Journal of Applied Biological Sciences
E-ISSN: 2146-0108 14(2): 211-224, 2020
Research Article

HERITABILITY AND GENE EFFECTS OF SOME ROOT TRAITS IN MAIZE UNDER WATER DEFICIT STRESS CONDITIONS

Armin Vahed Rezaei[1,a], Saeid Aharizad [1,b,*], Majid Norouzi[1,c]

[1]*Tabriz University, Faculty of Agriculture, Department of Plant Breeding and Biotechnology, Tabriz, Iran*

**Corresponding Author:*
E-mail: s.aharizad@yahoo.com

(Received 05th March 2020; accepted 10th Augus 2020)

a: ORCID 0000-0002-1493-1231, b: ORCID 0000-0002-6171-3851, c: ORCID 0000-0002-1558-7030

ABSTRACT. To study of genetic structure in maize generations under water deficit conditions, the seven maize generations (MO17 and B73 as parents, F1, F2, F3, BC1, and BC2) were grown under normal irrigation (N), 50 (I1) and 75 (I2) millimetre evaporation from class A evaporation pan at the University of Tabriz farm. Three experiments were conducted in a randomized complete block design with 20 replications. The root traits including root length, root volume, root diameter, root number, root fresh weight, root dry weight were measured. A combined analysis revealed that there was a significant difference between the studied generations for maize root traits. The results of the scaling test indicated the existence of epistatic effects for all traits except the root number under different irrigation conditions. In most of the traits, the dominant effect is significant. The three-parameter model was the best fit model for root number, in three irrigation conditions. For most of the studied traits, six parameters and five parameters models were significant in different irrigation conditions, however, some models were not significant under irrigation conditions, due to because of existing maternal effects, genetic affinities, and multiple epistasis. Estimation of the dominance degree above 1 in some of the traits under different irrigation conditions indicated that there was a phenomenon of overdominance incomplete dominance in the control of them. High levels of genetic broad sense and narrow sense heritability suggested that genetic effects and additive effects have a greater role in the inheritance of most traits under different irrigation conditions.

Keywords: *gene effects, generation mean analysis, heritability, root, water stress*

INTRODUCTION

The root is essential to plant survival and play a critical role in determining the yield of crops. However, they are hidden from view, often deep in the soil, and this makes them difficult to study and easy to ignore [1]. Roots also have a remarkable capacity to sense and respond to most of the physicochemical parameters of the soil by adjusting their growth and water transport properties accordingly; this function is tightly linked to shooting physiology. Therefore, under limiting soil water availability conditions, roots may play an important role in maintaining the water status of the whole plant [2]. One aspect of principal importance in this arena is the response of root growth and development to water-deficit conditions [3]. The roots are the first organ to sense a water shortage [4], therefore generally considered to be the most important organ with respect to improving crop adaptation to water deficit stress [5]. Some plants have the robust ability to increase root growth at the early stage of drought stress to absorb the water in deep soil [6]. The length, weight, volume, and density of plant roots were also reported being associated with the drought resistance in crops [7].

The maize root system is composed of a primary root, a variable number of seminal roots, nodal roots arising from below ground stem nodes (crown roots) and above ground stem nodes (brace roots), and lateral roots arising from these axes [8]. This plant responds to drought stress by redirecting root growth and dry matter accumulation away from the shoot to the root [9]. Maize nodal roots response to soil drying to continue elongation at water potentials that are low enough to inhibit shoot growth completely [10]. Also, reduced lateral root branching density can improve drought tolerance in maize by reducing the metabolic costs of soil exploration permitting greater axial root elongation, greater rooting depth, and thereby greater water acquisition from drying soil [11]. So understanding the nature of drought response in maize and some major strategies used for improving drought stress-tolerance maize lines will provide opportunities to improve the breeding process [12].

Estimation of the types of gene action involved in the expression of traits, the level of additive effects and degree of dominance are very important in designing a breeding method for improving interested, traits. Knowledge of the way genes act and interact will determine which breeding system can optimize gene action more efficiently and will help to elucidate the role of breeding systems in the evolution of crop plants [13]. So many workers developed genetic models for the estimation of different genetic effects. Although the majority of these genetic models are additive-dominance models or simply additive models. The non-allelic interactions are largely ignored to have a simplified interpretation of genetic variation. But, it has now been established that such inter-allelic expression for continuous variation [14,15]. Generation means analysis (GMA) is one of the quantitative biometric methods based on measurements of the phenotypic performance of certain quantitative traits on as many as possible plant individuals in a basic experimental breeding generation (parental, filial, backcross and segregation generations [15]. GMA is a useful technique in plant breeding for estimating main gene effects (additive and dominance) and epistatic effects (additive × additive, additive × dominance, and dominance × dominance) interactions relationship for the inheritance of quantitative traits [14]. This study was carried out to determine the potential of some root traits in P1, P2, F1, F2, F3, BC1 and BC2 generations of crosses between B73 and Mo17 inbred lines under drought tolerance in terms of heritability, genetic advance and type of gene action prevailing in maize.

MATERIALS AND METHODS

Development of Generation

Two inbred lines; B73 and MO17 were selected based on distinctiveness in responses to water deficit stress. Inbred line B73 was designated as drought susceptible parent (P1) while MO17 as the drought-tolerant parent (P2) [16]. These two most contrasting genotypes were used for further development of genetic material. During April 2013, both tolerant and susceptible parents were sown under normal field conditions and crosses were attempted to obtain filial generation one (F1) or hybrid (B73 × MO17) seed. One hundred fifty F1 plants along with parents (P1, P2) were raised in the field during April and May 2014. One hundred F1 plants were advanced by selfing to filial generation two (F2) and the other fifty F1 plants (twenty-five each) were crossed by pollinating with B73 (P1) and MO17 (P2) to develop backcrosses, BC1 (F1× B73) and BC2 (F1× MO17) generations, respectively. During May 2015, fifty F2 plants were advanced by selfing to filial generation three (F3).

Evaluation of Genetic Material

The experimental material consisted of MO17 (resistant to drought) and B73 (sensitive to drought) maize inbred lines. The experiment was carried out at the experimental farm of Faculty of Agriculture, University of Tabriz, Iran (46º 17′ E and 38º 3′ N), at an altitude of approximately 1360 m, during the successive growing seasons of 2017/2018. In this growing season, the plants were grown in three separate experiments in a randomized complete block design with 20 replicates for each one. Each replicate consisted of one plant in one PVC pipe measuring 1 meter in length and 20 cm diameter. To extract the roots easily, plastic was first inserted into the PVC pipes to be removed from the pipe at the end of the growing season and then filled with crop soil. Plastics also help increase the accuracy of work when washing roots. The soil in the experimental area is Sandy Loomis. The climate is semi-steppe and semi-arid according to the classification of Köppen, with hot summers and cold winters. The average annual temperature is 9.88°C. To apply the stress before planting, to determine the field capacity (FC), one of the PVC pipes was filled with soil and saturated by adding water and its surface was covered with plastic. After 72 hours, when no water came out from the bottom of the PVC gravity, samples were taken from the PVC pipe and it was transferred to the laboratory for estimation of some soil parameters [17]. To determine soil physical properties including soil bulk density (ρb) measurements on intact specimens and drying of soil samples from the oven was used. The particle size distribution on the samples was also measured by the hydrometric method [18]. Soil available water in millimeters was calculated using the following equation (Eqn.1) [17]:

$$AW = \frac{\theta_{FC} - \theta_{WP}}{100} \times D \times \frac{\rho_b}{\rho_w}$$

Eqn.1

From the beginning of the six-leaf stage until harvesting, daily the air relative humidity and evaporation from the class A evaporation pan surface were recorded based on three normal irrigation (N), 50 (I_1) and 75 (I_2) millimeter evaporation from class A evaporation pan and taking into account the vegetation coefficient and the amount of evapotranspiration, the amount of water required was calculated and the volume of water required for each PVC pipe was added to the pipe by the graduated cylinder [19]. After the maturity stage, pipes at ground level were removed carefully and all of the roots were washed and root length (cm), root volume (cm3), root diameter (mm), root number, root fresh weight (g), root dry weight (g) were measured.

Biometrical and Genetical analysis

Combined variance analysis and comparison of the mean of the characters among generations were carried out, using MSTAT-C [20] software. Generation means analysis (GMA) was applied, on parameters which showed significant differences among generations, to determine the mode of inheritance and magnitude of gene action for the traits under investigation. GMA was performed using Mather and Jinks [14] method. In this method the mean of each character is indicated as follows (Eqn. 2):

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

Eqn. 2

Where: Y = observed mean for generation; m = mean effect; a = average additive effects; d = average dominance effects; i = average interactions between additive effects; j = average interactions between additive and dominance effects; l = average interactions between dominance effects. α, β, α^2, $2\alpha\beta$, and β^2 are the coefficients of genetic parameters. To estimate the genetic effects $(e) = X\hat{\beta}$ and to select the most suitable model of estimated the weighted least square method (Eqn. 3) by utilizing matrix algebra (Eqn. 4) as describe by Rowe and Alexander [21] and the joint scaling test of Mather and Jinks [14] were employed.

$$(O) = \begin{bmatrix} \overline{P_1} \\ \overline{P_2} \\ \overline{F_1} \\ \overline{F_2} \\ \overline{F_3} \\ \overline{BC_1} \\ \overline{BC_2} \end{bmatrix}$$

$$\beta = (\mathrm{X'WX})^{-1}.(X'WY)$$

Eqn. 3

$$\chi^2 = \sum[(o_i - e_i)^2.\mathrm{W}]$$

$$\mathrm{X} = \begin{bmatrix} 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & -1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 0.5 & 0 & 0 & 0.25 \\ 1 & 0 & 0.25 & 0 & 0 & 0.0625 \\ 1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 \\ 1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 \end{bmatrix} \quad \mathrm{W} = \begin{bmatrix} \mathrm{W}_{\mathrm{P}_1} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathrm{W}_{\mathrm{P}_2} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathrm{W}_{\mathrm{F}_1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathrm{W}_{\mathrm{F}_2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathrm{W}_{\mathrm{F}_3} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathrm{W}_{\mathrm{BC}_1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathrm{W}_{\mathrm{BC}_2} \end{bmatrix} \quad Y = \begin{bmatrix} \overline{P_1} \\ \overline{P_2} \\ \overline{F_1} \\ \overline{F_2} \\ \overline{F_3} \\ \overline{BC_1} \\ \overline{BC_2} \end{bmatrix} \quad \beta = \begin{bmatrix} m \\ a \\ d \\ aa \\ ad \\ dd \end{bmatrix}$$

Eqn. 4

In this method, weights were calculated from Eqn. 5 [14]:

$$W = \frac{1}{\frac{V}{n}}$$

Eqn. 5

Standard error associated with each estimate of genetic effect was obtained as the diagonal elements of the solution equation (Eqn. 6). The significance of each genetic effect estimate was evaluated as described by Snedecore and Cochran [22], utilizing a t-test.

$$SE = \left((X'WX)^{-1}\right)^{0.5}$$

Eqn. 6

To test the adequacy of the model, the chi-square ($\chi 2$) test was performed as outlined (Eqn. 7).

Eqn. 7

The analysis of the values of A, B, C, and D should be equal within the range of this standard error. The significance of any of this scale is taken to indicate proceeded to compute the interaction types involved the six parameters genetic model of Hayman [23] (Eqn. 8). The significance of the genetic components was tested using a t-test.

$$A = 2\overline{BC_1} - \overline{P_1} - \overline{F_1} \qquad V_A = 4\overline{V}_{BC_1} + \overline{V}_{P_1} + \overline{V}_{F_1} \qquad t_A = \frac{A}{SEA} \qquad SEA = \sqrt{V_A}$$

$$B = \overline{2BC_2} - \overline{P_2} - \overline{F_1} \qquad V_B = 4\overline{V}_{BC_2} + \overline{V}_{P_2} + \overline{V}_{F_1} \qquad t_B = \frac{B}{SEB} \qquad SEB = \sqrt{V_B}$$

$$C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2} \qquad V_C = 16\overline{V}_{F_2} + 4\overline{V}_{F_1} + \overline{V}_{P_1} + \overline{V}_{P_2} \qquad t_C = \frac{C}{SEC} \qquad SEC = \sqrt{V_C}$$

$$D = 4\overline{F_3} - 2\overline{F_2} - \overline{P_1} - \overline{P_2} \qquad V_D = 16\overline{V}_{F_3} + 4\overline{V}_{F_2} + \overline{V}_{P_1} + \overline{V}_{P_2} \qquad t_D = \frac{D}{SED} \qquad SED = \sqrt{V_D}$$

Eqn. 8

To estimate the environmental variance (V_E), Additive variance (V_A) and dominance variance (V_D) the weighted least square method as describe by Nelder [24] was employed. In this method matrix of coefficients of the genetic and error variance (X) is the following matrix (Eqn. 9):

$$X = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 1 & 1 & 0 \\ 1 & 1.5 & 0.75 & 0 \\ 1 & 0.5 & 1 & -1 \\ 1 & 0.5 & 1 & 1 \end{bmatrix}$$

Eqn. 9

Broad-sense (Eqn. 10), narrow-sense heritability (Eqn. 11) and degree of dominance (Eqn.12) were estimated using the following formulae respectively [13]:

$$h_b^2 = \frac{V_A + V_D}{V_A + V_D + \frac{V_E}{r}} \qquad h_n^2 = \frac{V_A}{V_A + V_D + \frac{V_E}{r}} \qquad \bar{a} = \sqrt{\frac{2V_D}{V_A}}$$

Eqn. 10 **Eqn.11** **Eqn. 12**

RESULTS AND DISCUSSION

Combined Analysis of Variance

The combined analysis of variances for studied traits (Table 1) revealed significant differences between irrigation conditions (A) and generations (B) (p = 1%). The condition × generation interaction (A×B) was also significant for RL, RD, RN, RFW, and RDW (p = 5% or 1%) except RV. Therefore, the significant difference between generations makes possible genetic analysis. A comparison of seven generations means (Table 2) showed that water deficit reduced RV and RD, but increased RL, RN, and RDW in many generations. Certainly, in more generation, RL increased in I_1 and decreased in I_2, whereas RFW and RDW decreased in I_1 and increased in I_2. MO17 parents had the highest RV, RD, RN, and RFW under all irrigation conditions.

Table 1. *Analysis of variance for evaluated root.*

SOV	df	Mean square					
		RL	**RV**	**RD**	**RN**	**RFW**	**RDW**
Condition (A)	2	2850.11^{**}	4245.73^{*}	0.354^{**}	1081.66^{**}	19109.03^{**}	646.31^{**}
R/A	57	425.264	891.04	0.005	24.530	2211.90	91.09
Generations (B)	6	5475.28^{**}	8128.627^{**}	0.044^{**}	83.52^{**}	10526.64^{**}	323.17^{**}
A×B	12	636.176^{*}	1001.26^{ns}	0.022^{**}	20.76^{**}	4024.62^{**}	149.48^{**}
Error	342	291.22	722.30	0.005	21.49	1414.129	60.90
CV%		17.54	42.63	26.56	25.84	41.63	49.62

Where RL, RV, RD, RN, RFW and RDW denote; root length, root volume, root diameter, root number, root fresh weight and root dry weight, respectively.

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

Table 2. *Mean comparison of traits studied under normal and limited irrigation conditions.*

Generations	**Traits**					
	RL			**RV**		
	N	I_1	I_2	N	I_1	I_2
P_1 (B73)	89.27^{b}	94.17^{bc}	86.83^{cd}	53.2^{bc}	48.7^{b}	47.1^{c}
P_2 (Mo17)	82.2^{bc}	105.15^{ab}	103.25^{ab}	79.85^{a}	69.75^{a}	61.55^{abc}
F_1	107.6^{a}	108.7^{a}	108.87^{a}	83.3^{a}	76.2^{a}	77.05^{a}
F_2	100.15^{a}	101.42^{abc}	98.2^{ab}	85.7^{a}	69.9^{a}	69.5^{ab}
F_3	72.3^{c}	89.91^{c}	78.12^{d}	42.8^{c}	47.65^{c}	58.3^{bc}
BC_1	102.47^{a}	107.39^{a}	92.78^{bc}	58.3^{bc}	62.05^{ab}	60.55^{abc}
BC_2	101.15^{a}	109.60^{a}	103.85^{a}	68.55^{ab}	49.3^{b}	68.55^{bc}

Generations	**Traits**					
	RD			**RN**		
	N	I_1	I_2	N	I_1	I_2
P_1 (B73)	0.28^{b}	0.27^{a}	0.14^{c}	14.75^{b}	15.65^{b}	19.55^{b}
P_2 (Mo17)	0.31^{b}	0.31^{a}	0.20^{b}	15.35^{b}	16.35^{ab}	19^{b}
F_1	0.36^{a}	0.28^{a}	0.28^{c}	17.5^{a}	18.35^{a}	24.6^{a}
F_2	0.32^{ab}	0.29^{a}	0.21^{b}	16^{ab}	17.6^{ab}	22.2^{ab}
F_3	0.29^{b}	0.27^{a}	0.22^{b}	15.1^{b}	15.95^{ab}	22.05^{ab}
BC_1	0.30^{b}	0.19^{b}	0.19^{b}	15.5^{b}	16^{ab}	20.95^{ab}
BC_2	0.31^{b}	0.20^{b}	0.23^{b}	17.45^{a}	17.35^{ab}	19.45^{b}

Generations	**Traits**					
	RFW			**RDW**		
	N	I_1	I_2	N	I_1	I_2
P_1 (B73)	68.22^{bc}	65.56^{b}	82.37^{b}	14.63^{bc}	12.52^{b}	16.82^{ab}
P_2 (Mo17)	111.30^{a}	78.09^{ab}	85.86^{b}	20.09^{ab}	13.13^{b}	11.68^{bc}
F_1	123.70^{a}	82.83^{a}	122.45^{a}	20.10^{ab}	16.28^{ab}	18.53^{a}
F_2	121.87^{a}	82.55^{a}	100.71^{ab}	24.79^{a}	17.21^{a}	16.34^{abc}
F_3	62.74^{c}	81.37^{a}	83.16^{b}	11.12^{c}	14.58^{ab}	12.72^{bc}
BC_1	120.21^{a}	72.29^{ab}	81.25^{b}	17.38^{b}	13.12^{b}	13.02^{bc}
BC_2	95.04^{ab}	80.03^{ab}	95.04^{b}	19.25^{ab}	16.02^{ab}	10.87^{c}

N, I1 and I2; normal irrigation, 50 and 75 millimeter evaporation from class A evaporation pan , respectively.

Where RL, RV, RD, RN, RFW and RDW denote; root length, root volume, root diameter, root number, root fresh weight and root dry weight, respectively.

Scaling Test

The result of A, B, C and D tests under three environments, showed that significance of any of these tests in normal irrigation condition for RL, RV, RFW, RDW except RD and RN (Table 3), indicates the presence of non-allelic gene interactions on the scale measurement used. The scaling test was not significant for RL, RFW, and RDW at I1 and RL, RV, RD, RN, RFW, except RDW at I2 Irrigation condition.

Table 3. *Estimation of scaling test for all studied traits under normal irrigation and water deficit condition.*

Traits	Scals	Conditions		
		N	I_1	I_2
RL	A ± SE	8.07 ± 9.26 ^{ns}	8.91 ± 11.40 ^{ns}	-10.15 ± 7.75 ^{ns}
	B ± SE	12.5 ± 9.20 ^{ns}	8.36 ± 8.30 ^{ns}	-4.42 ± 7.47 ^{ns}
	C ± SE	13.92 ± 18.02 ^{ns}	-11.02 ± 19.48 ^{ns}	-15.03 ± 14.55 ^{ns}
	D ± SE	-82.57 ± 18.71**	-42.51 ± 23.69 ^{ns}	-73.98 ± 25.60 ^{ns}
RV	A ± SE	-19.9 ± 14.89 ^{ns}	-0.8 ± 13.01 ^{ns}	-3.05 ± 11.12 ^{ns}
	B ± SE	-26.05 ± 14.17 ^{ns}	-47.35 ± 12.18 **	-1.5 ± 13.34 ^{ns}
	C ± SE	43.15 ± 50.16 ^{ns}	8.75 ± 31.86 ^{ns}	15.25 ± 34.97 ^{ns}
	D ± SE	-133.25 ± 28.46 **	-67.65 ± 23.17 **	-14.45 ± 29.68 ^{ns}
RD	A ± SE	-0.033 ± 0.023 ^{ns}	-0.156 ± 0.048 **	-0.027 ± 0.047 ^{ns}
	B ± SE	-0.053 ± 0.040 ^{ns}	-0.191 ± 0.046 **	-0.014 ± 0.026 ^{ns}
	C ± SE	-0.027 ± 0.076 ^{ns}	0.023 ± 0.078 ^{ns}	-0.071 ± 0.062 ^{ns}
	D ± SE	-0.083 ± 0.066 ^{ns}	-0.093 ± 0.078 ^{ns}	0.114 ± 0.081 ^{ns}
RN	A ± SE	-1.25 ± 1.83 ^{ns}	-2.00 ± 1.88 ^{ns}	-2.25 ± 3.06 ns
	B ± SE	2.05 ± 1.86 ^{ns}	0.00 ± 1.57 ^{ns}	-4.7 ± 2.79 ^{ns}
	C ± SE	-1.1 ± 3.52 ^{ns}	1.7 ± 4.27 ^{ns}	1.5 ± 6.83 ^{ns}
	D ± SE	-1.7 ± 3.86 ^{ns}	-3.4 ± 4.14 ^{ns}	5.25 ± 5.72 ^{ns}
RFW	A ± SE	48.50 ± 31.65 ^{ns}	-3.80 ± 13.53 ^{ns}	-42.31 ± 21.51 ^{ns}
	B ± SE	-44.92 ± 19.57 *	-0.85 ± 11.23 ^{ns}	-18.22 ± 16.07 ^{ns}
	C ± SE	60.56 ± 67.93 ^{ns}	20.88 ± 29.80 ^{ns}	-10.27 ± 51.45 ^{ns}
	D ± SE	-127.29 ± 38.46 **	16.74 ± 21.45 ^{ns}	-37.01 ± 40.89 ^{ns}
RDW	A ± SE	0.033 ± 3.07 ^{ns}	-2.56 ± 2.99 ^{ns}	-9.31 ± 4.81 ^{ns}
	B ± SE	-1.69 ± 3.35 ^{ns}	2.63 ± 3.11 ^{ns}	-8.48 ± 2.59 **
	C ± SE	24.22 ± 15.29 ^{ns}	10.64 ± 6.72 ^{ns}	-0.19 ± 10.38 ^{ns}
	D ± SE	-39.81 ± 8.69 **	-1.75 ± 11.42 ^{ns}	-10.29 ± 7.33 ^{ns}

Where RL, RV, RD, RN, RFW and RDW denote; root length, root volume, root diameter, root number, root fresh weight and root dry weight, respectively.

^{ns},* and ** non-significant, significant at 5% and 1% levels of probability, respectively.

Model and Genetic Effects

Estimates of genetic effects from generation mean analysis according to the different parameter models and the joint scaling test ($\chi 2$) for root traits in three irrigation regimes are present in Table 4. Except for RD in the I1 condition, all models had non-significant $\chi 2$ statistics, indicating that the selected models are fitted the data obtained for different traits. The mean parameter [m] for all studied attributes in three conditions indicates that the contribution due to the overall mean plus the locus effects and interaction of the fixed loci was significant. Additive gene effect [a] was significant for RV, RFW, and RDW in normal irrigation, RL, RV, RD, RFW, and RDW in I1, and RL, RV, RD, and RN in I2 condition. On the other hand, the estimated dominance gene action [d] was significant for RL, RD, RN, RFW, and RDW in three conditions except for RV in I1 condition, indicating the importance of dominance gene effects in inheritance of these traits. The epistatic effects ([i], [j] and [l]) were significant for RL, RV, RFW, and RDW in normal irrigation, RV and RD in I1 and RL and RDW in I2 condition. Both additive

× additive [i] and dominance × dominance [l] effects were significant for RL, RFW, and RDW in normal condition. The opposite signs of dominance [d] and dominance × dominance [l] suggested duplicate type of epistasis. Opposite sign between additive [a] and additive × additive [i] gene effect in normal irrigation for RV, RFW, RDW, and RD in I1 and RL in I2 condition suggest the oppositional nature of interaction in these traits. In the I1 irrigation regime, significant additive × dominance [j] gene effects for RV indicated that this trait is under complex genetic control. In most of the traits except RN, the gene effects differed in three conditions.

Genetic Variance Components

The result of generation variance analysis indicated that the environmental variance in most traits except RL under normal and I2 condition, also RDW in both of I1 and I2 condition were higher than genetic variances (Table 5). In other words, estimates of variance components showed environmental and interaction variances in some traits were higher than additive and dominance variance and in other traits, dominance and additive variance were higher than these in three irrigation conditions. A negative estimate of VAD in most traits in different conditions except for RL, RD, and RN under normal irrigation, RN and RDW in I1 condition and RL and RV in I2 condition denote that dominant genes are in the low-performance parent. For RN in normal irrigation, RL, RN and RDW in I1 condition and RL, RV, RN and RFW in I2 condition VA was higher than VD which indicated that breeding for these traits would be different in three irrigation conditions.

Degree of Dominance

The degree of dominance for studied traits is presented in Table 5, which shows that the degree of dominance for all studied traits except RL and RN in normal irrigation and RD in I2 condition wasn’t estimated because the genetic variance component (VA, VD or both of them) are estimated negative and intended zero in calculations. Degree of dominance for RL and RN in normal irrigation and RD in I2 condition, indicating the presence of the overdominance type of gene action in the inheritance of these traits.

Table 4. *Estimates gene action types using generation means for maize root traits under normal irrigation and drought stress.*

Traits	C	Genetics parameter						χ^2	*df*
		m **± SE**	**[*a*] ± SE**	**[*d*] ± SE**	**[*i*] ± SE**	**[*j*] ± SE**	**[*l*] ± SE**		
RL	N	47.78± 8.07**	3.35± 2.39^{ns}	125.97± 24.14**	37.58± 8.15**	-4.72± 11.85^{ns}	-65.83± 18.41**	3.26 ^{ns}	1
	I_1	47.65± 2.52**	-5.61± 2.59*	11.26± 4.69*	-	-	-	7.55 ^{ns}	4
	I_2	79.35± 5.02**	-8.21± 2.39*	30.21± 6.46*	15.66± 5.71**	-5.72± 10.06 ^{ns}	-	3.52 ^{ns}	2
RV	N	30.51± 5.05**	-13.19± 4.14**	52.97± 9.57**	35.33± 6.42**	7.22± 17.77 ^{ns}	-	6.36 ^{ns}	2
	I_1	49.37± 8.91**	-10.40± 3.66**	-4.03± 28.30 ^{ns}	9.13± 9.12 ^{ns}	47.90± 14.08**	31.93± 25.14 ^{ns}	5.55 ^{ns}	1
	I_2	53.94± 3.24**	-7.41± 3.26*	22.62± 6.50**	-	-	-	0.41 ^{ns}	4
RD	N	0.29± 0.008**	-0.014± 0.009 ^{ns}	0.061± 0.015**	-	-	-	4.10 ^{ns}	4
	I_1	0.377± 0.036**	-0.021± 0.010*	-0.43± 0.011**	0.084± 0.036*	0.040± 0.063 ^{ns}	0.335± 0.089*	11.39 **	1
	I_2	0.17± 0.007**	-0.03± 0.007*	0.10± 0.013*	-	-	-	3.09 ^{ns}	4
RN	N	14.96± 0.39**	-0.52± 0.41 ^{ns}	2.52± 0.80**	-	-	-	2.47 ^{ns}	4
	I_1	15.78± 0.49**	-0.62± 0.49 ^{ns}	2.30± 1.02*	-	-	-	1.99 ^{ns}	4
	I_2	19.00± 0.87**	1.72± 0.90**	4.50± 1.57*	-	-	-	9.48 ^{ns}	4
RFW	N	21.62± 13.32**	-21.38± 6.58*	190.69± 55.35**	67.33± 13.91*	105.25± 32.34 ^{ns}	-87.68± 48.88*	3.38 ^{ns}	1
	I_1	74.01± 3.02**	-6.35± 3.08*	8.96± 6.89 ^{ns}	-	-	-	3.04 ^{ns}	4
	I_2	74.87± 5.46**	-9.63± 5.38 ^{ns}	36.95± 10.90*	-	-	-	4.72 ^{ns}	4
RDW	N	5.56± 1.95**	-2.28± 1.05*	25.98± 6.73**	11.46± 2.11*	-	-11.40± 5.47*	6.36 ^{ns}	2
	I_1	13.10± 0.94**	-1.16± 0.91*	3.57± 1.67 ^{ns}	-	-	-	4.83 ^{ns}	4
	I_2	15.88± 2.37**	2.45± 1.18 ^{ns}	-15.24± 7.09*	-1.80± 2.67 ^{ns}	-	18.20± 6.13**	2.78 ^{ns}	2

Where RL, RV, RD, RN, RFW and RDW denote; root length, root volume, root diameter, root number, root fresh weight and root dry weight, respectively.

m, [a], [d], [i], [j] and [l] denote; mean, additive effect, dominance effect, additive × additive, additive × dominance and dominance × dominance, respectively.

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

Heritability

High broad-sense heritability estimates RL, RD, RN, RFW, RDW, and RV under three environments (Table 5) revealed that the effective progress can be made through the selection and high effect of the genetic variance in control of these traits. Moderate narrow-sense heritability was shown for RN in normal irrigation and I2 condition. Narrow-sense heritability was lower than those broad-sense for RL in normal irrigation and for RD in I2 condition indicating that most of the genetic variance was due to non-additive effects i.e., dominance or epistasis. The similarity between broad-sense heritability and narrow-sense heritability exhibits the involvement of the additive effect and zero estimation of dominance effect in the genetic constitution of some traits under different conditions.

Table 5. *Estimates variance components, degree of dominance broad-sense and narrow- sense heritability for all studied traits under normal irrigation and drought stress.*

Traits	**conditions**	**Genetic variance components**				**DOD**	**Heritability**	
		V_E	V_A	V_D	V_{AD}		H^2_b	H^2_n
RL	N	155.11	61.09	103.17	25.27	1.08	95.49	28.53
	I_1	313.25	175.41	-83.01	-158.84	-	91.80	91.80
	I_2	154.29	184.52	-69.88	8.77	-	95.98	95.98
RV	N	696.65	-388.47	159.11	-97.19	-	82.03	-
	I_1	558.36	-12.51	-161.25	-86.09	-	-	-
	I_2	533.81	282.40	-209.16	109.28	-	91.36	91.36
RD	N	0.003	-0.0005	0.0017	0.0019	-	91.91	-
	I_1	0.004	-0.0017	0.0049	-0.0003	-	96.03	-
	I_2	0.0023	0.0009	0.0017	-0.0023	1.06	95.81	27.64
RN	N	8.80	2.42	2.11	0.41	1.51	91.14	48.70
	I_1	13.64	5.34	-6.07	0.47	-	88.67	88.67
	I_2	30.19	1.29	-13.10	-9.40	-	46.14	46.14
RFW	N	1769.66	-1755.20	1740.07	-1960.67	-	95.16	-
	I_1	556.70	-99.69	-87.28	-191.90	-	-	-
	I_2	890.22	438.50	-337.72	-84.95	-	90.78	90.78
RDW	N	35.88	-10.75	-5.17	-1.42	-	-	-
	I_1	39.62	59.91	-44.85	2.68	-	96.79	96.79
	I_2	18.13	-0.64	18.35	-23.35	-	95.29	-

Where RL, RV, RD, RN, RFW and RDW denote; root length, root volume, root diameter, root number, root fresh weight and root dry weight, respectively.

VE, VA, VD, VAD, DOD, H2b and H2ndenote; Environment variance, additive variance, dominance variance, additive × dominance co-variance, degree of dominance, broad-sense heritability and narrow-sense heritability, respectively.

Previous studies of maize have shown that drought stress induces morphological, physiological and biochemical changes, including changes to photosynthesis, plant height, dry matter production, leaf area and grain yield [25]. However, many studies have reported maize responses to water stress applied under unnatural conditions and for a short duration [26,27]. In maize Morphoanatomical changes in the canopy and root system are involved in mechanisms for efficient water absorption and conservation, and the identification of such mechanisms is crucial for the selection of genotypes tolerant to drought [28]. Maize, respond to water deficit by redirecting growth and dry matter accumulation away from the shoot to the root [29]. In the present study, the assessment of various root traits for drought tolerance revealed significant variability among the seven maize generations. The highest stress tolerance was revealed by the F_1, displaying the presence of heterosis for drought resistance in the F_1 hybrid. Also means of the F_1 were higher than either the highest parent or mid-parent value indicating over or partial dominance, respectively towards the respective parents for most studied traits, as well as, the transgressive segregation for more traits was also observed in the F_2 generation.

Dissection of genetic variation into different components using biometric methods is important for a plant breeder to exploit the potential genetic resources through plant selections and hybridization schemes. The procedure of generation means and variance analyses had extensively been used for drought-tolerance studies in cotton [30], wheat [31] and maize [32]. In this study, although the scaling test failed to detect non-allelic interaction for some of the traits in different irrigation conditions, the inadequacy of the additive-dominance model suggests the presence of non-allelic interactions. A negative estimate of additive and dominance gene effect in some cases might be due to parent arrangement in the cross and epistatic gene action in the cross combinations, respectively. The dominance gene effect was higher than the additive gene effect for most traits which confirms the important role of the dominance gene effect in the genetic system. This kind of epistasis generally hinders the improvement through the selection and, hence, a higher magnitude of dominance and dominance × dominance type of interaction effects would not be expected. It also indicated that selection should be delayed after several generations of selection (single seed descent) until a high level of gene fixation is attained. Besides the additive and dominance genetic effects and epistatic components have also contributed to genetic variations for most of the root traits studied. Data analysis revealed, there are many relations between scaling test, joint scaling test, and generation mean analysis results. Heritability estimates indicate the progress from selection for plant characters is relatively easy or difficult to make inbreeding program. Plant breeders, through experience, can perhaps rate a series of their response to selection. Heritability gave a numerical description of this concept. Assessment of heritability of various traits is of considerable importance in crop improvement programs, for example, to predict response to selection [33]. In this study, high levels of genetic broad sense and narrow sense heritability suggested that genetic effects and additive effects have a greater role in the inheritance of most traits under different irrigation conditions.

CONCLUSION

Since the studies of different traits in different environmental conditions have shown that with changing environmental conditions, the mode of action and estimate genetic parameters are changed, it can be better these studies in a few years and different environments. In this cross for many traits, epistasis effects under different irrigation conditions were seen, so for breeding hybrids, selection optimal epistatic compounds can be effective. As well as the results of the research necessary to benefit from the dominance gene effects in hybrid corn breeding programs. Due to the high impact of the environment on the estimated parameters to increase accuracy and determine the more accurate amount of these parameters, studies should be done in several years.

REFERENCE

[1] Ober, E.S., Sharp, R.E. (2007): Regulation of Root Growth Responses to Water Deficit. In: Jenks, M.A., Hasegawa, P.M., Jain, S.M. (eds.) Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops. Springer, Dordrecht, pp: 33-53.

[2] Bengough, A.G., McKenzie, B., Hallett, P., Valentine T. (2011): Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. Journal of Exprimental Botany 62(1): 59-68.

[3] Sharp, R.E., Poroyko, V., Hejlek, L.G., Spollen, W.G., Springer, G.K., Bohnert, H.J., Nguyen, H.T. (2004): Root growth maintenance during water deficits: physiology to functional genomics. Journal of Exprimental Botany 55(407): 2343-2351.

[4] Trachsel, S., Stamp, P., Hund, A. (2010): Growth of axile and lateral roots of maize: response to desiccation stress induced by polyethylene glycol 8000. Maydica 55(2): 101-109.

[5] Vadez, V. (2014): Root hydraulics: the forgotten side of roots in drought adaptation. Field Crops Research, 165: 15-24.

[6] Hu, H., Xiong, L. (2014): Genetic engineering and breeding of drought-resistant crops. Annual Review of Plant Biology 65: 715-741.

[7] Hammer, G.L., Dong, Z., McLean, G., Doherty, A., Messina, C., Schussler, J. Cooper, M. (2009): Can changes in canopy and/or root system architecture explain historical maize yield trends in the US corn belt?. Crop Science 49(1): 299-312.

[8] Hochholdinger, F., Woll, K., Sauer, M., Dembinsky, D. (2004): Genetic dissection of root formation in maize (*Zea mays* L.) reveals root-type specific developmental programmes. Annals of Botany 93(4): 359-368.

[9] Ribaut, J.M., Betran, J., Monneveux, P., Setter, T. (2009): Drought Tolerance in Maize. In: Bennetzen, J., Hake, S. (eds.) Handbook of Maize: Its Biology. Springer, NewYork, pp: 311-344.

[10] Sharp, R., Davies, W. (1979): Solute regulation and growth by roots and shoots of water-stressed maize plants. Planta 147(1): 43-49.

[11] Zhan, A., Schneider, H., Lynch, J. (2015): Reduced lateral root branching density improves drought tolerance in maize. Plant Physiology 168(4): 1603-1615.

[12] Maazou, A.R.S., Tu, J., Qiu, J., Liu, Z. (2016): Breeding for drought tolerance in maize (Zea mays L.). American Journal of Plant Science 7(14): 1858.

[13] Hallauer, A., Miranda Filho, J. (1988): Quantitative Genetics in Maize Breeding. Springer, NewYork.

[14] Mather, K., Jinks, J. (1982): Biometrical Genetics. Chapman and Hall CrossRef, Landon.

[15] Kearsey, M.J., Pooni, H.S. (1998): The Genetical Analysis of Quantitative Traits: Stanley Thornes (Publishers) Ltd.

[16] Dresselhaus, T., Hückelhoven, R. (2018): Biotic and Abiotic Stress Responses in Crop Plants. Multidisciplinary Digital Publishing Institute (MDPI), Belgrade.

[17] Schaap, M.G., Leij, F.J., Van Genuchten, M.T. (2001): Rosetta: A computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. Journal of Hydrology 251: 163-176.

[18] Jacob, H., Clarke, G. (2002): Methods of Soil Analysis, Part 4, Physical method. Soil Science Society of America, Inc, Madison, Wisconsin, USA.

[19] Allen, R.G., Pereira, L.S., Raes, D., Smith, M. (1998): Crop Evapotranspiration-Guidelines for Computing Crop Water Requirements-FAO Irrigation and Drainage Paper 56. Fao, Rome 300: D05109.

[20] MSTAT-C U. s. g. t. (1991): In: Michigan State University. USA.

[21] Rowe, K., Alexander, W. (1980): Computations for estimating the genetic parameters in joint-scaling tests 1. Crop Science 20(1): 109-110.

[22] Snedecor, G.W., Cochran, W.G. (1989): Statistical Methods. Ames: Iowa State University Press, Iowa.

[23] Hayman, B. (1958): The Separation of epistatic from additive and dominance variation in generation means. Journal of Heredity 12(3): 371.

[24] Nelder, J. (1960): The estimation of variance components in certain types of experiment on quantitative genetics. Biometrical Genetics 139-158.

[25] Zhao, W., Liu, B., Zhang, Z. (2010): Water requirements of maize in the middle heihe river basin, China. Agricultural Water Management 97: 215-223.

[26] Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S.M.A. (2009): Plant Drought Stress: Effects, Mechanisms and Management. Sustainable Agriculture. Springer, pp: 153-188.

[27] Kakani, V.G., Vu, J.C.V., Allen-Jr, L.H., Boote, K.J. (2011): Leaf photosynthesis and carbohydrates of CO2-enriched maize and grain sorghum exposed to a short period of soil water deficit during vegetative development. Journal of Plant Physiology 168: 2169-2176.

[28] Ge, T., Sui, F., Bai, L., Tong, C., Sun, N. (2012): Effects of water stress on growth, biomass partitioning, and water-use efficiency in summer maize (*Zea mays* L.) throughout the growth cycle. Acta Physiologiae Plantarum 34: 1043-1053.

[29] Hsiao, T.C., Xu, L.K. (2000): Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. Journal of Experimental Botany 51: 1595-1616.

[30] Khan, N., Azhar, F.M., Khan, A.A., Ahmad, R. (2014): Measurement of canopy temperature for heat tolerance in upland cotton: variability and its genetic basis. Pakestan Journal of Agricalural Science 51: 359-365.

[31] Munir, M., Chowdhry, M.A., Ahsan, M. (2007): Generation mean studies in bread wheat under drought condition. International Journal of Agricultural Biolology 9: 282-286.

[32] Ahsan, M., Farooq, A., Khaliq, I., Ali, Q., Aslam, M., Kashif, M. (2013): Inheritance of various yield contributing traits in maize (*Zea mays* L.) at low moisture condition. African Journal of Agricultural Research 8: 413-420.

[33] Nyguist, W.E. (1991): Estimation of heritability and prediction of response in plant populations. CRC Critical Review in Plant Science 10(3): 235–322.