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ORIGINAL ARTICLE

Genetic interaction and inheritance of biochemical traits can predict tolerance of hybrid maize cv. SC704 to drought

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Abstract

To study gene action and inheritance of some biochemical traits generation mean and generation variance analyses of basic seven generations B73 (as maternal line), MO17 (as paternal line), F_1, F_2, F_3, BC_1, and BC_2 were conducted at the University of Tabriz agricultural research station (NW-Iran) in 2017. The generations were sown in PVC pipes using a RCBD with 20 replications under three water regimes (100% FC, 55% and 75% available water depletion). The results revealed that based on percent increase of polyphenol oxidase, soluble sugars and proline, SC704 and MO17 were ranked as resistant (enhancement 41.39%, 58.39% and 55.47% in SC704 and 34.25%, 53.75% and 64.51% in MO17, respectively) under severe stress condition. Pearson's correlation and principal component analysis indicated polyphenol oxidase activity most correlated with proline and soluble sugars and suggest that the important role of these traits in antioxidative defense mechanisms. The findings of the generation mean analysis implied the existence of digenic interactions. The prevalence of dominance variance and low narrow-sense heritability (0.07–0.47) for catalase, peroxidases, and polyphenol oxidase activities under severe stress condition suggest the utilization of a hybrid breeding program such as heterosis and selection in the later generation to facilitate breeding for improvement of these traits. In contrast, additive genetic variance and high narrow-sense heritability (0.53–0.71) for protein content, proline concentration and soluble sugars under severe stress condition revealed that the selection in the parents' inbred lines or early segregating generations could be useful to improve the aforementioned traits in the maize.

Keywords Additive and dominance variances · Biochemical traits · Generation mean analysis · Heritability · Maize (*Zea mays* L.) · Water deficit stress

Introduction

The global demand for maize as one of the three leading global cereals, will increase to 50% by 2050 (Ignaciuk and Mason-D'Croz 2014). One of the most critical environmental factors is water deficit stress that affects maize yield adversely (Nelson et al. 2007; Nuccio et al. 2015). According to FAO (2016) the maize production has been reduced to 31% in 2016 compared to 2015 due to drought stress. Then, the study of maize capacity to tolerate abiotic stress such as drought is one of the most important goals of maize breeding programs because maize yield is very susceptible to abiotic stresses (Wattoo et al. 2009). Drought stress in plants not only reduce the yields of crops but also cause of leaf senescence, mechanical damage, excessive transpiration and imbalance which leading to deficiency or malfunction in plants (Cramer et al. 2011).

The maize genotype that known as the ideal genotype should have both high average yield and high stress tolerance

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(Bányai et al. 2020). It is worth to mention that MO17 was ranked as resistant inbred line based on proline, fresh weight and glycine betaine which has been reported by Moharramnejad et al. (2015) and grain yield and morphological traits which has been documented by Kravić et al. (2016) under drought stress. Also, B73 was demonstrated as sensitive inbred line to water stress based on relative water content of leaf (Chen et al. 2012).

Crops display various mechanisms of physiological and biochemical levels to withstand drought stress conditions (Fang and Xiong 2015). The reactive oxygen species (ROS) such as (singlet oxygen, $^1O_2$; superoxide, O_2^-; hydrogen peroxide, H_2O_2; hydroxyl radical, OH^-) are generated through normal cellular metabolism, but drought stress causes increase of ROS production (Moller et al. 2007; Gharibi et al. 2016). Accumulation of ROS causes toxicity, peroxidation of cellular membranes, synthesis and expression of compatible solutes such as proline, carbohydrate metabolism, oxidation of proteins, lipids peroxidation (Miller et al. 2010; Liu et al. 2015; Zhang et al. 2018).

Maintaining of the balance between the ROS generation and scavenging are undertaken by different antioxidant enzymes (superoxide dismutase, catalase, and peroxidases), and non-enzymatic antioxidants (Gill and Tuteja 2010). Under abiotic stress, the antioxidant enzymes respond towards the reduction of oxidative stress (Talaat 2014). In addition, polyphenol oxidase has a substantial contribution in the control of oxidative processes (Rachkovskaya and Kim 1980; Voskresenskaya 2006). Polyphenol oxidases (PPOs) enzymes able to catalyze the oxidation of diphenols to o-diquinones in the presence of oxygen (Mayer 2006). According to Thipayong et al. (2004) and Taranto et al. (2017), there is a high correlation between drought resistance and PPO expression. Recent studies have indicated that PPOs have a role in the Mehler reaction. Indeed, the contribution of PPOs in the Mehler reaction causing plants with high PPO, have improved stress tolerance (Boeckx et al. 2015a, b). In addition, PPOs have more other roles including contribution in cell division and primary differentiation (Van Huystee and Cairns 1982), electron cycling, regulation of oxygen levels (Vaughn and Duke 1984) and other physiological processes. Overexpressing of certain enzymes can enhance water deficit tolerance; however, they may delay in germination that reduces development of the plants which causing interference with the growing season. Overall, for improving of water stress tolerance in plants requires strategies which target a few pathways of metabolic simultaneously. According to the stress intensity and duration, other stress markers such as compatible solutes often increase along with the activity of the antioxidant systems (Laxa et al. 2019).

When the maize is under exposure to water stress, protein expression is changed and osmolytes accumulation and synthesis are observed during growth of the plant (Riccardi et al. 1998; Mohammadkhani and Heidari 2008; Zhao et al. 2016). This accumulation protects the plant cell to control water content in the absence of these osmolytes. Proline is one of the osmolytes that accumulate in different cell organelles of plants (e.g. chloroplast stroma and cytoplasm) as a compatible solute during drought stress. The significant accumulation of proline caused by water deficit stress has been documented in the different growth stages of maize to the maintenance of cell turgor and protection of cell structures for improvement under limited water (Köşkeroğlu and Tuna 2010; Soltani et al. 2013; Sinay et al. 2016). Moreover, soluble sugars are other osmolytes that have compatible metabolism and accumulate in the leaf cells of different plant species when they are exposed to water stress (Udomchalothorn et al. 2009; Abid et al. 2018). They protect the plant and cell membrane harms against water stress (LiXin et al. 2009; Bolouri-Moghaddam et al. 2010). High levels of soluble sugars like trehalose, mannitol, sorbitol (Anjum et al. 2016; Sharma et al. 2019), sucrose, hexoses and raffinose stabilize membranes and dehydrated tissues and act as ROS scavengers (Rosa et al. 2009). Especially cumulating of sucrose (glucose and fructose) in leaves and roots playing a major role in osmoregulation, stabilization of cells during drought, and interacting with biological macromolecules and cell membranes (Vieira et al. 2017a).

The knowledge of gene effects for maize or any other crop is important to selection and breeding procedures for different characters. Generation mean analysis as a biometrical tool, established by Mather and Jinks (1982), estimates genetic parameters of various traits including additive and dominance effects. Also, it can be used to estimate effects due to epistasis including interaction effects of additive × additive, additive × dominance and dominance × dominance (Kearsey and Pooni 2004). Many researchers have investigated that important roles of additive and non-additive effects in the inheritance patterns of quantitative characters in maize (Khan et al. 2014; Mbogo et al. 2015; Harakotr et al. 2016) and different crop plants (Khodambashi et al. 2012; Said 2014; Pathak et al. 2015; Prabhu et al. 2017). An effective breeding strategy for developing water deficit tolerant varieties considerably depends on knowledge of the inheritance mechanism of the stress tolerance in maize, high broad-sense heritability and additive genetic variance for the characters which are contributing to drought tolerance (Mather and Jinks 1982; Zaidi et al. 2010). However, there are no reports or studies on the inheritance of maize biochemical characters by applying the generation mean analysis method.

This study was carried out, for the first time, to ascertain the type of gene action involved in the biochemical traits inheritance through generation mean analysis to facilitate breeding programs using seven basic generations of a cross between

B73 and MO17 under the control and water deficit conditions. Ultimately, we used Pearson's correlation and PCA biplot to identify the most relevant biochemical traits under three water treatments.

Materials and methods

Plant materials and experiment

All the generations of MO17 as paternal line, early and dwarf, B73 as the maternal line of cytoplasmic male sterile, late and tall, SC704 as F_1 hybrid, F_2, BC_1, BC_2 and F_3 were grown in PVC pipes of 20 cm in diameter and 1 m in depth. Two maize seeds per pipe were sown then thinning was done at the tillering stage and left only one plant/seedling per pipe. Plant height of the generations in physiological maturity approximately ranged from 80 to 211 cm. The station was protected from any possible rain water by auto-rain-shelter in the water stress conditions. Mean temperature and relative humidity during growing season were about 37.5 °C and 29%, respectively. The generations were grown under natural sunlight in loamy sand soil with a bulk density (ρ_b) of 1.41 g.cm^{-3} at permanent wilting point (PWP) and field capacity (FC) equals 13.80% and 28.20%, respectively.

The present experiment was designed in a randomized complete block design with 20 replications and three water regimes including 100% FC (full irrigation), 55% available water depletion (mild water stress) and 75% available water depletion (severe water stress). It should be noted that evaporation and plant water requirement was measured daily using class A evaporation pan and according to recommended conditions by the FAO (Allen et al. 1998). By measuring the relative humidity, wind speed and position of the pan, the pan coefficient (K_P) was calculated and with its application, ET_O (reference crop evapotranspiration) was achieved. Then, using the three values of K_C (the maize crop coefficient) in initial, mid and the end of the late season stage provided by FAO Journal 56 (Allen et al. 1998), the K_C curve was plotted. The crop evapotranspiration (ET_C) was measured using the maize crop coefficient curve ($ET_C = K_C\ ET_O$). Irrigation was carried out when the amount of ET_C was equal to stress treatments level. Available water (AW) was calculated on volume basis using multiply gravimetric soil water content between FC and PWP regarding to bulk density as follows:

$$\mathrm{AW} = \left(\frac{\theta_{FC} - \theta_{PWP}}{100}\right)\mathrm{D}\frac{\rho_b}{\rho_w}$$

where ρ_w is the density of water which considered to 1 g. cm^{-3} and D is the root depth of maizeThese water regimes applied at 5 or 6 leaf stage till the silking.

Enzyme extraction and assay

Fresh leaves (200 mg each sample) were placed in a chilled pestle and were homogenized in 50 mM Tris–HCl buffer. The extract sample was centrifuged at 13,000 g, 4 °C for 20 min. The obtained supernatants were used for the catalase (CAT), peroxidases (PODs), and polyphenol oxidase (PPO) assays (Sudhakar et al. 2001). The activity of all three enzymes was determined using the method of Kar and Mishra (1976) and expressed in units per mg of protein (U/mg protein).

CAT activity assay: reaction mixture including of supernatant, 50 mM Tris-buffer (pH 7.0) and 5 mM H_2O_2 was prepared. Change in absorbance was carried by a spectrophotometer at 420 nm.

The activities of PODs and PPO assay: for measuring of PODs activity the reaction mixture contained of 100 mM Tris–buffer (pH 7.0), and 5 mM H_2O_2 and 10 mM pyrogallol was incubated for 5 min at 25 °C. The absorbance was estimated at 425 nm in the spectrophotometer. PPO activity was determined in the same method, with the difference that H_2O_2 was not added in the reaction mixture.

Biochemical traits

Protein content measurement: Briefly, 100 mg of the fresh leaf was weighed and ground with liquid nitrogen. Then, 100 mg Coomassie Brilliant Blue G-250 was dissolved in 50 mL 95% ethanol. After that, 100 mL of phosphoric acid (85%) was added and solution made up to 1 L with water, then, it was filtered and kept at 4 °C. For the assessments, 5 ml Bradford solution and 100 µL extract were mixed and incubated for 5 min. The absorbance value was determined at 595 nm with a spectrophotometer and the protein content by Bradford (1976) protein assay was determined using Bovine Serum Albumin (BSA) standard.

Soluble sugar measurement: sugar content was calculated based on the anthron (Irigoyen et al. 1992). The sample (0.5 g of fresh leaf) was ground in a mortar using 5 mL of 80% hot ethanol and centrifuged at 9000 g for 15 min. The extracted solution was decanted to other tube and 12.5 mL of 80% ethanol was added to it. 1 mL of the supernatant was taken and 1 mL of anthrone reagent (0.2%) was added to the extract. The resulting solution was placed in a water-bath set at 100 °C for 10 min and the absorbance was read at 625 nm. Then, the soluble sugars were calculated using a glucose standard by creating a standard curve.

Proline measurement: leaf proline concentration was assessed using the ninhydrin method of Bates et al. (1973). First, 0.2 g of fresh leaf was homogenized in 5 ml of 3% aqueous sulfosalicylic acid and the supernatant was removed by centrifugation. Then, 1 mL extract was mixed with 1 mL acid-ninhydrin and 1 mL of glacial acetic acid, and was boiled in a test tube at 100 °C for 1 h. The resulting solution was extracted with 2 mL of toluene at the same time toluene was considered as a blank sample. The absorbance was measured at 520 nm by the spectrophotometer. Finally, the proline content was measured using a series of pure proline for the standard curve. It is worth to mention that all three biochemical traits were expressed as mg/g of fresh weight.

Genetic studies and statistical analyses of biochemical traits

Generation mean analysis and genetic parameters including m (F∞ metric), d (additive effects), h (dominance effects), I (additive × additive interaction), j (additive × dominance interaction) and l (dominance × dominance interaction) were conducted by weighted least squares using the method of Mather and Jinks (1982). Furthermore, statistical significance of genetic parameters was determined using *t*-test. Validity test to the adequacy of the additive-dominance model was carried out by scaling tests of A, B, C and D (Kearsey and Pooni 2004). The existence of digenic epistasis was verified when the scales were significant. We applied the joint scaling test to assess goodness of fit for the six-parameters model (Cavalli 1952).

Additive, dominance and environmental variances (V_A, V_D and V_E respectively) were obtained following formulae (Mather and Jinks 1982):

$$V_A = 2V_{F2} - V_{BC1} - V_{BC2};\ V_D = 4\left(V_{BC1} + V_{BC2} - V_{F2} - V_E\right);\ \text{and}\ V_E = \tfrac{1}{4}\left(V_{P1} + V_{P2} + 2V_{F1}\right).$$

Broad sense and narrow sense heritability (h_b^2 and h_n^2 respectively) and average degree of dominance (a) were calculated using:

$$h_b^2 = (V_A + V_D)/(V_A + V_D + V_E);\ h_n^2 = (V_A)/(V_A + V_D + V_E)\ \text{and} = a\sqrt{(2V_D/V_A)}$$

The statistical analyses were done with software of Excel 2013, SAS 9.2 and Quattro Pro 6.

Pearson's correlation was used to explain the correlations among the traits using SPSS version 23. Furthermore, a combined principal component PCA biplot by using CANOCO software for Windows 4.5 (Lepš and Šmilauer 2003) was employed to graphically show relationship between the traits associated with experimental conditions.

Results

The results showed that differences among the studied generations in all biochemical traits were significant in the normal and water stress conditions (Table 1). Therefore, generation mean analysis was carried out for these traits to assay the gene action and the mode of inheritance. In addition, water regimes and generations interaction were significant for all characters except for the activities of CAT and PODs, which indicated the different response of the traits among seven generations under water regimes.

Changes in biochemical traits under water deficit stress

The mean values of PPO activity, protein content, soluble sugar and proline concentration based on the Duncan test are given in Fig. 1 (a, b, c and d respectively). The highest values of all mentioned characters belonged to MO17 and SC704 under the severe stress conditions. The water deficit did not have a significant impact on generations for activities of CAT and PODs (data not shown). As compared to normal irrigation, level of PPO activity, soluble sugars and proline concentration were increased significantly, whilst the level of protein content was decreased under two water deficit conditions. PPO activity (41.39%) and soluble sugars (58.39%) of SC704 were increased as compared with two inbred parents (B73 and MO17) and had the highest percent increase under severe stress condition (Table 2), while for proline concentration the highest percent increase was related to MO17 (64.51%). In addition to, protein content of B73 had the highest percent reduction (−25.08%) as compared with SC704 (−8.17%), however this value demonstrated 8.76% increase in MO17. The lowest value of PPO activity was related to BC_1 whilst this generation had the highest percent increase in protein content.

Pearson's correlation was measured among biochemical traits under control and water deficit conditions (Table 3). The statistical results of severe stress condition showed that all of the traits correlated significantly with each other. Furthermore, proline had a significant and high positive correlation with PPO activity ($r = 0.726$) and protein content ($r = 0.758$). Overall, among all traits soluble sugar had the most positive and significant correlation with PPO activity ($r = 0.861$) and proline ($r = 0.873$) respectively.

The relationship between biochemical traits based on the experimental conditions was depicted on the biplot of PCA (Fig. 2). It was found that the first axis (PC1) accounted 83.6% of total variance and for the second axis (PC2) 11.7% of total variance. Soluble sugar, proline, CAT, PODs, and PPO activity were contributed most to the PC1, while protein was contributed most to the PC2. The PCA biplot showed positive correlations among CAT, PODs, PPO, and proline. Also, the score plot of PCA demonstrated the presence of three different groups including control, mild and severe stress conditions.

Genetic components

The standard errors showed the significance values of scaling tests, which indicated the inadequacy of the simple additive-dominance model among generations for all studied traits except for proline content in the control treatment (Tables 4, 5 shows genetic effects and standard errors based on six-parameter models for the studied traits in the normal and water stress conditions. Non-significant of X^2 value under three conditions showed that related models were the best fit for the studied traits.

Both main effects (additive and dominance) were involved in governing of biochemical traits except for PODs activity under normal irrigation and 55% available water depletion (55% AWD) and proline in the control condition. The dominance effects were high in magnitude with comparison to the additive effects for almost traits under three conditions. Furthermore, digenic interaction was detected for all studied characters except for proline under full irrigation; however, dominance × dominance epistasis was more important than others (Table 5).

Additive × additive interaction was significant and negative for PPO activity and soluble sugar in 75% AWD whereas, dominance × dominance interaction was significant and positive in all of the traits except for proline under water deficit conditions. Also, the sign of additive × dominance interaction was negative and positive in the control and water stress conditions, respectively. There was duplicate epistasis for all characters except for proline concentration because the sign of dominance [h] and dominance × dominance interaction [l] were the opposite. Meantime, the existence of complementary gene action was estimated for proline concentration under water deficit condition because the same sign of [h] and [l] parameters.

Genetic variance components and heritability

Additive and dominance genetic variances for some characters were estimated negative values due to the effects of used method and environment which they were assumed zero in Table 6. It is noteworthy that the dominance variance was higher than the additive variance for all biochemical traits except for protein and proline under three regimes and soluble sugars under severe stress condition. The values of V_{AD} for PODs activity and soluble sugar were positive under three conditions. In contrast, the value of the other traits was negative at the same conditions.

The average degree of dominance for PPO activity in the control treatment and soluble sugar in 75% AWD were estimated less than unity showing the presence of incomplete dominance for these characters. At the same time, it was greater than unity for other studied traits, revealing the existence of over-dominance gene action in controlling these traits.

Discussion

The present study revealed that the high percent increase of PPO activity, protein, soluble sugars and proline in generations of MO17 and SC704 under water deficit condition might be attributed to their tolerance mechanism. Therefore, they had the best resistance to severe water stress on the basis of the percent increase in the aforementioned traits. It has been revealed by Moharramnejad et al. (2015) and Kravić et al. (2016) who documented that MO17 was ranked as resistant inbred line under drought stress. Whilst, B73 was

Table 1 Analysis of variance for biochemical traits of maize generations under control and water deficit conditions

Source of variation	D.F	Mean squares					
		Catalase	Peroxidase	Polyphenol oxidase	Protein	Soluble sugar	Proline
Water regimes (WR)	2	0.012**	0.0037*	90.197**	0.312**	217.913**	0.0058**
Replication/ WR	57	0.00035	0.00030	0.698	0.0067	1.624	0.00014
Generations (G)	6	0.0037**	0.0017**	37.248**	0.252**	36.124**	0.0027**
G × WR	12	0.000064ns	0.000028ns	3.907**	0.0293**	2.819*	0.00046**
Error	342	0.00039	0.00025	0.789	0.0080	1.323	0.00014
C.V. (%)		29.21	37.31	13.26	16.74	17.41	27.49

D.F degrees of freedom, *ns* *, **non-significant, significant at 0.05 and 0.01 probability levels, respectively

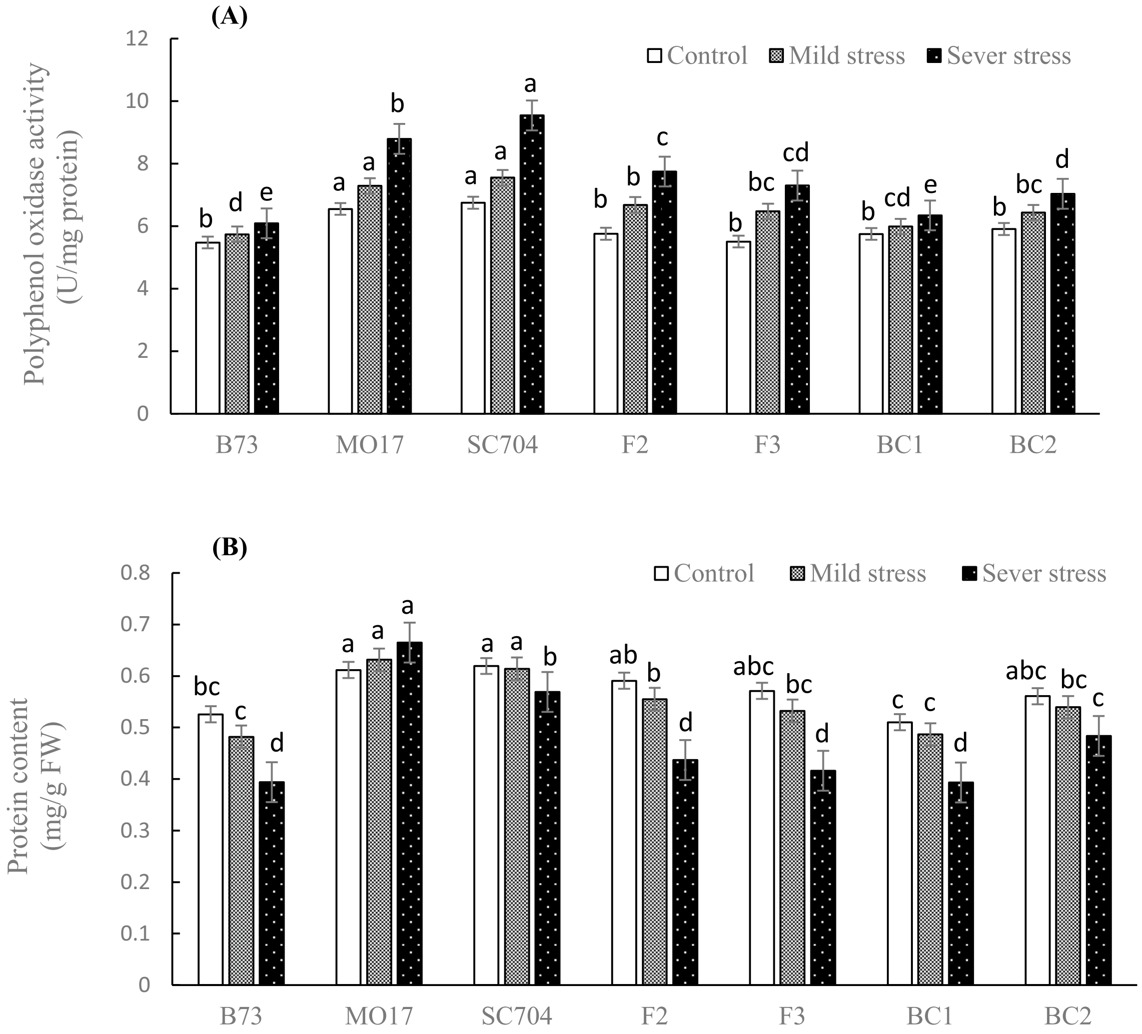

Fig. 1 Effect of control and water deficit conditions on **a**. Polyphenol oxidase activity; **b**. Protein content **c**. Soluble sugar and **d**. Proline concentration of maize generations. Bars represent standard errors of the mean. The different letters mean significant differences according to the Duncan test ($P \leq 0.05$)

indicated as sensitive inbred line which agree with results of Chen et al. (2012).

Enhancement of PPO activity and soluble sugars have been reported recently during the water deficit conditions (Shi et al. 2016; Akhtar and Mahmoo 2017) that are consistent with our findings. Soluble sugars have very complex roles within the cell under stress conditions such as stabilization of cellular membranes, maintaining cell turgor and regulation of the gene expression (Gibson 2005; Vieira et al. 2017a). In addition, enhancing of soluble sugar during the activation of the antioxidative defense system indicated its role on oxidative-stress-regulated and gene expression, as a result, it has been recommended that oxidative stress can control and modulate sugar gene expression and signaling (Bohnert and Jensen 1996; Couée et al. 2006; Vieira et al. 2017b).

According to Ge et al. (2006), the protein content decreased in root and leaves of maize subjected to water deficit stress which is coincident with the our results. However, Mohammadkhani and Heidari (2008) described that maize protein concentration of leaves at first stage increased and then decreased under drought treatment. Additionally, significant increase in proline concentration has been reported by Zenda et al. (2019) in the maize inbred lines with the high stress period. Similarly, our results showed that enhancement of proline concentration especially in the severe stress condition.

Today, correlation analysis and PCA are usually used as appropriate techniques to evaluate the association between

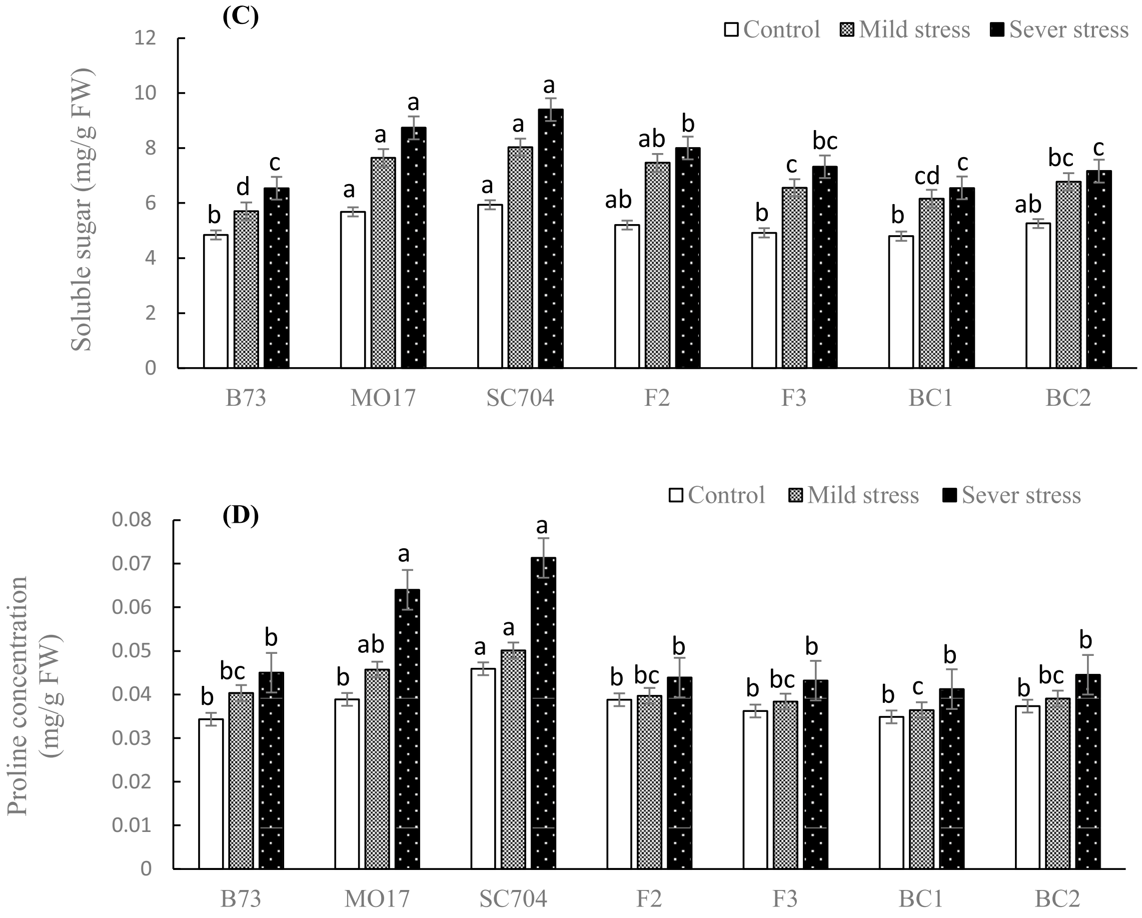

Fig. 1 (continued)

Table 2 Percent decrease/increase of polyphenol oxidase, protein, soluble sugar and proline under severe stress condition

Generations	Percent decrease/increase			
	Polyphenol oxidase	Protein	Soluble sugar	Proline
MO17	34.25	8.76	53.75	64.51
B73	11.29	−25.08	34.97	31.04
SC704	41.39	−8.17	58.39	55.47
F_2	34.59	−26.01	58.84	13.23
F_3	32.58	−27.14	48.93	19.24
BC_1	10.34	−22.90	36.51	18.37
BC_2	19.07	−13.79	36.25	19.35

AWD available water depletion, *FW* fresh weight of extracted tissue

the traits and their principal components for water deficit conditions (Nazari and Pakniyat 2010; Dehbalaei et al. 2013). In the present study, PCA and correlation analysis indicated that a significant differences among biochemical traits under severe stress condition. In other words, these results showed that the biochemical traits had a pattern which dependents to experimental conditions. A strong correlation between proline and protein content (Table 3) might indicate the role of proline in maintaining the structure of proteins within the cell (Verslues and Sharma, 2010). We also found that soluble sugars were more sensitive to water deficit stress. Indeed, it had the highest positive correlation with proline and PPO activity which affected strongly under severe stress condition. Our results were similar to the findings of Couée et al. (2006) who documented that a strong correlation between soluble sugars content and redox metabolism pathways in plant under stress conditions. Moreover, many studies have confirmed that there are a positive correlations among water stress, the antioxidant enzymes, and osmolytes of soluble sugars and proline (Mahajan and Tuteja 2005; Farooq et al. 2009; Laxa et al. 2019).

Since polygenic traits have many genes, each with a small additive effect, for all studied traits small magnitude of the additive effects are predictable (Mather and Jinks 1982). For all studied characters, additive gene effect had a negative sign because MO17 was the superior parent and chosen as

Table 3 Correlation among biochemical traits of maize generations under control and water deficit conditions

		Catalase	Peroxidase	Polyphenol oxidase	Protein	Soluble sugar	Proline
Catalase	Full irrigation	1					
	55% AWD	1					
	75% AWD	1					
Peroxidase	Full irrigation	0.274^{ns}	1				
	55% AWD	0.309^{ns}	1				
	75% AWD	0.391*	1				
Polyphenol oxidase	Full irrigation	0.477^{**}	0.310^{ns}	1			
	55% AWD	0.532**	0.376*	1			
	75% AWD	0.674**	0.447**	1			
Protein	Full irrigation	0.286^{ns}	0.176^{ns}	0.315^{ns}	1		
	55% AWD	0.494**	0.311^{ns}	0.597**	1		
	75% AWD	0.527**	0.552**	0.695**	1		
Soluble sugar	Full irrigation	0.311^{ns}	0.056^{ns}	0.423*	0.178^{ns}	1	
	55% AWD	0.218^{ns}	0.296^{ns}	0.598**	0.492**	1	
	75% AWD	0.501**	0.517**	0.861**	0.602**	1	
Proline	Full irrigation	0.075^{ns}	0.035^{ns}	0.396*	0.478**	0.385*	1
	55% AWD	0.196^{ns}	0.361*	0.452**	0.528**	0.349*	1
	75% AWD	0.570**	0.630**	0.726**	0.758**	0.873**	1

ns *, ** Correlation is non-significant, significant at 0.05 and 0.01 probability levels, respectively

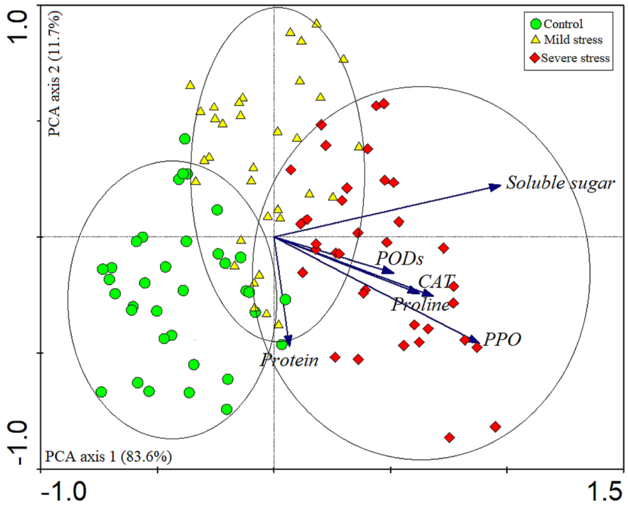

Fig. 2 Principal component analysis biplot of the catalase (CAT), peroxidases (PODs), polyphenol oxidase (PPO), protein, soluble sugar and proline concentration under control and water deficit conditions

P_2. At the same time, the negative sign of dominance gene effect implied that incomplete dominance was towards of reducing the biochemical traits levels. In contrast, the positive sign of dominance effect indicated enhancement of the alleles controlling the inheritance for soluble sugar in the control treatment. These findings suggest that in water deficit conditions, soluble sugars act as a strong osmotic regulation in maize. This result is consistent with Vieira et al. (2017b) who documented that increase of soluble sugars had a major contribution in the terms of tolerate water stress during the stress periods.

Generally, both main effects (additive and dominance gene effects) and digenic interaction (epistasis) governed the inheritance of studied traits. Though for most traits, higher dominance and dominance × dominance effects indicated the necessity of exploiting dominance gene action in the maize breeding programs by using the production of hybrid varieties.

The negative sign of additive × additive epistasis for PPO activity and soluble sugar implied that the existence of an interaction between decreasing and increasing alleles. Consequently, the dispersion was also present in the parents under severe stress condition. Similarly, the dispersion of genes in the parents under the control condition and association under both stress conditions was detected due to the negative and positive signs of [j] respectively. For almost all biochemical characters positive sign of dominance × dominance epistasis indicated unidirectional dominant in both normal and water deficit conditions. The presence of duplicate gene action for all studied characters, except for proline, causes a disturbance in the selection process by reducing the diversity in F_2 and segregating generations.

There are no reports about the inheritance of gene effects through generation mean analysis in maize for all biochemical characters. The present study is a first attempt to address the gene actions of studied biochemical traits using generation mean analysis. Our results showed that the higher

Table 4 Scaling tests (±SE) for biochemical traits of maize generations under control and water deficit conditions

Traits	Water Regimes	A	B	C	D
Catalase (U/mg protein)	Full irrigation	−0.025±0.0091**	−0.019±0.011 ns	−0.021±0.018 ns	−0.012±0.018ns
	55% AWD	−0.022±0.010**	−0.017±0.011 ns	−0.0050±0.019 ns	0.00043±0.018ns
	75% AWD	−0.020±0.09*	−0.023±0.011*	−0.0068±0.026 ns	−0.014±0.026ns
Peroxidase (U/mg protein)	Full irrigation	−0.016±0.0094ns	−0.015±0.0089 ns	−0.038±0.018*	−0.0027±0.016ns
	55% AWD	−0.018±0.0090*	−0.018±0.0092*	−0.046±0.014**	0.00041±0.016ns
	75% AWD	−0.021±0.0072**	−0.023±0.0086**	−0.047±0.016**	0.0036±0.014ns
Polyphenol oxidase (U/mg protein)	Full irrigation	−0.73±0.27**	−1.48±0.43**	−2.50±0.76**	−1.52±0.58**
	55% AWD	−1.30±0.46**	−1.97±0.48**	−1.39±0.96 ns	−0.50±0.99ns
	75% AWD	−2.95±0.52**	−4.27±0.56**	−2.99±1.36*	−1.19±1.15ns
Protein (mg/g FW)	Full irrigation	−0.12±0.051*	−0.11±0.058*	−0.13±0.11ns	−0.034±0.11ns
	55% AWD	−0.12±0.047**	−0.17±0.038**	−0.12±0.091^{ns}	−0.091±0.096ns
	75% AWD	−0.17±0.031**	−0.27±0.044**	−0.45±0.072**	−0.27±0.075**
Soluble sugar (mg/g FW)	Full irrigation	−1.18±0.59*	−1.10±0.66 ns	−1.59±1.052ns	−1.26±1.14ns
	55% AWD	−1.42±0.56*	−2.12±0.84**	0.45±1.34ns	−2.064±1.45 -ns
	75% AWD	−2.84±0.55**	−3.81±0.53**	−2.066±1.26ns	−1.99±3.18ns
Proline (mg/g FW)	Full irrigation	−0.010±0.0061ns	−0.010±0.0057 ns	−0.0099±0.012ns	−0.0059±0.0094ns
	55% AWD	−0.017±0.0063*	−0.018±0.0062*	−0.027±0.012*	−0.012±0.011ns
	75% AWD	−0.034±0.0049**	−0.046±0.0085**	−0.076±0.016**	−0.024±0.012*

ns, *, ** non-significant, significant at 0.05 and 0.01 probability levels, respectively. AWD: available water depletion, *FW* fresh weight of extracted tissue

dominance variance than the additive variance for all three antioxidant enzymes in both normal and water stress conditions. Also, the values of soluble sugar under control and 55% AWD conditions revealed that the dominance variance had a major role in the governing of this character. The positive value of V_{AD} for PODs activity and soluble sugar indicated that dominance genes were more prominent in the MO17, whilst the negative value of V_{AD} for the other traits revealed that dominance genes were in the low performance parent (B73).

The values of narrow-sense heritability for all three antioxidant enzymes activities were between low to moderate confirmed that again the importance of dominance variance in governing these enzymes. Based on Gorji et al. (2011) the narrow-sense heritability of antioxidant enzymes such as CAT activity of triticale was moderate under drought stress and low under normal condition, which indicated that more important role of dominance gene effect in controlling of these characters. According to Karmakar et al. (2013) and Nassourou et al. (2017), narrow-sense heritability of antioxidant activity was lower than 50% revealed that non-additive genetic effects had a major role in the genetics of these characters in ridge gourd and cowpea seed respectively.

The high values of additive variance and narrow-sense heritability of protein contents indicate the involvement of additive gene effects in the genetic controlling of this character under both control and water deficit conditions. Similar findings were obtained in the study of Akram et al. (2007) in bread wheat which by analysis of genetic component showed that the protein content is controlled by additive and incomplete dominance effects and recommended that selection can be effective in early segregating generations. In contrast, Abid et al. (2016) reported non-additive gene action with low h_n^2 in controlling of total soluble protein of leaves in cotton under water stress.

In the control and mild stress conditions, the low value of narrow-sense heritability for soluble sugar indicated the major role of dominance variance, while in the severe stress condition it was high and indicated the important role of additive variance. There is no report on gene effects of soluble sugar in crop plants leaves. Nevertheless, the important role of both main effects in super-sweet corn grains and dominance variance in cowpea seeds for soluble sugar have been documented by Qi et al. (2009) and Nassourou et al. (2017), respectively.

In both control and stress conditions, the high values of additive variance showed that additive effect has an important role in governing proline concentration. The same result was documented by Pourmohammad et al. (2014), who found proline concentration was controlled by additive gene action under drought stress in sunflower. Our results disagree with Naroui Rad et al. (2013) who using diallel cross design in bread wheat and Khalil et al. (2016) in sunflower indicated that non-additive genetic effects were more prominent than additive effects.

Table 5 Estimates of genetic parameters (±SE), x^2 and its degree of freedom (D.F.) for biochemical traits of maize generations under control and water deficit conditions using generation man analysis

Traits	Water regimes	m	d	h	i	j	l	x^2	D.F
Catalase (U/mg protein)	Full irrigation	0.07±0.008**	−0.007±0.002*	−0.04±0.03^{ns}	−0.006±0.008^{ns}	−0.007±0.01^{ns}	0.05±0.02*	1.16^{ns}	1
	55% AWD	0.08±0.008**	−0.006±0.002*	−0.05±0.03^{ns}	−0.01±0.008^{ns}	–	0.05±0.02*	1.65 ^{ns}	2
	75% AWD	0.09±0.01**	−0.009±0.003**	−0.05±0.03^{ns}	− 0.01±0.01^{ns}	–	0.06±0.02**	1.62^{ns}	2
Peroxidase (U/mg protein)	Full irrigation	0.04±0.003**	−0.002±0.003^{ns}	−0.03±0.01*	–	-0.001±0.01^{ns}	0.03±0.01*	0.14^{ns}	2
	55% AWD	0.04±0.002**	−0.003±0.003^{ns}	−0.04±0.01**	–	0.0002±0.01^{ns}	0.04±0.01**	0.67^{ns}	2
	75% AWD	0.05±0.006**	−0.004±0.002*	−0.03±0.01**	–	0.001±0.009^{ns}	0.04±0.01**	0.99^{ns}	2
Polyphenol oxidase (U/mg protein)	Full irrigation	5.96±0.09**	−0.52±0.09**	−1.83±0.47**	–	0.95±0.46*	2.64±0.45**	3.96^{ns}	2
	55% AWD	7.25±0.42**	−0.77±0.11**	−3.47±1.21**	−0.75±0.42^{ns}	0.66±0.53ns	3.81±1.00**	2.17^{ns}	1
	75% AWD	8.78±0.46**	−1.34±0.15**	−7.38±1.39**	−1.36±0.47**	1.30±0.70ns	8.16±1.08**	4.75^{ns}	1
Protein (mg/g FW)	Full irrigation	0.64±0.05**	−0.04±0.01**	−0.31±0.14*	−0.08±0.05^{ns}	−0.02±0.07^{ns}	0.28±0.11*	2.11^{ns}	1
	55% AWD	0.60±0.04**	−0.07±0.01**	−0.30±0.11*	−0.05±0.04^{ns}	0.05±0.04^{ns}	0.32±0.09**	2.59^{ns}	1
	75% AWD	0.46±0.03**	−0.13±0.009**	−0.26±0.09**	0.06±0.03^{ns}	0.08±0.05^{ns}	0.36±0.08**	0.85^{ns}	1
Soluble sugar (mg/g FW)	Full irrigation	4.47±0.28**	−0.4±0.17*	1.35±0.41**	0.74±0.33*	−0.25±0.84^{ns}	-	3.12^{ns}	2
	55% AWD	7.33±0.06**	−0.95±0.15**	−2.61±1.92^{ns}	−0.68±0.65^{ns}	0.27±0.91^{ns}	3.34±1.46**	6.46^{ns}	1
	75% AWD	9.09±0.64**	−1.10±0.16**	−7.23±1.71**	−1.48±0.64**	1.00±0.73^{ns}	7.55±1.15**	6.90^{ns}	1
Proline (mg/g FW)	Full irrigation	0.37±0.0006**	−0.002±0.0009**	–	–	–	–	5.47^{ns}	5
	55% AWD	0.04±0.004**	−0.003±0.001*	−0.03±0.01*	− 0.002±0.004^{ns}	–	− 0.03±0.01*	0.69^{ns}	2
	75% AWD	0.05±0.004**	−0.009±0.002**	−0.06±0.02**	0.0009±0.005^{ns}	0.012±0.0008^{ns}	− 0.08±0.01**	0.089^{ns}	2

ns, *, **: non-significant, significant at 0.05 and 0.01 probability levels, respectively. *AWD* available water depletion, *FW* fresh weight of extracted tissue

Conclusions

It can be concluded that protein content significantly decreased whilst PPO activity, soluble sugars and proline concentration increased in maize generations under water deficit stress. Comparing changes in the biochemical traits between control and two water deficit conditions allowed us to identify some of the defense mechanisms related to water deficit tolerance in maize. The positive strong correlation of antioxidant enzymes, especially PPO with proline and soluble sugars could suggest that the antioxidative defense mechanism is more activated by increasing proline and soluble sugars production. This result is important to improve water deficit stress tolerance in maize. Indeed, generation means analysis as an important method forward to identify gene effects for maize showed that additive and non-additive genetic effects were governed in the inheritance of biochemical traits. The high narrow-sense heritability and additive genetic variance of protein content, proline concentration and soluble sugars under severe stress condition indicated that these characters are useful for selecting resistant maize generations in the parents' inbred lines. Clearly, additional attention and research on molecular findings of response and resistance of maize generations are needed to identify most resistant crop varieties in field conditions particularly under water deficit stress.

Table 6 Estimates of genetic variances, broad-sense and narrow sense heritability and average degree of dominance for biochemical traits of maize generations under control and water deficit conditions

Traits	Water regimes	V_E	V_A	V_D	V_{AD}	h_b^2	h_n^2	ā
Catalase (U/mg protein)	Full irrigation	0.057	0.039	0.14	−0.089	0.76	0.16	2.68
	55% AWD	1.82	0.35	2.58	−2.16	0.62	0.07	3.84
	75% AWD	0.084	0.13	0.18	−0.14	0.79	0.33	1.66
Peroxidase (U/mg protein)	Full irrigation	2.68	0	4.23	2.44	0.61	0	–
	55% AWD	2.31	0	3.38	1.77	0.59	0	–
	75% AWD	1.80	1.38	6.19	5.60	0.83	0.15	2.99
Polyphenol oxidase (U/mg protein)	Full irrigation	0.43	0.48	0.18	−0.025	0.60	0.44	0.87
	55% AWD	0.12	0.31	0.24	−0.018	0.82	0.46	1.24
	75% AWD	0.093	0.19	0.12	−0.024	0.77	0.47	1.12
Protein (mg/g FW)	Full irrigation	0.034	0.085	0	−0.018	0.71	0.71	0
	55% AWD	0.058	0.094	0	−0.021	0.56	0.56	0
	75% AWD	0.039	0.058	0	−0.023	0.60	0.60	0
Soluble sugar (mg/g FW)	Full irrigation	0.38	0.14	0.57	0.20	0.65	0.13	2.85
	55% AWD	0.24	0.29	0.42	0.38	0.75	0.30	1.70
	75% AWD	0.97	1.65	0.51	0.54	0.69	0.53	0.79
Proline (mg/g FW)	Full irrigation	1.14	2.14	0	−2.02	0.65	0.65	0
	55% AWD	0.76	1.44	0	−1.03	0.65	0.65	0
	75% AWD	0.39	0.83	0	−0.46	0.68	0.68	0

V_E, V_A, V_D and V_{AD} environment, additive, dominance and additive × dominance co-variance respectively, h_b^2 and h_n^2: broad sense heritability and narrow sense heritability. ā average degree of dominance, *AWD* available water depletion, *FW* fresh weight of extracted tissue

Author contribution statement Mozhgan Shirinpour is written the manuscript, designed the experiment, analyzed the data and developed the idea. Ali Asghari is developed the idea, designed the experiment and written the manuscript. Saeid Aharizad is designed and developed the experiment. Ali Rasoulzadeh is designed the experiment and developed some part of the methods. Saeed Khavari Khorasani is designed the experiment.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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