Singh et al. (1990) observed significant differences in water potential among wheat genotypes under drought stress. Ludlow and Muchow (1990) proposed that leaf relative water content (RWC) was a better indicator of water status than was water potential. To formulate an efficient breeding program for developing drought-tolerant varieties, it is essential to comprehend 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 (Solomon and Labuschagne, 2004; Farshadfar et al., 2011b). The diallel cross designs are frequently used in plant breeding research to obtain information about genetic properties of parental lines or estimates of general combining ability (GCA), specific combining ability (SCA) and heritability (Baker, 1978; EL-Maghraby et al., 2005; Iqbal et al., 2007). In addition, the

Table 1. Analysis of variance for different characters investigated.

SOV	df	Mean square								
		PH	PL	NTP	TSW	RWC	SC	CHF	DTF	Ys
Rep	2	21.073 ^{ns}	5.253**	10.018 ^{ns}	93.507**	68.517	3870.694**	0.004**	1.159 ^{ns}	29.049 ^{ns}
Treat	20	122.302**	34.642*	7.802*	22.934*	86.153*	1026.712**	0.001**	13.230**	12.620**
Parent	5	33.943 ^{ns}	2.440**	0.779 ^{ns}	3.683 ^{ns}	13.619 ^{ns}	448.263 ^{ns}	0.014 ^{ns}	6.463 ^{ns}	14.781**
Cross (F ₁)	14	42.411 ^{ns}	14.423 ^{ns}	1.723 ^{ns}	8.022 ^{ns}	34.603 ^{ns}	280.129 ^{ns}	0.000 ^{ns}	3.690 ^{ns}	4.414 ^{ns}
Parent versus F1	1	1682.570**	214.180**	128.020**	327.950**	117.520**	14371.120**	0.054**	180.620**	116.690**
Error	40	46.145	4.043	3.880	11.124	43.688	416.043	0.000	2.792	5.507
CV(%)	--	7.310	5.790	22.300	11.510	8.770	22.450	2.430	1.020	24.590

* p<0.05; ** p<0.01 ; ^{ns}: non significant

diallel cross technique was reported to provide early information on the genetic behavior of these attributes in the first generation (Chowdhry et al., 1992; Topal et al., 2004).

Combining ability describes the breeding value of parental lines to produce hybrids. GCA refers to the average performance of a parent in hybrid combinations and SCA is the performance of a parent relatively better or worse than expected on the basis of the average performance of the other parents involved (Sprague and Tatum, 1942; Griffing, 1956). Combining ability analysis helps in the identification of parents with high GCA and parental combinations with high SCA. Based on combining ability analysis of different characters, higher SCA values refer to dominance gene effects and higher GCA effects indicate a greater role of additive gene effects controlling the characters. If both the GCA and SCA values are not significant, epistatic gene effects may play an important role in the genetic of characters (Sprague and Tatum, 1942). The estimation of additive and non-additive gene action through this technique could be useful in determining the possibility of commercial exploitation of heterosis and isolation of pure lines among the progenies of the desirable hybrids (Stuber, 1994). The diallel genetic design and its various modifications have been used by breeders to estimate the potential of populations for intrapopulational improvement and the usefulness of parents in interpopulational breeding programs, and to select inbred lines in hybrid development programs. The best-known methods for diallelic analysis are those developed by Hayman (1954), both exclusively for homozygous parents, that by Griffing (1956), for circulate diallel cross, that by Gardner and Eberhart (1966), normally used when the parents are open-pollinated populations and those by Miranda-Filho and Geraldi (1984), which are adapted with the Gardner and Eberhart (1966) and the Griffing (1956) methods for partial diallel. Of these, the Griffing and Gardner and Eberhart methods are doubtless the most frequently applied. The main reasons that justify the widespread use of the Griffing method are its generality, since the parents can be clones, pure lines, inbred lines, or populations of a self-pollinated, cross-pollinated or intermediate species, and the ease of analysis and interpretation; the latter also characterizes the method developed by Gardner and Eberhart (1966). The objectives of the present investigation were to study (i) specific and general combining ability as well as (ii) the genetic properties of morpho-physiological indicators in bread wheat under drought stress condition.

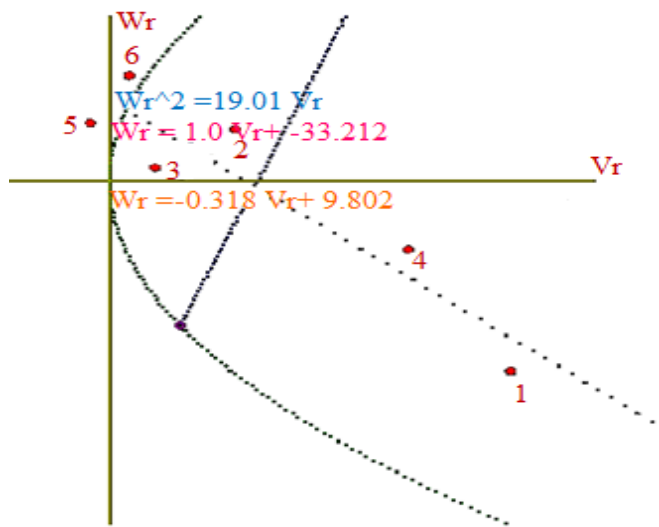


Fig 1. Regression line and dispersion of parents around origin for PH under drought condition.

Results and discussion

In order to study the parents separately and their resulted crosses the value of the mean square for treatments has been classified in three groups: parents, crosses (F₁) and parents versus crosses. The result of analysis of variance (ANOVA) revealed significant differences among parents and hybrids for all traits, indicating the presence of genotypic variability, different responses of genotypes to water stress condition and possible selection of drought tolerant genotypes under water deficit (Table 1). The results suggested significant heterosis among parents and hybrids (Rastogi et al., 2010). 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 (Farshadfar et al., 2011a).

Combining ability analysis

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.

Table 2. Combining ability analysis of significant traits.

Mean square										
SOV	df	PH	PL	NTP	TSW	RWC	SC	CHF	DTF	Ys
GCA	5	183.71*	2.07**	3.34 ^{ns}	33.10 ^{ns}	124.21 ^{ns}	447.75 ^{ns}	0.00 ^{ns}	22.81**	8.35 ^{ns}
SCA	9	102.93*	1.60**	6.47 ^{ns}	20.20 ^{ns}	98.24**	1105.21*	0.00 ^{ns}	5.17 ^{ns}	16.70 ^{ns}
Error	28	45.22	0.24	3.28	12.02	42.39	455.88	0.00	3.41	24.67
MSgca/MSsca		1.78 ^{ns}	1.25 ^{ns}	0.52 ^{ns}	1.64 ^{ns}	1.26 ^{ns}	0.40 ^{ns}	0.00 ^{ns}	4.41**	0.50 ^{ns}
Baker Ratio		0.78	0.71	0.51	0.76	0.72	0.44	0.00	0.89	0.50

* p<0.05; ** p<0.01 ;^{ns} non significant

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 et al., 1990; Singh and Narayanan, 1993). The results of combining ability analysis exhibited that general combining ability (GCA) and special combining ability (SCA) were significant for PH and PL indicating the involvement of additive and non-additive effects (dominance and epistasis) in their inheritance, and also GCA was significant for DTF displaying that DTF is controlled by additive type of gene action, while SCA was significant for RWC and SC indicating that they are monitored by non-additive type of gene action (Table 2). The amount of Baker's ratio (Table 2) for PH, PL, TSW, RWC, DTF and Ys was closer to 1 (more than 0.7) that reveals additive effects play more significant roles. Low coefficient of Baker's ratio for the traits SC and CHF indicates the role of non-additive effects in controlling them. The ratio of MSgca/MSsca was significant for DTF and Ys, therefore they are predominantly controlled by additive gene effects, so 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 (EL-Maghraby et al., 2005; Shiri et al., 2010). Estimate of GCA for plant height of the six genotypes revealed that parent 5 has the least negative GCA and therefore, parent 5 can be effective to reduce plant height. The best general combiners with positive effects, for improvement of PH, PL, NTP, TSW, RWC, SC, CHE, DTE and Ys under drought conditions were parents 5, 1, 6, 1, 2, 1, 1, 2 and 2, respectively. Accordingly parents 2 and 6 are the best general combiners for improvement of drought tolerance (Table 3). Dahanda and Sethi (1998) in their study on wheat showed that additive effect of genes plays an important role in controlling trait of water lost from detached leaves. In examining combining ability for durum wheat, Topal et al. (2003) exhibited that GCA for seed length and thousand seed weight and SCA for breakage rate of seed and grain width were significant. The estimates of SCA for the nine characters are presented in Table 4. The 1×3 cross has the most SCA in the negative direction that can be used in breeding programs to reduce the height of the plant. Cross of 1×4 exhibited high SCA effects for PL while, crosses 2×5 and 2×6 indicated the highest SCA effects for SL and NTP respectively. The crosses 1×6 and 1×4 were good combiners for TSW and RWC, respectively.

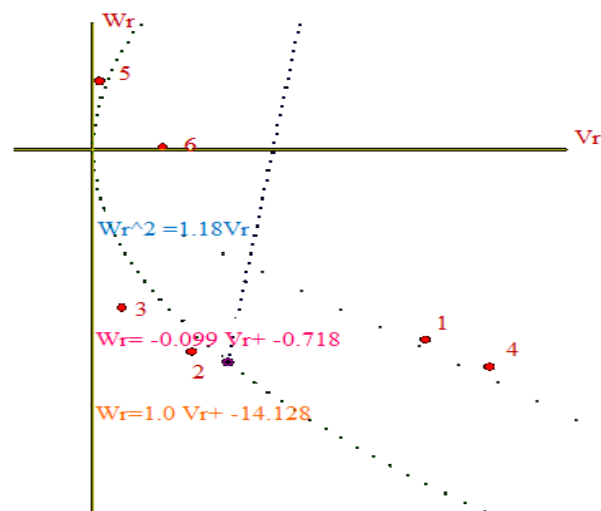


Fig 2. Regression line and dispersion of parents around origin for PL under drought condition.

The best specific combinations for SC and CHF were crosses 1×3 and 3×4, respectively. For DTM, high-positive SCA effects were displayed by the crosses 4×5 and 2×3. While the cross 3×5 and 1×2 indicated the highest SCA effects for grain yield under drought stress (Table 4).

Morley-Jones analysis of variance

The model proposed by Morley-Jones (1965) considers the homozygous varieties taken as random from some base population about which the conclusion are to be drawn. Consequently, his model is concerned with variances and not the estimates of genetic constants (Singh et al., 1990; Farshadfar et al., 2011b). In this model the sum of squares corresponding to a , b_1 , b_2 and b_3 can be obtained. The general ANOVA in half-diallel analysis will take the form given in Table 5. An important advantage of Morley-Jones ANOVA components is that it is free of the assumptions 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 (Miranda-Filho and Geraldi, 1984; Farshadfar et al., 2011a). Here "a" signifies additive genetic variance in the absence of the b_2 item. If b_2 is significant, the "a" item will not measure additive variance unambiguously, but it will also be contaminated with non-additive variance. The b_1 item measures the mean deviations of the $F_{1,s}$ from the mid-parental values and becomes significant when the dominance effects at various loci are predominantly in one direction. That is, there is a directional dominance effect. The absence of significance of this item in

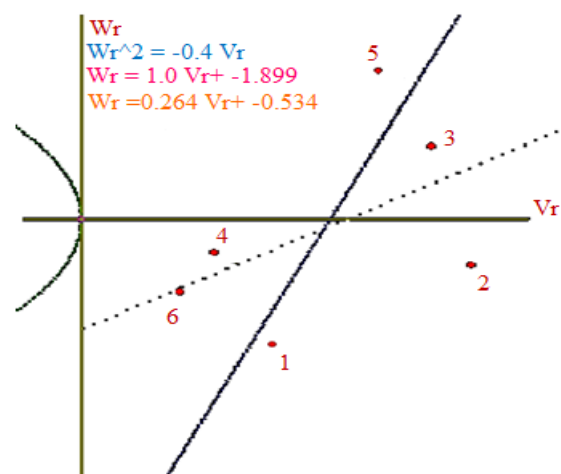
Table 3. General combining ability (GCA) of parents in a 6×6 diallel design for significant traits.

parents	characters								
	PH	PL	NTP	TSW	RWC	SC	CHF	DTF	Ys
1	2.49	3.41	-0.82	2.49	3.34	7.46	0.01	-1.83	-0.49
2	-1.60	-1.05	-0.06	1.49	3.39	5.57	0.00	1.33	1.37
3	-2.06	0.44	0.35	0.24	1.27	-0.23	0.01	-1.58	-0.43
4	6.07	1.88	-0.29	-1.11	-1.66	-6.16	-0.01	0.17	-0.76
5	-4.91	-2.30	0.11	-0.80	-4.69	1.14	-0.01	1.00	-0.38
6	-0.42	-2.38	0.71	-2.31	-1.65	-7.78	0.00	0.92	0.68

this case suggested an ambidirectional nature of dominance. The significance of the b_2 item indicated that the mean dominance deviation of the F_1 's from their mid-parental values differed significantly over the F_1 arrays and these arrays differ if some parents contain more dominant alleles than others, implying asymmetry of gene distribution (Hayman, 1954; Farshadfar et al., 2011b). 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 . The b_3 is equivalent to specific combining ability variance (Singh and Narayanan, 1993). In breeding jargon, estimation of items (a) and (b) amounts to estimation of general combining ability and specific combining ability, respectively (Farshadfar et al., 2012). Highly significant differences were observed for additive ("a") effect for PL, RWC, DTF and CHF in Morley-Jones method, while dominance ("b") item was significant for all traits except for CHF and Ys (Table 5) indicating that the inheritance of PL, RWC, DTF and CHF was mainly controlled by additive gene effects, while PH, NTP, TSW, SC and Ys by dominance type of gene action. Both ("a") and ("b") items were significant for PL, RWC and DTF, accordingly these traits are controlled by both additive as well as dominance type of gene action. As (b_2) and (b_3) were not significant for NTP, CHF and Ys, hence interallelic interaction (epistasis) is not involved in their genetics. As the component (b_1) was significant for NTP and Ys (Table 5), therefore dominance effects were due to directional dominance. Significant (b_2) item for PH, PL, TSW, SC and DTF indicating imbalance of gene distribution for these traits. Significant (b_3) item for PH, PL, RWC and SC exhibited residual dominance effect (b_3) resulted from additive × additive, additive × dominance and dominance × dominance interaction effects (Table 5).

Hayman numerical analysis

The parameters H_1 and H_2 were significant for the characters PL, NTP, TSW, SC and DTF which confirms the existence of dominance in the inheritance of all the traits (Table 6), but as component D was also significant for DTF, hence simultaneous effect of additive and dominant gene action is involved for DTF. Difference between ($H_1 - H_2$) was positive for PH, PL, TSW, RWC, SC and DTF, 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 PH, PL, TSW, SC, and DTF exhibiting that the distribution of alleles in the parents is unknown. As the ratio of $\sqrt{H_1 / D}$ is greater than one for PH, PL, SL, SC and DTF, hence, over dominance is involved in the genetic of these traits, but this ratio is zero for NTP and TSW which implies that type of dominance is unknown.

**Fig 3.** Regression line and dispersion of parents around origin for NTP under drought condition.

The proportion of genes with positive and negative effects in the parents is estimated as ($H_2/4H_1$). If positive and negative alleles are symmetrically distributed this ratio equals 0.25. Estimates of the proportion of positive and negative genes ($H_2/4H_1$) in the parents ranged from 0.16 for DTF to 0.25 for NTP (Table 6) hence, positive and negative alleles are symmetrically distributed in this trait. This reconfirms that H_2 was not different from H_1 in this trait. 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 (Rastogi et al., 2010; Farshadfar et al., 2011b). Solomon and Labuschagne (2004) reported that high estimate of heritability (greater than 0.5; Stansfield, 2005) for all the traits studied may be probably for the involvement of few major genes in the control of inheritance of these traits. High broad-sense heritability observed for PH, PL, TSW, RWC, SC and DTF confirmed that these traits are more genetic, but because of low narrow-sense heritability the role of additive part is low. Broad-sense heritability's of all true-sense heritability, or the proportion of additive variance out of the total variance of accessions composed of mainly additive and environmental variation, is viewed as eventual heritability (Farshadfar et al., 2012).

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 over dominance for the characters investigated. The position of regression line on Vr-Wr graph provides information about the average degree of dominance (Singh and Narayanan, 1993).

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

Crosses	Characters								
	PH	PL	NTP	TSW	RWC	SC	CHF	DTF	Ys
1×2	1.77	0.99	0.82	0.56	-1.28	-6.09	0.00	-0.28	3.24
1×3	-9.59	-2.72	-0.69	-1.54	0.20	32.07	0.00	0.8	-2.85
1×4	10.27	5.63	1.39	-2.65	6.83	-7.47	0.01	0.22	0.67
1×5	-2.82	-3.95	-0.90	-0.42	-1.87	-9.75	0.00	-1.62	-1.70
1×6	0.37	0.05	-0.61	4.05	-3.87	-8.74	0.00	0.88	0.65
2×3	2.49	1.06	-1.79	0.86	5.88	17.39	0.01	1.88	0.95
2×4	-0.98	-1.08	-1.93	-0.93	-11.3	-3.81	-0.02	-1.03	0.51
2×5	0.39	0.97	1.17	0.87	0.85	-10.41	-0.01	0.53	-2.26
2×6	-3.66	-1.94	1.74	-1.36	5.85	2.92	0.01	-0.03	-2.43
3×4	-0.59	0.73	1.22	1.27	-0.53	-20.68	1.00	-0.28	-1.77
3×5	3.79	0.39	1.04	-1.44	-2.3	-14.52	-0.01	-0.78	3.35
3×6	3.90	0.54	0.22	0.85	-3.25	-14.25	0.00	-1.62	0.33
4×5	-4.72	-2.02	-0.32	3.41	-3.52	23.29	0.02	3.62	-0.12
4×6	-3.98	-3.26	-0.36	-1.11	1.48	8.69	-0.01	-0.53	0.72
5×6	3.37	4.61	-0.99	-2.43	-0.21	11.39	0.00	1.30	0.74

Regression line passes below the origin cutting W_r axis in the negative region (intercept= $a < 0$ (negative)) for PH, PL, NTP, TSW and SC (Fig. 1, 2, 3, 4, and 5, respectively) indicating the presence of overdominance, while DTF was under the control of partial-dominance (Fig. 6). High difference between regression line and regression line with slope of one for PH and PL, suggesting the presence of non-allelic interaction therefore, selection through selfing are not effective for improvement of PH and PL. Non-allelic interaction related to a number of interacting genes, lead to inefficient selection, but if the number of interacting genes reduced, selection will be efficient. Detection of epistasis suggested that variation for PH and PL were 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 Ph and PL (Farshadfar et al., 2011b). The dispersion of parents around the regression line for PH (Fig. 1) showed that parents 5 and 6 are close to the origin of the coordinate, and accordingly have more than 75% dominant genes, parents 2 and 3 have 50-75% of dominant genes, while parents 1 and 4 are far from the origin, therefore they have < 25% of dominant genes. Parents 2 and 3 have more than 75% dominant genes for PL (Fig. 2), while recessive and dominant genes are equally distributed in parent 1, 4, 5 and 6. Almost 50% of the dominant genes are distributed in parents 4 and 6 for NTP (Fig. 3), while 50% of the recessive genes are located in parents 2, 3 and 5, recessive and dominant genes are equally distributed in parent 1. The dispersion of parents around the regression line for TSW (Fig. 4) reveals that parent 3 is close to the origin of the coordinate, and accordingly have > 75% of dominant genes parents 1, 4 and 5 have 50-75% of dominant genes, while parents 2 and 6 are far from the origin and therefore has < 25% of dominant genes. Most of the dominant genes for SC (Fig. 5) were distributed in parents 2, 4, 5 and 6, while recessive genes were mostly distributed in parents 1 and 3. The dispersion of parents around the regression line for DTF showed that parents 1 and 4 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes (Fig. 6), parents 2 and 3 have 50-75% of dominant genes, while parents 5 and 6 are far from the origin, therefore they have < 25% of dominant genes.

Materials and methods

Plant materials and experimental conditions

The plant material consisted of six-parent diallel cross excluding reciprocals. The experiment was carried out at Razi

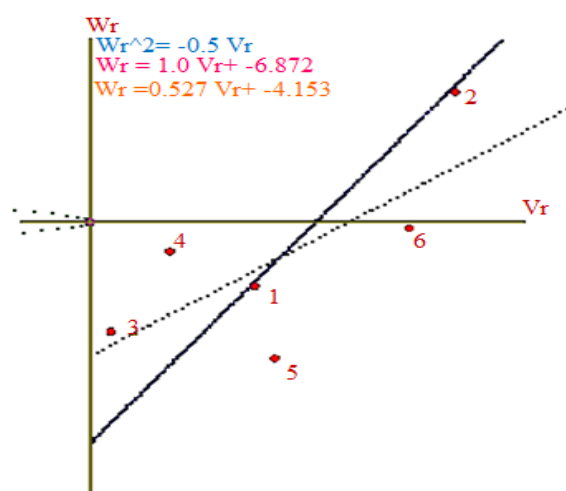


Fig 4. Regression line and dispersion of parents around origin for TSW under drought condition.

University, Kermanshah, Iran during year 2008 to 2009 (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 named Pishtase (1), CHAM-4DOVN-2ICW93-0001-AP-OL-1AP-2AP-OAP (2), Zagross (3), Ns732.HER//Darab (4), TEVEE S/KARAWAN "S" ICW93-0073-1AP-OL-8AP-OL-... (5) and URES/3//FURY//SLN/ALDAN "S"/4/NS732/HER ICW93-0531-... (6), respectively. The plant genetic materials (parents and F_1 s) were grown in a randomized complete block design with three replications under rainfed conditions. Single seeds were sown in 2.5 m rows and at 15 × 30 cm plant to plant and row to row distances, respectively. From each entry (parents and F_1 s), five competitive plants were randomly selected from each replication for recording observations on the following morpho-physiological characters:

Grain yield (GY)

GY was recorded under stress (Y_s) conditions at physiological maturity stage. The physiological maturity stage was considered when 90% of seed changed color from green to yellowish and stopped photosynthetic activity.

Table 5. Morley-Jones analysis of variance for significant traits in the six-parent diallel crosses of wheat.

Mean Square		PH	PL	NTP	TSW	RWC	SC	CHF	DTF	Y _s
SOV	df									
a	5	109.07 ^{ns}	17.39**	3.04 ^{ns}	14.28 ^{ns}	137.50*	287.62 ^{ns}	0.02*	24.78**	26.97 ^{ns}
b	15	126.71**	40.39**	9.39**	25.62*	69.03**	1273.07**	0.01 ^{ns}	9.38**	20.12 ^{ns}
b ₁	1	92.01 ^{ns}	28.66*	69.41**	53.10*	13.54 ^{ns}	1624.69 ^{ns}	0.01 ^{ns}	7.13 ^{ns}	22.85 ^{ns}
b ₂	5	176.46**	55.70**	2.63 ^{ns}	34.30*	27.57 ^{ns}	1504.91**	0.02 ^{ns}	17.44**	25.72 ^{ns}
b ₃	9	102.94*	33.19**	6.47 ^{ns}	17.74 ^{ns}	98.22*	1105.21*	0.00 ^{ns}	5.15 ^{ns}	16.70 ^{ns}
Error	40	46.15	4.04	3.88	11.14	137.50*	416.04	0.01	2.79	19.01

* p<0.05; ** p<0.01 ;^{ns}: non significant

Morphological traits

In order to measure morphological traits such as: plant height (PH), peduncle length (PL) and number of tillers per plant (NTP), 3 plants randomly selected and measurements were performed. Data were collected on number of days to flowering (DTF) from day of planting to 50% flowering per plot.

Physiological characters

1- Relative water content (RWC)

A sample of 5 leaves were taken randomly from the flag leaves of each genotype and fresh weight (FW) was measured. Then, samples were placed in distilled water for 24 h and reweighed to obtain turgor weight (TW). Leaf samples were oven dried and weight in 70°C for 72 h (DW). RWC was calculated using the following formula (Eric et al., 2005).

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

2- 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:

$$QY = Fv/Fm$$

where, Fv and Fm are variable and maximum fluorescence, respectively.

3- Stomatal conductance (SC)

Using three points of a flag leaf in each plot SC was measured by a Porometer.

Biometrical genetic analyses

1- Griffing - model I, method 2

This method was calculated by following model:

$$X_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b} \sum e_{ijk}$$

where, u = the population mean, g_i = the general combining ability effect of the ith parent, g_j = the general combining ability effect of the jth parent, s_{ij} = the specific combining ability effect of the cross between ith and jth parents such that s_{ij} = s_{ji} and e_{ijk} the environmental effect associated with ijkth observation.

2- Baker's ratio

To evaluate the role of additive and non-additive gene effects, Baker's ratio (2 MS_{Gca}/2 MS_{Gca} + MS_{Sca}) was used

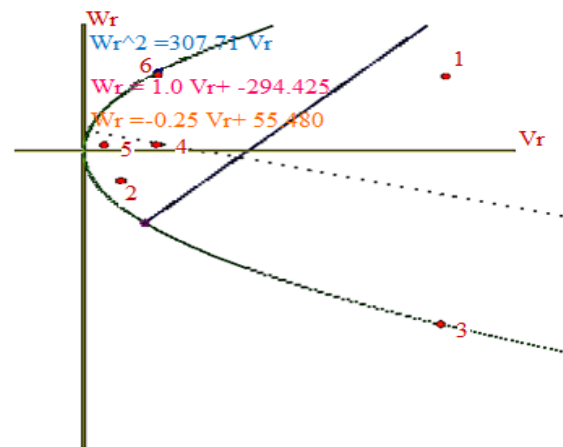


Fig 5. Regression line and dispersion of parents around origin for SC under drought condition.

(Table 2). Baker's ratio gives a clear picture of additive and non-additive effects of the genes. If this ratio equals to 1, it means that all effects are the result of additive effect (Baker, 1978). If this ratio equals to 0.5, it means that variance of additive effects and non-additive effects are equal and if it is less than 0.5 it shows the superiority of non-additive gene effects (dominance, over dominance and epistasis) in controlling the traits of interest (Farshadfar et al., 2012).

3- 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 ith parent = "a" component, l = mean dominance deviation = b₁, l_i = further dominance deviation due to the ith parent = b₂ and l_{ij} = dominance deviation that is unique to each F₁ and unexplained by above two dominance deviations = b₃. Also b₁ + b₂ + b₃ = b. Statistical analysis of Morley-Jones and Hayman performed by MSTAT-C version L42, SPSS ver. 17 and Dial 98 statistical packages to estimate genetic parameters.

4- 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 formula: $Wri = (Vri \times VOLO)^{1/2}$ where, Vri is the variance of rth 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

Table 6. Hayman analysis of variance for significant traits in the six-parent diallel crosses of wheat.

Characters	PH	PL	NTP	TSW	SC	DTF
Genetic Parameters						
D	19.01 ^{ns}	1.18 ^{ns}	-0.40 ^{ns}	-0.02 ^{ns}	307.71 ^{ns}	5.48*
H ₁	151.85**	57.69**	7.19*	27.43**	1485.41**	12.19**
H ₂	110.35 ^{ns}	42.09**	7.26**	19.95*	1114.02**	7.74**
F	40.32 ^{ns}	10.08 ^{ns}	-0.62 ^{ns}	4.38 ^{ns}	680.79 ^{ns}	5.67
h ²	12.27 ^{ns}	5.55 ^{ns}	14.39 ^{ns}	9.53 ^{ns}	279.43 ^{ns}	1.04
E	14.93**	1.25**	1.17**	3.73**	140.54**	0.99**
$\sqrt{H_1/D}$	2.82 ^{ns}	6.98 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	2.19*	1.49**
kd/(kd+kr)	0.68**	0.80**	0.00 ^{ns}	0.00 ^{ns}	0.75**	0.67
h ² /H ₂	0.13 ^{ns}	0.15 ^{ns}	2.37**	0.57 ^{ns}	0.29 ^{ns}	0.16
h	4.45 ^{ns}	2.48**	-3.87 ^{ns}	3.38*	18.73**	-1.24
H ₂ /4H ₁	0.18**	0.18**	0.25**	0.18**	0.19**	0.16**
D/D+E	0.56*	0.48 ^{ns}	-0.51 ^{ns}	-0.01 ^{ns}	0.68**	0.84**
H ² b	0.71**	0.91**	0.61**	0.63**	0.65**	0.80**
H ² n	0.19*	0.22**	0.02 ^{ns}	0.14 ^{ns}	-0.03 ^{ns}	0.42**

* p<0.05; ** p<0.01 ;^{ns}: non significant.

D=Additive variance, H₁= Dominance variance, H₂= Dominance variance, F= Relative frequency of dominant and recessive alleles, h²= square of difference P vs. all, E= Environment variance, $\sqrt{H_1/D}$ = 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, (H²b)= Broad-sense heritability, (H²n)= Narrow-sense heritability, (H₂/4H₁)= Proportion of dominance and recessive genes.

regression line, where, Wr is array mean of variances, Vr array mean of covariance's 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 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 et al., 1990; Singh and Narayanan, 1993).

Conclusion

The results obtained from the present study showed significant genetic variation between the genotypes for morpho-physiological traits investigated under rainfed condition. PH, PL, RWC and SC revealed significant differences for SCA; hence non-additive gene action was predominant for these traits. The best GCA with positive effects, for improvement of PH, PL, NTP, TSW, RWC, SC, CHE, DTE and Ys under drought conditions were parents 5, 1, 6, 1, 2, 1, 1, 2 and 2, respectively. Also the best SCA with heterobeltiosis over the best parents for improvement of these traits were crosses 1 × 3, 5 × 6, 2 × 6, 1 × 6, 1 × 4, 1 × 3, 3 × 4, 2 × 3 and 1 × 2, respectively indicating that parents of these crosses are genetically diverse. Hayman and Morley-Jones analysis of variance indicated that PL, DTF and RWC were controlled by additive and non-additive types of gene action, NTP by dominance type of gene action, while PH, TSW and SC were controlled by additive type of gene action.

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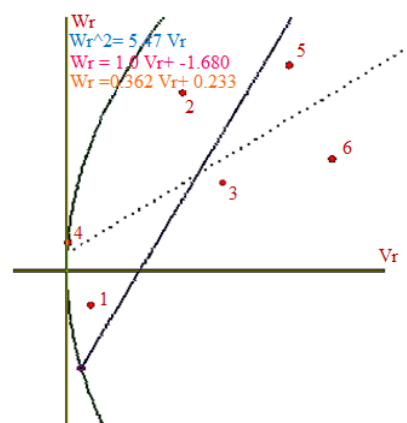


Fig 6. Regression line and dispersion of parents around origin for DTF under drought condition.

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