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GENETIC BEHAVIOR OF MORPHO-PHYSIOLOGICAL TRAITS AND THEIR ROLE FOR BREEDING DROUGHT TOLERANT WHEAT

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Abstract

The development of drought tolerant and high yielding varieties/germplasm is the major objective of any wheat breeding program. In the present study genetic architecture of physiological traits, yield and yield related parameters were studied using the generation mean analysis to improve grain yield under drought stress. A drought tolerant line, 9877 and a drought susceptible line, NR371 were crossed to develop six generations (P_1, P_2, F_1, BC_1, BC_2, and F_2). Results revealed additive, dominant and epistatic effects involved in the inheritance of characters which varied with trait and stress. Additive gene action was observed for canopy temperature, Chlorophyll 'a' and turgor potential. Although narrow sense heritability estimates for some traits were low but canopy temperature, chlorophyll 'a' and turgor potential expressed reasonably high heritability that supports the results of gene action providing an opportunity for early generation selection to use in a breeding program. The estimation of heritability for leaf carotenoids and turgor potential along with gene action for leaf carotenoids is a new work in wheat. The findings of present study suggested that physiological and bio-chemical traits are the indicators of stress tolerance and their utilization in developing high yielding drought tolerant wheat germplasm can expedite the breeding for stress tolerance.

Key worlds: Drought, Gene action, Heritability, Yield potential.

Introduction

Wheat is an important food crop which is grown on largest area with total production of 651 million tons all over the world (Anon., 2013). A small yield increment per unit area would give a quantum jump to total production. Water stress is limiting factor in harvesting potential yields in semiarid regions of the world. In most of the developing countries wheat is grown under limited irrigation or rainfed conditions where the crop experiences periodical water shortage spells during one or more growth stages causing overall potential decrease in the grain yield (Pokharel & Pandey, 2012). Present emerging climate change is another future threat that will affect agriculture to a great extent. Food security issues may arise in the developing world due to change in rain fall patterns leading to yield reduction. The yield loss disturbs the equilibrium of supply and demand, causing food security issues. Less sensitive well adapted germplasm can perform better in changing climate (Hellin *et al*., 2012). Reduction in uptake of nutrients, hampered flowering, less and small spikes, shortening of grain filling period and reduction in grain number and weight is also featured with water stress (Taiz & Zeiger, 2006; Hussain *et al.,* 2008). The present scenario demands systematic efforts to improve food availability for ever increasing population. Water relation directly or indirectly provides the information about the water status of plants under water deficit conditions that may be in the form of relative water content, leaf water potential, leaf osmotic potential and turgor potential (Ashraf *et al.,* 1994a and Akram, 2011). Water is necessary to maintain the optimum growth and physiological activities involved in different processes necessary for plant growth, development and ultimately yield (Taiz & Zeiger, 2006; Hussain *et al.,* 2008). The yield potential, yield stability and drought tolerance are complex quantitative characters affected by genotype × environment interaction. The need is to develop physiologically and genetically more stable genotypes which could perform better under limited moisture.

Generation mean analysis is a biomaterial technique that deals with the phenotypic performance of the traits under investigation (Kearsey & Pooni, 1996; Sharma & Sain, 2004) and is useful to estimate main gene effects (additive and dominance) and epistatic effects such as (dominance × dominance), (additive × additive) and (dominance × additive). The information generated will be helpful in estimating the performance of parents and their crosses used in the study. This study will provide guideline for selecting and designing a wheat breeding program.

Materials and Methods

Genetic material: The experimental material consisted of wheat lines as parents and their generations. The generations were derived from two contrasting lines, selected on the basis of relative water content. The line 9877 (P1) exhibited maximum relative water content, used as male parent while line NR371 (P2) maintained minimum relative water content under drought conditions was used as female parent and subsequent generations were developed as F_1 (1st Filial generation), BC_1 and BC_2 (Backcross 1 and 2) and F_2 (2nd Filial generation).

Experimental layout: The experiment was conducted in the field of Wheat Research Institute, Ayub Agricultural Research Institute, Faisalabad, Pakistan. The experiment was laid out under Split plot design with two treatments and three replications in a randomized complete block design. Sowing was done with the help of dibbler, keeping the row length of 5 m, plant to plant and row to row distance of 15 and 30 cm, respectively. A border of non-experimental lines was sown to minimize border effect. To control rainfall, movable rain shelter was used which was stretched over the experimental area only at the time of rain. The treatments consisted of normal irrigation (control) and water stress (drought stress). Water stress block received half the number of irrigations: first at the time of sowing and second at heading, whereas the normal block was irrigated four times i.e. at sowing, tillering, booting and grain filling stages. All other crop production practices were kept uniform. Data were collected on well-guarded 30 plants of Parent 1 (P_1), Parent 2 (P_2) and F_1, 200 plants from F_2, 50 from Backcross 1 ($P_1 \times F_1 = BC_1$) and Backcross 2 ($P_2 \times F_1 = BC_2$) in each replication.

To determine relative water content (RWC) method and formula given by Malik & Wright (1995) was used. Chlorophyll 'a' (Ch 'a'), chlorophyll 'b' (Ch 'b') and carotenoid (Car) contents were extracted by the method of Arnon (1949) from fresh leaves and calculated according to Davies (1976). Leaf water potential (Ψ_w) was measured using the third leaf from the top of main tiller of plant. The measurements were made from 10.00 to 12.00 am with Scholander type pressure chamber (Arimad 2, ELE International, Israel). Same leaves were used for osmotic potential (Ψ_s). Leaf was frozen at -20°C for osmotic potential determination. The frozen leaf material was thawed and cell sap was extracted after crushing the leaves with a glass rod and the sap was sucked with a disposable syringe. The sap so extracted was directly used for the determination of osmotic potential using an Osmometer (Wescor 5520, USA). Leaf turgor potential (Ψ_p) was calculated as the difference between leaf water potential (Ψ_w) and leaf osmotic potential (Ψ_s) values. Canopy temperature measurements were made using a hand-held infrared thermometer (LT300 infrared, Sixth Sense) as described by Reynolds *et al.* (1998) during 12:00 to 4:00 pm on a clear day when wind was slow.

Main spikes were harvested at maturity and threshed manually to record grain weight (g) per spike using electronic balance (OHAUS-GT400, USA). Hundred grain weight from each plant was taken as fraction and multiplied with10 to convert it into 1000-grain weight. Grain yield of individual plants was recorded in grams and then total yield per plant was calculated by adding the yield of the mother shoot of each plant.

Statistical analysis: Analysis of variance was performed on mean data according to the method given by Steel *et al.* (1997) and generation mean analysis was conducted following Mather & Jinks (1982) using a computer program supplied by Dr. H.S Pooni, School of Biological Sciences, University of Birmingham. Mean and variances of each population (Parents, Backcrosses, F_1 and F_2) used in the analysis were calculated from individual plants pooled over replications. Heritability in narrow sense (h^2_{ns}) was calculated (Mather & Jinks, 1982) using the components of variance from the best fit model of weighed least squares analysis.

Results and Discussion

Pooled analysis of variance (Table 1) for the generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) was significant for all the traits under study. Significant differences among the parents and generations under both treatments were observed. This genetic variability is the basic prerequisite for success in a breeding program. Farshadfar *et al.* (2013), Razzaq *et al.* (2013) and Rad *et al.* (2013) have also reported genetic variability for the studied characters. Significant genotype × environment interaction is an indication of changed behavior of breeding material under different moisture regimes (Mustafa *et al.*, 1996; Sayar *et al.*, 2008; Akram, 2011).

Table 1. Mean square values of six generations for all the traits studied at vegetative stage under normal and water stress conditions.

Traits	Replications (r)	Treatment (t)	Error (r × t)	Generations (g)	(t × g)	Error (r × t × g)
Relative water content %	0.4600	992.670**	0.02	26.260**	4.770**	0.19
Chlorophyll 'a' (mg g-1 FW)	0.0002	0.618**	0.00005	0.002**	0.003**	0.00005
Chlorophyll 'b' (mg g-1 FW)	0.0002	0.084**	0.00006	0.0009**	0.0002**	0.00007
Leaf carotenoids (mg g-1 FW)	0.0006	0.062**	0.00005	0.001**	0.0004**	0.00003
Water potential (-Mpa)	0.0010	4.120**	0.009	0.025**	0.004**	0.0005
Osmotic potential (-Mpa)	0.0040	0.875**	0.0001	0.084**	0.012**	0.002
Turgor potential (-Mpa)	0.0013	1.048**	0.008	0.017**	0.008**	0.002
Canopy temperature (C^0)	0.0400	33.770**	0.110	0.514**	0.050**	0.080
No. of tillers	0.1100	305.670**	0.040	1.740**	0.430**	0.080
Grain wt. spike^{-1} (g)	0.0060	7.909**	0.008	0.036**	0.160**	0.006
1000-grian wt. (g)	0.5400	844.180**	0.870	16.840**	9.860**	0.130
Grain wt. plant^{-1} (g)	0.0100	1048.270**	0.030	2.280**	0.330*	0.090

** = Significant at 0.01 level of probability. * = Significant at 0.05 level of probability

Table 2. Comparison of two treatment means of six generations under normal and water stress conditions.

Traits	**Treatments**		**Percentage increase/decrease**
	Normal	**Water stress**	
Relative water content %	89.500	68.990	-23.00
Chlorophyll 'a' (mg g-1 FW)	1.522	1.211	-20.42
Chlorophyll 'b' (mg g-1 FW)	0.551	0.454	-17.58
Leaf carotenoids (mg g-1 FW)	0.474	0.391	-17.63
Water potential (-Mpa)	-0.867	-1.448	-66.94
Osmotic potential (-Mpa)	-1.762	-1.978	-12.21
Turgor potential (-Mpa)	0.894	0.527	-41.06
Canopy temperature (C^0)	24.040	25.970	8.05
No. of tillers	11.180	4.110	-63.24
Grain wt. spike^{-1} (g)	2.520	1.580	-37.27
1000-grian wt.. (g)	44.090	33.610	-23.77
Grain wt. plant^{-1} (g)	19.930	5.480	-72.48

Growth and yield performance: The pooled means of two treatments and generations exhibited that the most drought sensitive parameter was grain yield with a decrease of 72.48% followed by number of tillers (63.24%). In contrast osmotic potential showed the lowest decrease of 12.21% under stress (Table 2). Observing the individual performance of generations and parents, highest relative water content 93.13% was recorded in P_1 under irrigated conditions (Fig. 1) and the lowest relative water content in P_2. A general decrease in relative water content in all the genotypes was observed under water stress conditions. However maximum decrease of 27.42% was recorded in genotype P_2 while the minimum relative water loss of 18.19% in P_1. All the segregating material remained within parental loss range. The highest relative water content of 76.19% was obtained in $P_{1.}$ Relative water content provides useful information regarding screening against drought tolerance (Rahman *et al.,* 2000; Grzesiak *et al.,* 2003; Arjenaki *et al.,* 2012). It has been reported in the literature that genotypes with higher relative water content were tolerant to drought stress and produced higher biomass by maintaining optimum physiological and bio-chemical activities (Ashraf *et al*., 1994a; Akram, 2011; Mushtaq *et al.,* 2011).

Physiological and biochemical traits: Leaf water potential varied from -0.78 to 1.60 Mpa between normal and water stress conditions indicating that plants were facing severe drought. The results were in accordance with earlier findings of Fahliani & Assad (2005) and Akram (2011). Leaf water potential decreases with increase in water deficit, however it was more pronounced in P_2 than P_1 indicating its sensitivity to water stress (Fig. 5). The leaf water potential gives the information about the genetic behavior of plant under water stress conditions (Fahliani & Assad 2005). Reports also showed that water potential may differentiate between resistant and susceptible cultivars (Bhutta *et al*., 2006; Fahliani & Assad 2005; Sayar *et al*., 2008).

Osmotic adjustment results from the accumulation of solutes in the cell which lowers the osmotic potential and helps in maintaining turgor potential of the plants facing drought stress (Sayar *et al*., 2008; Taiz & Zeiger, 2006). This mechanism of compensation is essential for the survival of the plants with increasing drought intensity and decreasing soil matric potential. Maintenance of potential difference is necessary to allow the water uptake by the roots. Parents and generations showed a parallel decrease in soil water and osmotic potential. Many other workers including Ashraf *et al.,* 1994b, Fahliani & Assad, 2005 and Akram, 2011 reported similar behavior. The reduction in osmotic potential in P_1 (Fig. 6) was minimum showing its lack of adaptability and sensitivity to drought stress whereas P_2 maintained its high turgor potential by decreasing osmotic potential. The hybrid generations also performed better than the sensitive parent. Ashraf *et al.* (1994b) and Akram (2011) reported that wheat genotypes with lower osmotic potential were better adapted to drought stress. Those genotypes which had greater decrease in osmotic potential also showed high turgor potential. P_1 had the lowest decrease in osmotic potential and hence could attain lowest turgor potential in comparison to all the generations including P_2 (Fig. 7). Most of the physiological and morphological activities like leaf elongation, stomatal opening and photosynthetic activities are directly affected by turgor potential under drought stress conditions. Plant loses the turgor potential under drought to a point restricting cell expansion, that is why, plants remain stunted and having smaller leaf size than those which are grown in normal conditions (Farooq *et al*., 2009). But in present research, P_2 and hybrid generations were successful in maintaining their higher turgor potential and ultimately yield, this may be due to decrease in osmotic potential resulting due to accumulation of solutes allowing the uptake of water necessary to maintain cell turgor potential.

The comparative performance of the chlorophyll pigments is given in Figs. 2 to 4. Stress caused a decrease in Chlorophyll 'a', 'b' and leaf carotenoids. The reduction in above mentioned parameters was expected because chlorophyll is membrane bounded organelle and drought stress effects the membrane stability as reported by Tas & Tas (2007), Ghobadi *et al*. (2011), Arjenaki *et al*. (2012) and Koscielniak *et al*. (2014). The reduction may be due to the production of chlorophylase and peroxydase activities which promote break down of chlorophyll and slow down its synthesis (Taiz & Zeiger, 2006; Arjenaki *et al*., 2012). Some reports have also indicated the production of phenolic compounds stimulated under water deficit conditions which reduced the synthesis of chlorophyll 'a' and 'b' and degraded the already existing chlorophyll in the leaf that reduces the photosynthetic activities and ultimately yield (Tas & Tas, 2007; Arjenaki *et al*., 2012). Leaf carotenoids are considered accessory to harvest light from 400 to 500 nm and transfer this energy to chlorophyll, however, some researchers reported that they protect the photosynthetic apparatus from different types of stresses (Deltoro *et al*., 1998; Farooq *et al*., 2009; Loutfy *et al*., 2012). In present study carotenoids decreased due to water stress in parents and their generations. However the decrease in carotenoid content was more in P_2 as compared to generations and P_1, which indicated their better adaptability and genetic makeup towards water stress conditions. Similarly the canopy temperature (Fig. 8) was also found to increase under water stress which was due to the closing of stomata and preventive measures to conserve water by the plant (Rashid *et al.,* 1999 and Fahliani & Assad, 2005).

Agronomic and yield related parameters: The yield related parameters (Figs. 9-12) like 1000 grain weight, number of tillers, grain weight per spike and grain weight per plant were advisedly affected by the water stress and yield showed maximum decrease because all the other yield component traits add up to express grain yield.

Gene action: Gene action study revealed the presence of both additive and non-additive components governing the traits. Epistatic effects were present in all the traits except canopy temperature which was driven by additive genes under normal irrigation and both by additive and dominant genes under water stress. Similar reports are available in the literature where Pierre *et al*. (2010) found additive × additive and dominant × dominant as most important epistatic effects along with dominant gene action controlling the trait. Hosary *et al.* (2012) found leaf temperature under the influence of additive gene control. Additive component was found in all the traits under both moisture regimes, whereas the dominant and epistatic effects varied with the trait and treatment (Table 3). For relative water content under normal irrigation conditions, strong dominant × dominant epistatic effect was observed along with high magnitude of additive component responsible for the expression of the trait. Stress conditions changed the gene action by increasing the epistatic effects, [mdhij] was the best fit parameter model for relative water content under stress regime. Presence of high degree of epistasis made the gene action complex which indicated towards the delay in selection process. Farshadfar *et al.* (2011) also reported both additive and non-additive effects, while non-additive genetic control was reported by Golparvar *et al.* (2006). In such a situation, selection may not be effective and may be delayed until the trait is fixed. Four parameter model [mdjl] was found best fit to explain the genetic variability in chlorophyll 'a' under normal irrigated conditions the magnitude of epistatic effects j and l were high as compared to d. However under stress regime additive d was complemented by additive × additive epistasis which made the gene action fixable and allowed early generation selection for high chlorophyll content under water stress. These results are congruent to that of Rad *et al.* (2013). For Chlorophyll 'b' [mdj] explained the genetic variability of the trait with higher magnitude of j under both moisture regimes, as j is additive × dominant epistasis that tends to segregate in next generations. It suggests delay in selection for chlorophyll content. Rad *et al.* (2013) also reported the predominance of non-fixable genetic component in the expression of chlorophyll 'b'. Leaf carotenoids were found under the influence of [mdhij] under both the moisture regimes. The magnitude of additive and additive × additive component was lower as compared to the dominant and additive × dominant epistasis which pointed to a complex inheritance of this trait. Due to both additive and dominant genetic nature it would be better to delay selection for stable expression. No report was available in literature regarding the inheritance of the leaf carotenoids in wheat, however, Cheema & Sadaqat (2005) have reported additive genetic control of the trait in Brassica. Duplicate type of epistasis was observed in case of leaf water potential under normal irrigation conditions and under stress conditions additive, dominant and additive × dominant epistasis was observed. The trait was largely under the control of epistasis as competed to main effects which indicated the complexity of inheritance pattern. A similar situation was observed by Farshadfar *et al*. (2011) in contrast to dominant gene action as reported by Ghotbi *et al.* (2004). For osmotic potential both additive and dominant main effects were present under normal irrigation and under stress, additional additive × dominant component was involved for driving the trait. The material studied may be subjected to reciprocal recurrent selection before using it in any breeding program either for variety development or heterosis breeding. The presence of appreciable magnitude of both additive and dominant components suggested a delay in selection. While Ghotbi *et al.* (2004) reported dominant nature of the trait. Leaf turgor potential was governed by additive and dominant components of inheritance along with epistasis under normal irrigation but absent under stress conditions. Literature on the genetic study of turgor potential in wheat was not available however Akbar *et al.* (2009) reported both additive and non-additive nature of the trait in maize. Four to five parameters model explained the genetic nature of yield related traits like number of tillers, grain weight per spike and 1000 grain weight. Under stress conditions 1000 grain weight was governed by three parameter model [mdi] but the epistasis was of duplicate nature exhibiting the complexity of the genetic makeup and high involvement of epistasis in controlling the traits. In such case early generation gain is difficult to achieve so selection may be delayed to fix the character. Grain weight per plant was mostly under the control of strong epistatic effects. Both additive and dominant components of inheritance were evident. Khattab *et al.* (2010) and Zaazaa *et al.* (2012) also reported predominance of epistasis. Nazeer *et al*. (2010) reported over-dominance and Ahmed *et al.* (2007) reported additive nature of the trait. Whereas, some of the researchers like Majid *et al.* (2007) and Laghari *et al.* (2010) suggested indirect selection of component traits to improve overall yield.

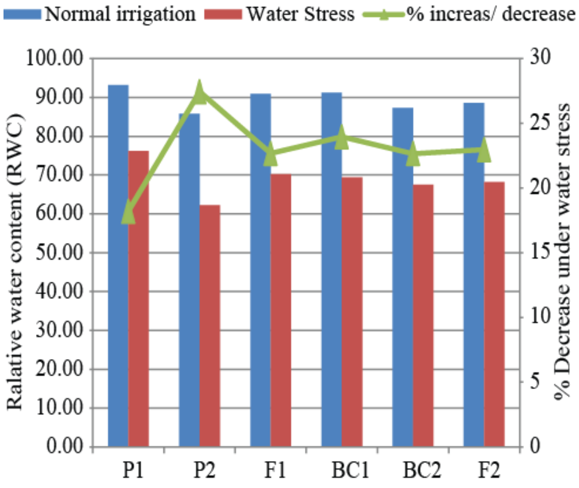

Fig. 1. Ralative water content of six generations under normal and water stress environments along with % increase and decrease.

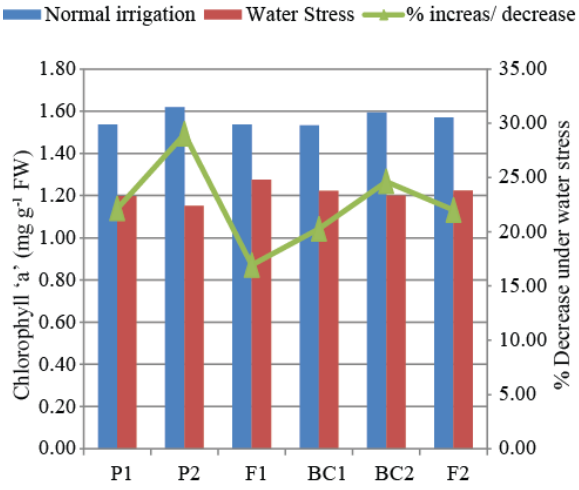

Fig. 2. Chlorophyll "a" of six generations under normal and water stress environments along with % increase and decrease.

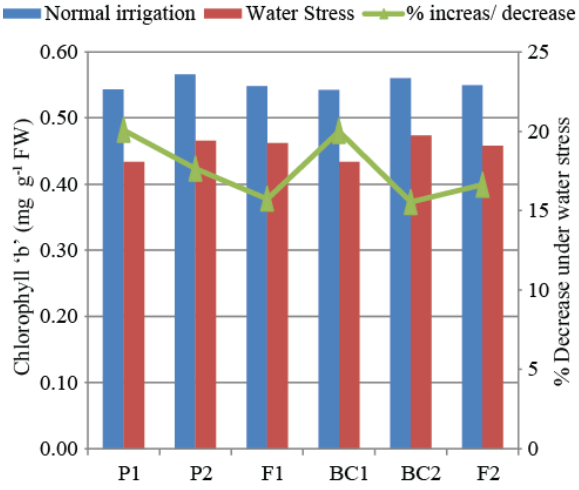

Fig. 3. Chlorophyll "b" of six generations under normal and water stress environments along with % increase and decrease.

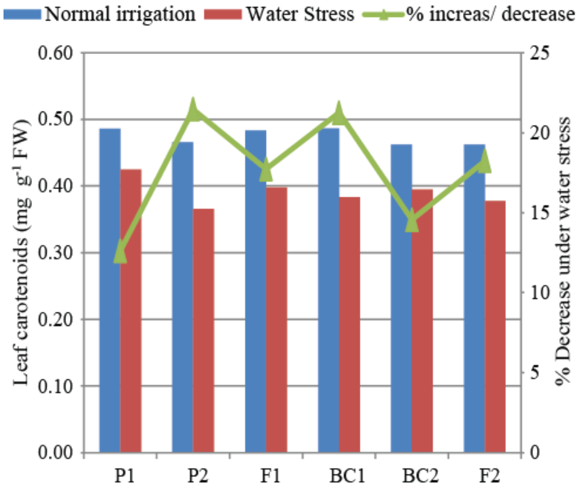

Fig. 4. Leaf carotenoids of six generations under normal and water stress environments along with % increase and decrease.

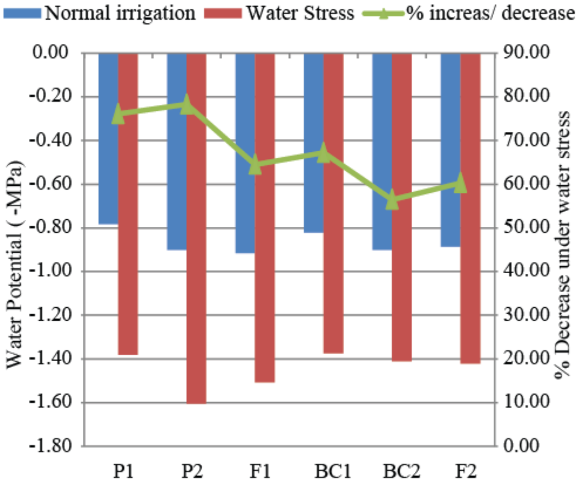

Fig. 5. Leaf water potential of six generations under normal and water stress environments along with % increase and decrease.

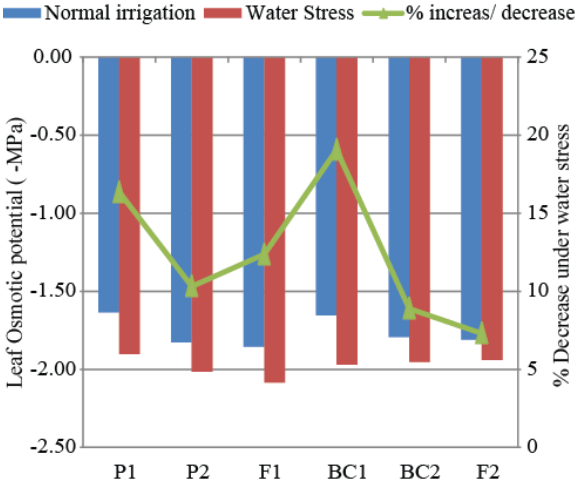

Fig. 6. Leaf osmotic potential of six generations under normal and water stress environments along with % increase and decrease.

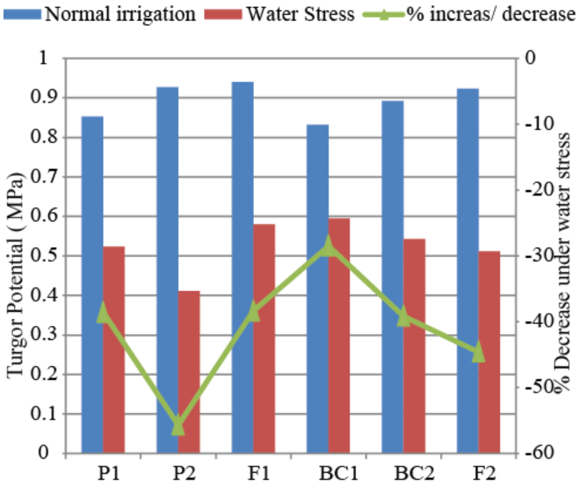

Fig. 7. Turgor potential of six generations under normal and water stress environments along with % increase and decrease.

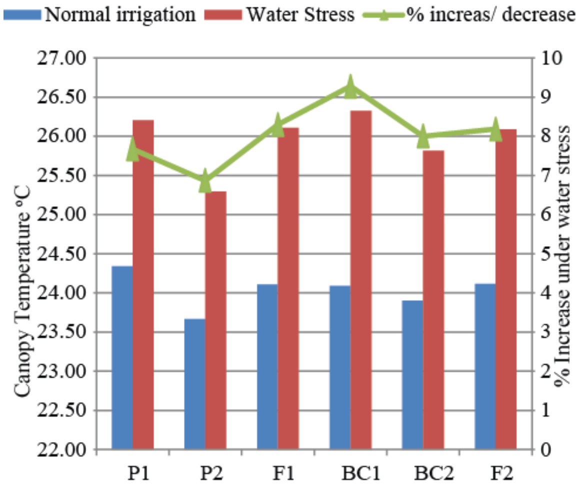

Fig. 8. Canopy temperature of six generations under normal and water stress environments along with % increase and decrease.

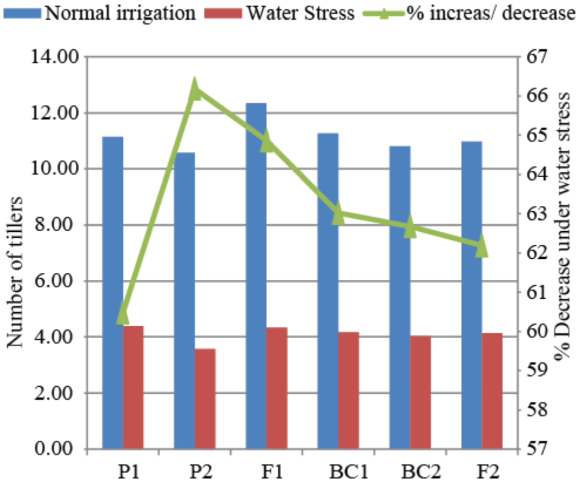

Fig. 9. Number of tillers per plant in six generations under normal and water stress environments along with % increase and decrease.

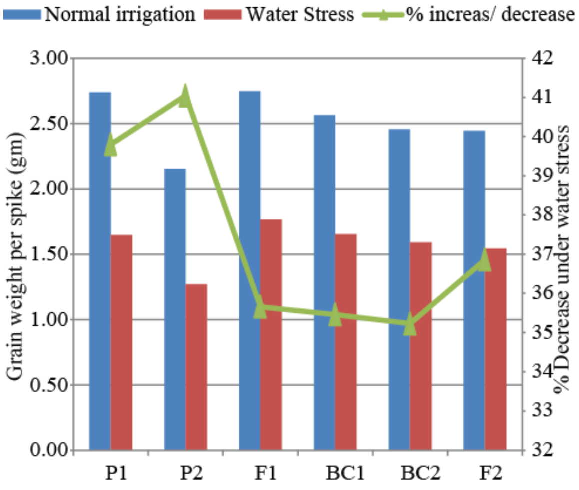

Fig. 10. Grain weight per spike of six generations under normal and water stress environments along with % increase and decrease.

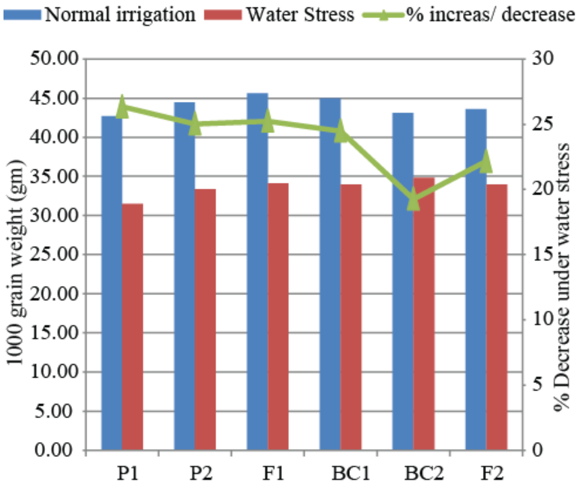

Fig. 11.1000 grain weight of six generations under normal and water stress environments along with % increase and decrease.

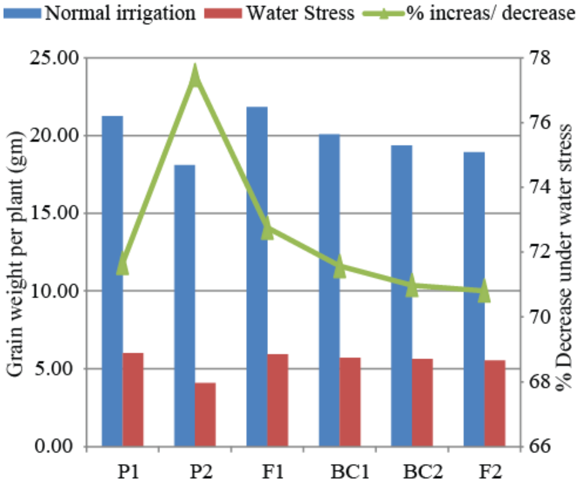

Fig. 12. Grain weight per plant of six generations under normal and water stress environments along with % increase and decrease.

Table 3. Estimation of best fit models on generation means of all the traits at vegetative stage and maturity under normal and water stress conditions.

Plant traits	m ± S.E	[d] ± S.E	[h] ± S.E	[i] ± S.E	[j] ± S.E	[l] ± S.E	χ^2 (df)
				Under normal irrigation			
Relative water content	88.44 ± 0.11	4.64 ± 0.11				2.26 ± 0.41	4.21 (3)
Chlorophyll ‘a’	1.58 ± 0.02	0.05 ± 0.04			-0.21 ± 0.01	-0.05 ± 0.01	0.82(2)
Chlorophyll ‘b’	0.55 ± 0.02	0.09 ± 0.01			-0.06 ± 0.02		0.99(3)
Leaf carotenoids	0.05 ± 0.07	0.09 ± 0.01	0.05 ± 0.01	0.05 ± 0.01	0.04 ± 0.01		0.63(1)
Water potential	1.17 ± 0.09	0.06 ± 0.01		-0.08 ± 0.01			5.87(3)
Osmotic potential	1.94 ± 0.01	0.19 ± 0.01	0.13 ± 0.01				3.64(3)
Turgor potential	0.82 ± 0.03	0.23 ± 0.02	0.14 ± 0.04	0.17 ± 0.02	-0.23 ± 0.09		0.23(1)
Canopy temperature	24.05 ± 0.04	0.33 ± 0.06					1.98 (4)
No. of tillers	9.56 ± 0.34	0.32 ± 0.13	2.69 ± 0.50	1.25 ± 0.36			1.82 (2)
Grain wt. spike^{-1}	2.14 ± 0.05	0.29 ± 0.02	0.61 ± 0.06	0.31 ± 0.05	-0.36 ± 0.11		0.14 (1)
1000-grian wt.	41.56 ± 0.40	0.88 ± 0.09	4.07 ± 0.47	2.05 ± 0.41	1.87 ± 0.82		0.09 (1)
Grain wt. plant^{-1}	15.98 ± 0.45	3.07 ± 0.13	5.81 ± 0.62	5.17 ± 0.48	-3.33 ± 0.85		0.32 (1)
				Under water stress			
Relative water content	66.10 ± 0.92	6.94 ± 0.18	4.00 ± 1.40	3.11 ± 0.94	-9.93 ± 1.87		1.09 (1)
Chlorophyll ‘a’	1.27 ± 0.81	0.12 ± 0.03		0.05 ± 0.01			0.20 (3)
Chlorophyll ‘b’	0.46 ± 0.02	0.15 ± 0.01			-0.11 ± 0.02		2.05(3)
Leaf carotenoids	0.36 ± 0.09	0.19 ± 0.01	0.04 ± 0.02	0.04 ± 0.01	-0.08 ± 0.01		0.17(1)
Water potential	1.71 ± 0.02	0.13 ± 0.01	0.17 ± 0.03		-0.34 ± 0.07		3.54 (2)
Osmotic potential	2.24 ± 0.02	0.25 ± 0.02	0.14 ± 0.03		-0.41 ± 0.11		2.67 (2)
Turgor potential	0.47 ± 0.09	0.07 ± 0.01	0.14 ± 0.02				4.51 (3)
Canopy temperature	25.78 ± 0.79	0.48 ± 0.08	0.43 ± 0.15				1.69 (3)
No. of tillers	4.35 ± 0.12	0.68 ± 0.11	-1.67 ± 0.47		-1.68 ± 0.49	1.63 ± 0.50	0.18 (1)
Grain wt. spike^{-1}	1.56 ± 0.014	0.13 ± 0.02		0.08 ± 0.02	-0.39 ± 0.10		3.98 (2)
1000-grian wt.	34.37 ± 0.08	0.62 ± 0.10		-0.49 ± 0.05			5.86 (3)
Grain wt. plant^{-1}	7.12 ± 0.055	0.99 ± 0.061		-0.84 ± 0.08	-2.25 ± 0.40		3.07 (2)

where: m = Mean, [d] = Additive effects, [h] = Dominance effects, [i] = Additive × additive effects, [j] = Additive × dominance effects, [l] = Dominance × dominance effects, χ^2 = Chi square and (df) = Degree of freedom

Table 4. Heritability estimates of morph-physiological traits.

Traits	Normal irrigation	Water stress
Relative water content %	0.75	0.51
Chlorophyll ‘a’ (mg g^{-1} FW)	0.71	0.63
Chlorophyll ‘b’ (mg g^{-1} FW)	0.35	0.39
Leaf carotenoids (mg g^{-1} FW)	0.68	0.59
Water potential (-Mpa)	0.29	0.43
Osmotic potential (-Mpa)	0.65	0.62
Turgor potential (-Mpa)	0.73	0.70
Canopy temperature (^{o}C)	0.72	0.69
No. of tillers	0.40	0.38
Grain wt. spike^{-1} (g)	0.82	0.60
1000-grian wt. (g)	0.85	0.63
Grain wt. plant^{-1} (g)	0.58	0.82

Heritability studies: The heritability of plant material varied with the experimental condition (Table 4). Under non-stress conditions relative water content, 1000 grain weight and grain weight per spike showed high heritability while under stress regime only grain weight per plant expressed high heritability. This indicated that high proportion of genetic component of variance can be fixed by early generation selection in segregating generations (Munir *et al.,* 2007). The inconsistency of the results between the generation mean analysis and heritability may be due to estimation precision of the procedures. However, the results of generation mean analysis were more reliable (Singh & Narayanan, 2000). With the exception of few, majority of the traits had the involvement of epistatic effects. Appreciable range of heritability was observed in most of the traits which supported the results of gene action studies. The lowest heritability estimate of 0.29 was given by water potential under normal irrigation conditions. Contrary to this most of the physiological traits like chlorophyll ‘a’, leaf carotenoids, osmotic potential, turgor potential and canopy temperature gave moderate to high heritability estimates under both the regimes. Low to moderate heritability of these traits were reported by several workers (Ghotbi *et al*., 2005; Bhutta *et al.,* 2006; Farshadfar *et al*., 2011; Rad *et al.,* 2013). Literature on heritability and gene action for turgor potential and leaf carotenoids was not reported in wheat, however, in sunflower, brassica and maize, scientists including Cheema & Sadaqat (2005); Akbar *et al*. (2009) and Rauf *et al.* (2009) reported medium to low heritability estimates for these traits. An early generation selection of traits with high heritability is quite useful and single plant selections are even more effective. However, heritability may be influenced by environment due to genotype environment interaction.

Conclusion

Epistatic effects were present in majority of the traits studied but physiological traits like chlorophyll ‘a’, leaf carotenoids, osmotic potential, turgor potential and canopy temperature were comparatively under the less influence of epistatic inheritance as compared to agronomic and yield related traits. This indicated that the manipulation of these traits was comparatively easier in a breeding program using conventional breeding techniques. From the findings of present study, it is suggested that wheat germplasm can be identified for drought tolerance by using physiological and biochemical markers (like Chlorophyll *a*, turgor potential and canopy temperature) as screening tools and helpful in developing high yielding drought tolerant wheat cultivars.

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