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Genetic analysis of yield, yield-components and related phenological traits of maize (*Zea mays* L.) to breed under moisture stress conditions

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Abstract

Improved drought-tolerant maize hybrids would significantly reduce water consumption and increase yield in arid environments. Our knowledge about genetic parameters is very essential before starting a successful breeding program. The present research was carried out throughout three successive years between 2013-15 to reveal the pattern of inheritance in yield, yield-components and related phenological traits under moisture stress conditions. There was a positive and significant heterosis for grain yield/plant (GY), ear biomass/plant (EB), ear length (EL), grain number/row (GN) and plant height (pH). Inadequacy of additive-dominance model for the majority of the traits, indicate the role of epistatic in governing inheritance of those traits. There was a big-difference between dominance and additive effects for some traits, showing complete dominance and over dominance control the traits. Although dominance variation was greater than additive effect for phenological traits, however, the effect of additive effects was greater than dominance for GY, EB, ear-harvest index (EHI), row number/ear (RN) and ear-wood percent (EWP). Broad sense and narrow sense heritability ranged between 43.33-87.67 and 12.28-47.41, respectively. Meanwhile, the minimum gene number ranged between 1 to 6.53 in the studied traits. Due to the notable role of additive effects in governing the important traits of EB, EHI and RN, selection in early generations using the pedigree method for them, can be efficient to improve drought-tolerance and stabilize GY under moisture stress conditions.

***Keywords*:** Generation mean analysis; Genetic parameters; Water stress

1. Introduction

Scarcity of water in recent decades has been the most important problem in the worldwide (Ribot *et al.,* 2012). Iran, as an arid and semi-arid country, suffers severe moisture stress problems. In reality, moisture stress is the most important a-biotic stress, limiting crop productivity (Khan *et al.,* 2016; Betran *et al.,* 2003a). Therefore, the development of well-adapted cultivars with a wide range of environments is the basic and prior goal of maize breeders (Ndhlela *et al.,* 2015). Maize is one of the most important tropical cereals with a rich grain of protein and necessary amino acid (Badu-Apraku and Akinwale, 2011).Several genes control maize grain yield (GY) under moisture stress conditions, hence, indirect selection for GY improvement using the other traits will be an efficient method to improve GY (Campos *et al.,* 2004). In other words, breeding for drought tolerance, is an economic and a permanent strategy to resolve moisture stress problems (Ashraf and Harris, 2005). Our knowledge about heritability and the genetic analysis of a trait is very essential before starting a successful breeding program (Ullah *et al.,* 2013). Indeed, insufficient information about gene action leads to deficiency of breeding for yield improvement (Roff and Emerson, 2006). In reality, in a quantitative trait, the number of genes, the type of gene action, and the genotype by environment interaction are three major factors that must be

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evacuated and which may limit progress in the analysis of genetic variation (Sprague, 1963). Therefore, breeders need to assess genetic analysis (gene action, heritability, hybrid vigor and inbreeding depression) of different traits to improve yield and yield components under varied environments. The response to selection is influenced by the genetic variability, heritability and selection intensity (Sharma, 2003). Heritability estimates are influenced by the type of genetic material, sample size, method of sampling, type of experiment, the method of calculation and effect of linkage (Ali-Said, 2014). Many different genetic models have been developed for the estimation of genetic effects. Among the different genetic analysis methods, generation mean analysis is one of the most valuable methods involving estimation of genetic effects (Kearsey and Pooni, 2004). Although, the majority of these proposed genetic models estimate only additive and/or dominance effects, but, generation mean analysis (Mather and Jinks, 1982) provides information on additive, dominance and epistatic (additive by additive, dominance by dominance and additive by dominance effects) effects. Genetic analysis of different traits in maize has been studied previously by other researchers (Hinze and Lamkey, 2003; Zdunic *et al.,* 2008; Jebaraj *et al.,* 2010; Sher *et al.,* 2012; Carretero *et al.,* 2014; Meena *et al.,* 2014). The majority of these researchers indicated that epistatic effects play a major role in governing inheritance of some economic traits of maize. Thus, plant breeders cannot ignore epistatic effects. Sher *et al.* (2012) suggested that both dominance and epistatic gene action played a major role in operating the inheritance of days to pollen shedding, days to 50% silking, anthesis silking interval, and maturity. Meanwhile, over dominance, complete dominance, and epistatic gene actions were responsible for yield and yield-components (Butruille *et al.,* 2004; Meena *et al.,* 2014). Some previous researchers (Makumbi *et al.,* 2011; Ndhlela *et al.,* 2015) indicated that additive effect has a preponderant role than dominance effect in controlling the inheritance of grain yield, ear length, ear diameter, and grain yield/ ear. However, Badu-Apraku *et al.* (2011) reported that both dominance and additive effects played major role in governing the yield and yield-components of maize. Generally, the number and type of generations, the type of genetic material, sample size, method of sampling, type of experiment, method of calculation, accuracy of statistical hypothesis and effect of linkage lead to different results in different researches. The present research was carried out: (i) to detect the type of gene action, and (ii) to estimate genetic parameters and the number of genes that play an important role in governing the studied traits for an efficient breeding program under moisture stress conditions.

2. Materials and Methods

2.1. Plant material and experimental location

The experimental material consisted of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) derived from a cross between S0200237-7 (P_1) and S0200237-5 (P_2) lines (Table 1). The study was carried out at the research-farm of Agriculture and Natural Resources Research and Education Center of Golestan, in Gorgan-Iran, throughout three successive growing seasons of 2013-15. In 2013, the crosses were made between the parents to produce F_1 hybrid. In 2014, F_1 progenies were selfed to produce F_2 and they crossed to the parents to produce BC_1 and BC_2 generations. In 2015, the seeds of the six generations were planted based on a randomized complete block design with three replicates for each generation. Rows were 5 m long with a distance of 75 cm between the rows and 17.5 cm between plants in rows. Each replicate consisted of more than 10 plants in one row for each of the parents and F_1, and more than 20 plants in two rows for each of back cross and the F_2 population. In reality, the traits were recorded on 10 individual plants for P_1, P_2 and F_1, as well as 20 plants for BC_1 and BC_2 and F_2 for each replicate for the below traits. The traits of days to 50% silking, grain filling period, days to physiological maturity, plant height, row number/ear, grain number/row, ear diameter, grain depth, 250-grain weight, grain humidity percent, ear-wood percent, ear-biomass/plant, grain yield/plant, and ear-harvest index were measured during the 2015 growing season and after harvesting the plants.

The plants were normally watered until established and after that, they were watered when the soil-moisture was about 70% field capacity. Soil-weighted moisture was used to detect required water in each irrigation time.

Table 1. Characters of the used parental inbred lines

Name	Pedigree	Drought response	Maturity
P_1 (male)	S0200237-7	drought susceptible	Late (110-120 days)
P_2 (female)	S0200237-5	drought tolerant	Semi early (100-110 days)

2.2. Statistical analysis

Analysis of variance and Duncan's multiple range test of the traits was conducted using SAS software. Generation mean analysis was performed using Mather and Jinks method according to six generation data (1982). Heterosis was calculated according to Matzinger (1963) and Kang (1994). Inbreeding depression was estimated by Kang's (1994) method. The variance components, average of gene dominance, dominance deviation and dominance degree of the traits were performed using Mather and Jinks (1982). Broad and narrow scene heritability was calculated by them method of Mahmud and Krammer (1951) and Warnner (1952). Gene number was estimated by the method of Lande (1981).

3. Results

Analysis of variance (Table 2) showed significant differences ($P<0.05$) among the generations for all traits. Therefore, generation mean analysis was carried out to reveal the mode of inheritance in the traits. Grain yield/plant (GY) and plant height (PH) showed the maximum relative heterosis and heterobeltiosis, respectively (Table 2). Relative heterosis value was negative for the traits of grain humidity percent (GHP), ear-wood percent (EWP), and row number/ear (RN), indicating the means of F_1 trend to the mean of undesirable parent (Table 2).

For some traits such as, grain-filling period (GFP), RN and ear diameter (ED), the means of F_1 were in the range of the parents means (Table 3). In contrast, for the trait of grain number/row (GN), the means of F_1 were similar to the means of one of the parents (Table 3).

For the traits of days to 50% silking (DS), PH, EWP, ear-biomass/plant (EB), and GY, the means of F_2 were less than the means of F_1 (Table 3). The results (Table 3) revealed that the means of F_2 were greater than the parents' means for the traits of days to physiological maturity (DPM), PH, RN, GN, ED, grain depth (GD), and 250-grain weight (TGW).

Results (Table 4) showed that all six parameter models were significant for TGW, but due to the lack of information, it was not possible to perform a related Chi-Square test, and it required more generations' information. The parameter of [h], is not significant for the traits of RN, EB, GY, and ear-harvest index (EHI) (Table 4), although there were significant values of additive by additive ([I]) effect, for the traits of PH, GN, ED, GD, TGW, GHP and EWP. Significant values of additive by dominance ([j]), for the traits of GN, TGW and EWP indicated that the mentioned epistatic plays a major role in the inheritance of these traits (Table 4). The significant values of parameters of [h] and [l] with opposite signs, for GFP, DPM, PH, ED, GD, TGW and GHP were shown in Table 4.

The $(H/D)^{½}$ ratio was greater than unity for days to 50% silking (DS), GFP, DPM, PH, GN, ED, GD, and GHP (Table 5). The $(F/(H\times D)^{1/2})$ ratio was less than unity and nearly zero for all traits (Table 5). Additive variance and partial dominance showed a big effect on the traits of RN, TGW, EWP, EB, GY, and EHI (Table 5). In other traits, including DS, GFP, DPM, PH, GN, ED, GD, and GHP, dominance variation was greater than additive variation (Table 5). The numbers of genes that were involved in governing the different traits ranged between 1- 6.53 (Table 6). The traits of EB and PH had maximum and EWP had minimum broad sense heritability (Table 6). The maximum and minimum narrow sense heritability was observed in TGW and GFP, respectively (Table 6).

4. Discussion

Our knowledge about genetic parameters is very essential before starting a successful breeding program (Ullah *et al*. 2013). The means of F_1 progenies were in the range of the parents' means for GFP, RN and ED, indicating the additive and partial-dominance gene actions involved in the genetic controlling of these traits. Thus, selection in early generations will be a suitable method for the trait genetic improvement. Although, Dofing and co-workers (1991) suggested that the ear length (EL) and ED were mainly controlled by dominance effect, but Makumbi *et al.* (2011) indicated that additive effect has a preponderant role than dominance effect in controlling the mentioned traits. For a specific trait, the similarity of F_1 progenies means that the means of one parent represents the role of partial or complete dominance effect in governing that trait. For PH, the means of F_1 progenies is out of the range of the means of the parents. In other words, over-dominance effects play an important role in controlling the traits. Vidal-Martinez *et al.* (2001), suggested that ear weight (EW), GN, RN, EL, and GY were mainly controlled by dominance effects. Oching and Compton (1994) reported that dominance effects operated the GY, while ear per plant, was controlled by additive gene action. Alok *et al.* (1998), showed that although additive and non-additive effects simultaneously controlled the PH and EL, but ED and RN were governed by partial dominance. Generally, hybridization methods have been suggested to breed the traits controlled by the dominance and over-dominance effects (Ishfaq, 2011 and El-Badawy, 2012).

Due to inbreeding depression, the means of F_2 progenies were less than the means of F_1 for DS, PH, EWP, EB, and GY. According to the above results, transgressive segregation was observed for DPM, PH, RN, GN, ED, GD, and TGW. These results were also supported by El-Badawy (2012) in maize.

The additive gene action does not have an important role in controlling a trait when there is a significant heterosis effect. Zdunic *et al.* (2008) reported the maximum heterobeltiosis and mid-parent heterosis for GY, and EW, respectively. Several previous researchers (Premalatha *et al.*, 2010; Bhavana *et al.*, 2011; Ram Reddy *et al.*, 2011; Sumalini *et al.*, 2011; Jawaharlal *et al.*, 2012; Raghu *et al.*, 2012) reported high and significant heterosis for grain yield and yield components.

The significant effect of [h] parameter shows the major contributors of dominance action in the inheritance of the trait. In other words, it indicates that the additive gene action did not play a major role in the inheritance of these traits. Significant values of [h] with negative signs for some traits, indicate the relative dominance for reduction of those traits. These results are in accordance with the findings of other researchers (Makumbi *et al.*, 2011; Betran *et al.*, 2003b; Ndhlela 2015). The least amount of dominance effect in the ear-wood percent can be related to undetermined directions of this effect and low genetic variation. The roles of non-additive effects have previously been reported for grain yield, and 1000-grain weight (Butruille *et al.*, 2004; Abrha *et al.*, 2013; Watto *et al.*, 2009).

Table 2. ANOVA, heterosis, heterobeltiosis and inbreeding depression of the different traits of maize in six generations of $(P_1) \times (P_2)$

S.O.V.	df	Mean of squares of traits						
		DS	GFP	DPM	PH	RN	GN	ED
Block	2	17.54^{**}	12.05^{**}	1.50^{ns}	189.53^{ns}	0.02^{ns}	18.64^{*}	7.78^{*}
Generations	5	4.98^{*}	6.05^{**}	8.66^{*}	376.60^{*}	4.40^{**}	13.30^{*}	34.51^{**}
Error	10	0.95	0.85	2.76	102.44	0.44	2.68	1.79
C. V.	-	2.04	1.36	1.42	4.82	5.11	5.59	3.19
Heterosis	-	6.01	0.00	2.48	9.23	-1.88	9.24	1.85
Heterobeltiosis	-	4.17	-1.47	2.33	8.59	-9.41	4.93	-5.47
Inbreeding depression	-	3.33	-2.99	-0.28	1.67	-22.40	-5.31	-13.30

S.O.V.	df	Mean of squares of traits						
		GD	TGW	GHP	EWP	EB	GY	EHI
Block	2	5.53^{*}	61.21^{**}	2.65^{ns}	2.57^{ns}	882.74^{ns}	607.44^{ns}	1.59^{ns}
Generations	5	17.69^{**}	61.00^{**}	25.09^{**}	7.81^{*}	2759.30^{**}	2474.60^{**}	57.77^{**}
Error	10	1.46	4.87	3.51	2.29	287.46	219.85	7.67
C. V.	-	4.12	3.32	7.22	6.93	14.88	16.10	3.45
Heterosis	-	2.53	0.72	-2.08	-9.10	15.04	15.72	1.62
Heterobeltiosis	-	-4.98	-1.63	-13.02	-15.84	-11.65	-13.30	-1.76
Inbreeding depression	-	-12.88	-9.55	-13.77	0.89	10.18	10.15	-0.24

S.O.V., Sources of variance; df, Degrees of freedom; DS, Days to 50% silking; GFP, Grain filling period; DPM, Days to physiological maturity; PH, Plant height; RN, Row number/ear; GN, Grain number/row; ED, Ear diameter; GD, Grain depth; TGW= 250- Grain weight; GHP, Grain humidity percent; EWP, Ear-wood percent; EB, Ear-biomass/ plant; GY, Grain yield/plant and EHI, Ear-harvest index. ^{ns}, not significant; *, significant at $P \leq 0.05$; **, significant at $P \leq 0.01$.

Table 3. Duncan s' mean comparison of the different traits of maize in six generations of (P_1) × (P_2)

Generation	DS	GFP	DPM	pH (cm)	RN	GN	ED (mm)
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
P_1	$46.33^{c} \pm 0.11$	$69^{ab} \pm 0.48$	$115.33^{b} \pm 0.38$	$203.93^{bc} \pm 2.41$	$11.40^{c} \pm 0.48$	$25.99^{c} \pm 0.21$	$37.23^{e} \pm 0.36$
P_2	$48^{bc} \pm 0.18$	$62^{d} \pm 0.28$	$110^{c} \pm 0.18$	$206.33^{abc} \pm 5.47$	$13.47^{b} \pm 1.33$	$28.22^{bc} \pm 0.57$	$43.49^{bc} \pm 1.28$
F_1	$50^{a} \pm 0.36$	$67^{cd} \pm 0.38$	$117^{ab} \pm 0.18$	$224.07^{a} \pm 4.50$	$12.20^{bc} \pm 0.99$	$29.61^{ab} \pm 0.19$	$41.11^{cd} \pm 0.50$
F_2	$48.33^{ab} \pm 0.28$	$69^{ab} \pm 0.18$	$117.33^{ab} \pm 0.11$	$220.33^{ab} \pm 2.60$	$14.93^{a} \pm 1.30$	$31.18^{ab} \pm 0.45$	$46.57^{a} \pm 0.72$
BC_1	$47.67^{bc} \pm 0.53$	$70^{a} \pm 0.18$	$117.67^{a} \pm 0.38$	$193.47^{c} \pm 3.29$	$12.60^{bc} \pm 0.10$	$28.98^{abc} \pm 0.25$	$39.44^{de} \pm 0.57$
BC_2	$49.33^{ab} \pm 0.46$	$68.33^{bc} \pm 0.28$	$117.67^{a} \pm 0.38$	$210^{abc} \pm 2.22$	$13.20^{b} \pm 1.10$	$31.81^{abc} \pm 0.21$	$44.08^{b} \pm 0.49$

Generation	GD (mm)	TGW (g)	GHP	EWP	EB (g)	GY (g)	EHI (%)
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
P_1	$25.88^{d} \pm 0.21$	$64.88^{b} \pm 0.76$	$22.47^{c} \pm 0.33$	$24.84^{a} \pm 0.06$	$72.80^{d} \pm 2.42$	$54.65^{d} \pm 0.78$	$75.16^{b} \pm 1.40$
P_2	$30.32^{ab} \pm 0.76$	$68.05^{b} \pm 0.96$	$28.93^{a} \pm 0.22$	$21.15^{b} \pm 0.34$	$135.82^{ab} \pm 8.20$	$109.65^{ab} \pm 9.50$	$80.51^{b} \pm 2.73$
F_1	$28.81^{bc} \pm 0.29$	$66.95^{b} \pm 0.71$	$25.17^{bc} \pm 0.24$	$20.90^{b} \pm 0.21$	$120^{bc} \pm 14.89$	$95.06^{bc} \pm 12.29$	$79.10^{b} \pm 0.66$
F_2	$32.52^{a} \pm 0.49$	$73.34^{a} \pm 0.08$	$28.63^{ab} \pm 0.30$	$20.72^{b} \pm 0.18$	$107.78^{bc} \pm 8.28$	$85.41^{bc} \pm 6.38$	$79.28^{b} \pm 0.58$
BC_1	$27.42^{cd} \pm 0.31$	$59.47^{c} \pm 0.75$	$22.80^{c} \pm 0.43$	$20.88^{b} \pm 0.21$	$90.55^{dc} \pm 12.68$	$71.56^{cd} \pm 10.69$	$78.79^{b} \pm 0.94$
BC_2	$30.91^{ab} \pm 0.29$	$66.03^{b} \pm 0.54$	$27.70^{ab} \pm 0.47$	$22.56^{ab} \pm 0.10$	$156.43^{a} \pm 15.77$	$136.13^{a} \pm 13.11$	$88.37^{a} \pm 3.01$

DS, Days to 50% silking; GFP, Grain filling period; DPM, Days to physiological maturity; PH, Plant height; RN, Row number/ear; GN, Grain number/row; ED, Ear diameter; GD, Grain depth; TGW= 250- Grain weight; GHP, Grain humidity percent; EWP, Ear-wood percent; EB, Ear-biomass/plant; GY, Grain yield/plant and EHI, Ear-harvest index. The means in each column followed by similar letter (s), are not significantly different at $p \leq 0.\ 05$. P_1, P_2, parental inbred lines; F_1, F_2, first and second filial generations; BC_1, BC_2, first and second backcrosses and SE, standard error.

Table 4. Estimation of genetic components for different traits of maize in six generations of (P1) × (P2)

Traits	[m]± SE	[d]± SE	[h] ± SE	[i] ± SE	[j] ± SE	[l] ± SE	Chi-square ($\chi 2$)
Days to 50% silking	47.17 ± 0.10**	-0.85 ± 0.10**	2.70 ± 0.31**	-	-	-	1.97^{ns}
Grain filling period	67 ± 0.26**	1.31 ± 0.21**	8.08 ± 1.01**	-	-	-8.24 ± 1.06**	3.37^{ns}
Days to physiological maturity	114.15 ± 0.21**	0.14 ± 0.20^{ns}	10.05 ± 0.75**	-	-	-7.20 ± 0.68**	1.42^{ns}
Plant height	295.21 ± 15.70**	-3.55 ± 2.75^{ns}	-229.87± 41.59**	-88.99 ± 15.91**	-	158.23±27.5**	4.02^{ns}
Row number/ear	12.78 ± 0.42**	-1.24 ± 0.53*	-	-	-	-	3.56^{ns}
Grain number/row	34.15 ± 0.65**	-1.24 ± 0.30**	-4.47 ± 0.76**	-6.87 ± 0.78**	-3.32 ±0.09**	-	4.67^{ns}
Ear diameter	59.91 ± 3.30**	-3.79 ± 0.50**	-34.55 ± 7.55**	-18.98 ± 3.23**	-	15.74 ± 4.45**	2.29^{ns}
Grain depth	41.95 ± 2.17**	-2.80 ± 0.29**	-24.58 ± 4.8**	-13.35 ± 2.14**	-	11.93 ± 2.76**	4.71^{ns}
250- grain weight	108.83 ± 1.98**	-1.59 ± 0.61**	-100.07 ± 5.93**	-42.36 ± 1.89**	-9.93 ± 2.22**	58.18 ± 4.16**	0.00
Grain humidity percent	39.40 ± 1.77**	-3.38 ± 0.19**	-28.83 ± 4.56**	-13.75 ± 1.75**	-	14.60 ± 2.88**	6.27^{ns}
Ear-wood percent	20.80 ±0.40**	1.76 ± 0.17**	0.23 ± 0.55^{ns}	2.28 ± 0.45**	-6.93 ± 0.67**	-	4.15^{ns}
Ear biomass/ plant	108.31 ± 3.45**	-35.20 ± 3.6**	-	-	-	-	5.26^{ns}
Grain yield/plant	88 ± 3.33**	-33.32 ± 3.38**	-	-	-	-	7.77^{ns}
Ear-harvest index	79.43 ± 0.40**	-3.33 ± 1.09**	-	-	-	-	8.45^{ns}

^{ns}, not significant; *, significant at $P \leq 0.05$; ** , significant at $P \leq 0.01$; [m], mid-parent value; [d], pooled additive effects; [h], pooled dominance effects; [i], pooled interactions between additive effects; [j], pooled interactions between additive and dominance effects; [l], pooled interactions between dominance effects and SE, standard error.

Table 5. Components of variance, average of gene dominance, dominance deviation and dominance degree of different traits of maize in six generations of (P1) × (P2)

Traits	D	H	F	E_W	$(H/D)^{1/2}$	$F/(H \times D)^{1/2}$
Days to 50% silking	20.04	40.12	-2	34.23	1.41	-0.07
Grain filling period	2.68	8.65	1.34	10.50	1.80	0.28
Days to physiological maturity	15.96	25.94	0	21.83	1.27	0
Plant height	2156.72	2837.47	834.32	779.05	1.15	0.34
Row number/ear	70.87	56.57	6.68	39.69	0.89	0.11
Grain number/row	17.26	24.31	-0.59	13.40	1.19	0.03
Ear diameter	28.49	62.86	-2.54	26.99	1.48	-0.06
Grain depth	17.91	30.29	-0.33	15.85	1.30	-0.01
250- grain weight	50.67	27.53	-8.35	28.26	0.74	0.22
Grain humidity percent	13.22	29.37	0.89	22.02	1.49	0.04
Ear-wood percent	0.85	0.32	-0.13	1.53	0.61	-0.26
Ear biomass/ plant	2542.87	1635.58	263.70	587.71	0.80	0.13
Grain yield/plant	1762.94	1226.53	172.67	494.85	0.83	0.12
Ear-harvest index	84.71	55.73	24.59	27.71	0.81	0.36

D, additive variance; H, dominance variance; F, the correlation of D and H on all loci of any trait; V_E , environmental variance or non-genetic variance; $(H/D)^{½}$, average of gene dominance; and $(F/ (H \times D)^{1/2})$, modulus of dominance deviation

Table 6. Heritability and gene number of different traits of maize in six generations of (P1) × (P2)

Traits	The used formulas of the number of genes for various traits						Heritability	
	1	2	3	4	5	6	(H_b)	(H_n)
Days to 50% silking	0.52	0.03	0.54	0.26	-	-	63.73	21.23
Grain filling period	0.42	-	-	-	-	-	51.90	12.28
Days to physiological maturity	0.01	-	1.06	0.68	-	-	65.74	25.02
Plant height	0.00	0.00	-	0.19	-	-	86.50	37.36
Row number/ear	0.01	0.00	0.01	-	0.00	0.00	76.25	42.40
Grain number/row	0.07	0.23	5.00	-	0.05	0.03	75.62	31.40
Ear diameter	0.19	0.12	0.94	-	0.08	0.05	77.19	24.07
Grain depth	0.23	0.27	2.00	-	0.06	0.03	75.12	27.96
250- grain weight	0.32	0.04	1.07	-	-	-	73.18	47.41
Grain humidity percent	1.69	0.14	0.58	0.72	1.67	-	65.92	40.46
Ear-wood percent	1.36	-	6.53	-	-	-	43.33	31.48
Ear biomass/ plant	-	0.01	3.95	0.20	-	-	87.67	34.32
Grain yield/plant	-	0.01	3.53	0.35	-	-	85.79	35.20
Ear-harvest index	0.48	0.04	-	0.03	-	-	83.52	33.14

H_b, broad sense heritability; H_n, narrow sense heritability

Additive gene action as well as additive-by-additive effect influenced the inheritance of the traits of GN, ED, GD, TGW, GHP and EWP. Therefore, selection in early generations can be an efficient method for genetic improvement of these traits. Significant values of additive by dominance effect for the traits of GN, TGW and EWP indicate that the mentioned epistatic play a major role in the inheritance of these traits. Indeed, stabilizing these apostates is not possible in earlier generations (Watto *et al.,* 2009). These findings are in agreement with the results of other researchers (Iqbal *et al.,* 2010; El- Badawy 2012). The significant values for dominance and dominance by dominance effects, with opposite signs, indicate the duplicated epistatic in the inheritance of the GFP, DPM, PH, ED, GD, TGW and GHP. This kind of epistatic is a barrier for early selection; therefore, it reduces the speed of the breeding process (Sandeep *et al.,* 2012). Inversely, complementary epistatic, namely significant values for [h] and [l] with the same signs, was not observed for any trait. Mather and Jinks (1982) proposed that complementary epistatic is not a barrio for selection in early generations. According to a research (Vidal-Martinez *et al.,* 2001), dominance effects controlled the traits of EW, GN, RN, EL, and GY. Butruille *et al.* (2004), revealed the greater role of dominance effect in controlling the grain yield. Some previous results (Makumbi *et al.,*. 2011; Ndhlela *et al.,* 2015) indicated that additive effect has a preponderant role than dominance effect in controlling the inheritance of grain yield, ear length, ear diameter, and grain yield/ ear. Blank *et al.* (2006) suggested that the additive effect played a greater role than dominance effect in governing the inheritance of grain yield. Melani and Carena (2003) showed that additive effect has a greater role than dominance effect in genetic governing the inheritance of grain yield, and grain humidity. The result of the components of variance (Table 5) showed that the F parameter was positive for the majority of the traits. Indeed, it indicates that the high-parent alleles dominated on mid-parent alleles on the majority of loci. In other words, the dominant alleles increased the traits. When F is less than unity, it means that dominant alleles have been dispread between the parents (Sandeep *et al.,* 2012). When F is close to zero, it means that there is no directional dominance (Roy 2000). Because the average of gene dominance was greater than unity for DS, GFP, DPM, PH, and GHP, therefore, dominance and over-dominance played an important role in inheritance of the mentioned traits. Mihailov and Chernov (2006) suggested that epistatic interaction played a major role in operating the inheritance of GY, ED, GN, EN, DS, and DPM, while the traits of EWP, TGW, days from anthesis to silking, tassel length were controlled by both additive and dominance effects simultaneously.

Other traits, for example, in the GY, [H/D] $^{1/2}$ were less than unity, therefore additive and partial dominance effects played an important role in governing the traits. The modulus of dominance deviation (F/ [H×D] $^{1/2}$) was less than unity and nearly zero for all traits, hence, it indicates that the alleles at different loci, have different effects with opposite sign in governing a given trait. In other words, dominant alleles have been distributed to both parents. In the above situation, dominance degree (h/d) is not a suitable criterion for dominance effect, while $[H/D]^{1/2}$ indicates an average of gene dominance (Mather and Jinks 1982). The present results for different traits are in accordance with those of Prakash *et al*. (2004) and Kumar *et al.* (2005) who reported dominance and over dominance type of gene action for the same trait.

Because the majority of the traits dominance degree were greater than unity (Table 5), non-additive gene action was shown to have been predominant in the inheritance of the traits. Moreover, the average of gene dominance was greater than unity for the afore-mentioned traits. Indeed, the role of dominance effect in governing the traits resulted in reducing narrow sense heritability of the above-mentioned traits (Hussain *et al.*, 2009). In the traits of RN, TGW, EWP, EB, GY, and EHI, additive variance, [D], and partial dominance, had demonstrated to have played a significant and greater role than non-additive gene action in the heritance of the traits. The results (Table 5) revealed that, the average of gene dominance was less than unity for the traits. Saleem *et al.* (2002), Wattoo *et al.* (2009) and Irshad ul Haq *et al.* (2010) obtained similar results.

In other traits, including days to 50% silking, grain filling period, days to physiological maturity, plant height, grain number/row, ear diameter, grain depth, and grain humidity percent, dominance variation, [H], was greater than additive variation. In these traits average of gene dominance, $[H/D]^{1/2}$ was greater than unity. Consequently, and according to the above results, the dominance gene action was important in governing the inheritance of the above traits. Indeed, in the traits, there is a big distance between narrow and broad sense heritability. In this case, selection in early generations is not an efficient breeding method. Meanwhile, using bi-parental crosses (hybridization) and recurrent selection are proposed. There was an agreement with the results of the previous study (Sher *et al.*, 2012) which stated that for phenological traits, the dominance gene action played a major role in its inheritance. While, Irshad-U1-Haq *et al.* (2010) reported both dominance and additive gene action in the traits of days to silking, days to tasselling, plant height, ear length, and grain yield, Spaner *et al.* (1996) and Alexander *et al.* (2008) suggested the more important role of additive variation in controlling the inheritance of grain yield. Melchinger *et al.* (1990) showed that epistatic effect (additive by additive) plays an important role in controlling of maize grain yield.

The estimation of gene number is a crucial strategy for detection of breeding method. The numbers of genes that are involved in governing the different traits ranged between 1- 6.53. It indicated that probably seven groups of genes were controlling the traits (Irshad-ul-haq *et al.*, 2010). Because different methods have different hypothesis for estimation of gene number (Lande, 1981), the estimated gene number varied in different methods.

The traits of EB showed the maximum broad sense heritability, indicating that genotype-environmental interaction will result in the low heritability of the traits (Sandeep *et al.*, 2012). The maximum narrow sense heritability was observed in TGW. The small difference between broad and narrow sense heritability indicated that the given trait was mainly controlled by the additive effect (Waqar-UL-Haq *et al.*, 2008). High heritability of grain yield showed the greatest effect of additive variation in governing GY heredity. Indeed, high level of narrow sense heritability for a given trait will increase its response to selection (Falconer and Mackay, 1996). Therefore, selection in early generations is considered as a valuable and suitable method for improving the trait (Ndhlela *et al.*, 2015). High broad sense heritability is due to a high genetic diversity or happens by the polling genotype environment interaction in a population (Mikic *et al.*, 2016; Ding *et al.*, 2016). Garcia *et al.* (2005) reported that the degree of heritability varied for plant height and ear length. Broad and narrow sense heritability of GY was reported with about 57 and 30% (Sher *et al.*, 2012), 88 and 16% (Sandeep *et al.*, 2012), 87 and 30% (Jebaraj *et al.*, 2010) and 67 and 25%, respectively (Ifie *et al.*, 2014) by different researchers. Genotype environment interaction will result in low heritability of a trait (Sandeep *et al.*, 2012). The obtained results are in concurrence with some previous researches (Unay *et al.*, 2004) and they are not in close conformity with other findings. Indeed, different methodologies and different genetic materials will obtain the different results.

5. Conclusion

In total, the studied traits are categorized in three groups based on the mode of inheritance. The first group, included GY, EB, EHI, RN, and EWP, in which the additive effects were greater than dominance variation. Therefore, selection in early-generations will result in response to selection in these traits. Inversely, in the second group, dominance gene action and epistatic interaction played a major role in governing the traits of DPM and PH. Finally, in the third group, i.e. DS, GFP, GN, ED, GD, TGW and GHP, both additive and dominance effects were involved in the operating of the traits simultaneously. When the average of gene dominance is greater than unity for a given trait, it indicates the role of dominance effect in governing the trait, so that dominance gene action results in reducing the narrow sense heritability of the given trait. The smaller difference between broad and narrow sense heritability for a trait indicating the given trait is mainly controlled by additive effect. High heritability of grain yield showed the greatest effect of additive variation in governing the grain yield heredity. Meanwhile, due to the notable role of additive effects in governing the important traits of EB, EHI and RN, selection in early generations using pedigree and multiple-seed-descent methods for them, can be efficient to improve drought-tolerance and stabilizing GY under moisture stress conditions.

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