ESTIMATES OF GENE EFFECTS FOR EAR LENGTH AND EAR DIAMETER AMONG GENERATION MEANS OF CORN, *ZEA MAYS* L.

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Introduction

In corn, ear length and ear diameter are the two component characters of yield which mutually express the size and shape of ears. Some computed data from the studies of ROBINSON et al. (1951) and MOCHIZUKI et al. (1967) displayed that these have highly positive correlation value with grain yield. According to corn breeders' experiences and the authors', the variability of ear length in response to different conditions of growing is quite similar to that of yield of individual plant. However, these two characters receive less attention than others by corn breeders in breeding program.

The purpose of the paper is to test for gene effects attributable to the both characters: additive, dominance, and epistasis effects for 10 possible crosses of five inbred lines of same and diverse origins. The obtained results of gene effects especially for ear length will be refered in order to plan more effectively the breeding procedure which emphasizes the non-additive gene effects.

Materials and method

Ten inbred lines were used as parents in this study of which 5 lines, N207, N208, N209, N210 and N211 are derived from same origin, whereas the others are of diverse origin, namely N56, N146, N206, T6 and T113. The ancestral varieties of these lines can be refered from HO (1970). All of the inbred lines are assumed to be homozygous. In the study, all possible crosses (F_1, single crosses selfed or F_2, and back crosses (P_1F_1 and P_2F_1)) were used.

In reference to each origin, same or diverse origin, fourty five populations consisting of five inbred lines, 10 F_1's, 10 F_2's, 10 B_1's, 10 B_2's were tested at the field of Hokkaido university in 1972. Simple lattice design with three replications was practiced in the experiment.

Measurements for the two traits were made on individual plants. These plants were identified so that measurements for ear length and ear diameter are associated with the same plants. Length of ear was measured as the length of cob, and ear diameter was measured at the approximate center of ear. Both attributes were measured in centimeters.

Statistical analysis:

The analysis method of GAMBLE (1962) was applied to each cross for each character. Gene effects' parameters are listed below:

m : means based on the F_2,
a : pooled additive effects,
d : pooled dominance effects,
aa : pooled additive × additive epistasis effects,
ad : pooled additive × dominance epistasis effects, and
dd : pooled dominance × dominance epistasis effects.

Then, the expectations of the means of two inbred lines and their descendants resulting from additional selfing and crossing can be listed in matrix notation as follows:

$$Y = BX \qquad \text{where,}$$

$$Y = \begin{bmatrix} P_1 \\ P_2 \\ F_1 \\ F_2 \\ B_1 \\ B_2 \end{bmatrix} \quad X = \begin{bmatrix} 1.0 & 1.0 & -.5 & 1.0 & -1.0 & 0.25 \\ 1.0 & -1.0 & -.5 & 1.0 & 1.0 & 0.25 \\ 1.0 & 0.0 & 0.5 & 0.0 & 0.0 & 0.25 \\ 1.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 \\ 1.0 & 0.5 & 0.0 & 0.25 & 0.0 & 0.0 \\ 1.0 & -.5 & 0.0 & 0.25 & 0.0 & 0.0 \end{bmatrix} \quad B = \begin{bmatrix} m \\ a \\ d \\ aa \\ ad \\ dd \end{bmatrix}$$

The six parameters for each of 10 crosses were estimated from population means using the relationship listed above. The variances of population means were used to estimate variance of the estimated parameters. The estimates of the gene effects calculated from the population mean over 3 replications will be discussed below.

Results

The mean performance of parents and crosses for two traits are shown in TABLE 1, 2, 3, and FIG. 1. In the designation of the cross, the first inbred was considered as P_1, and the second inbred as P_2. In same origin, the performance per se. of parents for ear length and ear diameter was relatively close to each other while it scatters largely in diverse origin with the range of 21.61–21.83 in same origin and 15.32–27.70 in diverse origin for ear length, respectively. And the range of performances of cross was also larger in diverse than in same origin.

All the crosses of the F_1 population exceeded their mid-parent values, and most of them showed superior than the higher parent of the cross. The performances of F_2 and back crosses were also considerably higher than the higher parents' for many cases as noted in TABLE 2 indicating high heterotic effect. The advantage of F_1 population expressed in term of average heterosis as the value of (F_1–M.P.) approved that it is more

TABLE 1. Mean performances of the parents and crosses averaged over replications for the two traits (same origin).

CROSSES	POPULATIONS					
	P_1	P_2	F_1	F_2	B_1	B_2
	Ear length (cm)					
N207×N208	21.61	21.85	24.17	23.43	22.70	22.30
N207×N209	21.61	21.89	22.17	23.40	23.58	22.34
N207×N210	21.61	21.87	22.30	21.76	21.90	23.28
N207×N211	21.61	19.24	21.30	21.31	22.44	21.36
N208×N209	21.85	21.89	27.93	22.59	21.02	21.45
N208×N210	21.85	21.87	24.58	21.74	21.82	20.15
N208×N211	21.85	19.24	23.68	22.85	20.43	20.59
N209×N210	21.89	21.87	21.77	21.30	21.27	21.21
N209×N211	21.89	19.24	22.08	21.95	22.46	21.30
N210×N211	21.87	19.24	21.77	22.47	22.77	20.98
	Ear diameter (cm)					
N207×N208	3.50	3.64	3.67	3.75	3.48	3.79
N207×N209	3.50	3.50	3.47	4.08	3.73	3.61
N207×N210	3.50	3.59	3.59	3.53	3.67	3.69
N207×N211	3.50	3.52	3.55	4.61	3.76	3.69
N208×N209	3.64	3.50	3.80	3.60	3.50	3.66
N208×N210	3.64	3.59	3.78	3.80	3.60	3.54
N208×N211	3.64	3.52	3.81	3.71	3.46	3.47
N209×N210	3.50	3.59	3.67	3.46	3.46	3.51
N209×N211	3.50	3.52	3.61	3.49	3.66	3.62
N210×N211	3.59	3.52	3.55	3.40	3.66	3.58

TABLE 2. Mean performances of the parents and crosses averaged over replications for the two traits (diverse origin).

CROSSES	POPULATIONS					
	P_1	P_2	F_1	F_2	B_1	B_2
			Ear length (cm)			
N 56×N146	19.16	20.64	24.70	22.90	21.98	22.28
N 56×N206	19.61	27.70	26.45	22.17	24.93	20.57
N 56×T 6	19.16	15.34	23.40	18.01	21.77	21.62
N 56×T113	19.61	18.54	23.62	17.18	21.75	24.98
N146×N206	20.64	27.70	26.18	22.06	21.90	24.33
N146×T 6	20.64	15.32	25.34	23.62	16.74	25.51
N146×T113	20.64	18.54	24.86	23.12	22.74	20.95
N206×T 6	27.70	15.32	24.98	22.25	24.02	24.73
N206×T113	27.70	18.54	25.65	22.80	24.60	18.75
T 6×T113	15.32	18.54	23.78	23.31	23.31	24.70
			Ear diameter (cm)			
N 56×N146	3.47	3.89	3.99	4.06	3.68	3.69
N 56×N206	3.47	4.21	4.29	4.07	4.10	4.43
N 56×T 6	3.47	4.37	4.92	4.48	3.57	3.76
N 56×T113	3.47	3.76	3.98	4.64	4.02	3.96
N146×N206	3.89	4.21	4.19	4.32	4.49	4.21
N146×T 6	3.89	4.37	4.61	4.10	4.64	4.34
N146×T113	3.89	3.76	3.95	4.16	4.60	4.08
N206×T 6	4.21	4.37	5.02	3.56	4.46	4.02
N206×T113	4.21	3.76	4.05	4.00	3.94	4.74
T 6×T113	4.37	3.76	4.75	4.62	4.00	4.10

TABLE 3. Mean performances of F_1, mid-parents and average heterosis for the two characters (same and diverse origins).

CHARACTERS		M.P.	F_1	AVERAGE HETEROSIS#
SAME ORIGIN				
ear length	(cm)	21.29	23.17	1.88 ± 1.71
ear diameter	)cm)	3.54	3.65	0.10 ± 0.08
DIVERSE ORIGIN				
ear length	(cm)	20.27	24.89	4.62 ± 1.74*
ear diameter	(cm)	3.93	4.37	0.42 ± 0.21

* significant at 5%. # measured as F_1-M.P.

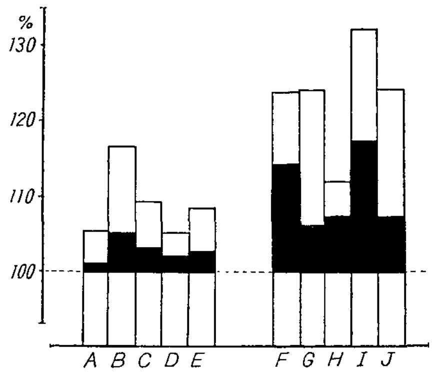

Fig. 1. Average heterosis expected by percentage of (F_1/M.P.) for ear length (□) and ear diameter (■)

A : N207; B : N208; C : N209; D : N210; E : N211;
F : N 56; G : N146; H : N206; I : T 6; J : T113

apparent in diverse origin and for ear length. The largest heterosis ratio was considered in diverse origin as 122.79% and 111.98% comparable with 108.83 and 103.10% of same origin for ear length and ear diameter, respectively.

The gene effects were computed for every single cross, and then, the results are shown in TABLE 4, 5 and 6. Instead of attaching the standard errors of the estimates, the significant estimates have been indicated in their usual manner, and in addition, those estimates larger than their standard error are indicated by ♯.

The number of crosses being significant for dominance effects is larger for ear diameter than for ear length. In regard to the inheritance of ear

TABLE 4. Number of crosses showed significant estimates of gene effects.

CHARACTERS	GENE EFFECTS					
	m	a	d	aa	ad	dd
SAME ORIGIN						
ear length	10	5(6)	4	4(5)	2(4)	4(7)
ear diameter	10	3(5)	6(7)	7	3(5)	6(8)
DIVERSE ORIGIN						
ear length	10	6(7)	6(9)	7(9)	5(7)	6(8)
ear diameter	10	5(6)	9	9	7(9)	7(8)

( ): indicates the number of crosses owning the estimates larger than standard error.

TABLE 5. Mean estimates of 6 gene effects for the two characters in same origin.

CROSSES	GENE EFFECTS m	a	d	aa	ad	dd
			Ear length (cm)			
N207×N208	23.43**	0.40	−1.28	−3.72	0.52	5.52*
N207×N209	23.40**	1.24#	−1.34	−1.76	1.38#	−2.24
N207×N210	21.76**	−1.38#	3.87*	3.32*	−1.25	−5.60#
N207×N211	21.31**	1.08*	3.24*	2.36#	−1.00#	−6.51**
N208×N209	25.59**	−0.43	0.63	−5.42**	−0.41	20.06**
N208×N210	21.74**	−2.33**	7.70**	4.98*	−2.32**	−4.04#
N208×N211	22.85**	−0.16	−6.22**	−9.36**	−1.46*	15.77**
N209×N210	21.30**	0.06	−0.35	−0.24	0.05	2.58
N209×N211	21.95**	1.16*	1.24	−0.28	−0.16	−2.90#
N210×N211	22.47**	1.79*	−1.16	−2.38	0.48	−0.47
			Ear diameter (cm)			
N207×N208	3.75**	−0.31**	−0.36	0.46	−0.24**	0.40
N207×N209	4.08**	0.12#	−1.67**	−1.64**	0.12#	0.90#
N207×N210	3.53**	−0.07	1.55**	0.70**	−0.05	−1.25**
N207×N211	4.61**	0.07*	−3.50**	−3.54**	0.08*	2.76**
N208×N209	3.60**	0.16#	0.15	0.08	−0.23#	0.59#
N208×N210	3.80**	0.06	−0.75**	−0.92**	0.04	1.43**
N208×N211	3.71**	−0.01	−0.57#	−0.98**	−0.07	1.90**
N209×N210	3.46**	−0.05	0.23	0.10**	−0.07	0.39
N209×N211	3.49**	0.04	0.70**	0.60**	0.05	−0.87**
N210×N211	3.40**	0.10**	0.06*	0.60**	0.07**	−0.59**

*, ** indicate significant at the 5 and 1% levels, respectively.
estimate larger than its standard error.

length, the relative importance of additive or dominance effects is different between the two materials (TABLE 4). Six crosses of same origin (S.O.) have estimates of (a) larger than standard error while 4 crosses are dealt with dominance (d); and the number is 7 for (a) against 9 for (d) in diverse origin (D.O.), respectively.

It should be noted that the sign of parameters of (a) and (ad), taking whether negative sign or positive sign, is quite dependent upon either parent being as P_1 or P_2 (as can be refered from the expectation method). Thus the sign is meaningless and can be disregarded for these. Estimates of dominance effects shown in Table 6 were positive for almost the crosses :

TABLE 6. Mean estimates of gene effects for the two characters in diverse origin.

CROSSES	GENE EFFECTS					
	m	a	d	aa	ad	dd
			Ear length (cm)			
N 56×N146	22.90**	−0.30	2.33#	−2.47#	0.44	3.76#
N 56×N206	22.17**	4.36**	5.34#	2.32	8.63**	6.44#
N 56×T 6	18.01**	0.15	20.89**	14.74**	−1.76#	−20.22**
N 56×T113	17.18**	−3.23**	29.51**	24.74**	−3.34*	−32.26**
N146×N206	22.06**	−2.43*	6.23*	4.22*	1.10	4.02
N146×T 6	23.62**	−8.77**	−2.62#	−9.98**	−11.43**	12.12**
N146×T113	32.12**	−8.21**	−15.83**	−21.10**	−9.25**	2.62
N206×T 6	22.25**	−0.71	11.97**	8.50**	−6.90**	−13.02**
N206×T113	22.80**	5.85**	−1.97	−4.50#	1.27#	15.34**
T 6×T113	20.58**	−1.39#	20.87**	14.62**	0.19	−29.62**
			Ear diameter (cm)			
N 56×N146	4.06**	−0.01	−1.19**	−1.50**	0.20#	3.10**
N 56×N206	4.07**	−0.33*	1.23**	0.78*	0.04	−3.10
N 56×T 6	4.48**	−0.19#	−2.26**	−3.26**	0.26#	3.79**
N 56×T113	4.64**	0.06	−2.23**	−2.66**	0.20*	1.85*
N146×N206	4.32**	0.28**	0.26**	0.12	0.44**	−0.05
N146×T 6	4.10**	0.30*	2.04**	1.56**	0.54**	−2.04**
N146×T113	4.16**	0.52**	0.85*	0.73*	0.46**	−2.53**
N206×T 6	3.56**	0.44*	3.43**	2.72**	0.52*	−1.06#
N206×T113	4.00**	−0.08	1.43*	1.36*	−1.02**	2.65*
T 6×T113	4.62**	−0.10	−1.59**	−2.28**	−0.45**	3.44**

*, ** indicate significant at the and 1% levels, respectively.
estimate larger than its standard error.

1, 2, 3, 4, 5, 8, 10; and 5 among the sixe significant crosses were of plus sign with high magnitude. Consequently, positive dominance effects are relatively important in the inheritance of ear length when parents are native of diverse origin.

Epistasis effects existed greatly in diverse origin rather than in same origin (TABLE 15). Nine crosses in diverse origin and 7 crosses in same origin exhibited significant estimates for epistasis for one or more of three types of espistasis in regard to ear diameter. Same origin showed 7 crosses being significant for additive×additive effect, and 3, 6 crosses in respect to the other two types of epistasis, additive×dominance and dominance×

dominance, respectively. There was only one cross, N210 × N211, showed significant estimates for all three types of epistasis at 1% level.

Diverse origin showed a similar trend of appearance for epistatic effect; the number of crosses exhibiting significant estimates for additive × additive was largest and then, additive × dominance or dominance × dominance. However, 5 crosses had estimates being significant for all three types of epistasis (TABLE 6).

As for the inheritance of ear length in same origin, epistatic effects were considered significantly for the two types of additive × additive and dominance × dominance at 4 crosses. The first effect seemed unimportant because it was computed in small magnitude and almost the estimates for the effect were of negative values. The dominance × dominance effect took important role in the inheritance of this character. Epistasis appeared more frequently in diverse origin with larger scale than in same origin. Seven, five and six crosses had significant estimates for additive × additive, additive × dominance, and dominance × dominance, respectively.

The effect of additive × additive owned relatively high values comparable with the others. However, we could not affirm in reference to the number of crosses showing estimates larger than their standard error that which epistatic effect among the two types, a × a and d × d, was more advantage.

Considering the three crosses, namely, N56 × T113, N56 × T6 and T6 × T113 which were made from the parents (P_1 and P_2) of low performance per se.. All the crosses showed very high average heterosis amount in F_1. It is striking that dominance effects were so important in all three of them with very high magnitudes being significant at 1% level. The magnitudes of dominance effect of the so-called crosses were 20.89, 29.51 and 20.89, respectively. The significance at 1% level was also considered for other two types as additive × dominance and dominance × dominance. The role of additive effects were minor with magnitudes being several times smaller than those of dominance effects.

Discussion

The first generation of synthetic varieties is a composite of all possible crosses among parental inbred lines. The investigation on gene effects from each of single crosses is more natural to help our nnderstanding about the intrinsic expression of gene action in contributing to heterosis in SYN. 1.

As can be refered from the TABLE 7, the high values of correlation between the two characters with either ear weight and grain yield were computed. Ear length always shows high relationship with yield potentiality

TABLE 7. Matrix of correlation values between five yield component characters in same and diverse origin.

SAME ORIGIN					
ear length	1.000	.296*	.393**	.397**	.339**
ear diameter		1.000	.282	.125	.076
100 kernel w.			1.000	.319*	.226
ear weight				1.000	.891***
shelled corn w.					1.000
DIVERSE ORIGIN					
ear length	1.000	.005	.358*	.470**	.474**
ear diameter		1.000	.047	.375**	.306*
100 kernel w.			1.000	.654**	.643***
ear weight				1.000	.981***
shelled corn w.					1.000

*, **, *** significant at 5, 1 and 0.1%, respectively.

in corn. As a matter of fact, the ear length is quite proportional to the number of kernels per row, the factor concerns deeply with yield of its ear. On the other hand, the kernel row number is morphologically not so variable between varieties or lines and F_1 rarely exceeds their higher parent; therefore, advantage in F_1 population would not be expected greatly in both same and diverse origins (Table 1, 2 and 3). There were nine and six crosses which showed significant estimates for dominance gene effects in diverse and same origin ; but about a half of the numbers or more had negative sign. The additive × additive effects are found relatively larger than other digenic epistasis ; but we could not have an explicit conclusion from the obtained results that which gene effects are important in the inheritance of ear diameter. GAMBLE (1962) quoted that estimates of dominance effects are no more important than the others.

The difference in gene effects between two sources of materials is more apparent in the study of ear length. In same origin, additive effects are apparently important in the inheritance of the character. The result states the effects of long progress of selection of the materials from a narrow genetic base.

The additive effect is, in contrast, minor important than the dominance effect in case of diverse origin. ROBINSON et al. (1949) reported that additive genetic variance is very large to the total genetic variances of open-pollinated population in regard to the inheritance of yield. Nevertheless, genetic variances in ROBINSON's paper were computed regardless of epistasis which exhibited a relative importance in GAMBLE,s (1962). With regard to the importance of dominance effect, the study herein shows similar results with the GAMBLE's for ear length.

The crosses made between the parents of low performances per se. display a consistent trend of gene effects that the high heterosis in hpbrid may be as the result of contributing by dominance gene effect, and in addition, one digenic epistasis. The presence of dominance effect with high magnitude and the minor importance of additive effect in diverse origin force us to pay more attention on breeding procedures which emphasize the dominance and epistasis. The method of selection named as the recurrent selection for specific combining ability proposed by HULL (1949) may be one of the procedures which is available to meet the requirements.

Summary

Estimates of gene effects for the two yield component characters, ear diameter and ear length, were computed comparatively for the two synthetic varieties of same and diverse origin, respectively.

In general, the synthetic variety of diverse origin had large number of crosses showing significant estimates of dominance effect while the synthetic variety of same origin was of additive effect. The trend was more apparent in the analysis of ear length. Five crosses among ten in same origin exhibited significant additive effect's estimates and the number is relatively larger than those of the other effects. Additive effect is very important in the inheritance of ear length of same origin. However, the dominance effect is more important than additive effect in case of diverse origin. Besides, the relative importance of epistasis especially for the digenic type of "additive × additive" was considered. The authors also found that the extremely high heterosis which often occurs in crosses made between lines of low performance per se. is resulted by the contribution of dominance and at least one digenic epistasis.

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