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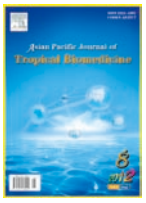

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Genetic analysis of maturity and flowering characteristics in maize (*Zea mays* L.)

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ABSTRACT

Objective: To elucidate the pattern of inheritance and determine the relative magnitude of various genetic effects for maturity and flowering attributes in subtropical maize. **Methods:** Four white grain maize inbred lines from flint group of corn, two with late maturity and two with early maturity, were used. These contrasting inbred lines were crossed to form four crosses. Six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2) were developed for each individual cross. These were evaluated in triplicate trial for two consecutive years. **Results:** Both dominance gene action and epistatic interaction played major role in governing inheritance of days to pollen shedding, 50% silking, anthesis silking interval and maturity. **Conclusions:** Preponderance of dominance gene action for these traits indicated their usefulness in hybrid programs of subtropical maize.

1. Introduction

Knowledge about flowering habit, type of gene action and mode of inheritance of maize inbred populations is very essential before launching a successful hybrid development program. Generation mean analysis (GMA) is one of those biometrical techniques that involves estimation of the magnitude of various genetic effects (additive, dominance and epistatic effects). The estimates of genetic effects can help the plant breeders to decide the breeding procedures better suited for the improvement of trait(s) being analyzed[1]. Generation mean analysis, a biometrical method developed[2], greatly helps in the estimation of various components of genetic variance. Estimation of the types of gene action involved in the expression of traits, the level of additive effects and the degree of dominance are very important in designing a breeding method for improving the trait of interest. Knowledge of the way genes act and interact will determine which breeding system can optimize gene action more efficiently and will help elucidate the role of breeding systems in the evolution of crop plants[3].

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Dominance effects of genes for days to silk have been observed. Researchers have evaluated some maize populations and concluded that additive effects were more important for silking, while for tasselling the additive x dominance effects were predominant[4]. While studying the inheritance of anthesis silking interval (ASI) through generation means analysis using eight maize inbred lines, recessive genes were found to control the inheritance of interval between anthesis and silking with prominent additive gene effects[5]. Additive genetic variance was shown to have been predominant in the inheritance of days taken to silk[6].

Over dominance type of gene action has been found responsible for the number of days to tasselling[7] , whereas partial dominance was reported for number of days to silking. Non-additive gene action has been shown to have played a significant role in the inheritance of days to tasselling, days to silking, and days to maturity[8]. An obvious additive gene action is reported in the inheritance of days to silking[9]. The importance of additive gene action was noticed in the inheritance of days to 50% tasselling and days to 50% silking[10]. The non-additive gene action was also found to prevail for days to 50% husk browning[11]. Similarly, investigation of six generations in maize crosses (P_1, P_2, F_1, F_2, BC_1 and BC_2) revealed preponderance of

non-additive gene actions for the expression of most of the traits studied except for days to 50% husk browning *i.e.*, maturity[12]. The inheritance of days to 75% tasselling and days to 75% silking was found to be operated by non-additive gene action, while days to maturity was seen to have been governed by the additive type of gene effects[13].

The present study was, therefore, designed with the objectives to elucidate the type of gene action and interaction that governed the inheritance of maturity and flowering attributes in subtropical germplasm of maize.

2. Materials and methods

2.1. Genetic material

The breeding material used in this experiment comprised a set of four white kernel flint maize inbred lines, each developed by manual self pollination for 6-8 generations having distinct genetic make-up as shown in Table 1. Two out of the 4 inbreds were tall in stature with late maturity (100-120 days) and the other two were dwarf having early maturity (90-100 days). These lines were grown at the Cereal Crops Research Institute (CCRI) Pirsabak, Nowshera NWFP (Pakistan) which is located about 1 540 km north of Indian Ocean at 34 °N latitude, 72 °E longitude and an altitude of 288 meters above sea level, thus representing a continental climate. Six generations were developed over two growing seasons for each cross by using manual pollination procedures for crossing and selfing as described[14].

Table 1
Name, pedigree and maturity of the parental inbred lines.

S. No.	Name	Pedigree	Maturity
1.	Pop. 9804	CHSW X Sahard White	Late (110-120 days)
2.	Pop. 9805	Sarhad White X Azam	Late (100-110 days)
3.	Pop. 9801	Pahari X Swabi White	Early (90-95 days)
4.	FRW-4	Shaheen X Peshawer White	Early (95-100 days)

2.2. Development of F1 generations

During the first growing season (Spring 2005), all the four parental lines were crossed with each other to produce four F1 hybrids in the following crossing pattern.

S. No.	Female	Male
1.	Pop.9804	X Pop.9801
2.	Pop.9804	X FRW-4
3.	Pop.9805	X Pop.9801
4.	Pop.9805	X FRW-4

2.3. Development of F2 and back cross (BC1 & BC2) generation

Part of seed from each of the four parental inbred lines and their four resultant F1 hybrids was planted in the field during summer 2005 to produce F2, BC1 and BC2 generations. F2 generation of each cross was produced by selfing the F1 plants while BC1 and BC2 generations were developed by crossing back each F1 hybrid with its respective male and female parents in the 2nd crop season as given below:

BC_1 Generations		BC_2 enerations	
Female	Male	Female	Male
(Pop.9804 X Pop.9801) X	Pop.9804	(Pop.9804 X Pop.9801) X	Pop.9801
(Pop.9804 X FRW-4) X	Pop.9804	(Pop.9804 X FRW-4)	X FRW-4
(Pop.9805 X Pop.9801) X	Pop.9805	(Pop.9805 X Pop.9801)	X Pop.9801
(Pop.9805 X FRW-4) X	Pop.9805	(Pop.9805 X FRW-4)	XFRW-4

2.4. Field evaluation

The material for field evaluation comprised 20 entries, generated from the above crossed and selfed combinations *i.e.*, 4 parents, 4 F1s, 4 F2s, 4 BC1s and 4 BC2s. The 20 entries were planted in the field in triplicate, using randomized complete block (RCB) design for evaluation at Cereal Crops Research Institute (CCRI) Pirsabak, Nowshera for two consecutive years *i.e.*, 2006 and 2007 in the summer growing season (July-October). The experimental plot size comprised two rows for non-segregating P1, P2 and F1 generations, four rows each for BC1 and BC2 generations while seed of F2 generation of each cross was planted in eight rows. The rows were 5 m long with row spacing of 75 cm and 25 cm between plants within row. Two seeds were planted in each hill resulting in a plant population of 53 333 plants ha-1 which was later thinned to maintain one plant hill-1. A uniform fertilizer dose of 200 kg N, 90 kg $P_2O_5$and 90 kg K_2SO_4 hectare-1 was applied. Whole P_2O_5 in the form of Single Super Phosphate (SSP) and potash as Sulphate of Potash and half Nitrogen in the form of urea were applied just before planting during land preparation, while remaining half N was applied as side dressing in the form of urea, about 3 weeks after emergence. Weeds were controlled by pre-emergence application of Primextra gold @ 600 mL $acre^{-1}$. Insects control was carried out through seed treatment with Confidor WP-60 before planting and with the application of Furadon granules (3%) one month after planting by applying in the leaf whirls. Hand weeding and earthing-up operations were practiced for weed control in later stages, *i.e.* four weeks after emergence. The crop was irrigated, as and when required, till one week before maturity. The average maximum (35.30 ℃) and minimum (22.68 ℃) temperature recorded during the crop season in the year 2006[15], whereas 34.83 ℃ and 14.68 ℃ were recorded, respectively as maximum and minimum temperature during the crop season from July - October in the year 2007[16]. The total precipitation during the crop growth period was 143.25 mm[15] during the year 2006 while 180 mm[16] during 2007. Ten plants were selected at random from each plot in each replication from P1, P2 and F1 generations while 20 and 30 plants were taken from back crosses and F2 generations, respectively, to record data on individual plant basis for generation means analysis. Moreover, data for genotypic and phenotypic correlation coefficients, broad and narrow sense heritability and mid parent and high parent heterosis for the following plant parameters were recorded on plot and/or

hectare basis.

2.4.1. Days to 50% pollen shedding

In each plot the number of days from planting to 50% pollen shedding was recorded when pollen shedding started after dehiscence of anthers on central branch of the tassel on 50 % plants in a plot[17].

2.4.2. Days to 50% silk emergence

Silking date was recorded when the first day silks became visible on the topmost ear of at least 50% of plants in a plot[18,19]. The number of days from planting to 50% silk emergence was then recorded as days to 50 % silk emergence[20,21].

2.4.3. Anthesis silking interval (ASI)

The difference in number of days from 50% pollen shedding to 50% silk emergence was recorded as ASI for each plot in each replication[17].

2.4.4. Days to maturity

Date of maturity was recorded when grain of at least 50% of plants in a plot attained black layer[18,19] and number of days were then calculated from planting to maturity and recorded as days to maturity.

2.5. Statistical Analysis

Ordinary combined analysis of variance[22] was run on the data using MSTAT-C (Table 2), to detect if significant differences exist among the various generations for the standard plant parameters.

Table 2
Analysis of variance for generations combined across years.

Source of variation	Degrees of freedom	Mean squares	Expected mean square
Years	y-1	= 1 M1	--
Reps (years)	y(r-1)	= 4 M2	--
Genotypes	g-1	= 5 M3	$\delta^2_e + r\delta^2_{gy} + ry\delta^2_g$
Genotypes x Years	(g-1)(y-1)	= 5 M4	$\delta^2_e + r\delta^2_{gy}$
Pooled Error	y(g-1)(r-1)	= 20 M5	δ^2_e
Total	ryg-1	= 35 --	--

Generation means analysis was applied, on parameters which showed significant differences among generations, to determine the mode of inheritance and the magnitude of gene action for maturity and flowering traits in sub-tropical maize germplasm. This analysis was accomplished in several steps:

1)For parameters having significant differences among generations in the combined analysis of variance, averages were calculated from the data obtained for two years for each generation in each replication, using Microsoft Excel computer program.

2)For a given trait, each generation mean was expressed in terms of its genetic effects, using the following equation[23].

$G = m + \alpha a + \beta d + \alpha 2aa + 2\alpha \beta ad + \beta 2dd$

Where G = observed mean for generation; m = the mean effect; a = average additive effects; d = average dominance effects; aa = average interactions between additive effects; ad = average interactions between additive and dominance effects; dd = average interactions between dominance effects, α and β are the coefficients of a and d which are listed in Table 3 as below:

Table 3
Coefficients of α and β utilized for the construction of different models in the generation means analysis.

Generation	Genetic effects					
	m	A	d	aa	ad	dd
P1	1	1	-0.5	1	-1	0.25
P2	1	-1	-0.5	1	1	0.25
F1	1	0	0.5	0	0	0.25
F2	1	0	0	0	0	0
BC1	1	0.5	0	0.25	0	0
BC2	1	-0.5	0	0.25	0	0

3)Because the various generation means are not known with equal precision[17], weights were calculated for each generation, the appropriate weights being the reciprocals of the squared standard errors of each mean[24].

4)With the set of equations obtained in step 2, and considering the weights associated with each generation, genetic effects were estimated by the method of weighted least squares (multiple linear regression), utilizing matrix algebra[25]. Briefly these three matrices were defined as: W (weights matrix), X (matrix of coefficients of the genetic effects), Y (column vector of observed generation means). The estimates of genetic effects were derived from the column vector β, defined as: $\beta = (X2WX)-1(X2WY)$.

5) Standard error associated to each estimate of a genetic effect was obtained as the diagonal elements of the solution equation $SE(\beta) = \sqrt{(XX)-1\sigma 2}$, where $\sigma 2$ was the error variance, estimated by the mean square of the two years average[26,27].

6) Significance of each genetic effect estimate was evaluated as described by[28], utilizing a t-test.

7) In order to test the adequacy of the model, chi-square (χ^2) tests were performed[25].

Steps three to seven were accomplished utilizing the Microsoft Excel computer program.

The joint scaling test[29], was used to detect epistasis for all traits measured. In the presence of epistasis, additive (d), dominance (h) effects and non-allelic interaction components (i, j and l) of generation means were estimated to explain the inheritance of various traits, using models of Hayman[23] and Mather & Jinks[24]. A three parameter model also known as additive-dominance model was used to explain the genetic variability for those traits which showed non significant magnitudes for chi-square (χ^2). By observing a significant χ^2 value, the six parameter model was applied to accommodate the digenic epistatic interactions.

3. Results

Mean squares (not given) showed significant differences

among various genetic generations in all the four crosses, therefore, generation means analysis was applied on all the traits studied to determine the mode of inheritance and the magnitude of gene action for maturity and flowering characteristics.

3.1.Days to 50% pollen shedding

Six parameter model was adequate to explain the inheritance pattern of days to 50% pollen shedding since χ^2 estimates were found significant for all the four crosses (Table 4). The dominance gene action as well as additive x dominance digenic non-allelic gene interaction were important in governing the inheritance of days to pollen shed in cross Pop.9804 x FRW-4, whereas these two genetic components along with additive x additive gene interaction played major role in the inheritance of this trait in cross Pop.9805 x FRW-4. The gene interactions between additive x dominance were predominated in operating the inheritance of days to pollen shed in cross Pop.9805 x Pop.9801. The digenic non-allelic epistasis of additive x dominance and dominance x dominance were considered the major contributors in the inheritance of this trait in a cross Pop.9804 x Pop.9801.

3.2.Days to 50% silk emergence

The estimates of joint scaling test and magnitudes of components of genetic variation for this trait are presented in Table 4. The non significant value of χ^2 for days to 50 % silking in a Pop.9805 x Pop.9801 indicated the adequacy of the additive-dominance model to explain inheritance pattern of this trait, whereas χ^2 values were significant in the remaining three crosses for days to silk, showing that thee parameter model did not adequately explain the quantum of genetic variability for this trait. The inadequacy of additive-dominance model also indicated the presence of epistasis, which is also inferred from the generation means. As the three parameter model did not satisfactorily explain the genetic variability for days to 50 % silking in these three crosses, therefore, a six parameter model was applied to accommodate epistatic interactions. As shown in Table 4, the genetic effects for h (dominance), are significant indicating the involvement of dominance gene action in the inheritance of days to silk in a cross Pop.9805 x Pop.9801. The significant values for genetic components, dominance (h) and dominance x dominance (l), with opposite signs are indicative of the duplicate type of epistasis in the inheritance of this trait in two crosses (Pop.9804 x FRW-4 and Pop.9805 x FRW-4). In cross Pop.9804 x Pop.9801, the significant effects of h and j indicated that the inheritance of days to silk was controlled by dominance gene action as well as additive x dominance epistasis in this cross.

3.3. Anthesis silking interval (ASI)

Estimates of genetic effects presented in Table 4 showed that χ^2 values were significant for all the four crosses that revealed the adequacy of six parameter model in explaining the inheritance of anthesis silking interval. Significant values of h (dominance) and l (dominance x dominance) with opposite signs indicated that digenic non-allelic interaction of duplicate type predominantly explained the inheritance of ASI in cross 1 (Pop.9804 x FRW-4). Preponderance of dominance gene action as well as additive x additive gene interaction was found to play an important role in governing the inheritance of this trait in crosses Pop.9804 x Pop.9801 and Pop.9805 x Pop.9805 x FRW-4. Additive, dominance and additive x additive type of gene action and interaction were equally important in controlling the inheritance of anthesis silking interval in cross Pop.9805 x Pop.9801.

3.4. Days to maturity

Table 4

Estimates of genetic effects for maturity and flowering characteristics in 4 maize crosses evaluated at Cereal Crops Research Institute (CCRI) Pirsabak Nowshera combined over 2 years (Summer, 2006 and Summer, 2007).

Parameter	Cross	Mean	Additive	Dominance	Additive × Additive	Additive × Dominance	Dominance × Dominance	χ^2	Type of non-allelic interaction
Days to Poll. Shed	Pop.9804 X FRW-4	52.77*	0.19ns	-4.96*	0.02ns	-3.45*	3.58ns	97.41**	----
	Pop.9804 X Pop.9801	54.95*	-0.12ns	-1.99ns	2.46ns	-3.87*	-9.43*	76.80**	----
	Pop.9805 X FRW-4	53.23*	0.83ns	-8.88*	-3.62*	-1.27*	2.22ns	19.92**	----
	Pop.9805 X Pop.9801	52.32*	0.33ns	-2.01ns	-2.18ns	-1.87*	-4.01ns	12.23**	----
Days to 50% Silk	Pop.9804 X FRW-4	53.23*	0.43ns	-6.12*	-1.45ns	-3.62*	10.52*	216.5 0**	Duplicate
	Pop.9804 X Pop.9801	55.06*	0.29ns	-4.70*	0.29ns	-4.32*	-3.15ns	19.10**	----
	Pop.9805 X FRW-4	54.61*	1.54*	-10.15*	-5.69*	-0.55ns	6.46*	16.52**	Duplicate
	Pop.9805 X Pop.9801	53.49*	0.72ns	-3.12*	----	----	----	7.71ns	----
ASI	Pop.9804 X FRW-4	1.50*	-0.67*	3.67*	4.00*	-1.00*	-6.00*	190.70**	Duplicate
	Pop.9804 X Pop.9801	2.33*	0.00ns	-0.75*	-0.67*	-0.25*	0.63ns	16.60**	----
	Pop.9805 X FRW-4	2.50*	0.00ns	-2.00*	-2.00*	0.17ns	0.67ns	90.40**	----
	Pop.9805 X Pop.9801	2.30*	-0.17*	-1.58*	-2.33*	0.08ns	3.83ns	74.1**	----
Days to Maturity	Pop.9804 X FRW-4	110.30*	-1.52ns	-14.00*	-29.47*	-12.90*	29.33*	169.10**	Duplicate
	Pop.9804 X Pop.9801	103.14*	0.97ns	-9.09ns	-1.58ns	-13.71*	-2.94ns	66.00**	----
	Pop.9805 X FRW-4	98.73*	-0.63ns	2.59ns	5.93*	-2.76*	-15.85*	50.50**	----
	Pop.9805 X Pop.9801	95.41*	-2.79*	31.61*	27.14*	-8.21*	-42.52*	101.32**	Duplicate

The additive-dominance model was insufficient to explain the genetic variability for days to maturity as the chi-square value for all the crosses were significant (Table 4). The inadequacy of the model also indicated the presence of epistasis, therefore, six parameter model was applied to explain the inheritance pattern of days to maturity in the four maize crosses examined in this study. The two crosses *i.e.*, Pop.9804 x FRW-4 and Pop.9805 x Pop.9801 exhibited duplicate types of epistatic gene action in the regulation of inheritance of this trait as significant effects of opposite sign for genetic components, h and l, were observed in Table 4. In cross Pop.9805 x FRW-4, although all the three types of epistatic effects (additive x additive, additive x dominance and dominance x dominance) were significant but dominance x dominance epistasis had predominant influence in the inheritance of days to maturity. The significant value of j in cross Pop.9804 x Pop.9801 suggests that additive x dominance gene effects made a major contribution to the inheritance of days to maturity in this cross.

4. Discussion

4.1.Days to 50 % pollen shedding

Prevalence of additive x dominance genes interaction was common in the inheritance of days to pollen shed in all the four crosses. In addition to this interaction, dominance gene effects of the most important nature were seen in crosses Pop.9804 x FRW-4 and Pop.9805 x FRW-4, with the least importance of additive x additive and dominance x dominance gene interaction. Frequent appearance of epistasis indicated the greater genetic diversity in the parents involved in the formation of these crosses. In case if dominance and additive x additive effects are present, it can be inferred that these types of gene effects would help in promoting earliness in these materials. The tendencies found in the present data for days to 50 % pollen shedding were similar to those observed in the earlier data[4,8,13] where non additive epistatic effects were among the most important affecting this parameter. There was partial agreement with the conclusions reached in earlier studies[7,30] which stated that for days to tasselling, dominance (incomplete to over dominance) effects played major role in its inheritance. Contrasting effects have also been reported in some studies[10] for the inheritance of days to tasselling in maize, and they were of the opinion that this trait was mainly controlled by additive type of gene action[5].

4.2.Days to 50 % silking

The dominance gene effect was common in all the four crosses studied for governing the inheritance of days to 50 % silking. In cross-1 and cross-3, the dominance x dominance gene interaction was of primary importance among the digenic non-allelic interactions for controlling the inheritance of days to silk. The non-allelic interaction of additive x additive was also observed to be important contributor in the expression of days to silk in cross-3. The involvement of additive x dominance genes interaction was also seen in controlling the inheritance of this trait in cross-1 and cross-2. In case where dominance was of major importance, the trait could be successfully utilized in the formation of hybrids and promoting earliness in the material. The presence of epistasis is mostly indicative of greater genetic diversity in the parents. The findings that the dominance effects seemed to be the most substantial in the inheritance of days to silk concurred with other conclusions[31]. Partial dominance genetic effects[35] and over dominance gene action[26] in governing inheritance of days to silk in maize have been reported. The epistatic effects in controlling the inheritance of days to silk in maize are in agreement with the results obtained in earlier investigations[8,13,31]. However, additive genetic effects in explaining the genetic variability for days to silking in maize have been reported[4,6,9,10,33].

4.3.Anthesis silking interval (ASI)

Inheritance of anthesis silking interval was governed mainly by additive, dominance and additive x additive gene interaction in the all the four crosses. Preponderance of dominance gene action indicated that this trait could be utilized successfully in the formation of hybrids. The additive and additive x additive genetic effects for ASI is indicative of a good potential in the improvement of this trait. These results were in line with those of a generation mean analysis study on eight maize inbred lines where the inheritance of interval between anthesis and silking were controlled by recessive genes with prominent additive effects[31].

4.4.Days to maturity

The most important in terms of its absolute magnitude was the epistatic dominance x dominance effect for days to maturity in three crosses, whereas in one cross the effect of additive x dominance interaction was predominant for this trait. In cross-4, dominance effect was more important than additive effects in governing the inheritance of the trait. Moreover, additive x additive gene interaction also played paramount role in controlling this character in three crosses. Prevalence of epistasis is indicative of greater genetic diversity in the parental lines. The presence of dominance and additive x additive effects appears to have promoted earliness in days to maturity. The preponderance of non-additive gene effects in controlling the inheritance of days to maturity is in concurrence with other conclusions where the non-additive effects for days to 50 % husk browning (maturity) were important[10,34,35]. The additive effects observed for days to maturity in cross-4 are in close conformity with other findings in which days to maturity appeared under the control of additive gene action[12,13,16].

Conflict of interest statement

We declare that we have no conflict of interest.

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