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GENERATION MEAN ANALYSIS FOR DIFFERENT MORPHO-PHYSIOLOGICAL PARAMETERS OF MAIZE SEEDLING UNDER DIFFERENT REGIMES OF WATER

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ABSTRACT

Maize being the leading cereal grain crop is widely used throughout the world including Pakistan. About thirty-three percent of world's arable land experiences a deficiency of water and the greatest harvest yields are frequently decreased by dry spell. The current research was considered to examine the genetic traits governing the drought tolerance of morphological and physiological parameters during the seedling stage in maize. The breeding stock consisted of two parental lines, YP12 and US-17 with variable traits concerning their ability to bear water shortage and their succeeding generations F_1 and F_2 along with back crosses (BC_1 and BC_2). The combined analysis of variance for all traits yielded significant differences among generations and water treatments suggesting the presence of a wide range of genetic variability. Relative water contents, leaf water potential, osmotic potential and turgor potential decreased under water stress environment. All morphological parameters like root and shoot length, fresh root and shoot weight and dry root and shoot weight exhibited a decrease in response to water stress. Dry shoot weight, turgor potential and osmotic potential under water stress have additive nature suggesting that early selection based on one of these traits may also complement the other resulting in the development of better-yielding maize material for stress tolerance. Further, root characters such as root length, fresh and dry weight can play a crucial role in efficiently evaluating the maize genotypes to drought stress during the seedling stage.

Key words: Epistasis, Dominance, Genetic basis, Maize, Drought tolerance

INTRODUCTION

Maize being the leading cereal grain crop is widely used for corn syrup, flakes, corn oil, gluten etc. in the world including Pakistan. Additionally, it is also grown for fodder and silage purposes. Several abiotic stresses such as drought, reduce the growth and yield of plants below the optimal level (Cramer *et al*., 2011). About thirty-three percent of the world's arable land experiences a deficiency of water and the greatest harvest yields are frequently decreased by dry spells (Khan *et al*., 2004). It is an unavoidable and frequent feature of agriculture in the world as well as in Pakistan. Despite noticeable improvements in agriculture, climate plays a significant role in agriculture production. Considering the climate changes and increasing threat of global warming in areas where frequent and severe droughts are expected, enhancing the tolerance of the crops to water shortage through the use of drought tolerance cultivars is considered the cost-effective and most efficient technique to combat the impact of drought stress, particularly in low-value cropping systems (Shankar *et al*., 2022).

The severity of the negative impact caused by drought increased when it happened simultaneously during the process of germination and seedling growth (Tsago *et al*., 2014 and Khayatnezhad *et al*., 2010). The phenotypic expressions of seedling traits are reduced due to the effects of water stress (Avramova *et al*., 2016). Drought tolerance screening often involves the utilization of shoot and root growth, which are susceptible to inhibition under a water stress environment (Kaydan and Yagmur, 2008; Li *et al*., 2014). During the initial phases of cultivation, water stress conditions lead to a notable reduction in the rate of seed germination and an increase in the mortality of seedlings. To attain improved crop growth and yield, it is essential to assess the ability of seedlings to tolerate water stress conditions during their early growth stage, as it aids in predicting favorable crop growth at maturity (Meeks *et al*., 2013). Hence, biometric characteristics during the initial growth phases can serve as selecting criteria to enhance crop resilience to drought (Blum, 2011; Comas *et al*., 2013). The use of various seedling growth and germination indices as predictive measures in crop screening for drought tolerance is often backed by supporting evidence (Queiroz *et al*., 2019; Khan *et al*., 2016; Shamim *et al*., 2014; Obidiegwu *et al*., 2015).

Understanding the genetic regulation and mechanism of drought tolerance is critical for maize, as it appears to be less adapted to water deficit environment. Generation mean analysis, a biometrical method developed by Mather and Jinks, (1982) is a valuable method for assessing genetic effects which are related to polygenic traits with its greatest benefit being the competence to estimate epistatic genetic effects such as additive × additive [i], additive × dominance [j] and dominance × dominance [l] interactions (Singh and Singh, 1992).The present research aims to offer essential information regarding the performance of both parents and their crosses during the seedling stage which could be served as a reference for selecting parents and designing a breeding strategy in the future.

MATERIALS AND METHODS

The research material comprised maize inbred lines (YP-12 and US-17) serving as the parents (P_1, P_2) and their filial generations (F_1, F_2, BC_1 and BC_2). Parents were selected based on distinctiveness in response to water stress. Inbred line YP-12 as tolerant parent (P_1) with maximum dry root weight and relative water content while inbred line US-17 as susceptible parent (P_2) with lowest dry root weight and relative water content under water stress environments (Saleem *et al*., 2020). During spring 2021, these two genotypes were sown under normal field environments and the cross was attempted to obtain first filial generation (F_1) seed. During Autumn 2021, an experimental field was planted with the parents as well as one hundred twenty F_1 plants. Half of the F_1 plants were selfed to develop second filial generation (F_2) whereas sixty remaining plants (thirty each) were crossed with YP-12 (P_1) and US-17 (P_2) to develop back crosses BC_1 and BC_2, respectively.

During February 2022, two sets each having the generations (P_1, P_2, F_1, BC_1, BC_2, and F_2) were planted in polyethene bags (18 × 9 cm) filled with pre-washed equal quantities of sand in two-factor factorial completely randomized design with three repeats under water stress and normal environments in the wire house of College of Agriculture, University of Sargodha. Two seeds of each generation were planted at a uniform depth of 2.5 cm at 18 % moisture level. Humidity and temperature ranged from 49.3 % to 58.4 % and 20.3°C to 25.1°C during the whole experiment. Ten seedlings of P_1, P_2 and F_1each, twenty seedlings of BC_1 and BC_2 each and fifty seedlings of F_2 were maintained in each replication under both normal and water-stress environments. Hoagland solution (140ml) was applied to both treatments after seven days of sowing. However, following two weeks from planting, the same quantity of distilled water was solely applied to the normal set. Upon the completion of the third week, irrigation was administered to both treatments before uprooting the seedlings. Seedlings were gently washed with water to remove sand and then wrapped in blotting paper for 10 minutes to remove the surface water. Measurements were taken for various parameters including relative water content, water potential, osmotic potential, turgor potential, shoot length, root length, fresh shoot weight, fresh root weight, dry shoot weight and dry root weight during the experiment and at the end of the experiment. Relative water content was measured by the formula and procedure described by Malik and Wright, (1995), whereas, leaf water potential and osmotic potential was recorded according to the procedure described Ashraf *et al*., (1994). Leaf turgor potential was determined by subtracting the values of osmotic potential from the values of leaf water potential Saleem *et al.*, (2016).

Statistical Analysis: The recorded data was analyzed for variances using the method given by Steel *et al*., (1997) and generation means were analyzed using SAS® 9.4 (SAS, 2014).

RESULTS AND DISCUSSION

The availability of genetic variation within the breeding material is a major determining factor of any breeding program. To determine the variation among various physiological and morphological parameters in water-stressed environments, a recent study was conducted. This information is crucial in the development of comprehensive maize breeding strategies for water stress conditions in the future.

The pooled analysis of variance for seedling's physiological and morphological characteristics for parents (P_1 and P_2) and segregating (F_1, F_2, BC_1 and BC_2) was significant (Table 1) indicating the presence of extensive variability. This variation suggested presence of an extensive range of quantitative trait loci influencing numerous traits in both the parental lines and subsequent generations (Saleem *et al*., 2016b; Sehar *et al*., 2015). The presence of such differentiating behavior was also recorded by Saleem *et al*., (2016a).

Table 1. Mean squared values obtained from pooled analysis of variance for seedling characteristics.

	Generations	Treatments	T×G	Error
Relative Water content	0.03^{**}	0.021^{**}	0.0002^{*}	0.002
Water Potential	0.026^{**}	4.221^{**}	0.0121^{**}	0.0004
Osmotic Potential	0.095^{**}	0.796^{**}	0.0115^{**}	0.003
Turgor Potential	0.015^{**}	1.052^{**}	0.0092^{**}	0.003
Shoot length	30.86^{**}	402.41^{**}	0.71^{*}	0.25
Root length	49.80^{**}	240.96^{**}	1.25^{**}	0.20
Fresh shoot weight	19.84^{**}	71.18^{**}	0.21	0.09
Dry shoot weight	25.09^{**}	50.08^{**}	0.93^{**}	0.06
Fresh root weight	3.45^{**}	14.34^{**}	0.45^{**}	0.03
Dry root weight	16.15^{**}	27.73^{**}	0.02	0.05

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

Seedling's physiological and morphological characteristics were noticeably affected by drought stress (Figs. 1-10) and it also influenced the gene expression. The study revealed that the expression of genes was influenced by the physiological response of the plant and its surrounding environmental conditions. Physiological changes induced by stress have also been found to affect gene expression (Saleem *et al*., 2016a). Relative water contents, leaf water potential, osmotic potential and turgor potential decreased under water stress environment (Fig.1-4). Maximum reduction of 33 % from normal environment for relative water contents was recorded in Parent line US-17 (P_2) which exhibited its sensitivity to water stress environment while a minimum reduction was observed in BC_1 generation (Fig.1). Maximum reduction of 30.17% in leaf water potential (Fig.2) and 27.5% in turgor potential (Fig. 4) was detected in Parent Line US-17 (P_2) whereas 11.81% reduction in osmotic potential (Fig. 3) from the normal environment was observed in F_2 generation, which demonstrated sensitivity and intolerance to the water shortage. While all generations and P_1 exhibited improved tolerance to the stress environments. When solutes build up inside a cell, it leads to osmotic adjustment. This adjustment reduces the cell's osmotic potential and aids in preserving the turgor potential of plants experiencing water stress (Sayar *et al*., 2008). This compensation mechanism aids in the survival of the plants during times of escalating and diminishing soil moisture levels by preserving the critical potential difference required for water uptake through the roots.

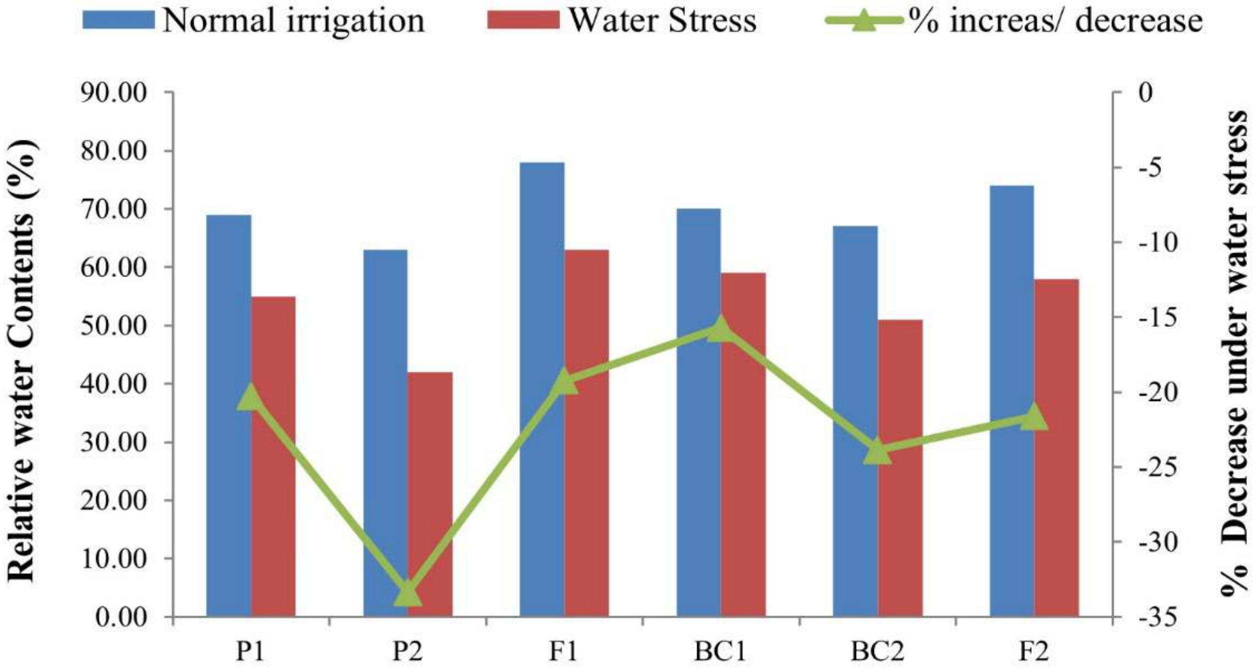

Fig. 1: Performance of parents and generations under irrigated and water stress conditions for relative water contents

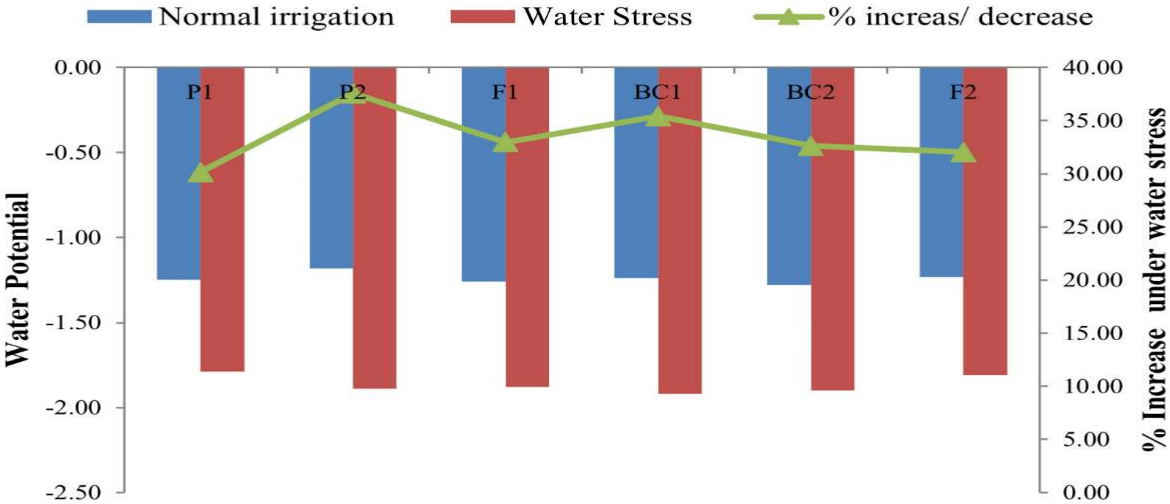

Fig. 2: Performance of parents and generations under irrigated and water stress conditions for water potential

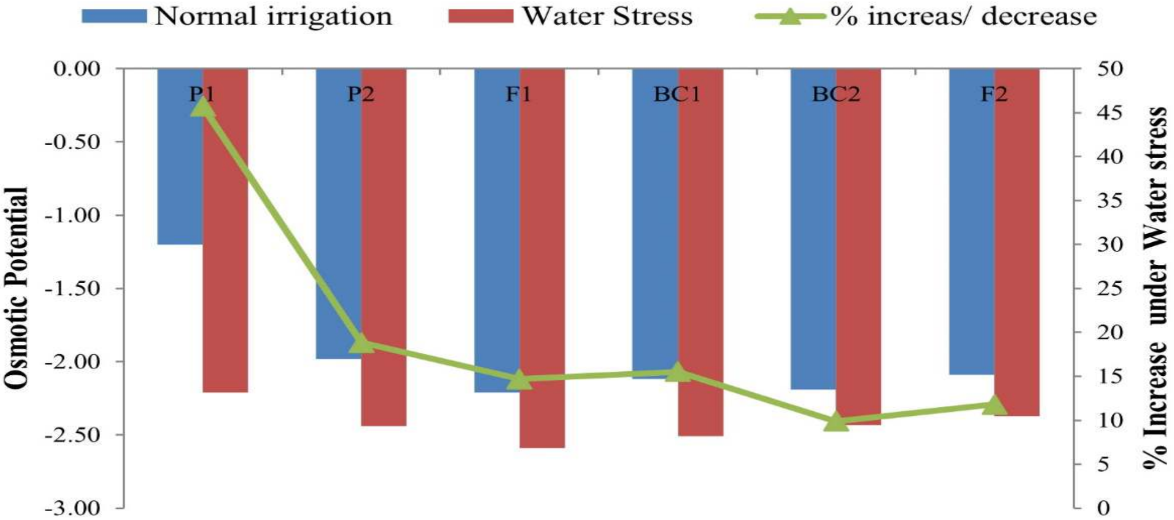

Fig. 3: Performance of parents and generations under irrigated and water stress conditions for osmotic potential l

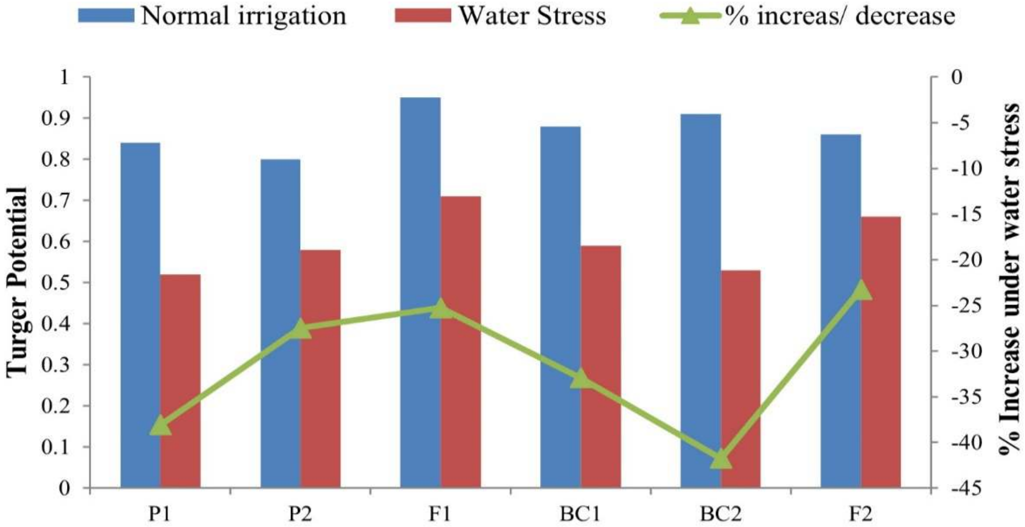

Fig. 4: Performance of parents and generations under irrigated and water stress conditions for turger potential

All of the seedling's morphological parameters investigated exhibited a decrease in response to water stress which was also confirmed by Saleem *et al*., 2020 during studies on seedling parameters under water limited environment. Parental line P_2 (US-17) exhibited a maximum reduction in shoot length (32%) and root length (37%) than the normal environment which showed its sensitivity to the water stress environment, While Parental line P_1 (YP-12) showed a minimum reduction (Fig. 5-6). All remaining generations (F_1, F_2, BC_1 and BC_2) showed a reduction between these two generations (parents). Water stress inhibits cell expansion and division, leading to a decrease in shoot and root elongation. Under water deficit conditions, the growth of meristematic cells is affected, resulting in shorter shoots and roots (Zhu, 2002). Plants may experience an imbalance between the production of reactive oxygen species (ROS) and their detoxification mechanisms under water stress environment. ROS accumulation causes oxidative stress and damage cellular structures, leading to reduced shoot and root growth (Mittler, 2002). Fresh shoot and dry shoot weight also showed a reduction in all generations under water stress environment (Fig. 7-8). A maximum reduction of 41 % was recorded for parental line P_2 (US-17) for fresh shoot weight whereas maximum reduction of 52% for dry shoot weight was observed in BC_1 generation. When faced with drought conditions, the plant undergoes a reduction in leaf area and leaf number as well as plant height while increasing the growth of roots. (Ali *et al*., 2011; Schuppler *et al*.,1998). BC_1 generation exhibited minimum reduction of 24 % for fresh shoot weight whereas 35% reduction of dry shoot weight was recorded for BC_2 generation. Like shoot fresh and dry weight, fresh root and dry root weight also decreased in all the generations (Fig. 9-10). A maximum reduction of 56 % was recorded for parental line P_2 (US-17) for fresh root weight whereas maximum reduction of 35% for dry root weight was observed in BC_1 generation. Root growth was significantly hampered, as it obstructed their ability to penetrate the dry soil and decreased their respiratory efficiency (Ali *et al*., 2011; Thomas and Howarth, 2000). BC_2 generation exhibited minimum reduction of 23 % for fresh root weight whereas 23% reduction of dry root weight was recorded for Parental line P_2 (US-17). Water stress limits the availability of water in soil, which subsequently affects the uptake of essential nutrients by the roots. Inadequate nutrient absorption negatively impacts plant growth and leads to reduced shoot and root weight (Chaves *et al*., 2008). Similarly, water stress also affects the stomatal conductance of plants leading to reduced carbon dioxide uptake and subsequently decline in photosynthetic activity. This decrease in photosynthesis results in reduced biomass accumulation and lower shoot and root weight (Flexas *et al*., 2002).

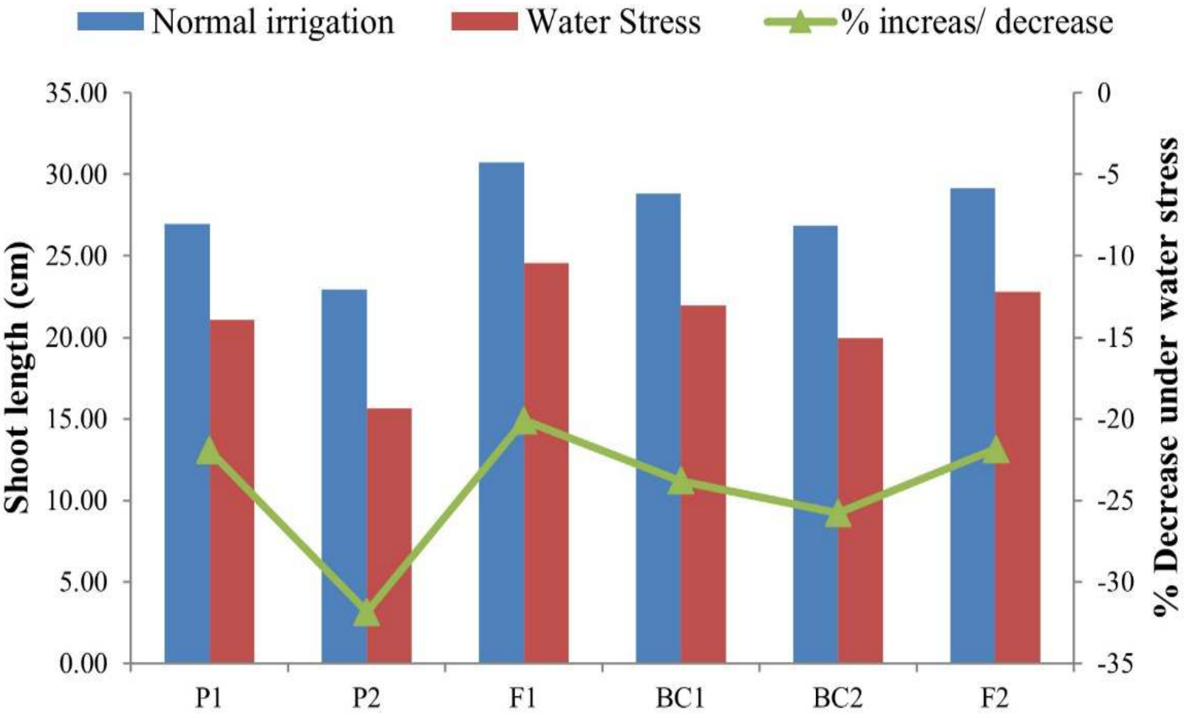

Fig. 5: Performance of parents and generations under irrigated and water stress conditions for shoot length

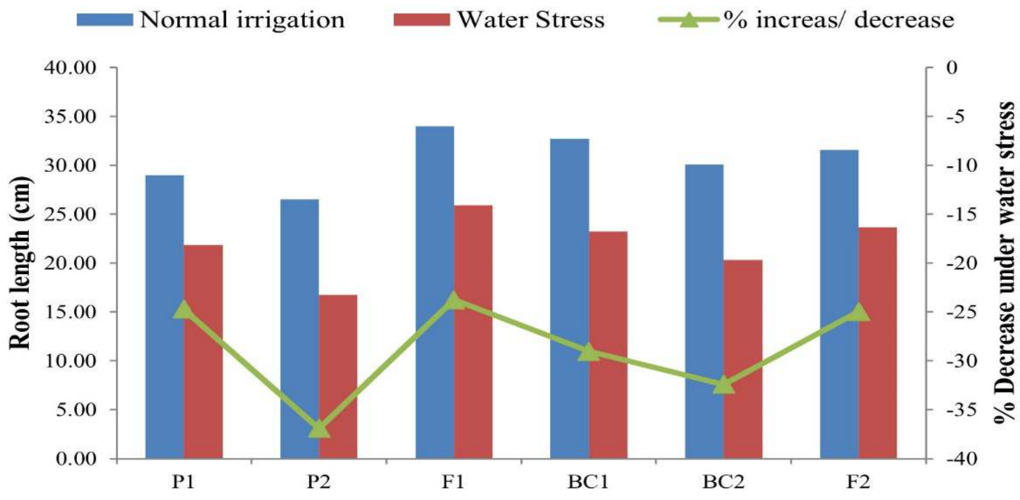

Fig. 6: Performance of parents and generations under irrigated and water stress conditions for root length

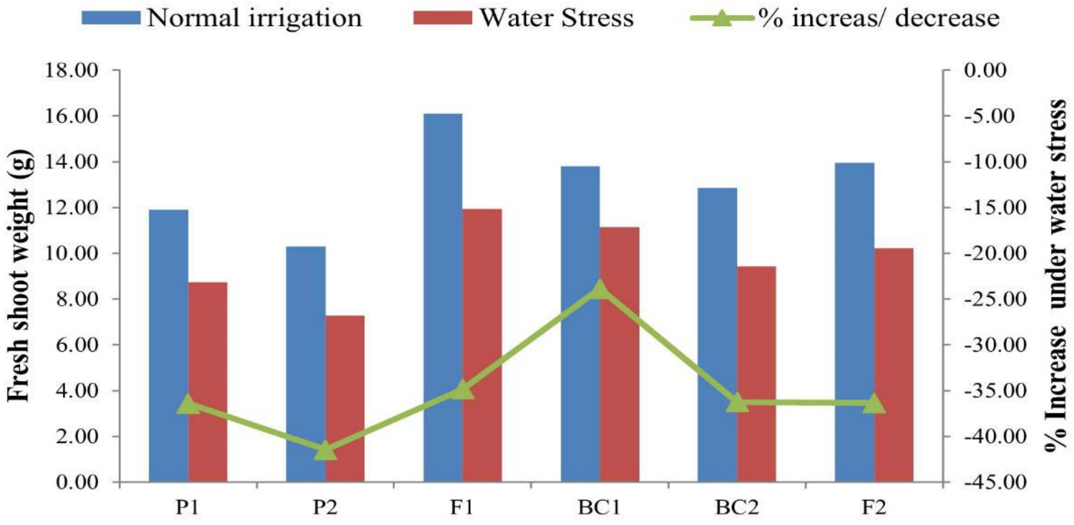

Fig. 7: Performance of parents and generations under irrigated and water stress conditions for fresh shoot weight

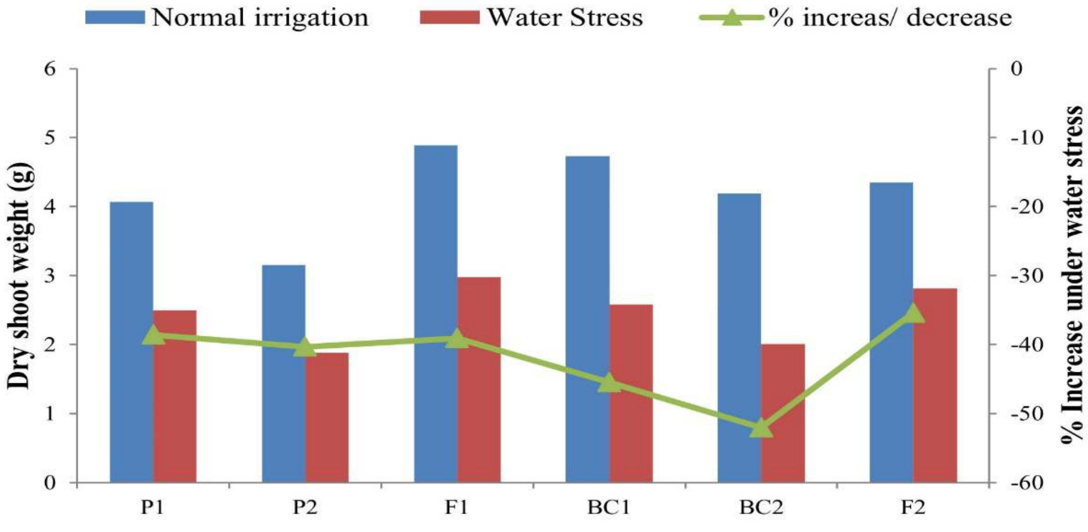

Fig. 8: Performance of parents and generations under irrigated and water stress conditions for dry shoot weight

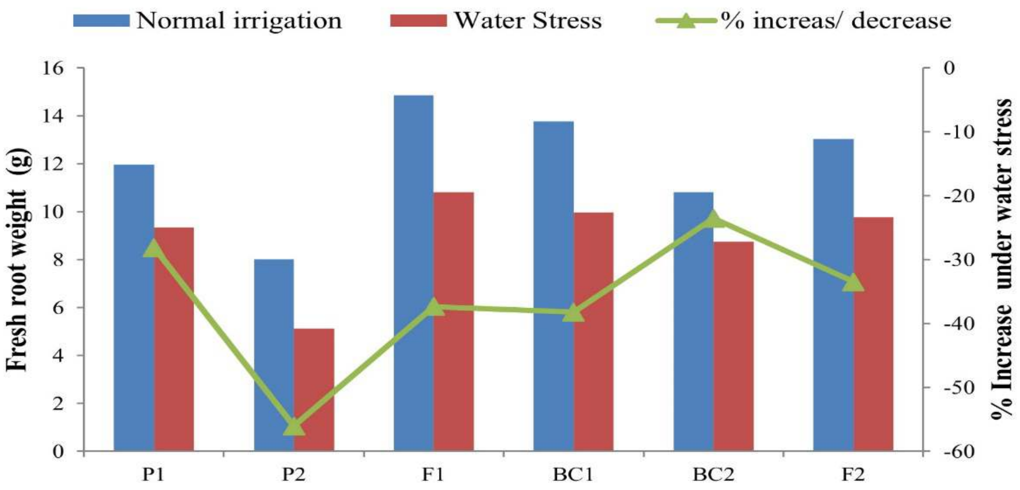

Fig. 9: Performance of parents and generations under irrigated and water stress conditions for fresh root weight

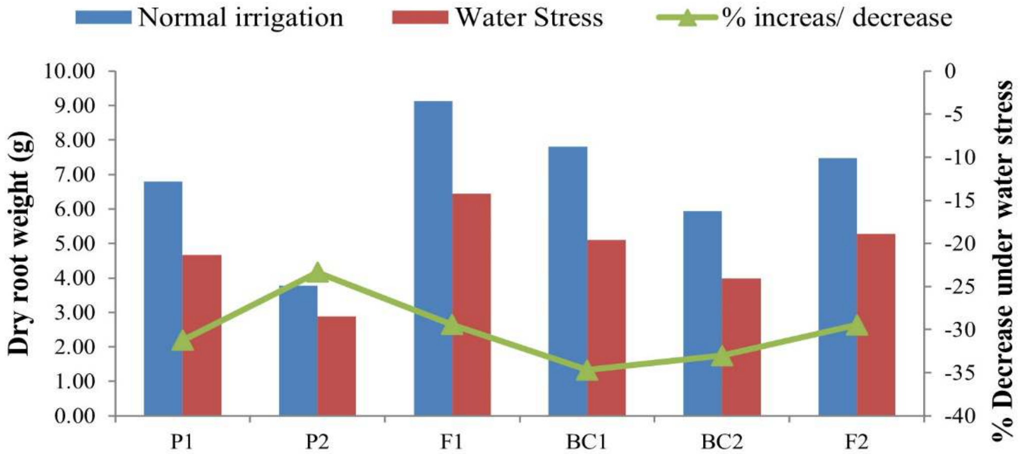

Fig. 10: Performance of parents and generations under irrigated and water stress conditions for dry root weight.

The genetic analysis of parents, generations and back crosses showed that the studied parameters are under the effect of both dominant and additive gene action along with variable degree of epistasis in almost all the parameters under study, except relative water content under non stress regime. (Table 2). Relative water content was found under the influence of fixable additive genetic component and three-parameter model under both moisture regimes. The substantial size of fixable additive component shows that selection for relative water content can be carried out in studied material to fix the trait.

Complex gene action was found responsible for the control of water potential under stress conditions with five-parameter model [mdhij] controlling the expression of the trait. Although fixable additive [d] component shared a reasonable portion in the appearance of the character, the presence of high degree of duplicate epistasis [i] and non-fixable additive x dominant [j] may hinder the process of selection. Under the non-stress regime four-parameter model [mdhj] controlled the expression of water potential in studied generations with a high degree of contribution from additive x dominant [j] component of inheritance suggesting a delay in selection. The control of osmotic potential and turgor potential under a water stress regime was primarily controlled by additive genetic component [d] and its corresponding additive x additive epistemic component [i] whereas the dominant [h] showed meager magnitude indicating additive nature of the traits and hence selection can yield better results (Saleem *et al*., 2016a). A Four-parameter model [mdhj] was found to be the optimal explaining the genetic variation of osmotic potential under anon-stress regime whereasa five-parameter model [mdhjl] controlled the expression of turgor potential. The high magnitude of epistasis observed in both osmotic and turgor potential suggests a potential delay in the process of selection (Saleem *et al*., 2016b).

A higher magnitude of non-fixable genetic [h] and its corresponding epistatic factor [l] under both regimes advocated the presence of complementary gene

Table 2. Generation mean analysis for morpho-physiological parameters of maize seedling under two different water regimes.

Traits	**Genetic effects**						
	M	**[d]**	**[h]**	**[i]**	**[j]**	**[l]**	**χ2 (df)**
Normal							
Relative Water content	0.75±0.08	1.101±.12	0.09±0.07	-	-	-	0.354(3)
Water Potential	1.33±0.13	1.18±0.04	0.18±0.04	-	0.90±0.12	-	0.311(2)
Osmotic Potential	1.73±0.02	0.92±0.06	0.61±0.04	-	0.80±0.02	-	0.031(2)
Turgor Potential	0.98±0.09	0.65±0.024	0.25±0.015	-	0.90±0.081	0.60±0.055	0.121(3)
Shoot length	27.98±0.49	-1.18±0.22	3.159±0.65	-	-	1.035±0.18	0.468(2)
Root length	29.06±0.43	1.595±0.21	5.165±0.48	-1.76±0.39	-	-	1.035(2)
Fresh shoot weight	10.83±0.16	-1.03±0.09	3.976±0.26	-	-1.37±0.35	-	0.807(2)
Dry shoot weight	3.58±0.12	-0.74±0.18	1.782±0.26	-0.13±0.09	-	-	0.267(2)
Fresh root weight	12.09±0.18	1.812±0.08	0.43±0.43	-1.25±0.33	-	3.075±0.28	0.758(1)
Dry root weight	7.12±0.08	1.89±0.13	0.839±0.23	-1.48±0.13	-	1.178±0.33	0.715(1)
Water deficit condition							
Relative Water content	0.68±.25	0.29±0.15	-	1.09±0.25	-	-	0.235(3)
Water Potential	1.43±0.09	0.58±0.03	0.25±0.02	-0.45±0.02	0.64±0.08	-	0.357(2)
Osmotic Potential	1.38±0.05	0.72±0.02	0.38±0.09	0.65±0.035			0.412(3)
Turgor Potential	0.91±0.09	0.94±0.08	0.12±0.07	0.35±0.015			0.035(3)
Shoot length	19.95±0.19	-1.14±0.17	3.913±0.32	-	-	1.124±0.21	0.541(2)
Root length	26.15±0.15	3.12±0.17	1.09±0.12	-3.68±0.25	-	2.45±0.28	0.917(1)
Fresh shoot weight	8.79±0.35	0.832±0.19	2.892±0.63	-	-1.11±0.38	-	1.237(2)
Dry shoot weight	4.79±0.53	1.139±0.54	4.154±1.05	-	-	-	0.485(3)
Fresh root weight	9.93±0.24	1.183±0.08	0.773±0.27	-2.14±0.17	-	1.168±0.34	0.318(1)
Dry root weight	5.03±0.09	1.73±0.19	1.064±0.15	-1.67±0.25	-	2.03±0.14	0.832(1)

action. Higher magnitude of dominance [h] genetic effects in comparison to additive genetic effects proposed that shoot length might be utilized for hybrid maize improvement program in both normal as well as water deficit regimes. Complex gene action was found responsible for the control of root length under stress conditions with a five-parameter model controlling the expression of the trait. Although fixable additive [d] component contributed a reasonable portion to the expression of the trait, the presence of a high degree of duplicate epistasis [i] may hinder the process of selection, however the dominate [d] was complimented by its corresponding epistasis [l] with a reasonable magnitude. A comparable behaviour was conveyed by Haq *et al.*, 2015 showing the complex nature of root length in which both the fixable and non-fixable components of inheritance were controlling the trait. Under normal irrigation condition, dominant [d] component was found to have significant control over the trait, predicting better results if the material is used for hybrid development. Under both water regimes, a four-parameter model [mdhj] controls the expression of fresh shoot weight. Values of non-fixable [h] genetic effects were observed higher in comparison to the additive [d] genetic component in both water treatments. Non-fixable epistatic component [j] was found negative under stress and normal regimes. Haq *et al.*, (2015) also reported that fresh shoot weight was controlled by non-fixable genetic factors. However, Khotyleva and Lemesh, (1994) and Akbar *et al.*, (2009) advocated that both additive and non-fixable factors of the model were accountable for transmission of this parameter. Wang *et al.*, (2000) described the importance of additive component for fresh shoot weight inheritance. A significantly higher value of non-additive genetic component [h] under water-limited regimes pointed out that the character might be exploited to develop hybrids for water shortage environments. Three parameters [mdh] were responsible for the inheritance of dry shoot weight under stress regimes as compared to normal water regimes where the trait was under the influence of four parameters [mdhi]. Magnitude of non-fixable genetic components was greater under both water treatments as compared to the fixable [d] main component suggesting that the effects of [h] components had a vital role in the inheritance of dry shoot weight. Genetic variation for fresh root weight was controlled by five parameter model [mdhil] under both the moisture regimes but the contribution of genetic effects varied with the environment. The contribution of the additive portion remained almost the same however the share of dominant and epistatic components of inheritance increased under water stress environment. In this situation either selection may be delayed or a reciprocal recurrent selection method may be used for selection (Haq *et al.*, 2015). Complex gene action was found responsible for the control of dry root weight under both regimes with a five-parameter model [mdhil] controlling the expression of the trait. Fixable genetic components were more as compared to non-fixable genetic components but due to the complementary genetic behaviour of non-fixable components it is smarter to defer the selection till further generations. The existence of additive components (Haq, 2014; Akbar *et al.*, 2008) whereas the impact of non-additive and additive factors for the transmission of dry root weight was reported by Khan, (2014). Every character can be attributed to a combination of both its genotype and the environment in which it develops. Therefore, the differences observed in a character can be traced back to variations in both the genetic material and the environmental factors that influence its development.

Conclusion: Assessing basic physiological (water potential, osmotic potential) and morphological characteristics of roots such as length and fresh & dry weight can play a crucial role in efficiently evaluating the maize genotypes to drought stress during the seedling stage. Furthermore, the utilization of hybridization and the adoption of a recombinant breeding strategy may pave the way for the creation of drought-tolerant genotypes.

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