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GENETICS OF WATER DEFICIT TOLERANCE FOR SOME PHYSIOLOGICAL AND YIELD VARIABLES IN *TRITICUM AESTIVUM* L.

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ABSTRACT

Breeding material consisted of two parental lines NR371 and 8126 bearing contrasting traits for water stress tolerance, their subsequent generations F_1, F_2 and their backcrosses BC_1, BC_2. The experiment was sown under rain shelter to control and avoid any excessive water delivery. Stable performance under both moisture regimes was observed for drought tolerant parent (8126) for almost all the physiological traits. The subsequent generations and backcrosses also gave better results as compared to the susceptible parent (NR371). Moreover, the presence of fixable genetic effects and high heritability estimates for proline content, osmotic potential and canopy temperature were 0.76, 0.71 and 0.70 respectively under water stress regime indicated the use of these traits for breeding stress tolerant varieties. The heritability for leaf carotenoids increased under water stress, contrary to it turgor potential decreased under stress regime. Th7e gene action study of leaf carotenoids and turgor potential is a novel piece of work in this study. Physiological traits are mostly overlooked by the plant breeders in breeding programs having major focus on yield and agronomic variables. The study indicates the possibility of yield enhancement for stress prone areas by breeding physiologically stable and efficient genotypes.

Keywords: Generation mean analysis, Heritability, Water stress, Wheat, Yield.

INTRODUCTION

Among food crops, wheat is the most important cereal grown on largest area world over. Globally it occupies 3rd position in production after maize and rice which is also true for per acre yields of cereals in the country (FAO, 2013). Evolution of high-potential varieties with sustained research efforts has increased the production of the country to the extent of self-sufficiency. However, the need to further accelerate research efforts for genetic improvement according to changing environment and ever increasing population is greater today than ever before. Wheat demand will increase up to 850 million tons during 2050 as compared to the present produce of 642 million tons which excludes the demand of animal feed all over the world (Sharma *et al*., 2015). Availability of adequate water supply at proper growth stage is an important factor which influences the crop production. Therefore, biochemical and physiological traits are of greater importance for a deeper understanding of the complex response of the plant to water stress and ultimately development of new varieties (Rad *et al.*, 2013), and further these variables can be used as selection criteria (Sehar *et al*., 2015).

Water stress is a limiting factor for harvesting potential yields in water scarce areas and semiarid regions of the world. Wheat is grown under natural precipitation or under limited irrigation in most of the countries where crop faces periodical spells of water shortage during growth stages leading to potential grain yield decrease (Ilyas *et al*., 2014). The current threat of climate change is another factor which is to affect agriculture greatly in near future. Changes in rainfall patterns causes yield losses, leading to disturb equilibrium of supply and demand, ultimately agitating food security issues of the developing world in the succeeding years (Sharma *et al*., 2015). Well adapted and less sensitive crop cultivars can perform better in varied climate to address the food security issues (Hellin *et al*., 2012). Reduction in uptake of nutrients and negative effect on yield components like hampered flowering, small and few spikes, grain filling period, grain number and weight are featured with water stress (Taiz and Zeiger, 2006; Hussain *et al.*, 2008). The exiting scenario demands for concerted and systematic efforts to not only sustain but also go beyond self-sufficiency to meet future country needs and global demand. The yield potential, drought tolerance and stability are complex quantitative characters affected by genotype × environment interaction. The need is of finding out suitable parents to tailor physiologically and genetically more stable and productive genotypes which could perform better under marginal moisture conditions.

Phenotypic performance of traits under investigation are best evaluated with quantitative biometrical methods based on generation mean analysis (Kearsey & Pooni, 1996; Sharma & Sain, 2004).The generation mean is also useful to estimate main gene effects (additive and dominance) and epistatic effects i.e. dominance × dominance, additive × additive and dominance × additive. The information generated here in this study about the performance of parental lines and their crosses will provide hopefully a guideline for identifying the desirable genotypes and designing a future breeding program.

MATERIALS AND METHODS

Two wheat lines NR371 (P_1) and 8126 (P_2), having maximum and minimum relative water loss of excised leaf were used in the study. Both the contrasting parents identified at the University of Agriculture Faisalabad, Pakistan and were crossed to raise F_1, F_2, BC_1 ($P_1 \times F_1$) and BC_2 ($P_2 \times F_1$). The study was carried out at Ayub Agriculture Research Institute, Faisalabad, Pakistan under a permanent installation having movable shelter, against precipitation. The experiment was laid out in split plot design having two treatments: normal irrigation and water stress with three replications in randomized complete block design. The seeds were dibbled 15 cm apart and distance of 30 cm was maintained between adjacent rows and one plant per hill after successful emergence of seedling was maintained. Border effect was minimized by planting non-experimental rows on either sides. Normal irrigation block was irrigated four times during critical stages of crop growth i.e. sowing, tillering, booting and grain filling stages. While, stress block was given two irrigations, first at the time of sowing and second at heading stage. All other agronomic crop production practices were kept uniform. Data for various traits was recorded on well-guarded 30 plants each of P_1, P_2 and F_1, 50 plants from backcrosses BC_1 and BC_2, while 250 plants from F_2 in each replication.

Relative water loss of excised leaf was measured as water loss per hour (gH_2O loss $g^{-1}DW\ hr^{-1}$) by the method of Clarke (1992). Leaf Chlorophyll *a*, Chlorophyll *b*, and leaf carotenoid contents were determined from fresh leaves with the method described by Arnon (1949) and calculated according to Davies (1976). Leaf water potential ψ_w and osmotic potential ψ_s. was taken by the method of Ashraf *et al*. (1994). Leaf turgor potential ψ_p was calculated as the difference between leaf water potential ψ_w and leaf osmotic potential ψ_s values. Proline content was determined following the method of Bates *et al.* (1973). Canopy temperature measurements were taken using hand-held infrared thermometer (LT300 infrared, Sixth Sense) as described by Reynolds *et al*. (1998). Grain yield per plant was recorded using electrical balance (OHAUS-GT400, USA). The data recorded was subjected to analysis of variance given by Steel *et al.* (1997) while generation mean analysis was carried out as by Mather and Jinks (1982) using computer program provided by Dr. H.S Pooni, School of Biological Sciences, and University of Birmingham. Narrow sense heritability (h^2_{ns}) was also calculated using the components of variance from the best-fit model of weighted least squares analysis (Mather and Jinks, 1982).

RESULTS AND DISCUSSION

Significant genetic variation for all the traits and generations was depicted in analysis of variance (Table 1). These significant differences can be attributed to a range of quantitative trait loci (QTLs) distributed among the parents and generations responsible for the expression of traits under study. Such genetic variability is fundamental requirement of the breeder for success of any breeding program. Under different moisture regimes, presence of significant generation × environment interaction (Table 1) was an evidence for varied behavior of breeding material under different environments. Similar response of physiological and agronomic traits in wheat material has been reported in the work of Rad *et al.* (2013) and Sehar *et al*. (2015).

The performance of generations for all the studied variables is given in the Figures 1 to 10. Maximum relative water loss was observed in P_1 (parental line NR371) and minimum by P_2 (parental line 8126).While, all the generations performed between the highest and lowest limit of the parents (Figure 1). Low relative water loss of excised leaf reflected the ability of plants for most economical and efficient water use. This attributes to the inherited ability of the material towards drought tolerance. Genotypes/lines having low leaf water loss were tolerant to water deficit conditions, indicating the evapo-transpiration efficiency of the genotype. Scientists including Clarke (1992), Malik and Wright (1995), Ghobadi*et al.* (2011) and Farshadfar*et al.* (2012) have reported the presence of genetic variability for this trait and accepted it as good screening criteria against drought. Chlorophyll *a*, *b*, and leaf carotenoids also decreased under water stress condition (Figure 2-4). The reduction in these variables is expected because chlorophyll is membrane bounded and drought stress affects the membrane stability as reported by Tas and Tas (2007), Hussain *et al.,* (2008). The production of chlorophylase and peroxydase activities promote break down of already existing chlorophyll and slows down its synthesis. In addition, production of phenolic compounds degrade the existing chlorophyll which reduces the photosynthetic activity Taiz and Zeiger (2006). The Parental line 8126 (P_2)showed minimum leaf carotenoid decrease which indicated its superiority to resist drought stress as compared to parental line NR371 (P_1) and the subsequent generations. However, the backcrosses and filial generations remained between the ranges of parents.

Similarly, leaf water potential, osmotic potential and turgor potential decreased under drought stress conditions (Figures 5-7). The accumulation of solutes within the cell results in osmotic adjustment which lowers the osmotic potential and helps in maintaining turgor potential of the stressed plants (Sayar *et al*., 2008; Taiz and Zeiger, 2006). This mechanism of compensation helps the survival of plants in conditions of increasing drought intensity and decreasing soil moisture by maintaining essential potential difference which allows the water up take through the roots. Maximum decrease in leaf water potential and turgor potential was observed in the Parental line 8126 (P_2) which showed its sensitivity and lack of tolerance to drought stress. While, all the generations and P_1 showed better tolerance to the stress conditions. Canopy temperature and proline content showed increase under drought conditions (Figures 8 & 9) and similar behavior was reported by Mohammadi *et al*. (2012) and Sehar *et al*. (2015). Proline content is important under drought stress it increases tolerance against drought and improves osmotic adjustment as also reported by Maleki *et al*. (2010). P_2 (8126) produced maximum proline content as compared to P_1 (NR371)having minimum proline content under drought stress. The overall yield loss in all the generations and parents was more than 50% under stress conditions while the maximum loss of 77% was observed in P_2 (8126) when the minimum yield loss of 51% occurred in P_1 (NR371).The F_1 yielded better than either of the parents whereas, F_2 and backcross (BC_1 and BC_2) were better in yield than P_2 (8126). Many researchers like Bhutta *et al*. (2006), Khakwani*et al.* (2012) and Razzaq *et al*. (2013) noted decrease in yield under water stress in wheat accessions. Sehar *et al*. (2015) also reported that the accessions performing better for physiological and agronomic traits also perform better for yield.

Gene action study revealed that the traits under observation were governed by additive dominant and epistatic interactions (Table 2). To explain the genetic variability of the relative water content under normal and water stress conditions the best-fit models were [mdj] and [mdhj], respectively. Although, additive gene action is there but presence of additive × dominant (j) epistasis made the gene action complex leading towards a delay in selection. The presence of non-additive nature of the trait is also reported by Farshadfar *et al*. (2011). Chlorophyll *a* and chlorophyll *b* also showed additive × dominant [j] epistasis along with additive [m] and dominate [d] gene action under normal irrigation. Similarly, epistatic effects were also present under stress regime and [mdij] and [mdl] were the best fit models for chlorophyll *a* and *b* which suggested delay in selection. Rad *et al*. (2013) has reported non-additive genetic control of these traits. Leaf carotenoids were under the strong influence of additive × dominant [j] epistasis which indicates complex nature of inheritance (Table 2). Reports on the gene action of carotenoids in wheat crop was not available in wheat however, Cheema and Sadaqat (2005) reported additive nature of gene control for leaf carotenoids in brassica. Leaf water potential under both stress and non-stress moisture regimes and osmotic potential under non-stress regime were driven by additive [d], dominant [h] and additive × dominant [j] epistasis, respectively. The magnitude of non-fixable [j] was found higher as compared to [d] and [h] which suggests improvement in trait before using it for a breeding program. Ghotbi *et al*. (2004) found dominant nature of the trait while Farshadfar *et al*. (2011) reported the presence of both additive and dominant gene action along with epistasis controlling the traits. They recommended reciprocal recurrent selection to harvest full potential of this trait. Turgor potential and proline were under the influence of additive component of inheritance under non-stress regime, while under water stress regime osmotic potential and canopy temperature were under the influence of fixable additive [d] gene action. The proline was controlled by additive [d] and additive × additive [i] component of inheritance (Table 2). The presence of fixable additive gene action in these traits permits early generation selection for tailoring drought tolerant wheat. Maleki *et al*. (2010) reported additive while Rad *et al*. (2013) reported dominant non-additive nature of proline. Similarly, additive nature of canopy temperature was reported in wheat by Hosary *et al.* (2012) however, literature on gene action of turgor potential in wheat is silent. While Akbar *et al*. (2009) found non-additive nature of the trait in maize crop. Grain yield was highly under the influence of non-fixable gene action which indicates complex inheritance. Therefore instead of direct focusing on yield it would be better to improve yield through improvement of component physiological traits which ultimately contribute to grain yield enhancement.

Heritability estimates varied depending upon the trait and stress regime (Table 2). Low to high range of heritability was observed for the traits under consideration which supported the results of gene action studies. The lowest heritability estimate of 0.24 was recorded in chlorophyll *a* under normal irrigation conditions while, the highest heritability estimate of 0.76 was displayed by proline under water stress regime. Proline content under both moisture regimes and canopy temperature along with osmotic potential under moisture stress regime gave high heritability under drought stress environment which permits early generation selection for these traits and their use in breeding program to tailor drought tolerant wheat. Moderate heritability for osmotic potential was reported in the work of Bhutta *et al*. (2006), while Coskun *et al*. (2010) and Maleki *et al*. (2010) reported high heritability for canopy temperature and proline content, respectively. Low to medium heritability was recorded for the remaining variables (Table 2), similar response was recorded by Farshadfar *et al.* (2012 & 13) and Rad *et al.*, (2013). Literature regarding heritability of turgor potential and leaf carotenoids was not found in wheat, however, Cheema and Sadaqat (2005), Akbar *et al.* (2009) and Rauf *et al.* (2009) have reported medium to low heritability in *brassica napus*, maize and sunflower for these physiological variables in their studies.

Table 1. Mean square values of some physiological traits in wheat under water stress conditions.

Traits	Replications (r)	Treatment (t)	Error (r × t)	Generations (g)	Interaction (t × g)	Error (r × t × g)
Relative water loss of excised leaf	0.0008	1.40**	0.001	0.07**	0.0033**	0.0002
Chlorophyll 'a'	0.0002	0.618**	0.00005	0.0020**	0.0030**	0.00005
Chlorophyll 'b'	0.0002	0.084**	0.00006	0.0009**	0.0002**	0.00007
Leaf carotenoids	0.0006	0.062**	0.00005	0.0010**	0.0004**	0.00003
Water potential	0.0010	4.120**	0.0090	0.0250**	0.0040**	0.0005
Osmotic potential	0.0040	0.875**	0.0001	0.0840**	0.0120**	0.0020
Turgor potential	0.0013	1.048**	0.0080	0.0170**	0.0080**	0.0020
Proline	0.0044	0.891**	0.0002	0.0880**	0.0140**	0.0030
Canopy Temperature	0.0650	30.64**	0.0700	1.5100**	0.0600**	0.0900
Grain wt. plant^{-1}	0.0400	1689.79**	0.0030	4.9000**	11.5900**	0.1500

Table 3. Generation means and heritability estimates of some physiological traits and yield in wheat sown under two moisture regimes.

Under Normal Irrigation								
Plant Traits	m ± S.E	[d] ± S.E	[h] ± S.E	[i] ± S.E	[j] ± S.E	[l] ± S.E	χ^2 (df)	h^2ns
Relative water loss of excised leaf	0.56±0.01	0.48±0.01			-0.29±0.04		3.36(3)	0.60
Chlorophyll 'a'	1.59±0.03	0.032±0.01	-0.05±0.01		-0.09±0.02		3.82(2)	0.24
Chlorophyll 'b'	0.53±0.05	0.12±0.01	0.04±0.01		-0.06±0.03		1.46(2)	0.64
Leaf carotenoids	0.46±0.02	0.04±0.001			-0.06±0.02		4.60(3)	0.48
Water potential	1.08±0.09	0.06±0.01	0.08±0.02		-0.10±0.04		4.01(2)	0.36
Osmotic potential	1.98±0.01	0.05±0.01	0.11±0.02		-0.16±0.06		2.51(2)	0.49
Turgor potential	0.89±0.05	0.05±0.014					5.35(4)	0.70
Proline	1.24±0.06	0.54±0.01					1.63(4)	0.73
Canopy temperature	27.13±0.74	0.67±0.07	-7.48±1.92	-2.83±0.74		4.78±1.26	1.74(1)	0.65
Grain wt. plant^{-1}	17.31±0.12	0.64±0.14	0.67±0.22		-2.65±0.66		4.31(2)	0.76
Under Water stress								
Relative water loss of excised leaf	0.52±0.07	0.182±0.01	0.06±0.01		-0.45±0.04		0.86(2)	0.60
Chlorophyll 'a'	1.3±0.06	0.162±0.04		-0.04±0.01	-0.25±0.02		4.18(2)	0.64
Chlorophyll 'b'	0.47±0.04	0.12±0.01				0.04±0.01	4.16(3)	0.33
Leaf carotenoids	0.38±0.03	0.05±0.01	0.05±0.01		-0.11±0.02		2.22(2)	0.68
Water potential	1.76±0.01	0.05±0.01	0.05±0.01		-0.14±0.05		3.85(2)	0.61
Osmotic potential	2.38±0.01	0.12±0.02					1.22(4)	0.71
Turgor potential	0.55±0.09	0.014±0.01	0.17±0.02				2.50(3)	0.39
Proline	3.51±0.41	1.67±0.53		0.72±0.16			3.13(3)	0.76
Canopy temperature	26.19±0.04	0.77±0.064					7.10(4)	0.70
Grain wt. plant^{-1}	6.16±0.18	1.48±0.05	1.08±0.24	-0.60±0.19	-1.84±0.32		1.55(1)	0.73

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, h^2ns = Heritability in narrow sense.

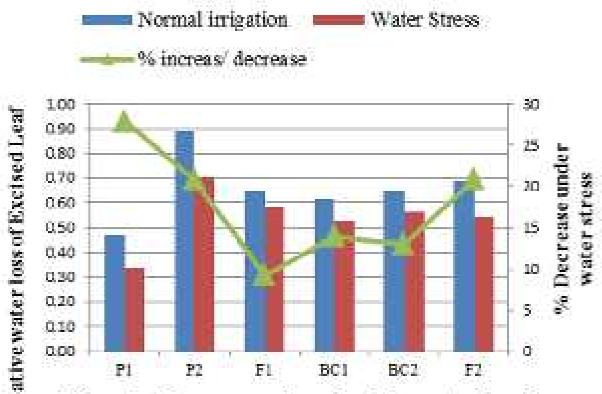

Figure 1: Mean comparison of relative water loss of excised leaf for six generations along with % increase and decrease

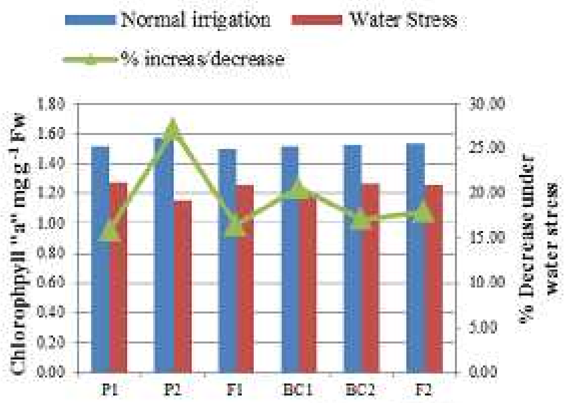

Figure 2: Mean comparison of Chlorophyll "a" for six generations along with % increase and decrease

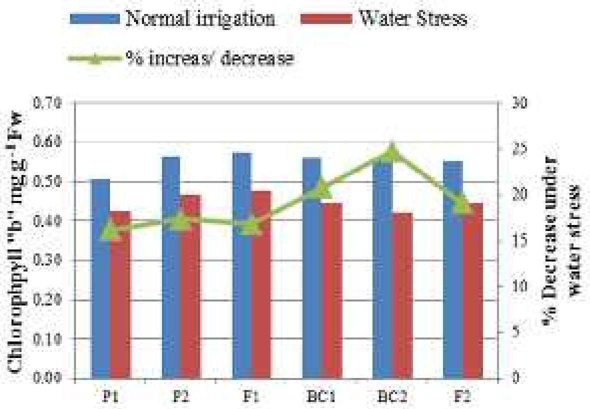

Figure 3: Mean comparison of Chlorophyll "b" for six generations along with % increase and decrease

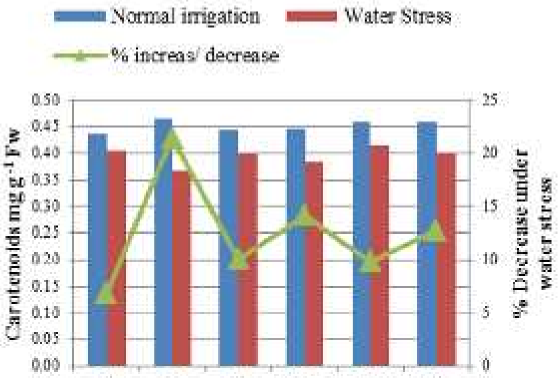

Figure 4: Mean comparison of Leaf Carotenoids for six generations along with % increase and decrease

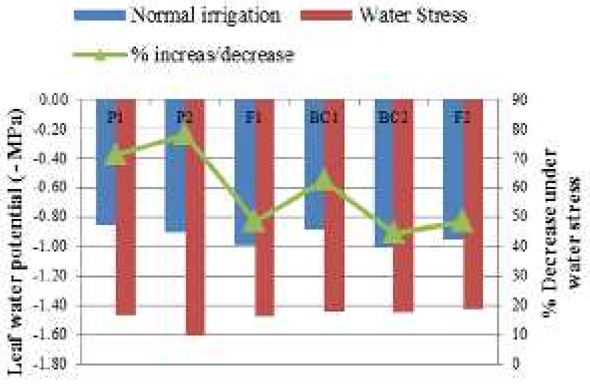

Figure 5: Mean comparison of Water Potential for six generations along with % increase and decrease

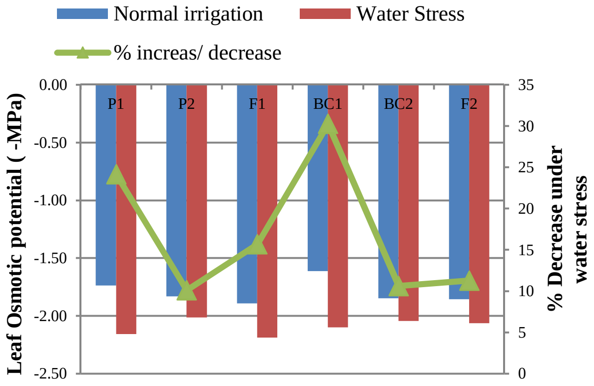

Figure 6: Mean comparison of Leaf Osmotic Potential for six generations along with % increase and decrease

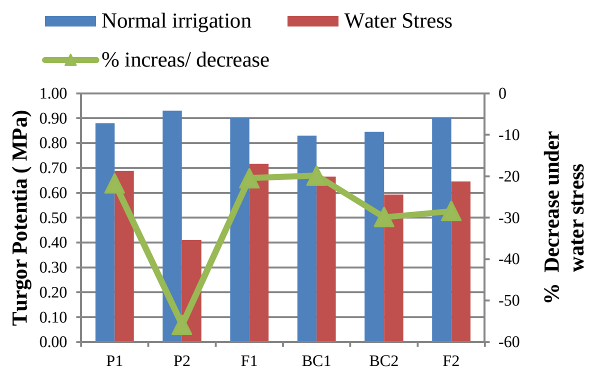

Figure 7: Mean comparison of Leaf Turgor Potential for six generations along with % increase and decrease

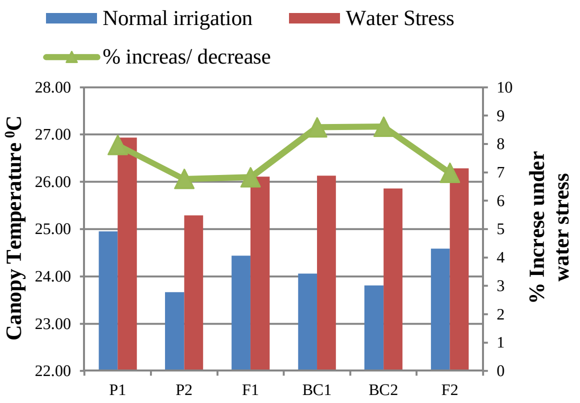

Figure 8: Mean comparison of Canopy Temperature for six generations along with % increase and decrease

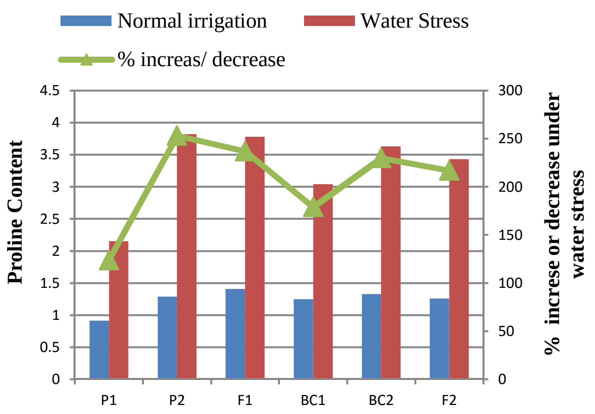

Figure 9: Mean comparison of Proline for six generations along with % increase and decrease

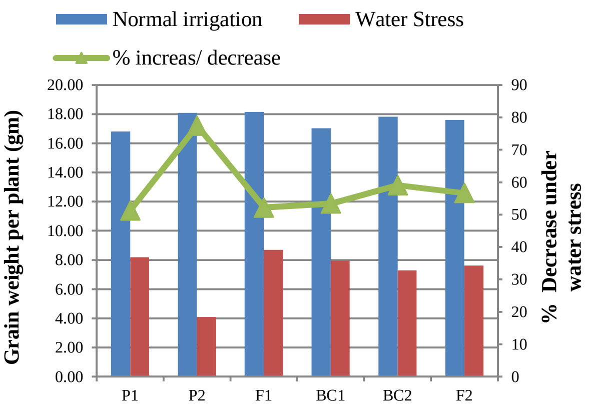

Figure 10: Mean comparison of grain weight perplant for six generations along with % increase and decrease

Conclusion: The presence of fixable genetic nature supported by high heritability for the physiological variables like osmotic potential, proline and canopy temperature provides an opportunity for early generation selection in these traits for tailoring drought tolerance in wheat genotypes. Previously plant breeders have mainly focused on the yield and yield related components and generation after generation selection has not only narrow down the genetic base but at the same time further improvement has become dawdling under stressful environment. This study suggests that yield enhancement can be achieved by breeding physiologically stable and efficient genotypes for stress prone areas.

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