

## Inheritance of drought tolerance indicators in bread wheat (*Triticum aestivum* L.) using a diallel technique

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### Abstract

In order to study the inheritance of field and physiological indicators of drought tolerance in bread wheat (*Triticum aestivum* L.), plants from an eight-parental diallel cross, excluding reciprocals, were grown in a field in a randomized complete block design with three replications under two different water regimes (irrigated and rainfed). Significant differences were found for yield potential (Yp), stress yield (Ys), stress tolerance index (STI), leaf water potential (LWP), water use efficiency (WUE), evapotranspiration efficiency (ETE), relative water loss (RWL) and chlorophyll fluorescence (CHF). There were significant differences for both general combining ability (GCA) and specific combining ability (SCA) except GCA for Ys, CHF and RWL and SCA for LWP, CHF and RWL, indicating the involvement of additive and non-additive types of genes in controlling all agronomic and physiological characters except for Ys, LWP, CHF and RWL. Parents and crosses thus have different GCA and SCA, respectively. The best general combiner for improvement of drought tolerance was Plainsman. The best specific combination with heterobeltiosis over the best parents for improvement of drought tolerance was the 3×6 cross. Hayman analysis of variance (ANOVA) indicated that Yp, Ys, STI, WUE and ETE were controlled by additive and non-additive types of gene action, LWP by a dominance type of gene action while CHF and RWL were controlled by an additive type of gene action. A high narrow sense heritability estimate was observed for all agronomic and physiological characters measured.

**Keywords:** Bread wheat; Drought tolerance; Diallel; Genetic analysis; Gene action; Heritability.

**Abbreviations:** CHF- chlorophyll fluorescence; CRD- completely randomized design; DW- dry weight; ETE-evapotranspiration efficiency; Fm- maximum fluorescence; Fv- variable fluorescence; FW- fresh weight; GCA- general combining ability; GY- grain yield; LWP- leaf water potential; RWC- relative water content; RWL- relative water loss; SCA- specific combining ability; STI- stress tolerance index; TDM- total dry matter; TW- turgor weight; TWU- total water used; W5H- wilted for 5 hours; WUE- water use efficiency; Yp- yield potential; Ys- stress yield.

### Introduction

Water stress is a problem that affects 45% of the world's geographic area and is a major constraint in wheat production and the most important contributor to yield reduction in semi-arid regions (Andrew et al., 2000; Amjad Ali et al., 2011). Improving drought resistance is, therefore, a major objective in plant breeding programs for rainfed agriculture in these regions (Ehdaie and Waines, 1993). Knowledge of genetic behavior and type of gene action controlling target traits is a basic principle for designing an appropriate breeding procedure for the purpose of genetic improvement. Hence, the success of any selection or hybridization breeding program for developing drought-tolerant varieties depends on precise estimates of genetic variation components for traits of interest consisting of additive, dominant and non-allelic interaction effects (Farshadfar et al., 2008; Mohammadi et al., 2010; Nouri et al., 2011). As drought resistance is a complex physiological phenomenon, its genetic basis has received limited attention. Therefore, little information is

available on the 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., 2008; Nouri et al., 2011). The potential for improving crop performance under drought stress can not be achieved until we have identified genes or gene products which are responsible for desired characteristics of drought resistance at different stages of plant growth and development (Dhanda et al., 2002). One of the most complex designs that has been used extensively for the genetic analysis of quantitative characters such as drought is the diallel cross. 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 (Iqbal et al., 2007). In addition, diallel crosses provide early information on the genetic behavior of these attributes in the first

**Table 1.** Analysis of variance for agronomic and physiological characters under rainfed condition.

S.O.V	df	Mean squares									
		Yp	Ys	STI	RWC	WUE	LWP	ETE	TAWU	CHF	RWL
Replication	2	24.8	0.473ns	0.31ns	64.82	0.268	10.62	0.28	1.98	0.01	0.013
Genotype	35	21.05**	1.858**	0.82**	77.37ns	0.238**	12.88**	0.63**	1.247ns	0.01**	0.014*
Error	70	2.16	0.709	0.016	57.48	0.025	5.46	0.11	1.155	0.01	0.007
CV%	--	15.91	20.08	23.7	9.6	15.98	12.83	15.69	11.65	15.16	33.5

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

**Table 2.** Combining ability analysis of agronomic and physiological traits under rainfed condition.

S.O.V	df	Mean squares								
		Yp	Ys	STI	WUE	LWP	ETE	CHF	RWL	
Replication	2	31.7**	1.128ns	0.05ns	0.3**	5.3ns	0.6**	0.03ns	0.02ns	
GCA	7	19.4**	1.607ns	0.10**	0.2**	30.8**	0.5**	0.009ns	0.014ns	
SCA	20	22.1**	1.677**	0.07**	0.3**	7.6ns	0.6**	0.003ns	0.005ns	
Error	54	1.9	0.644	0.02	0.02	5.6	0.1**	0.05	0.004	

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

**Table 3.** General combining ability of parents in an 8x8 diallel design for significant agronomic and physiological traits.

	Parents	characters								
		Yp	Ys	STI	WUE	LWP	ETE	CHF	RWL	
1	Painsman	1.8	0.482	0.14	0.2	2.1	0.2	0	0	
2	Chinese Spring	0.5	-0.192	0.00	0	1.6	0.1	0	0	
3	Sakha	-0.2	0.173	0.01	0	-0.7	0.2	0	0	
4	Saberbeg	0.1	-0.217	-0.03	0	0.4	-0.1	0	0	
5	Karckia	0.5	0.276	0.06	0.1	-0.1	-0.1	0	0	
6	Kobomugi	-1.4	-0.301	-0.08	-0.1	-0.3	-0.2	0	0	
7	Regina	-1.3	-3.32	-0.09	-0.1	-1.7	-0.2	0	0	
8	Capelle Despreza	0.1	0.099	0.00	0	-1.3	0.1	0	0	

generation (Topal et al., 2004). To date, several methods have been proposed for the genetic analysis of data from a diallel cross (Griffing, 1956a, b; Hayman, 1954a, 1954b). The approaches of Griffing (1956a) and Hayman (1954a, 1954b) are statistically similar, in their analyses of variance. Griffing's general combining ability (GCA) component is mathematically identical to Hayman's additive component. Griffing employs one specific combining ability (SCA) and one reciprocal effect component, while Hayman subdivides these into three dominance components ( $b_1$ ,  $b_2$  and  $b_3$ ), and two reciprocal effect components (c and d). They differ, however, in the genetic assumptions and interpretations which are associated with them. Griffing's analysis is a strict statistical treatment of main effects (GCA) and interactions (SCA) whereas Hayman's analysis incorporates genetic assumptions. In general, Hayman's method appears to extract more genetic information than Griffing's method from the same data set. Griffing's method involves only ANOVA and estimation of GCA and SCA effects. Hayman's method, on the other hand, may include statistical and graphical analyses of array variances and covariance, and the estimation of a number of genetic parameters. 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 ability as well as (ii) the genetic properties of agronomic and physiological characters in bread wheat.

## Results and discussion

### Parameters under rainfed conditions

ANOVA (Table 1) revealed significant differences among parents and hybrids for all agronomic (Ys) and physiological traits except for RWC and TWU, indicating the presence of genotypic variability, different responses of genotypes to water stress condition and possible selection of drought-tolerant genotypes under water deficit. LWP, WUE, RWC and RWL were suitable screening techniques for discriminating drought-tolerant genotypes in wheat, barley and chickpea (Suprunova et al., 2004; Bayoumi et al., 2008; Farshadfar et al., 2008; Cossani et al., 2009). In fact, the development of any plant breeding program is dependent upon the existence of genetic variability, the efficiency of selection and the expression of heterosis, and largely dependent upon the magnitude of genetic variability present in the plant population (Singh and Narayanan, 1993; Singh and Chaudhary, 1999).

### Combining ability analysis

The concept of combining ability 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 to evaluate inbreds in terms of their genetic value, and in the selection of suitable parents for hybridization and identification of superior cross combinations (Singh and Narayanan, 1993; Singh and Chaudhry, 1999).

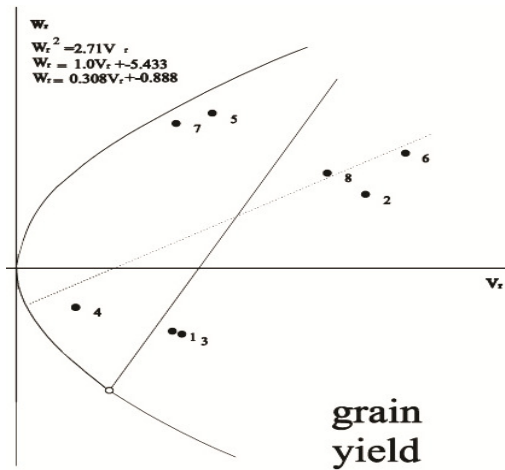


Fig 1. Regression line and dispersion of parents around origin for Yp under stress conditions

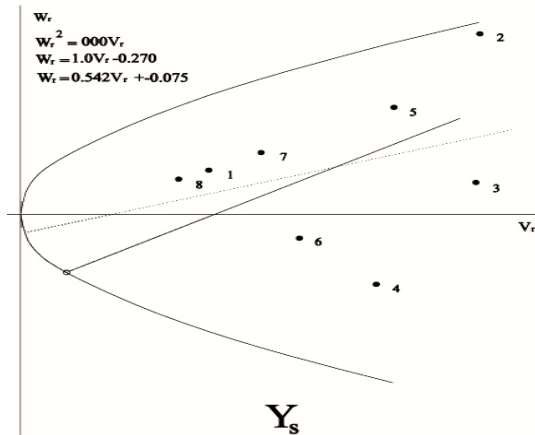


Fig 2. Regression line and dispersion of parents around origin for Ys under stress condition

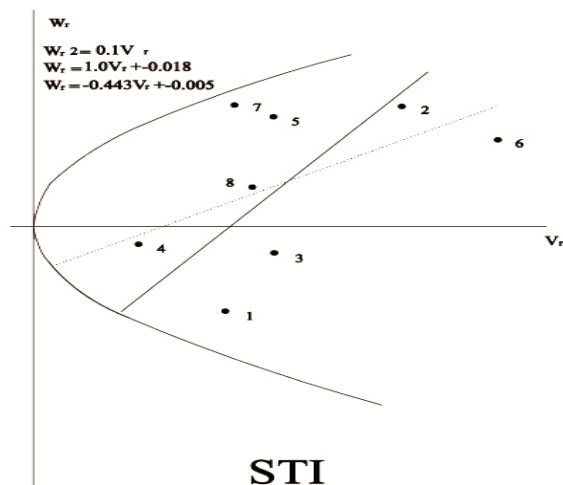


Fig 3. Regression line and dispersion of parents around origin for STI under stress conditions

Generally speaking, the choice of parental lines with high GCA effects increases the probability of obtaining heterotic hybrids in crops. Combining ability analysis for significant agronomic and physiological traits (Tables 2, 3) exhibited significant differences for both GCA and SCA except for GCA for Ys, CHF and RWL and SCA for LWP, CHF and RWL, indicating the involvement of additive and non-additive types of gene action in controlling all agronomic and physiological characters except for Ys, LWP, CHF and RWL. Parents and crosses thus have different general and specific combining abilities, respectively. The best general combiner with positive effects for improvement of Ys, WUE, LWP and ETE was Plainsman (Table 3). The best specific combination (Table 4) with heterobeltiosis over the best parents for improvement of Ys, WUE, ETE and LWP were 2x4, 3x6, 3x6 and 1x5 crosses, respectively, indicating that parents of these crosses are genetically diverse. The best combination for improved drought tolerance was the cross 3x6 (Shakha x Kobomugi). The expression of positive heterosis in these hybrids reveals the preponderance of additive gene action. According to Topall et al. (2004), compared to other types of gene effects, highly additive gene effects for a specific trait will increase the success of selection for that trait.

#### Gene action and genetic properties

Hayman ANOVA (Table 5) showed that components "a" and "b" were significant for Ys, WUE, ETE, CHF and RWL but not for LWP, while component "b" was significant for Ys, WUE, ETE but not for CHF and RWL. According to Mather and Jinks (1982) and Singh and Chaudhary (1999), "a" primarily tests the significance of the additive effects of the gene, while "b" tests the non-additive effects. Yates (1947), on the other hand, described that GCA may sometimes be called the additive genetic component or main effect while SCA may be referred to as the non-additive genetic component, dominance component or interaction effect. Therefore, the inheritance of Ys, WUE and ETE was controlled by a dominance and additive type of gene action. Simultaneous exploitation of both additive and dominant variance for improvement of Ys, STI, Yp, WUE and ETE is achieved by reciprocal recurrent selection (Chahal and Gosal, 2002). The physiological characters LWP, RWL and CHF were controlled by dominant, additive and additive type of gene action, respectively. "b<sub>1</sub>" tests the mean deviation of the F<sub>1</sub> plants from their mid-parental value. It is significant only if the dominant deviations of the genes in the various entries used are predominantly in one direction. In other words, there is a unidirectional dominance effect. "b<sub>2</sub>" tests whether the mean dominance deviation of the F<sub>1</sub> plants from their mid-parental values within each array differs over arrays. It will do so if some parents contain considerably more dominant alleles than others. That is, a significant "b<sub>2</sub>" implies asymmetry of the gene distribution in the parents at the loci exhibiting dominance. "b<sub>3</sub>" tests that part of dominance that is unique to each F<sub>1</sub>. Thus, from Table 5, it can be inferred that the significant dominance effects (b) were due to a directional dominance effect (b<sub>1</sub>), an asymmetry or imbalance of gene distribution (b<sub>2</sub>), and a residual dominance interaction effect (b<sub>3</sub>) originating from additive x additive, additive x dominant and dominant x dominant interaction effects. The directional dominance effect (b<sub>1</sub>) was not significant for Ys, LWP, CHF and RWL (Table 5). Inheritance of Ys was due to an asymmetry of the gene distribution (b<sub>2</sub>). As "b<sub>3</sub>" was significant for Ys, therefore interallelic interaction (additive x additive, additive x dominant and dominant x dominant) was also involved in its inheritance.

**Table 4.** Specific combining ability of the crosses for significant agronomic and physiological traits.

Crosses	Characters							
	Yp	Ys	STI	WUE	LWP	ETE	CHF	RWL
1×2	0.4	-0.473	-0.05	0.0	0.0	0.0	0.0	0.0
1×3	-1.8	0.597	-0.02	-0.2	-1.1	-0.6	0.0	0.0
1×4	-3.2	-0.62	-0.21	-0.3	-1.8	-5.0	0.0	0.0
1×5	-2.1	0.23	-0.08	-0.2	2.0	-0.4	0.0	0.0
1×6	2.8	0.515	0.19	0.3	0.8	0.4	0.0	-0.1
1×7	1.0	0.074	0.04	0.1	1.3	0.4	0.0	0.0
1×8	3.0	-0.323	0.13	0.3	-1.2	0.7	0.0	0.0
2×3	-1.0	-0.119	-0.07	-0.1	1.1	-0.5	0.0	0.0
2×4	-0.3	1.656	0.17	0.0	2.7	-0.3	0.0	0.0
2×5	2.1	0.75	0.19	0.2	-1.5	0.7	0.0	0.0
2×6	-5.2	-0.534	-0.26	-0.6	-2.4	-0.2	0.0	0.0
2×7	0.3	-0.751	-0.08	0.0	-1.2	0.0	0.0	-0.1
2×8	3.6	-0.528	0.09	0.4	1.3	0.3	0.0	0.0
3×4	-0.9	-1.381	-0.17	-0.1	1.0	-0.1	0.0	0.0
3×5	1.6	0.664	0.17	0.2	1.1	0.1	0.0	0.0
3×6	5.7	-0.012	0.25	0.6	0.6	0.8	0.0	0.0
3×7	-0.4	0.048	-0.02	0.0	-2.0	0.5	0.0	0.0
3×8	-3.2	0.203	-0.14	-0.3	-0.7	-0.1	0.0	0.0
4×5	2.2	-0.831	-0.02	0.2	-2.6	0.3	0.0	0.0
4×6	-0.3	0.489	0.03	0.0	0.9	0.0	0.0	0.0
4×7	2.3	0.788	0.21	0.2	0.0	0.3	0.0	0.0
4×8	0.2	-0.102	0.00	0.0	-0.1	0.2	0.0	0.0
5×6	-1.7	-0.741	-0.17	-0.2	-1.0	-0.2	0.0	0.0
5×7	-0.9	0.110	-0.03	-0.1	0.8	-0.3	0.0	0.0
5×8	-1.2	-0.182	-0.07	-0.1	1.0	-0.2	0.0	0.0
6×7	-0.6	-0.459	-0.07	-0.1	1.3	-0.4	0.0	0.1
6×8	-0.7	0.742	0.03	-0.1	-0.2	-0.3	0.0	0.0
7×8	-1.7	0.190	-0.05	-0.2	-0.1	-0.6	0.0	0.0

As "b<sub>3</sub>" was significant for Ys, WUE, ETE and LWP but not for CHF and RWL and "b" was significant for all physiological traits except for CHF and RWL, therefore Ys, WUE, LWP and ETE are controlled by dominant and interaction effects, namely additive×dominant and dominant×dominant interactions, while CHF and RWL are controlled only by an additive type of gene action. The advantage of ANOVA components (Table 5) are 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 Jinks 1982).

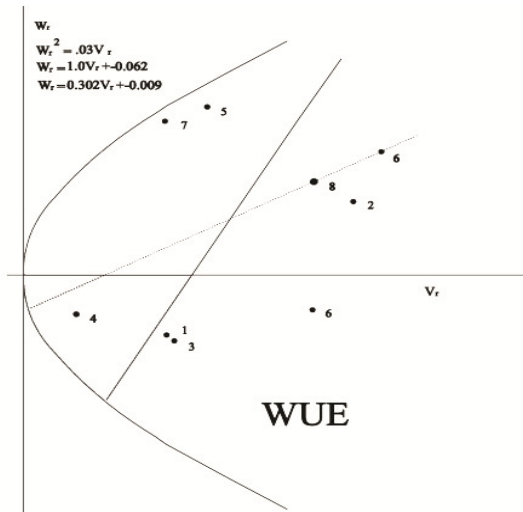
#### Genetic parameters

The ratio of  $\sqrt{H_1/D}$  is > 1 for Ys, WUE, LWP, ETE and RWL. Hence, overdominance is involved in the genetics of these traits. This ratio was < 1 for CHF. Accordingly, dominance is in the partial range. A comparison of additive and dominant components of genetic variance in the majority of crop plants excludes the possibility of overdominance as the major cause of heterosis. Though true overdominance at specific loci cannot be ruled out, the observed levels of overdominance have generally been traced to mimicking the effect of epistasis and linkage which do not warrant the production only of hybrids to exploit heterosis. Under such a situation there is every chance of producing inbred lines or populations as good as or even better than hybrids that would obviate the need of costly procedures of producing hybrid seed on a continuous basis. The exclusion of true overdominance as a major source of heterosis resulted in major shift in breeding procedures, even in maize (Chahal and Gosal, 2002). However, the existence of overdominance suggests the superiority of heterozygotes over homozygotes

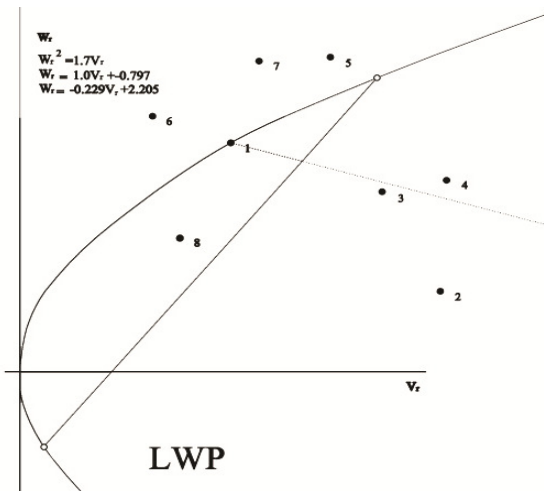
and thus warrants the development of hybrid varieties. In all other situations of incomplete to complete dominance, pure lines as good as hybrids can be developed (Chahal and Gosal, 2002). The parameter  $H_2/4H_1$  shows the proportion of dominant genes with positive or negative effects in parents. The maximum theoretical value of  $H_2/4H_1$  is equal to 0.25, which arises when  $p = q = 0.5$  at all loci. A deviation from 0.25 stems when  $p \neq q$ . Thus,  $H_2/4H_1 = 0.25$  indicates symmetrical distribution of positive and negative dominant genes in parents (Sharma, 1998). In the present case, Ys, WUE, LWP, ETE and RWL were  $\neq 0.25$ , hence dominant genes having increasing and decreasing effects on these traits are irregularly distributed in parents or they have an asymmetric distribution. As the ratio of  $H_2/4H_1 = 0.25$  for CHF, therefore dominant genes having increasing and decreasing effects on CHF are regularly distributed in parents or they have a symmetric distribution. The variation observed between genotypes for the characters studied revealed that selection may be effective for the improvement of yield under drought condition using physiological traits as a correlated response, although selection efficiency is related to the magnitude of heritability (Farshadfar et al., 2001). High broad-sense and narrow-sense heritability (Table 5) were observed for Ys, WUE, LWP, ETE, CHF and RWL, implying that the role of additive variance was higher than dominant variance. Solomon and Labuschagne (2004) reported that a high estimate of heritability (> 0.5; Stanfield, 2002) for all the traits studied may result from the involvement of a few major genes in the control of inheritance of these traits.

#### Graphical analysis

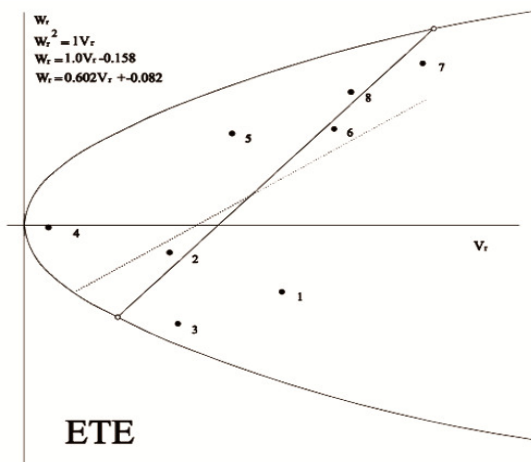
Hayman graphical analysis was conducted to evaluate the genetic relationships among parents. Graphic analysis of the



**Fig 4.** Regression line and dispersion of parents around origin for WUE under stress conditions



**Fig 5.** Regression line and dispersion of parents around origin for LWP under stress conditions



**Fig 6.** Regression line and dispersion of parents around origin for ETE under stress conditions

mode of inheritance varied from additive to overdominance for the characters investigated. The position of the regression line on a  $V_r$ - $W_r$  graph provides information about the average degree of dominance (Singh and Narayanan, 1993). In Hayman's approach of diallel analysis, a graph is drawn with the help of variances of arrays ( $V_r$ ) and covariances between parents and their offspring ( $W_r$ ). This graph is known as the  $V_r$ - $W_r$  graph. The position of a regression line on a  $V_r$ - $W_r$  graph provides information about the average degree of dominance. The regression line for  $Y_s$ , WUE, LWP, ETE and RWL (Figs. 2, 4, 5, 6, 8) passes below the origin cutting the  $W_r$ -axis in the negative region (intercept =  $a < 0$  (negative)) or  $D$  (additive variance)  $< H_1$  (dominant variance), indicating the presence of overdominance. When the regression line for CHF passes through the origin, it indicates the presence of complete dominance ( $D = H_1$ ). The dispersion of parents around the regression line for  $Y_s$  (Fig. 2) showed that parents 1, 4, 6, 7 and 8 are close to the origin of the coordinate, and accordingly have more than 75% dominant genes, while parents 2, 3 and 5 have mostly recessive genes. Most of the dominant genes for WUE (Fig. 4) were distributed in parents 1, 3 and 4, while recessive genes were mostly distributed in parents 2, 5, 6, 7 and 8. The distribution of genes in parent 6 is symmetric. Parents 1, 2, 3, 4, 5, 6 and 7 have more than 75% recessive genes for LWP (Fig. 5), while recessive and dominant genes are equally distributed in parent 8. Almost 50% of the dominant genes are distributed in parents 1, 2, 3 and 4 for ETE (Fig. 6), while 50% of the recessive genes are located in parents 6, 7 and 8; recessive and dominant genes are equally distributed in parent 5. The dispersion of parents around the regression line for CHF (Fig. 7) reveals that parents 2, 3 and 5 are close to the origin of the coordinate, and accordingly have  $> 75\%$  of dominant genes while parents 1, 4, 6 and 7 have 50-75% of dominant genes, while parent 8 is far from the origin and therefore has  $< 25\%$  of dominant genes. The dispersion of parents around the regression line for RWL showed that parents 2, 4 and 5 are close to the origin of the coordinate, and accordingly have  $> 75\%$  of dominant genes, parents 1 and 8 have 50-75% of dominant genes, while parents 6, 5 and 7 are far from the origin, therefore they have  $< 25\%$  of dominant genes.

#### Parameters under irrigated condition

Genotypes, including parents and their hybrids, varied significantly for yield under the irrigated condition ( $Y_p$ ) (Table 1) indicating the possible selection of genotypes with high grain yield under this condition.

Combining ability analysis showed highly significant differences for  $Y_p$  between the genotypes (Table 2). The best general combiner with positive effects for improvement of  $Y_p$  was Plainsman (Table 3) and the best specific combination (Table 4) with heterobeltiosis over the best parents for improvement of  $Y_p$  was the cross 3x6 (Shakha x Kobomugi) indicating that parents of this cross are genetically diverse. Hence, the best combination for improvement of high grain yield under irrigated conditions was cross 3x6. ANOVA (Table 5) revealed that "a" and "b" components were significant for  $Y_p$ . Therefore, the inheritance of  $Y_p$  was controlled by a dominant and additive type of gene action. A simultaneous exploitation of both additive and dominant variance for improvement of  $Y_p$  is achieved by reciprocal recurrent selection (Chahal and Gosal, 2002). Since "b<sub>3</sub>" was significant for  $Y_p$ , therefore the interallelic interaction (additive x additive, additive x dominant and dominant x dominant) was also involved in their

**Table 5.** Hayman analysis of variance and genetic properties of significant agronomic and physiological traits under water stress condition.

S.O.V	df	Mean squares							
		Yp	Ys	STI	WUE	LWP	ETE	CHF	RWL
Rep	2	24.8**	0.467ns	0.03ns	0.3**	6.4ns	0.3ns	0.009ns	0.008ns
a	7	10.2**	2.833**	0.06**	0.1**	10.4ns	0.4**	0.029**	0.014*
b	28	23.8**	1.614**	0.09**	0.3**	13.2**	0.7**	0.004ns	0.007ns
b <sub>1</sub>	1	88.5**	0.356ns	0.26**	1**	1.9ns	3.2**	0.000ns	0.009ns
b <sub>2</sub>	7	6*	1.615*	0.05*	0.1*	4.8ns	0.2ns	0.014**	0.014**
b <sub>3</sub>	20	26.8**	1.677**	0.09**	0.3**	16.6**	0.7**	0.000ns	0.005ns
Error	70	2.2	0.709	0.02	0.01	5.2	0.1	0.003	0.004
(H <sub>1</sub> /D) <sup>0.5</sup>	-	3.03*	1.59*	2.57*	2.9*	1.69ns	2.72*	0.96*	1.95*
(H <sub>2</sub> /4H <sub>1</sub> )	-	0.201*	0.185*	0.241*	0.197ns	0.45*	0.161*	0.252*	0.078ns
(H <sup>2</sup> b)	-	0.801*	0.762*	0.705*	0.812*	0.491*	0.74*	0.86*	0.648*
(H <sup>2</sup> n)	-	0.917*	0.69*	0.832*	0.916*	0.68*	0.859*	0.6*	0.566*

(H<sub>1</sub>/D)<sup>0.5</sup>=Average degree of dominance, H<sup>2</sup>b)= Broad-sense heritability, (H<sup>2</sup>n)= Narrow-sense heritability, (H<sub>2</sub>/4H<sub>1</sub>)= Proportion of dominance and recessive genes,

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

inheritance. The ratio of  $\sqrt{H_1/D}$  is > 1 for Yp thus overdominance is involved in the genetics of this character. The existence of overdominance suggests the superiority of heterozygotes over homozygotes and thus warrants the development of hybrid varieties. The parameter  $H_2/4H_1$  was  $\neq$  0.25 for Yp. Accordingly, dominant genes having increasing and decreasing effects on this trait and are irregularly distributed in parents or they have asymmetric distributions. High broad-sense and narrow-sense heritability (Table 5) was observed for Yp. Therefore, the role of additive variance was higher than dominant variance. The regression line for Yp (Fig. 1) passes below the origin cutting the Wr-axis in the negative region (intercept = a < 0 (negative)) or D (additive variance) < H<sub>1</sub> (dominant variance), indicating the presence of overdominance. Dispersion of parents around the regression line for Yp (Fig. 1) shows that parents 1, 3 and 4 are close to the origin of the coordinate, and accordingly have more than 75% of dominant genes while parents 2, 5, 6, 7 and 8 are far from the origin, therefore they have most of the recessive genes.

#### Parameter under both irrigated and rainfed conditions

In order to identify drought-tolerant genotypes in the field, several selection criteria have been proposed based on grain yield under stressed and non-stressed conditions. These indices are either based on drought resistance or the susceptibility of genotypes to drought (Talebi et al., 2009; Geravandi et al., 2011). Fernandes (1992) introduced a new advanced index named the stress tolerance index (STI), which can be used to identify genotypes that produce high yield under both stress and non-stress conditions. Genotypes can be categorized into four groups based on their performance in stressed and non-stressed environments: genotypes which express uniform superiority in both environments (Group A); genotypes which perform favourably only in non-stressed environments (Group B); genotypes which yield relatively well only in stressed environments (Group C) and genotypes which perform poorly in both environments (Group D). The optimal selection criteria should distinguish group A from the other three groups (Fernandez, 1992). STI is able to discriminate group A cultivars from the other groups, hence it is a better predictor of Yp and Ys than the other indices (Farshadfar and Sutka, 2002; Golabadi et al., 2006; Sio-Se Mardeh et al., 2006; Talebi et al., 2009; Shirinzadeh et al., 2010; Nouri et

al., 2011). That is why it was selected, measured and entered into the genetic analysis. Genotypes including parents and their hybrids varied significantly for yield under STI (Table 1), indicating the possible discrimination of drought-tolerant parents and F<sub>1</sub> hybrids with high grain yield under both rainfed and irrigated conditions. Combining ability analysis showed highly significant differences between the genotypes for STI (Table 2). The best general combiner with a positive effect for improvement of STI was Plainsman (Table 3) and the best specific combination (Table 4) with heterobeltiosis over the best parents for improvement of STI was the cross 3x6 indicating that parents of this cross are genetically diverse. Hence, the best combination for improvement of drought-tolerant genotypes with high grain yield under both stressed and non-stressed conditions was the cross 3x6. ANOVA (Table 5) revealed that "a" and "b" were significant for STI. Therefore, the inheritance of STI was controlled by dominant and additive type of gene action, which was also reported by Saba et al. (2001). A simultaneous exploitation of both additive and dominant variance for improvement of STI is achieved by reciprocal recurrent selection (Chahal and Gosal, 2002). As "b<sub>3</sub>" was significant for STI, the interallelic interaction (additive x additive, additive x dominant and dominant x dominant) was also involved in STI inheritance.

When the  $\sqrt{H_1/D}$  ratio is > 1 for STI, overdominance is involved in the genetics of these parameters. The existence of overdominance suggests the superiority of heterozygotes over homozygotes and thus warrants the developments of hybrid varieties. The parameter  $H_2/4H_1$  was  $\neq$  0.25 for STI. Accordingly, dominant genes having increasing and decreasing effects on these traits and are irregularly distributed in parents or they have an asymmetric distribution. High broad-sense and narrow-sense heritability (Table 5) was observed for STI. Therefore, the role of additive variance was higher than that of dominant variance. Genetic advance is directly related to the magnitude of narrow-sense heritability (Kearsey and Pooni, 2004). Thus, it seems that selection for drought resistance based on STI will be fruitful under drought-prone conditions (Saba et al., 2001). The regression line for STI (Fig. 3) passes below the origin cutting the Wr-axis in the negative region (intercept = a < 0 (negative)) or D (additive variance) < H<sub>1</sub> (dominant variance) indicating the presence of overdominance. The dispersion of parents around the regression line for STI (Fig. 3) indicates that parents 1 and 4 have most dominant genes: the proportion of recessive and dominant genes in parents 3



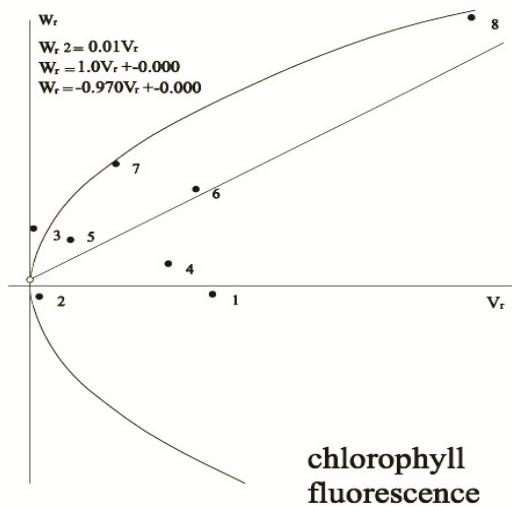


Fig 7. Regression line and dispersion of parents around origin for CHF under stress conditions

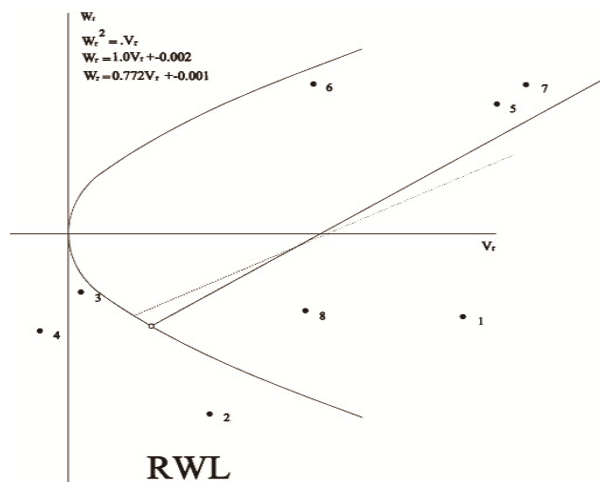


Fig 8. Regression line and dispersion of parents around origin for CHF under stress conditions

and 8 is almost equal while parents 2, 5, 6 and 7 have most of the recessive genes.

## Materials and methods

### Plant materials and experimental design

Eight varieties of wheat (*Triticum aestivum* L.), namely Plainsman, Chinese Spring, Shakha, Saberbeg, Karckia, Kobomugi, Regina and Capelle Desprez were crossed in a half diallel design at the Agricultural College of Razi University, Kermanshah, Iran (47° 20' N, 34° 20' E and 1351.6 m above sea level) during 2009 and 2010. Seeds of 28 F<sub>1</sub> along with their self-pollinated parents were sown in the field in November 2010 in a randomized complete block design with three replications under irrigated and rainfed conditions. Single seeds were sown in 2.5 m rows and at 15 × 30 cm inter-plant and inter-row distances, respectively.

### Parameters measured

At harvest time, following the measurement of yield potential (Yp) in the irrigated condition and stress yield (Ys) in the rainfed condition, the following physiological characters were recorded from the rainfed condition.

#### 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 24 h and reweighed to obtain turgor weight (TW). Thereafter the leaf segments were oven dried for 48 h at 72°C and reweighed to obtain 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)

The FW of 5 flag leaves was measured. The leaves were then wilted at 35°C for 5 h and reweighed (W5H). Then the samples were oven dried for 70°C and re-weighed to yield DW. RWL was calculated by the following formula (Farshadfar et al., 2001):

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

#### Chlorophyll fluorescence (CHF)

5 flag leaves were selected from each line in each replication and the quantum yield was recorded after dark adaptation using a MINI-PAM instrument according to the following equation (Gently et al., 1989):

$$\text{Quantum yield} = Fv/Fm$$

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

#### Leaf water potential (LWP)

LWP was measured on flag leaves of each replication using a pressure chamber (Model PMS Instrument Co.)

#### Water Use Efficiency (WUE)

To measure WUE, the genotypes were compared in a completely randomized design (CRD) with three replications. Three seeds from each line were sown in a 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 matter, TWU = total water used and GY = grain yield.

### Statistical analysis

Using yield under stress ( $Y_s$ ), yield under irrigated conditions and the mean of all genotypes under irrigated conditions ( $\bar{Y}_p$ ), stress tolerance index was calculated by the formula suggested by Fernandez (1992):

$$\text{Stress tolerance index} = \text{STI} = \frac{Y_p \times Y_s}{\bar{Y}_p^2}$$

Statistical analysis was performed according to Griffing (1956a, 1956b) and Hayman (1954a, 1954b) methods for diallel analysis using MSTAT-C, SPSS and Dial 98 software.

### Conclusion

In general, significant genetic variation was observed for the agronomic and physiological traits investigated in this study under rainfed and irrigated conditions. Analysis of combining ability indicated that the best general combiners with positive effects for improvement of  $Y_p$ ,  $Y_s$ , STI, WUE, LWP and ETE was Plainsman, while the best specific combination with heterobeltiosis over the best parents for improvement of drought-tolerant genotypes with high grain yield under rainfed and irrigated conditions was the cross 3×6 (Shakha × Kobomugi). Genetic analysis indicated the involvement of additive and dominant types of gene action in the inheritance of  $Y_p$ , STI,  $Y_s$ , WUE, ETE, CHF and RWL. Thus, a simultaneous exploitation of both additive and dominant variance to improve these parameters is achieved by reciprocal recurrent selection or a method such as diallel selective mating. High narrow-sense heritability was observed for  $Y_p$ , STI,  $Y_s$ , WUE, LWP, ETE, CHF and RWL, hence the role of additive variance was higher than dominant variance that is likely to involve a few major genes in the genetic control of these traits. STI is a suitable yield-based drought resistance index that can be employed in plant breeding programs because of its high narrow-sense heritability and the inherent ability of selecting high-yielding genotypes in either stressed or non-stressed conditions.

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