Biological Forum – An International Journal **7**(2): 722-733(2015)

ISSN No. (Print): 0975-1130
ISSN No. (Online): 2249-3239

Genetic analysis of some physiological traits in wheat by generations mean analysis under normal and water deficit conditions

Ali Akbar Asadi*, Mostafa Valizadeh**, Seyed Abolghasem Mohammadi** and Manochehr Khodarahmi***
**Ph.D. Student of Plant Breeding, Faculty of Agriculture, University of Tabriz, Tabriz, Iran*
***Department of Plant Breeding and Biotechnology, Faculty of Agriculture, University of Tabriz, Tabriz, Iran*
****Seed and Plant Improvement Institute, Karaj, Iran*

(Corresponding author: Ali Akbar Asadi)

(Received 02 September, 2015, Accepted 15 October, 2015)
(Published by Research Trend, Website: www.researchtrend.net)

ABSTRACT: The seven wheat populations (Gasspard and DN11 as parents line and their F1, F2, F3, BC1 and BC2) were grown under normal and water deficit conditions at the farm for two years to study the genetic background of wheat in normal and water deficit conditions. Significant differences were found among the generation means for most of the physiological traits in two conditions which revealed the presence of genetic diversity between selected parents. Generation mean analysis indicated that the mode of gene effects implicated in the control of the majority of traits was depending upon water regime. This research results revealed the implication of epistasis in inheritance of physiological traits under normal and water deficit conditions. Additive effect was significant for most of the traits except of F_v, F_v/F_m and F_v/F_0 and F_v/F_0 in normal condition. Relative water content, F_m and F_v revealed great importance of additive gene effects in genetic control of physiological traits in two conditions. Dominance effect was significant for all traits in normal condition but in water deficit condition at flag leaf area, relative water content, performance index, F_v/F_m and F_v/F_0 was not significant. These results indicated the importance of gene effects in inheritance of these traits. The results indicated that epistasis was significant components of the genetic architecture of studied traits in two conditions. Hence, detection, estimation and consideration of epistasis components are important in formulating of breeding strategies. Moderate to high broad sence heritability and low to moderate narrow sense heritability for most of traits were observed which indicates that there is appreciable amount of heritable variation, especially in relative water content, F_0, F_m, F_v, F_v/F_m and F_v/F_0 in two conditions. The considerable amount of heritable variation for important physiological traits imply the possibility of developing suitable lines for physiologic characters and the traits related to drought tolerance.

Key words: Generation mean analysis, heritability, water deficit, wheat

INTRODUCTION

Biotic and abiotic stresses cause changes in normal physiological functions of all plants, including economically important cereals as well. All stresses reduce biosynthetic capacity of plants and might cause some destructive damages on the plants (Lichtenhaler 1996). Drought is a significant limiting factor for agricultural productivity and generally inhibits plant growth through reduced water absorption and nutrient uptake. Decreased water availability generally results in reduced growth and final yield in crop plants. Plant drought tolerance is a highly complex trait that involves multiple genetic, physiological and biochemical mechanisms (Baik and Ullrich 2008 and Erdei *et al.* 2002).

While breeding programs in self pollination crops rely on selection for yield in advanced generations, alternatives to direct selection for yield have been adopted, as suggested by many researchers (Austin 1993). Indeed, the lake of identification of appropriate morphophysiological traits has been one major factor preventing improvement of yield in water limited environments, as well as the reason why plant breeders have not adapted more analytical approaches to selection. Moreover, any desirable physiological traits should be simple, rapid and more economical than yield to assess. Therefore such parameters should be easy to evaluate in large numbers of plants (e. g. in early generation) in a relatively short time and preferably in the target environment. Drought associated with high temperature and irradiance are the stresses which at present most limit the cereal yield under Mediterranean conditions because they usually occur together during the reproductive stages of the crops (Araus *et al.* 1998). Physiological approaches would be the most attractive way to develop new varieties (Araus *et al.* 2008). To be useful in breeding, a physiological character should be simple, rapid and more economical to assess than yield and stress resistance in order to evaluate large number of plants in a relatively short period of time (Austin 1993).

The experimental evidence indicates that there is a large inter and intra-specific genetic variability in photosynthesis rate (Nasyrov 1978; Isebrands *et al.* 1988; Kelly 1988 and Rocher *et al.* 1989), but attempts to use this variability in breeding programs have generally not been satisfactory (Austin 1988 and Nelson 1988).

Osmotic regulation will help to cell development and plant growth in water stress. It is defined that decrease of relative water content close stomata and also after blocking of stomata will reduce photosynthesis rate (Cornic 2000). It is reported that high RWC is a resistant mechanism to drought, and that high RWC is the result of more osmotic regulation or less elasticity of tissue cell wall (Ritchie *et al.* 1990). RWC is closely related with cell volume, it may more closely reflect the balance between water supply to the leaf and transpiration rate (Schonfeld *et al.* 1988). This influences the ability of the plant to recover from stress and consequently affects yield and yield stability (Lilley and ludlow 1996). Leaf relative water content has also been proposed as a more important indicator of water status than other water potential parameters under drought stress conditions (Dhanda and Sethi 2002).

chlorophyll content is one of the major chloroplast components for photosynthesis and has a positive relationship with photosynthetic rate (Guo and Li 1996). Although there is an argument about whether a higher CC (i.e. stay green trait) contributes to yield under drought conditions or not (Blum 1998), many studies indicated that stay-green is associated with improved yield and transpiration efficiency under water-limited conditions in wheat (Benbella and Paulsen 1998).

Photosynthesis is an essential process to maintain crop growth and development and it is well known that photosynthetic systems in higher plants are most sensitive to drought stress (Falk *et al.* 1996). The effect of water stress on photosynthesis has been a subject of controversy among plant physiologists for many years, and conflicting results have been reported depending on the plant material, and the experimental procedures used for investigations (Cornic and Massacci 1996). Several researches indicated that chlorophyll fluorescence parameters were strongly correlated with whole-plant mortality in response to environmental stresses (Greaves and Wilson 1987; Hakam *et al.* 2000; Percival and Sheriffs 2002; Baker and Rosenqvist 2004 and Valladares *et al.* 2005) and these parameters can be used as reliable indicators to evaluate the energetic/metabolic imbalance of photosynthesis and yield performance across genotypes under water deficit condition (Araus *et al.* 1998 and Li *et al.* 2006). Measurements of different physiological processes for plants responses to drought are important information on the various strategies of the plant intended to remove or to reduce the harmful effects of water deficit in soil or plant tissues. In the field indices of drought tolerance, the preference was given to the relations between the plant yield obtained under conditions of drought and that under conditions of optimum soil moistening (Dencic *et al.* 2000).

In theory, the biological yield of a crop can be improved through an increase in photosynthetic assimilates, a decline of respiration, and a desirable distribution of photosynthetic products. As photosynthesis is affected by physiological, biochemical and morphological factors and is closely dependent on environment, it is necessary to effectively combine these factors in order to increase biological or economical yield. Chlorophyll fluorescence is a fast, nondestructive and relatively simple technique for detecting the energetic and metabolic balance of photosynthesis because it uses chlorophyll as an internal fluorescence probe for the research on photosynthesis, and the fast induction kinetics of chlorophyll fluorescence is closely related to the photochemical reactions of photosynthesis (Moffatt *et al.* 1990; Krause and Weise, 1991). Being rapid, extremely sensitive and nondestructive, measurements of chlorophyll fluorescence from photosystem II (PSII) has become a useful method for the determination of mechanisms of photosynthesis and to study the effects of various environmental conditions on photosynthetic reactions (Bolhar-Nordenkampf *et al.* 1989, Krause and Weise 1991, Demmig-Adams and Adams 1992). Measurements of chlorophyll fluorescence have often been also proposed as a useful tool in screening for yield or stress tolerance in crops (Havaux and Lannoye 1985; Pastore *et al.* 1989; Flagella *et al.* 1995), measurements of chlorophyll fluorescence in the field to determine the actual response of the photosynthetic apparatus in different genotypes of crops under natural conditions have been limited in number (Bilger *et al.* 1995; Earl and Tollenaar 1999), and also have not been used in genetics and breeding programs. however Zhang *et al.* (2000) reported that the additive gene effect for Fm and non additive gene effect for $\mathbf{F_0}$ and Fv/Fm were found in sugarcane; they showed that parameters of chlorophyll florescence had large broad since heritability's which indicated that these parameters could be selected in sexual generation, that is, in the segregating generation of breeding program. Moreover, Shahbazy *et al.* (2009) indicated that dominance effect were higher than additive effect in chlorophyll fluorescence parameters in wheat and these traits are controlled with over dominance effects thus these traits had great broad sense and small narrow sense heritability. Breeding for specific, sub-optimal environments involves a deeper understanding of yield determining process.

Generally, different strategies have been proposed for the selection of relative drought tolerance and resistance, so some researchers have proposed selection under non-stress conditions (Richards 1996; Rajaram and Van Ginkle 2001), others have suggested selection in the target stress conditions (Ceccarelli and Grando 1991; Rathjen 1994) while, several of them have chosen the mid-way and believe in selection under both non-stress and stress conditions (Fischer and Maurer, 1978; Clarke *et al.* 1992; Fernandez, 1992; Byrne *et al.* 1995). Dencic *et al.* (2000) reported that many morphological and physiological characteristics were affected by drought stress. 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). 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, dominance and non-allelic interaction effects (Farshadfar *et al.* 2008; Mohammadi *et al.* 2010 and Nouri *et al.* 2011).

To determine the genetic parameters, one of the best methods is the generation mean analysis (Kearsey and pooni 1998 and Singh and Singh 1992). Generation mean analysis provides information on the relative importance of average effects of the genes (additive effects), dominance deviations and effects due to non allelic genetic interactions, in determining genotypic values of the individuals and consequently, mean genotypic values of families and generations (Viana 2000). This technique helps to understand the performance of selected parents and the potential of the resulting population to employ either for heterosis exploitation or pedigree selection (Singh and Chaudahry 1985).

Besides gene effects, breeders would also like to know how much of the variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment and interaction between genotype and environment. The aims of this study were genetic assessment of physiological traits and determination of the effective breeding strategy for genetic improvement of these traits in normal and water deficit conditions.

MATERIAL S AND METHODS

This study was carried out at the experimental farm in Science and Technology Research Institute (NSTRI) Agriculture, Medicine and Industry Research School, Karaj. Two wheat cultivars, Ggasspard (drought susceptible) and DN11 (drought tolerant) were chosen for this study. In 2011/2013 season, crosses were made among the parents to produce F1, BC1 (P1×F1), BC2 (P2×F1), F2 and F3 generations. In the 2013/2014 and 2014/2015 seasons, the seven populations were sown in two experiments in two conditions (normal and water deficit conditions) in a randomized complete blocks design (RCBD) with three replications. Each experiment replication consisted of 60 grains in 4 row for each of the parents, 45 grains in 3 rows for F1, 60 grains in 4 rows of each backcross, 60 grains in 4 rows for the F2 and 15 grains in 1 row (50 row or family) for F3 populations. Rows were 1.5 m long and 60 cm apart and 10 cm between plants. Recommended cultural practices for wheat production were adopted in all the growing seasons. Normal condition experiment were irrigated two times after anthesis, while water deficit condition experiment received no water. Fertilizer was applied at 100 kg ha^{-1} N. Data were recorded on 10 competitive individual plants for non-segregate generations (P1, P2 and F1) and 30 plants for BC1 and BC2, 40 plants for F2 and 5 plants for each F3 families in each replication for two conditions and two years.

Studied traits were as follow:

Flag leaf area (FLA): From the fully developed flag leaf of selected mother shoots, the maximum length and width was measured in millimeters (14 days after anthesis). FLA was calculated using the following function according to Muller (1991).

$$FLA = \text{Flag leaf length} \times \text{Flag leaf width} \times 0.74$$

Relative water content (RWC): Relative water content was determined according to Turner (1986) where fresh leaves were collected from each genotype and each replication 15 days after anthesis and weighted immediately to record fresh weight (FW). Then they were placed in distilled water for 24 h and weighted again to record their turgid weight (TW). Finally, they were subjected to oven drying at 72°C for 24h to record their dry weight (DW). The RWC was calculated using the following equation:

$$RWC = ((FW - DW)/(TW - DW)) \times 100$$

Chlorophyll content (CC): The CC in the flag leaf was determined by portable chlorophyll meter (CL-01, Hansatech, Kings Lynn, UK). Flag leaves of each genotype grown in water deficit and normal conditions were measured 15 days after anthesis stage and one measurement in the middle of the flag leaf were made randomly for each plant.

Stomatal conductance (SC): SC (mmol $m^{-2}s^{-1}$) was measured by the Leaf Porometer (SC-1 Decagon Devices, Pullman, WA) 20 days after anthesis stage.

Chlorophyll fluorescence: Chlorophyll fluorescence was measured using a portable fluorescence spectrometer Handy PEA (Hansatech Instruments, Norfolk, UK) 22 days after anthesis stage. Prior to measurements the leaves were dark adapted for 5 min in order to relax all energy depend fluorescence quenching. Fluorescence was induced by leaf radiation 650 µmol m^{-2} s^{-1} for 5 second. The measurements were made immediately after completing the measurements of gaseous exchange parameters. Fluorescence values recorded included: PI, performance index or vitality index; F_0, minimal fluorescence, a measure of the stability of the light harvesting complex; F_m maximal fluorescence value; F_V, variable fluorescence = F_M- F_0; F_V/F_M, represents the maximum quantum yield of PS II, which in turn is highly correlated with the quantum yield of net photosynthesis and F_V/ F_0, estimates the maximum primary yield of photochemistry of photosystem II (PS II). The photochemistry efficiency of PS II was determinate based on Fv/Fm value (the ratio of variable to the maximal fluorescence of dark-adapted leaves).

Statistical and genetic analysis

Analysis of variance and mean comparison were performed using SAS software. Depending on the characters, six or seven generations were used to estimate the genetic parameters (Mather and Jinks 1982). For the generation mean analysis, at first, additive-dominance model was conducted using weighted least squares. The joint scaling test was carried out to verify the goodness of fit of the model (Kearsey and Pooni 2004).

The analysis of the values of A, B, C and D should be equal zero within the limits of this standard error. The significance of any one of these scales are taken to indicate proceeded to compute the interaction types involved the six parameters genetic model of Hayman (1958). The significance of the genetic components were tested using "t" test Where ± t = effect / (variance effect) 1/2.

$A = 2BC_1 - P_1 - F_1$
$B = 2BC_2 - P_2 - F_1$
$C= 4F_2 - 2F_1 - P_1 - P_2$
$D = 2F_2 - BC_1 - BC_2$ (6 generations)
$D = 4F3 - 2F2 - P1 - P2$ (7 generations)

$VA = 4V(BC_1) + V(P_1) + V(F_1)$
$VB = 4V(BC_2) + V(P_2) + V(F_1)$
$VC = 16\,V(F_2) + 4V(F_1) + V(P_1) + V(P_2)$
$VD = 4\,V(F_2) + V(BC_1) + V(BC_2)$
$VC = 16\,V(F_3) + 4V(F_2) + V(P_1) + V(P_2)$

Generation mean analysis was done using the Mather and Jinks model (1982) as follows:

$Y = m + \alpha[d] + \beta[h] + \alpha_2[i] + 2\alpha\beta[j] + \beta^2[l]$

where y, m, d, h, i, l and j represent mean of generation, mean of all generation, sum of additive effects, sum of dominance effect, sum of additive × additive (complementary), sum of additive × dominant (duplicate) and sum of dominant × dominant interactions, respectively.

The terms α, β, α^2, 2 α β and β^2 represent coefficients of genetic parameters. A weighted least square analysis was performed on the generation means. Six parameters including m, d, h, i, j and l were estimated after testing adequacy three parameter models through joint scaling test. The genetic parameters [m, (d), (h), (i), (j), and (l)] were tested for significance using an unpaired t-test. Further models of increasing complexity were fitted if the chi-square value was significant. The best fit model was the one which had significant estimates of all parameters along with non significant chi-square value and high adjusted R^2.

Furthermore homogeneity of variances of non-segregation generations was tested by using Bartlett's test (Bartlett 1937) and when the variances were heterogeneous, the environmental variance σ^2_e was replaced by an adequate number of separate parameters and pooled to produce a single environmental variance. Additive, dominance, environmental variance and additive-dominance covariance components were estimated using the weighted least square test with the observed variance of the six or seven basic generations being used as the initial weights ($df/(2\times S^2)^2$) until the chi-squared test value reached a minimum (Lynch and Walsh 1998).

Environmental variance (σ^2_e), genetic variance (σ^2_G) and phenotypic variance (σ^2_P) were estimated as described by Mather and Jinks (1982) using the following equations:

$\sigma^2e = 0.25\,(\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})$
$\sigma^2_G = \sigma^2_A + \sigma^2_D$
$\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2e$

Broad-sense (h^2_b) and narrow-sense (h^2_n) heritability were estimated using the following formulae:

$h^2_b = \sigma^2_G / \sigma^2_P$
$h^2_n = \sigma^2_A / \sigma_{2P}$

Degree of dominance was calculated as below, based on the additive (A) and dominance (D) variance components estimated from the within-generation variances.

Degree of dominance = $\sqrt{}\,(V_A/V_D)$

Dominance deviation was estimated using following equation.

Dominance deviation=$V_{AD}/\sqrt{}\,(V_A+V_D)$

RESULT AND DISCUSSION

A. Analysis of variances

Analysis of variances and means comparisons for studied traits in different generations and two conditions are shown in Table 1. Analysis of variance showed significant differences among generations except of F_v/F_m and F_v/F_0 in water deficit condition.

Therefore, the significant difference between generations makes possible generation mean analysis and surveys of their inheritance. Water deficit condition reduced FLA, relative water content and CC but increased performance index, F_m, F_V, F_V/F_m and F_V/F_0 in many of the generations. For SC water deficit reduced in parents and F_1 but increased in segregate generations.

Table 1: Analysis of variance and means comparisons for physiological traits of wheat generations in normal and water deficit conditions.

	FLA		**RWC**		**CC**		**SC**		**PI**	
	NC	**WDC**	**NC**	**WDC**	**NC**	**WDC**	**NC**	**WDC**	**NC**	**WDC**
Year	23.89 **	2.1 ns	0.29 ns	0.9 ns	0.11 ns	0.17 ns	0.76 ns	3.13 ns	19.28 *	3.03 ns
Year (block)	0.4719	1.66	230.64	104.84	12.05	10.77	19.81	16.28	0.065	6.78
Trait	3.62 **	4.66 **	3.22 **	14.09 **	8.88**	14.96 **	4.95 **	32.28 **	12.66**	7.07 **
Trait* year	1.27 ns	4.61 **	4.95 **	14.7 **	3.08**	6.31 **	3.58 **	4.49 **	1.59 ns	2.18 ns
CV%	27.81%	28.15%	8.16%	8.94%	23.15%	26.06%	31.26%	34.49%	38.27%	30.46%
Means comparison										
DN11	28.2367 a	24.21 b	0.7898 d	0.7377 e	34.589 cd	31.903 c	38.52 c	56.488 b	3.1396 b	2.9587 c
Gasspard	26.47 b	22.23 c	0.835 c	0.8404 a	41.577 a	32.688 c	31.304 d	43.848 c	4.4918 a	5.197 a
F1	28.83 a	25.96 a	0.8441 bc	.8163 bc	36.87 b	36.258 b	42.706 c	55.493 b	2.5385 c	4.1713 b
F2	26.11 b	23.5 bc	0.8448 bc	0.8016 cd	34.499 cd	35.43 b	59.08 b	52.903.ab	3.013 b	4.3173 b
F3	26.05 b	23.19 b	.8328 c	0.8003 cd	35.367 bc	32.228 c	--------	------------	---------	----------
BC1	25.94 b	24.17 b	0.858 ab	0.7922 d	32.719 d	37.066 b	67.431 a	62.553 a	3.1061 b	4.205 b
BC2	25.96 b	26.55 a	0.865 a	0.8232 b	37.056 b	40.656 a	70.438 a	60.75 a	3.1019 b	4.4099 b

	F_0		**F_m**		**F_v**		**F_V/F_m**		**F_V/F_0**	
	NC	**WDC**	**NC**	**WDC**	**NC**	**WDC**	**NC**	**WDC**	**NC**	**WDC**
Year	37.12 *	8.2 ns	12.09 ns	6.91 ns	8.34 ns	5.71 ns	0.56 ns	0.12 ns	19.28 *	0.49 ns
Year (block)	1.75	2.09	7.12	1.93	8.12	1.76	10.07	0.94	8.25	1.18
Trait	3.43 *	2.29 *	13.39 **	2.24*	13.14 **	1.87 ns	8.49 **	1.45 ns	7.17 **	0.35 ns
Trait* year	1.06 ns	0.67 ns	4.57**	0.39 ns	4.7 *	0.38 ns	2.8 *	0.63 ns	2.76 *	0.36 ns
CV%	9.53%	10.57%	12.96%	15.3%	16.32%	18.68%	4.51%	4.38%	17.55%	19.6
Means comparison										
DN11	6091.5 a	6085.5 a	26483.9 a	28975.4 a	20392.4 a	22906.9 a	0.7668 a	0.7895 a	3.3588 a	3.778 a
Gasspard	5731.8 cd	5627.2 b	2521 b	26801.8 b	19479.2 ab	21174.6 b	0.7711 a	.78862 a	3.3948 a	3.7582 a
F1	5968 ab	5659 b	24539.1 b	26777.3 b	18571.1bc	21118.3 b	0.7536 b	0.7866 a	3.1197 b	3.7332 a
F2	5732.8 cd	5674 b	23171.5 c	26222 b	17438.8 d	20548 b	0.7474 bc	0.7777 a	3.0659 b	3.667 a
F3	----------	---------	----------	-----------	--------------	---------	------------	----------	-------------	------------
BC1	5887.2 bc	5727.1 b	24180.3 b	27116.1 b	18293.2 dc	21388.9 b	0.752 b	0.7851 a	3.1234 b	3.7645 a
BC2	5675.7 d	5521.7 b	21974.2 d	25730.4 b	16298.5 e	20208.7 b	0.7378 c	0.7803 a	2.8968 c	3.6959 a

NC and WDC: normal condition and water deficit condition, respectively

ns, * and **: non significant, Significant at 5% and 1% levels of probability, respectively.

FLA, RWC, CC and SC: Flag leaf area, Relative water content, Chlorophyll conductance and Stomatal conductance

PI, F_0, F_m, F_V, F_V/F_M and F_V/F_0: Performance index, Minimal fluorescence, maximal fluorescence value, variable fluorescence, represents the maximum quantum yield of PS II and estimates the maximum primary yield of photochemistry of photosystem II (PS II), respectively

B. Scaling tests

Scaling tests were not significant for FLA, RWC, F_0, F_m, F_v and F_v/F_m suggesting the lack of epistasis for the above mentioned traits at water deficit condition and were significant for other traits (Table 2) but in normal condition they were significant for all of the traits. Although scaling test failed to detect non-allelic interaction for some of the traits in water deficit condition, the inadequacy of additive-dominance model suggests the presence of non-allelic interactions.

C. Models and genetic effects

The results of the generations mean analysis showed that the additive dominance model was not enough to justify all traits. The results of genetic effects estimates, R^2, adjusted R^2 and chi-square (X^2) statistics for the selected models are shown in Table 3. Except of FLA in water deficit condition, all models had non-significant σ^2 statistics, indicating that the selected models are fitted the data obtained for different characters. However, some of the genetic effects were not significant in the selected models, probably due to small sample size. A negative estimate of dominance in some cases might be due to epistasic gene action in the cross combinations. Significancy of (j) for some of traits revealed that selection through selfing is not effective for improving those traits (Farshadfar *et al.* 2001; Sharifi 2005), because among the digenic interactions, additive × dominance type is more fixable and more useful for plant breeders. In addition, the opposite signs of [h] and [l] suggested duplicate type of epistasis (Sunil Kumar 2005). V_{AD} is an indicator of correlation between V_A and V_D over all loci. If V_{AD} is zero it means that dominance genes are in the parent with high performance, while negative V_{AD} exhibits that dominance genes are in the low performance parent.

Table 2: Results of scaling tests A, B, C and D for the studied traits under two conditions.

		A	B	C	D
FLA	**NC**	-5.7369*±1.777	-4.9473**±1.574	-8.7976**±2.827	-2.7292 ^{ns}±1.63
	WDC	-2.26677^{ns}±1.716	-0.00765 ^{ns}±0.017	0.02285 ^{ns}±0.04567	0.01979 ^{ns}±0.02536
RWC	**NC**	0.09398**±0.016	0.039*±0.016	0.08224**±0.0297	0.0086 ^{ns}±0.0187
	WDC	0.0032 ^{ns}±0.01856	-0.00765 ^{ns}±0.01722	0.02285 ^{ns}±0.04567	0.01979^{ns}±0.02536
CC	**NC**	-3.7327*±1.69	-3.198 ^{ns}±1.7	-8.1854*±3.55	-3.698 ^{ns}±2.1147
	WDC	6.038**±2.224	10.7881**±1.7081	4.8301 ^{ns}±3.835	-6.5343**±2.31
SC	**NC**	24.027**±6.78	30.88**±5.38	28.04*±10.97	-13.43 ^{ns}±64.131
	WDC	66.719**±6.43	70.9**±5.37	84.83**±10.77	-26.39 ^{ns}±71.35
	NC	0.534 ^{ns} ±0.363	-0823*±0.37	-0.656 ^{ns}±0.6342	-0.1818 ^{ns}±3.5619
PI	**WDC**	1.2802**±0.4773	-0.5486 ^{ns}±0.3799	1.3494 ^{ns}±0.9598	0.3089 ^{ns}±4.4795
F_0	**NC**	-285.21 ^{ns}±191.476	-348.42*±165.015	-828.39*±329.057	-97.38 ns±1688.47
	WDC	-273.31 ^{ns}±191.694	-242.83 ^{ns}±179.909	-317.783 ^{ns}±353.537	99.18 ^{ns}±1771.4
F_m	**NC**	-2662.39*±1148.32	-5748.4**±956.867	-8087.03**±1964.8	161.88 ^{ns}±9657.15
	WDC	-1520.67 ^{ns} ±1286.25	-2118.31 ^{ns}±1286.99	-4444.04 ^{ns}±2501.47	-402.53 ^{ns}±11751.2
F_v	**NC**	-2377.17*±1071.09	5453.31**±908.739	-7258.62**±1840.24	285.93 ns±9066.87
	WDC	-1247.36 ^{ns}±1191.34	-1857.48 ^{ns}±1231.59	-4126.26 ^{ns}±2411.17	-501.71 ^{ns}±1288.9
F_v/F_m	**NC**	-0.0183 ^{ns}±0.0109	-0.049**±0.01	-0.057*±0.019	0.0051 ns±0.0986
	WDC	-0.00556 ^{ns}±0.00952	-0.01452 ^{ns}±0.0117	-0.04044 *±0.02022	-0.01018 ^{ns}±0.09842
F_v/F_0	**NC**	-0.2317 ^{ns}±0.1668	-0.72**±0.1578	-0.7287*±0.299	0.1115 ^{ns}±0.0698
	WDC	0.01779 ^{ns}±0.04083	0.09967 ^{ns}±0.2225	0.3346 ^{ns}±0.44332	-0.1263 ^{ns}±2.13

NC and WDC: normal condition and water deficit condition, respectively

ns, * and **: non-significant, Significant at 5% and 1% levels of probability, respectively

FLA, RWC, CC and SC: Flag leaf area, Relative water content, Chlorophyll conductance and Stomatal conductance

PI, F_0, F_m, F_V, F_V/F_M and F_V/F_0: Performance index, Minimal fluorescence, maximal fluorescence value, variable fluorescence, represents the maximum quantum yield of PS II and estimates the maximum primary yield of photochemistry of photosystem II (PS II), respectively.

If dominance deviation is equal to or near one will confirms that the magnitude and sign of dominance for all the genes monitoring the character is equal. Therefore, the degree of dominance is a good estimator of dominance. If dominance deviation is equal to zero or close to zero, the magnitude and sign of the genes controlling the character is not equal and hence degree of dominance explains average dominance.

The data analysis revealed, most of the traits studied have significant differences among the six or seven generations. This is in good agreement with the result of Shahbazy *et al.* (2008), Zhang *et al.* (2000) and Araus *et al.* (1998) that these traits could be used as a selection criterion for grain yield in plant under drought conditions. The generation mean analysis for most of the characters showed the importance of both additive, dominance and epistasis type of gene effects. Small additive effect for polygenic traits is predictable, because parameters that determine gene effects are average effect of total segregating loci. Therefore, because additive parameter or interaction effect related with additive effect is the function of dispersion degree of increasing genes between parents, additive effect estimates may be small (Mather and jinks, 1982). Estimation of additive effects for RWC and CC in two conditions is negative, while these traits have positive additive genetic variance (Table 4). This problem is due to that in generation mean analysis method additive parameters or interaction effect related with dispersion degree of increasing genes between parents. On the other hand, genetic variances are not affected by equilibrate effect and are mean of squares of loci that expressed in form of sum of additive effect deviation (Mather and Jinks 1982). Additive × additive effect is important for plant breeders and genetic improvement of traits via selection. Among the physiological traits studied additive × additive effect was significant for RWC and SC in normal condition and CC, SC and PI in water deficit condition. Dominance effect was significant for all traits in normal condition but in water deficit condition at FLA, RWC, PI, F_v/F_m and F_v/ F_0 was not significant. These results indicated the importance gene effects in inheritance of these traits. On the other hand, significant additive and dominance effect indicated that both of them were important in the inheritance of studied traits. The dominance effects were greater than the additive effects for studied traits except RWC in two conditions. The results showed that dominance gene action was important in the inheritance of these traits. Epistasis was significant components of the genetic architecture of studied traits in two conditions. Hence, detection, estimation and consideration of these components are important in formulating of breeding strategies. Positive and significant epistatic gene effects indicated that these traits had increasing genes and selection for the development of these traits could be effective.

The dominance × dominance effect in normal condition was significant and positive for FLA, CC, F_0, F_m, F_v, F_v/F_m and F_v/F_0 while was significant and negative for RWC and SC. On the other hand, in water deficit condition this effect was significant and positive for CC and negative and significant for SC. In water deficit condition none-significant additive and dominance gene effects for F_v/F_m and F_v/F_0 indicated that these traits are under the complex genetic control and breeding for these traits is not an effortless task for breeders. The signs of dominance and dominance × dominance gene effects were opposite for studied traits at two conditions except of PI in water deficit condition suggesting duplicate type of non-allelic interaction in these traits. In some traits additive effect was higher than dominance gene effect and in the other traits dominance effect was higher than additive effects in two conditions. In three traits (CC, PI and F_0) the gene effects were differed in two conditions. Moderate to high broad sense heritability and low to moderate narrow sense heritability for most of traits were observed in this study for two conditions. This indicates that there is appreciable amount of heritable variation, especially for RWC, F_0, F_m, F_v, F_v/F_m and F_v/F_0 in two conditions. The estimates may be biased upward by the epistasis interaction observed in the generation mean analysis.

Flag leaf Area (FLA). Importance of FLA is obvious for grain yield because it is the major site of photosynthesis and provides stored carbohydrates during grain filling. In normal condition the genetic analysis showed that five parameters model [m-d-h-i-l] was the best fit for this trait. The signs of [h] and [l] were opposite suggesting duplicate type of non allelic interaction in this trait. Additive and dominance gene effects were significant positive and negative respectively which revealed that both types of additive and dominance effects are involved in the genetics of FLA in this condition. Negative sign for dominance gene effect indicated that partial dominance exist for decreasing FLA in the cross under study. In water deficit condition, generation mean analysis did not fit a simple epistatic model, which indicated that improvement of this trait would be more difficult as compared to the situation pertaining to more simple models of inheritance (additive-dominance and digenic epistatic model). In two conditions, dominance variance (V_D) was higher than additive variance (V_A). Degree of dominance, Degree of dominance was greater than than unity for this trait in two conditions. On the other hand, in both conditions H^2b was high and H^2n was low; thus breeding by hybridization would be more effective than population selection in two conditions.

Relative water content (RWC). In normal condition the generation means analysis showed six parameter model [m-d-h-i-j-l] as the best for RWC (Table 3). The significant additive and dominance gene effect in the inheritance of RWC revealed that both types of additive and dominance effects are involved in the genetics of this trait (Manette *et al.* 1988; Tammam 2005). Additive × additive effect is important for plant breeders and genetic improvement of traits via selection (Dhanda and sethi 1998; Yadav and Narsinghani 1999). In water deficit condition the generation means study revealed that four parameter model [m-d-h-j] could be best fit for RWC (Table 3). Golparvar *et al.* (2006) reported that [m-d-h-i-j] was the best fit for this trait in water stress condition. The additive genetic effects [d] significantly involved in the inheritance of RWC and indicated that the selection in early segregating generations will be fruitful. Absence of epistasis makes it possible to fix the additive genetic effect to increase the RWC to achieve the goal of breeding cultivars for stress environment. In the absence of non-allelic interaction the additive genetic effect found to be outstanding as reported before by Ijaz *et. al.* (2013), Golparavar *et al.* (2006) and Kumar and Sharma (2007). For RWC in two conditions V_A was higher than V_D. The degree of dominance was less than unity in two conditions. Estimation of broad-sense heritability's (Table 4) in two conditions indicated higher importance of genetic effects in control of traits. Comparison between broad and narrow-sense heritability's revealed equal importance of additive and non- additive effects in genetic control of this trait but H^2n is high which means possibility of selection for improvement of RWC in early generations which is in agreement with Dhanda and Sethi (2002) reports. Said, (2014) reported that RWC was controlled by the additive type of gene action in normal condition and the pedigree method of selection can be used for improved of this trait, hence, breeding of this trait in both condition can be effective with the early generations selection. These results inconstant of El-Sayed and El-Shaarawy (2006) reports.

Chlorophyll Content (CC). In this study, the CC for non segregating generations was decreased in water deficit condition (Table 1). Analysis of variance showed significant differences among generations. In normal condition additive, dominance and dominance × dominance epistasis effects were involved in controlling the inheritance of this trait and significant additive and dominance gene effects revealed that both types of additive and dominance effects are involved in the genetics of this trait in this condition. In water deficit condition genetic analysis revealed that the six parameters model [m-d-h-i-j-l] showed fit best for these trait. The results indicated that dominance effect and non allelic interaction effects were significant. V_A in normal condition were higher than V_D for this trait whereas in water deficit condition dominance variance were higher which was consistent with Golparvar *et al.* (2006) reports. In normal condition H^2n was higher than H^2b but in water deficit condition was reverse.

Table 3: Estimates of six and seven generations genetic models for wheat physiological traits studied in normal and water deficit conditions

		M	d	h	i	j	l	X^2(df)	R^2	R^2 adj
FLA	**NC**	27.57019**± 0.7329	0.8293**± 0.3655	-8.5925**± 3.27	-2.3866ns± 0.305	-	10.3047**± 2.88	0.40034 ^{ns} (2)	0.988	0.964
	WDC	22.9811**± 0.7227	0.9748**± 0.3522	3.5958ns± 3.2561	0.3185 ns± 0.7624	-7.3238** ±2.167	-0.3757 ns± 2.821	5.74998* (1)	0.861	0.169
(RWC)	**NC**	0.795**± 0.00755	-0.02226**± 0.00511	0.18274**± 0.0323	0.01765*± 0.0082	0.04506*± 0.02159	-0.1342**± 0.0277	0.586 ^{ns} (1)	0.936	0.807
	WDC	0.7949**± 0.00302	-0.05058**± 0.0045	0.012606 ns± 0.007525	-	0.03783 ns± 0.0235	-	2.95 ^{ns} (3)	0.978	0.957
CC	**NC**	37.8036**± 0.4637	-3.5508**± 0.45077	-11.1024**± 2.2767	-	-	8.5033**± 2.2299	1.8319 ^{ns} (4)	0.98	0.961
	WDC	25.1594**± 0.9419	-0.3916 ns± 0.5118	33.7742**± 4.075	7.1893**± 0.9992	-5.1704*± 2.63	-22.713**± 3.4188	1.474 ^{ns} (1)	0.99	0.938
SC	**NC**	21.78*± 11.16	5.3**± 1.76	118.77**± 27.13	28.27*± 11.02	-	-85.06**± 17.01	0.7584 ^{ns} (2)	.987	.934
	WDC	-19.87*± 11.49	2.2764*± 1.14	253.865**± 30.28	53.4807**± 12.45	-	-191.915**± 18.48	0.27 ^{ns} (1)	1	1
(PI)	**NC**	3.4975**± 0.277	-0.669**± 0.0767	-0.9578**± 0.33	0.3122ns± 0.2925	1.3487**± 0.499	-	0.0053 ^{ns} (1)	1	1
	WDC	4.077**± 0.1255	-1.1193**± 0.1254	-0.8387 ns± 0.5822	1.18327**± 0.5615	-	-0.7448 ns± 0.5579	.00201 ^{ns} (1)	1	1
F_0	**NC**	5913.58**± 46.23	184.27**± 4297	-657.04**± 228.24	-	-	711.5**± 236.3	.0.355 ^{ns} (2)	0.986	0.966
	WDC	5814.85**± 41.56	222.86**± 42.05	-197.837**± 67.76	-	-	-	3.8847 ^{ns} (3)	0.908	0.846
F_m	**NC**	25847.46**± 2871.5	636.43*± 287.155	-9603.93*± 1380.6	-	3118.53*± 1325.4	8295.59**± 1465.5	0.0254 ^{ns} (1)	1	1
	WDC	27540.9**± 328.53	1193.96**± 325.9	-1369.73*± 592.66	-	-	-	5.2284 ^{ns} (3)	0.8	0.666
F_v	**NC**	19935.8**± 264.245	456.6 ns± 264.24	-8989.91**± 1288.25	-	3127.94*± 1247.59	7625.18**± 1374.9	0.08982 ^{ns} (1)	0.999	0.994
	WDC	21749.7**± 306.84	955.08**± 304.18	-1172.84*± 559.42	-	-	-	4.59818 ^{ns} (3)	0.772	0.62
F_v/F_m	**NC**	0.76998**± 0.0022	-0.00119 ns± 0.0022	-0.0800167**± 0.0129	-	0.030996*± 0.0135	0.06361**± 0.01426	0.24125 ^{ns}(1)	0.996	0.981
	WDC	0.7692**± 0.0089	0.00089 ns± 0.00198	0.01746 ns± 0.01138	0.01982ns± 0.0093	-	-	0.4477 ^{ns} (2)	0.9341	0.838
F_v/F_0	**NC**	3.3764**± 0.0397	-0.01765 ns± 0.0397	-1.12807**± 0.207	-	0.4928*± 0.2168	0.08713**± 0.201	0.2412 ^{ns} (1)	0.991	0.953
	WDC	3.7597**± 0.04513	0.01667 ns± 0.045	.0478 ns± 0.8675	-	-	-	0.7474 ^{ns} (3)	0.369	0.051

NC and WDC: normal condition and water deficit condition, respectively

ns, * and **: non significant, Significant at 5% and 1% levels of probability, respectively

FLA, RWC, CC and SC: Flag leaf area, Relative water content, Chlorophyll conductance and Stomatal conductance

PI, F_0, F_m, F_V, F_V/F_M and F_V/F_0: Performance index, Minimal fluorescence, maximal fluorescence Value, Variable fluorescence, represents the maximum quantum yield of PS II and estimates the maximum primary yield of photochemistry of photosystem II (PS II), respectively.

Hence, breeding for this trait can be effective with the later generations selection and hybrid production in water deficit condition but in normal condition breeding could be effective in early generations selection.

Stomatal Conductance (SC)

The results indicated that five parameters model [m-d-h-i-l] was the best fit in normal and water deficit conditions. In the inheritance of these traits, additive and dominance effects were significant and dominance effects were higher than additive effects. In two conditions, V_D was higher than V_A and Degree of dominance was greater than one in two conditions. On the other hand, in both conditions H^2b was high and H^2n was low; thus, breeding for this trait can be effective with the later generations selection and hybrid production if breeders can overcome the hybridization barriers.

D. Chlorophyll fluorescence

Performance index (PI). In normal condition five parameters model [m-d-h-i-j] showed the best fit for this trait (Table 3). In the inheritance of (PI), additive, dominance and additive× dominance interaction effects were significant and dominance effects were higher than additive effect. Degree of dominance was higher than unity and H^2n was low. In water deficit condition five parameters model [m-d-h-i-l] showed the best fit for PI and additive and additive × additive effects were significant that involved in the inheritance of this trait and indicated that the selection in early segregating generations will be useful. In normal condition V_D was higher than V_A but in water deficit condition V_A was higher which indicated that breeding procedure for this trait differed in two conditions. Therefore, breeding of this trait can be effective with the later generations selection in normal condition and early generation selection in water deficit condition.

F_0. In normal condition the four parameters model [m-d-h-l] was determined as the best model for the F_0 and significant additive and dominance gene effect in the inheritance of F_0 revealed that both types of additive and dominance effects are involved in the genetics of F_0. Furthermore, dominance × dominance non allelic interaction effect had a major role in the inheritance of this trait. Additive and dominance effects were significant and additive effects were higher than dominance effect.

V_A was higher than V_D and H^2n was high, therefore, breeding of this trait can be effective with the early generations selection. In water deficit condition tree parameters model [m-d-h] showed the best fit for this trait and both types of additive and dominance effects are significant and involved in the genetics of F_0. Degree of dominance was higher than unity and H^2b and H^2n was high and moderate respectively. Hence breeding of this trait can be effective with the later generations selection.

F_m. In normal condition the five parameters model [m-d-h-j-l] was determined as the best model for the F_m. The significant additive and dominance gene effects in the inheritance of F_m revealed that both types of additive and dominance effects are involved in the genetics of F_m. Furthermore, additive × dominance and dominance × dominance non allelic interaction effects had a major role in the inheritance of this trait.

Whereas in water deficit condition tree parameters model [m-d-h] showed the best fit for F_m. Additive and dominance effects were significant and dominance effects were higher than additive effect. For this traits in two conditions V_A was higher than V_D and estimation of H^2b and H^2n (Table 4) in two conditions indicated higher importance of genetic effects in control of F_m. Comparison between H^2b and H^2n revealed equal importance of additive and non- additive effects in genetic control of this trait in two conditions. The degree of dominance was less than unity in two conditions. So breeding of this trait in both condition can be effective with the early generations selection.

F_v. In normal condition the five-parameters model [m-d-h-j-l] was determined as the best model for the F_v. The significant dominance gene effect in the inheritance of F_v revealed that dominance effects are involved in the genetics of F_v. Furthermore, additive × dominance and dominance × dominance non allelic interaction effects had a major role in the inheritance of F_v. where as in water deficit condition tree parameters model [m-d-h] showed the best fit for F_v. In the inheritance of this trait, additive and dominance effects were significant and dominance effect was higher than additive effect. For F_v in two conditions V_A was higher than V_D and estimation of H^2b in two conditions indicated higher importance of genetic effects in control of F_v. The degree of dominance was less than unity in two conditions. Comparison between H^2b and H^2n revealed that additive effects had important role in genetic control of this trait in two conditions. So breeding of this trait in both condition can be effective with the early generations selection.

Table 4: Variance components, degree of dominance, dominance deviation, broad -sense and narrow sense heritability estimates of physiological traits under normal and water deficit conditions.

	condition	V_E	VA	V_D	VA_D	H^2_b	H^2_n	Degree of dominance	Dominance deviation	Bartlett's test
FLA	**NC**	19.27	9.1439	32.024	-7.4859	0.6811	0.1513	1.87	-1.166	3.761^{ns}
	WDC	16.43	6.67	32.29	-9.42	0.70336	0.12044	2.199	-1.51	2.6865^{ns}
RWC	**NC**	0.002395	0.003258	0.000974	0.000207	0.6386	0.4916	0.55	0.0031	4.108^{ns}
	WDC	0.002543	0.003212	0.002628	-0.00073	0.6966	0.3817	0.904	0.0095	1.27^{ns}
CC	**NC**	32.3	24.88	9.9	2.895	0.5185	0.371	0.63	0.49	0.5812^{ns}
	WDC	30.755	12.99	51.74	-33.93	0.678	0.13	1.99	-4.21	0.1472^{ns}
SC	**NC**	297.457	29.556	363.376	-151.292	0.5691	0.0428	3.5063	-7.63	1.989^{ns}
	WDC	106.78	109.108	650.87	-148.301	0.8768	0.1258	2.442	-5.38	4.589^{ns}
(PI)	**NC**	0.2863	0.2224	1.6428	0.2466	0.8669	0.1033	2.7177	0.1805	1.566^{ns}
	WDC	0.89081	1.0151	0.7576	-0.6115	0.6655	0.3811	0.8639	-4.669	0.237^{ns}
F_0	**NC**	135900.76	200033.86	172559.26	-33402.65	0.73	0.39	0.92879	-54.72	7.786^{ns}
	WDC	104054.57	177811.28	270757.38	-37767.02	0.81	0.32	1.23	-56.89	0.88^{ns}
F_m	**NC**	7190224.239	7445673.21	2148488.501	-3180714.38	0.5716	0.443	0.5371	-1026.88	3.12^{ns}
	WDC	7579436.541	12466324.89	5046930.809	-218425.245	0.69	0.49	0.6362	-52.19	0.87^{ns}
F_v	**NC**	6119129.69	6184666.32	2428339.418	-2478138.07	0.5846	0.4198	0.6266	-844.399	3.743^{ns}
	WDC	6733431.065	12551812.27	4046484.274	386801.205	0.71	0.53	0.5677	94.94	0.745^{ns}
F_v/F_m	**NC**	0.0003876	0.000478	0.0008357	-0.0000297	0.7721	0.28	1.322	-0.00081	0.543^{ns}
	WDC	0.0002895	0.0007019	0.0007399	0.000264	0.83	0.4053	1.026	0.0069	1.54^{ns}
F_v/F_0	**NC**	0.125716	0.178277	0.1508529	-0.004858	0.7236	0.3919	0.9198	-0.0084	3.78^{ns}
	WDC	0.150129	0.543265	0.1563696	0.0769196	0.8233	0.6393	0.5365	0.0919	4.19^{ns}

V_E, V_A, V_D and V_{AD}: Environment, additive, dominance and adative ×dominance co-variance, respectively

H^2_b and H^2_n: Broad -sense heritability and narrow sense heritability, respectively

NC and WDC: normal condition and water deficit condition, respectively

ns, * and **: non significant, Significant at 5% and 1% levels of probability, respectively

FLA, RWC, CC and SC: flag leaf area, Relative water content, chlorophyll conductance and stomatal conductance

PI, F_0, F_m, F_V, F_V/F_M and F_V/F_0: Performance index, Minimal fluorescence, maximal fluorescence Value, Variable fluorescence, represents the maximum quantum yield of PS II and estimates the maximum primary yield of photochemistry of photosystem II (PS II), respectively

F_v/F_m and F_v/F_0. Analysis of variance results showed F_v/ F_m and F_v/ F_0, in two condition were significant in normal condition but were not significant in water deficit condition. In normal condition the genetic analysis showed that five parameters model [m-d-h-j-l] was the best fit for these traits. Dominance gene effect was significant and negative. Furthermore, additive × dominance and dominance × dominance non allelic interaction effects had a major role in the inheritance of these traits. But in water deficit condition genetic analysis showed no model that fitted for this traits. Variance analysis showed no significant differences among generations and there was no reason for generation mean analysis too.

For F_v/F_0 in normal condition V_A was equal V_D, but in water deficit condition V_A was higher than V_D. Degree of dominance was less than unity for this trait in two conditions and in return H^2b and H^2n were high (H^2n in water deficit was higher than normal condition). Thus breeding of this trait in both condition can be effective with the early generations selection. For F_v/F_m in normal condition V_D was higher than V_A but in water deficit condition V_A was equal with V_D which indicated that breeding procedure for this trait differed in two conditions. Degree of dominance was greater than unity for F_v/F_m and less than unity for F_v/F_0 in two conditions. Estimation of H^2b in two conditions for both traits indicated higher importance of genetic effects. Comparison between H^2b and H^2n revealed equal importance of additive and non- additive effects in genetic control of these trait in water deficit condition. Thus breeding of these trait in water deficit condition can be effective with the early generations selection. Generally in water deficit condition additive effect had higher gene effect in both traits. Zhang *et al.* (2000) reported that chlorophyll fluorescence was affected by genes from both the female and the male parents, indicating co-control by nuclear and chloroplast genes. Therefore, these traits (especially photosynthetic traits) could be good indicators of adaptation of wheat to drought stress. Since the measurement for these traits is non-intrusive, fast and reliable, the approach is quite attractive. Both of maximum/potential quantum efficiency of PS I1 F_v/F_m and the maximum primary yield of photochemistry of PS I1 F_v/F_0, are related with photosynthetic efficiency of plant (Shangguan *et al.* 2000).

CONCLUSION

However, for initiation of an efficient breeding program other populations from different crosses should be included in the program. As it was mentioned earlier, over dominance was observed for some of characters at two conditions, suggesting the important role of dominance in controlling the traits under study. However, the estimates may be biased upwardly by the epistasis and/or linkage disequilibrium. Linkage disequilibrium could bias the estimation of degree of dominance, especially in the early segregating generations, so that an incomplete or complete dominance is estimated falsely as over dominance genetic effect. Linkage disequilibrium has been suggested as the possible cause of this apparent over dominance or pseudo-over dominance (Marzooghian *et al.* 2014).

This analysis concluded that some of the physiological traits controlled by additive type of gene action and the selection in early generations could be helpful for improvement and some of them controlled by dominance type of gene action and the selection in later generations could be better. In conclusion, the considerable amount of heritable variation for important physiological traits imply the possibility of extracting suitable lines for agronomic characters and the traits related to drought tolerance in this study. On the other hand, the existence of non-additive effects in governing the above mentioned traits suggest the production of hybrid varieties if the hybrid seed can be produced in the breeding programs. These results show the importance of certain gene effects for the appropriate selection of parents and its relevance in elucidating the genetic structure of breeding population critical for the assessment of exploitable genetic variation.

REFERENCES

Araus J. L., Amaro T., Voltas J., Nakkoul, H. and Nachit M. M., (1998). Chlorophyll florescence as a selection criterion for grain yield in durum wheat under Mediterranean conditions. *Field Crop Research*, **55**: 209-223.

Araus J. L., Salfer M. P., Royo C. and Serett M. D., (2008). Breeding for yield potential and stress adaptation in cereals. *Critical Reviews in Plant Sciences,* **27**: 377-412.

Arraudeau M. A., (1989). Breeding strategies for drought resistance. In: Baker FWG (eds.) Drought Resistance in Cereals. *CAB International, Wallingford,* UK. pp: 107-116.

Austin R. B., (1993). Augmenting yield based selection. In: Hayward, M. D., Bosemark, N. O. and Romagosa, I. (Eds), Plant Breeding: principals and prospects. Chapman and Hall, London, pp:391-405.

Austin R. B., 1988. New opportunities in breeding. *Horticulture Science*, **23**: 41-45.

Baker N, R. and Rosenqvist E., (2004). Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. *Journal of Experimental Botany,* **55**: 1607-1621.

Baik B. K. and Ullrich S. E., (2008). Barley for food: Characteristics, improvement, and renewed interest. *Journal of Cereal Science*, **48**(2):233-242.

Bartlett M., S., (1937). Some examples of statistical methods of research in agriculture and applied biology. *Supplement to the Journal of the Royal Statistical Society*, **4**:137-183.

Benbella M. and Paulsen G. M., (1998). Efficacy of treatments for delaying senescence of wheat leaves: 11. Senescence and grain yield under field conditions. *Agronomy Journal,* **90**: 332-338.

Bilger W., Schreiber U. and Bock M., (1995). Determination of the quantum efficiency of PSII and non photochemical quenching of chlorophyll fluorescence in the field. Oecologia, **102**: 425-432.

Blum A., (1998). Improving wheat grain filling under stress by stem reserve mobilization. *Euphytica*, **100**, 77-83.

Bolhar-Nordenkampf H. R., Long S. P. and Baker N. R., (1989). Chlorophyll Fluorescence as a probe of the synthetic competence of leaves in the field: a review of current instrumentation. *Functional Ecology,* **3**: 497-514.

Byrne P. F., Bolanos J., Edmeades G. O. and Eaton D. L., 1995. Grains from selection under drought versus multilocation testing in related tropical maize populations. *Crop Science,* **35**: 63-69.

Ceccarelli S. and Grando S., (1991). Selection environment and environmental sensitivity in barley. *Euphytica,* **57**: 157-167.

Clarke J. M., DePauw R. M. and Townley-Smith T. F., (1992). Evaluation of methods for quantification of drought tolerance in wheat, *Crop Science*, **32**: 723-728.

Cornic G. and Massacci, A., (1996). In: Baker N. R. (ed). AdVAnces in Photosynthesis, V.5, photosynthesis and the Environment. Kluwer Academic Publishers, Dordrech / Boston/ London. pp. 347-366.

Cornic G., (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture-not by affecting ATP synthesis. *Trends in Plant Science* **5**(5): 18-188.

Dhanda S. S. and Sethi G. S., (2002). Tolerance to drought stress among selected Indian wheat cultivars. *The Journal of Agricultural Science,* **139**(3): 319-326.

Demmig-Adams B. Adams I. I. I., (1992). Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology*. **43**: 599-626.

Dencic S., Kastori R. and Kobiljski D., (2000). EVAluation of grain yield and its components in wheat genotypes and landrace under near option and drought conditions. Euphytica, **113**: 43-52.

Earl H. J. and Tollenaar M., (1999). Using chlorophyll fluorometry to compare photosynthetic performance of commercial maize (*Zea mays* L.) hybrids in the field. *Field Crops Research*. **61**: 210-221.

El-Sayed E. A. M. and El-Shaarawy G. A., (2006). Genetical studies on yield and some Agronomic characters in some bread wheat (*Triticum aestivum* L.) crosses. *Journal of Agriculture Science, Mansoura University,* **31**(8): 4901-4914.

Erdei L., Tari I., Csisza´r J., Pe´csva´radi A., Horva´th F., Szabo M., Ordog M., Cseuz L., Zhiponova M., Szilak L. and Gyorgyey L., (2002). Osmotic stress responses of wheat species and genotypes differing in drought tolerance: some interesting genes (advices for gene hunting). *Acta Biological Szegediensis,* **46**: 63-65.

Falk S., Maxwell D. P., Laudenbach D. E., Huner N. P. A. and Baker N. R., (1996). In advances in photosynthesis, V. 5, Photosynthesis and the environment, Kluwer Academic publishers, Dordrecht/Boston/London. pp. 367-385.

Farshadfar E., Ghanadha M., Zahravi M. and Sutka J., (2001). Generation mean analysis of drought tolerance in wheat (*Triticum aestivum* L.). *Acta Agronomica Hungarica,* **49**(1): 55-66.

Farshadfar E., Mahjouri S. and Aghaee M., (2008). Detection of epistasis and estimation of additive and dominance components of genetic variation for drought tolerance in durum wheat. *Journal of Biological Science,* **8**(3): 548-603.

Fernandez G. CJ., (1992). Effective selection criteria for assessing plant stress tolerance. In: Kuo CG, ed. Adaptation of Food Crops to Temperature and Water Stress. Shanhua: Asian Vegetable Research and Development Center, Taiwan, 93-410: 257-270.

Fischer R. A., and Maurer R., (1978). Drought resistance in spring wheat genotypes?. Grain yields responses. *Australian Journal of Agricultural Research*, **29**: 897-912.

Flagella Z., Pastore D. and Campanile D., (1995). The quantum yield of photosynthetic electron transport evaluation by chlorophyll fluorescence as an indicator of drought tolerance in durum wheat. *Journal of Agricultural Science, Cambridge***,** **3**: 325-329.

Golpar VAr A. R., Ghasemi-pir-balouti A. and Madani H., 2006. Genetic control of some physiological attributes in wheat under drought stress conditions. *Pakistan Journal of Biological Science,* **9**(8): 1442-1446.

Greaves J. A. and Wilson J. M., (1987). Chlorophyll fluorescence analysis-an aid to plant breeders. *Biologist,* **34**: 209-214.

Guo P. and Li M., (1996). Studies on photosynthetic characteristics in rice hybrid progenies and their parents. I. CC, chlorophyll-protein complex and chlorophyll fluorescence kinetics. *Journal of tropical and Subtropical*, **4**: 60-65.

Hakam N., Khanizadeh S., Deell J. R. and Richer, C., (2000). Assessing chilling tolerance in roses using chlorophyll fluorescence. *Hort. Science*, **35**:184-186.

Havaux U. and Lannoye R., (1985). Drought resistance of hard wheat cultivars measured by a rapid chlorophyll fluorescence test. *Journal of Agriculture Science, Cambridge* **3**: 501-504.

Hayman B. I., (1958). The separation of epistatic from additive and dominance variation in generation means. *Heredity,* **12**: 371-390.

Ijaz U., Smiullah and Kashif M., (2013). Generation means analysis for five physiological traits of bread wheat under rainfed condition, *Universal Journal of Plant Science,* **1**(1): 21-26.

Isebrands J. G., Oxborough K., Rees, D. and Scholes J. D., 1988. Regulation of the photochemical efficiency of PSII; consequences for the light response of field photosynthesis. Plant Physiology Biochemistry, 26:453-469.

Kearsey M. J. and Pooni H. S., 1998. The genetical analysis of quantitative traits. Chapman and Hall, London, PP. 380.

Kearsey M. J. and Pooni H. S., (2004). The genetical analysis of quantitative traits, second ed. Chapman and Hall, UK, ISBN 0-7487-4082-1.

Kelly H., 1988. Corn bread successfully for higher photosynthesis rate. Agricultural Research. 36:13-14.

Krause G. H. and Weise E., (1991). Chlorophyll fluorescence and photosynthesis: Annual Review of Plant Physiology and Plant Molecular Biology, 42:313-349.

Kumar A. and Sharma S. C., (2007). Genetics of excised leaf water loss and relative water content in bread wheat (*Triticum aestivum* L.). *Cereal Research Communication,* **35**(1): 43-52.

Li, R., GUO P., Baumz M., Grando S. and Ceccarelli S., (2006). Evaluation of CC and fluoresence parameters as indicators of drought tolerance in barley. *Agriculture Science in China*, **5**(10): 751-757.

Lilley J. M. and Ludlow M. M., (1996). Expression of osmotic adjustment and dehydration tolerance in diverse rice lines. *Field Crop Research,* **48**: 185-197.

Lichtenhaler H. K., (1996). Photosynthesis and high light stress. *Journal of Plant Physiology,* **148**: 4-14.

Lynch M. and Walsh B., (1998). Genetics and Analysis of Quantitative Traits, Sinauer Associates, Inc, Sunderland, p. 980.

Manette A. Schonfeld C. Richard J. Carre B. and Morhinweg W. (1988). Water relations in winter wheat as drought resistance indicators. *Crop Science.* **28**: 526-531.

Marzooghian A., Moghaddam M., Toorchi M. and Shakiba M. R., (2014). Investigation of genetic structure and gene action in bread wheat affected by salt stress. *International Journal of Biosciences,* **5**(6):173-181.

Mather K. and Jinks J. L., (1982). Biometrical Genetics.3rd ed. Chapman and Hall, London, P.P. 396.

Moffatt J. M., Sears E. G. and Paulson G. M., (1990). Wheat high temperature tolerance during reproductive growth. I. Evaluation by chlorophyll fluorescence. *Crop Science,* **4**: 881-885.

Mohammadi A. A., Saeidi, G. and Arzani A., (2010). Genetic analysis of some agronomic traits in flax (*Linum usitatissimum* L.). *Australian Journal of Crop Science,* **4**(5):343-352.

Muller J., (1991). Determining leaf surface area by means of a wheat osmoregulation water use: the challenge *Agriculture Meteorology.* **14**: 311-320.

Nelson C. J., (1988). Genetic association between photosynthetic characteristics and yield: review of the evidence. *Plant Physiology and Biochemistry*. **26**: 543-554.

Nasyrov Y. S., (1978). Genetic control of photosynthesis and improving of crop productivity. *Annual Review of Plant Physiology,* **29**: 215-237.

Nouri A. and Etminan A., Teixeira da Silva J. A. and Mohammadi R., (2011). Assessment of yield, yield related traits and drought tolerance of durum wheat genotypes (*Triticum turjidum* var. durum Desf.). *Australian Journal Crop Science,* **5**(1):8-16.

Pastore D., Flagella Z. and Rascio A., (1989). Field studies on chlorophyll fluorescence as drought tolerance test in *Triticum durum* Desf. genotype, *Journal of Genetics and Breeding,* **1**: 45-51.

Percival G. C. and Sheriffs C. N., (2002). Identification of drought tolerance woody perennials using chlorophyll fluorescence. *Journal of Arboriculture,* **28**: 215-223.

Rajaram S. and VAn Ginkle M., (2001). Mexico, 50 years of international wheat breeding, Bonjean AP, Angus WJ, (Eds.), The World Wheat Book: A History of Wheat Breeding. Lavoisier Publishing, Paris, France, 579-604.

Rathjen A. J., (1994). The biological basis of genotype × environment interaction: its definition and management. Proceedings of the Seventh Assembly of the Wheat Breeding Society of Australia, Adelaide, Australia.

Richards R. A., (1996). Defining selection criteria to improve yield under drought. *Plant Growth Regulation,* **20**: 157-166.

Ritchie S. W., Nguyan H. T. and Holaday A. S., (1990). Leaf Water content and gas exchange parameters of two wheat genotypes differing in drought resistance. *Crop Science.* **30**: 105-111.

Rocher J. P., Prioul J. L. and Lecharny A., (1989). Genetic Variability in carbon fixation, sucrose-P-synthase and ADP glucose pyrophosphorylase in maize plants of differing growth rate. *Plant Physiology,* **89**: 416-420.

Said A. A., (2014). Generation mean analysis in wheat (*Triticum aestivum* L.) under drought stress conditions. *Annals of Agricultural Science,* **59**(2): 177-184.

Schonfeld M. A., Johnson R. C., Carver B. F., and Mornhigweg D. W., (1988). Water relations in winter wheat as drought resistance indicators. *Crop Science,* **28**: 526-531.

Sing R. F. and Chaudhary B D., (1985). Biometrical methods in quantitative genetic analysis. Kalyani puublishers, New Dehli.

Singh R. P. and Singh S., (1992). Estimation of genetic parameters through generation mean analysis in bread wheat. *Indian Journal of Genetics,* **52**: 369-357.

Shahbzy H., bihamta M. R., Taeb M. and Darvish, F., (2012). Germination characters of wheat under osmotic stress: inheritance and relation wheat drought tolerance, *International Journal of Agriculture, Research and Review,* **2**(6): 689-698.

Shangguan Z. P., Shao, M. A. and Dyckmans J., (2000). Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. *Journal of Plant Physiology,* **56**: 46-51.

Sharifi M., (2005). Genetic analysis of salt tolerance in barley. M. Sc. Thesis, College of agriculture, Razi University., Kermanshah, Iran.

Sunil Kumar B., (2005). Physiological and genetic basis of hetorosis for quantitative characters in mung bean (*Vigna radiate* (L.) Wilczek). Ph.D. Thesis, Annamalai University.

Tammam A. M., (2005). Generation mean analysis in bread wheat under different environmental conditions. *Minufiy Journal Agriculture Researches,* **30**(3):937-956.

Turner N. C., (1986). Crop water deficit: A decade of progress. *Advances in Agronomy,* **39**: 51.

V Alladares F., Dobarro I., Sanchez-Gomez D. and Pearcy R. W., (2005). Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. *Journal of Experimental Botany,* **56**: 483-494.

Viana J. M. S., (2000). Generation mean analysis to polygenic systems with epistsis and fixed genes. *Pesquisa Agropecuária Brasileira,* **35**(6): 1159-1167.

Yadav R. K. and Narshinghani V. G., (1999). Gene effects for yield and its components in wheat. Rachis newsletter, 18:79-81.

Zhang M. Q., Chen R. K., Luo J., Lu, J. L. and Xu J. S., (2000). Analyses for inheritance and combining ability of photochemical activities measured by chlorophyll fluorescence in the segregating generation of sugarcane. *Field Crops Research,* **65**: 31-39.