THE RELATIONSHIP BETWEEN THE DIVERGENT LEVEL OF SYN. O AND HETEROSIS APPEARANCE IN SYNTHETIC VARIETIES OF CORN, *Zea mays* L.

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Introduction

The awareness of the importance of genetic diversity of parents in crossing has been prevailing from the early stage of breeding program of corn when corn breeders found that the crosses made from unrelated inbred lines indicate greater heterosis amount than those made from related lines (EAST, 1936; EAST *et at.*, 1912; HAYES *et al.*, 1939; WU, 1939; HULL, 1948; JOHNSON *et al.*, 1940). The understanding about the diversity to heterosis relationship then has been more clarified by the studies of SENTZ *et al.* (1954), MOLL *et al.* (1962, 1964), PATERNIANI *et al.* (1963), TIMOTHY (1963): Heterosis appears to increase with the increased genetic diversity of the parental population. In breeding synthetic varieties of high yield in corn, the use of parental lines from diverse origin is always favorable and necessary for the procedures which emphasize the non-additive gene effects (HO *et al.*, 1973).

Nevertheless, there have been some opinions on the loss of heterosis effect due to the over large divergence of parents involved (GILBERT, 1960). The further study on the association of heterosis in Syn. 1 and the degree of divergence of components of synthetics becomes more and more requisite because of the increasing interest in exotic genotypes for future breeding program.

The study aims at providing more evidences on the problem as follows: What should be an indicator of genetic diversity from the standpoint of breeders? The relationship between the diversity level of Syn. 0 and heterosis appearance in Syn. 1; and the variation of gene effects, additive and non-additive effects, in respect to different diversity of components, in Syn. 1.

Materials and method

Four among ten inbred lines were selected at will from each source of same and diverse origin, based on the yield performance. Therefore, the authors had in total 8 inbred lines with 5 different genotypes. The selection of inbred lines from diverse origin was held in respect to the basis of wildly geographical seperation. A brief decription of these lines is presented as follows:

— N208, N209, N210, and N211 are those lines which were selected from ten derived from the offspring of the cross "*Iwanai zairai* A×N85", flint type, after 10 years of selfing.

— N56, inbred line of *European* type because the so-called line was improved from the local variety of Germany, namely *Meinerser Frühmais.*

— N146, northern american flint type, the ancestral is not clear but different with those of same origin in many agronomic characters.

— T6 is a tropical flint type, and its ancestral variety is introduced from *Italy.* In the study, it may be classified either into *European* or into tropical type.

— T113 was improved from Caribbean variety, and it is considered as a tropical line in the study.

N146 of diverse origin and those of same origin are from *Northern America* region but so divergent in many agronomic characters such as flowering time, yield performance, germinating viability, and therefore, they are supposedly to be unrelated in genetic background. In fact, they are originated from quite different ancestral varieties.

Seven levels of genetic diversity for parental population or Syn. 0 were postulated in this study, in reference to the relationship between ancestral varieties as follows:

Degree of diversity of the syn. 0

Levels:	I	II	III	IV	V	VI	VII
Genotypes:	4/4	4/5	4/6	4/8 or (3/6, 2/4)	3/7	2/6	0/4

The fraction below each level mark (I–VI) represents the corresponding constitution of parental lines of Syn. 0 where the numerator of the fraction expresses the number of similar genotypes among parental lines used and the denominator indicates the total of parental lines in the level. Therefore, the first level can be understood as within source (of same origin) and it means 0% of diversity, while the last level (VII) is of 100% of diversity since there is no related genotype in Syn. 0. Consequently, the fraction corresponding to the level IV may as 2/4 or 3/6.

Yield test of parents and 28 single crosses was conducted at the field of Hokkaido university in 1973. Simple lattice design with three replications was practised.

Row width was 85 cm while the distance between plants was 30 cm. Data on grain yield was measured as g/plant after drying until 10% of moisture in the oven.

Analysis of the data was applied following the method IV of model II presented by GRIFFING (1954). The results noted in the study are the averaged value from all possible synthetics in regard to each level of diversity.

The author made an attempt at classifying the tested lines into region or type, in reference to the relationship between their ancestral vareities, in order to illustrate the indicator of diversity.

Results

The average performance of F_1 population distributed largely with the lowest mean is dealt with one of the crosses between inbred lines within source of same origin, 88.57 g/pl, and the maximum value is in consequence of the cross made from two lines between sources, N208×T6, as 231.61 g/pl. The range of yield performance for F_1 was greater in the first four families of N208, N209, N210, and N211 than in others (Table 1). Mean

TABLE 1. Yield of grain (g/pl) of parents, the mean and range of their F_1 crosses and the mean relative heterosis of the F_1's expressed as a percent of mid parent, high parent, and constant parent.

	Parent	F_1 performance		%		
		range of F_1	mean	vs. M.P.	vs. HP	vs. CP
N 208	115.87	126.10–231.61	167.14	53.79*	22.81	44.25*
N 209	92.31	88.57–196.73	147.95	55.63*	32.88*	60.27*
N 210	85.55	88.57–190.72	139.06	49.26	27.70	62.55**
N 211	89.46	89.40–189.11	144.78	61.83*	45.70*	61.84**
N 56	83.11	136.63–173.29	153.65	62.10**	44.35**	84.87**
N 146	67.82	126.47–187.67	151.94	82.40**	59.91**	124.03**
T 6	37.41	170.95–231.61	190.56	159.87**	93.83**	409.38**
T 113	67.37	126.47–189.11	160.18	87.92**	63.95**	137.76**

*, ** indicate significant at the 5 and 1% levels, respectively.

performances of F_1 crosses were all superior than those of their parents and the average heterosis was of course very apparent in families of diverse origin. As can be seen from the fourth and fifth colum of the Table 1, the ratio of F_1 performance to mid-parent or to high parent was computed significantly at 1% of level for all lines derived from diverse origin.

It is striking to recognize that the greatest advantage of heterotic effect can be expected from the crosses with T6, the line has the lowest performance per se.. The minimum value of mean yield of the cross, T6 × T113, in this family is still very high and being of 170.95 gram per plant.

The average yield of parents of same origin were associated strictly

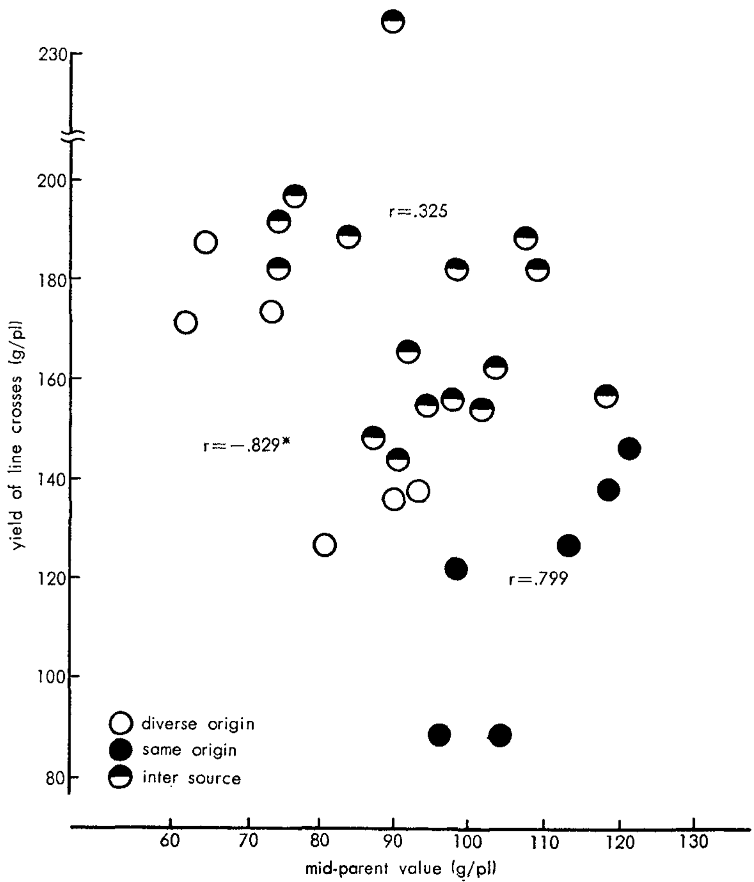

Fig. 1. Yields of line crosses in relation to the respective mid-parent.

with F_1's with a correlation value as 0.799. However, it showed a negative value for correlation between parents and F_1's performances ($r=-0.828$) in case of within source of diverse origin (Fig. 1). The correlation value computed from the data of between-source crosses was -0.347 indicating the gene effect must be complicated. The variances dealt with the first order, the second order, and the third order were accounted for the very small part of the total variance as 5.38%, 3.54%, and 1.46%, respectively, Table 2.

TABLE 2. Analysis of variance for grain yield (g/pl) from the data of the F_1 crosses and respective mid parent.

Source			d. f.	M. S.	F
within source	S. O.	additive	1	1906.409	7.039*
		deviation	4	270.788	
		total	5	597.921	
	D. O.	additive	1	2127.049	8.879*
		deviation	4	239.611	
		total	5	617.091	
inter sources	S. O. × D. O.	additive	1	425.187	0.854
		digenic	1	284.561	0.572
		trigenic	1	1451.672	2.916
		quadrigenic	1	115.807	0.232
		....			
		total	15	526.207	

* significant at 5%.

The differences among the within-region crosses is remarkable with the first group the best and the group IV is the poorest. Differences among the cross of *America* × *Asia* (*Caribbean* type), as the lowest to the cross, *America* × *Italy*, which is the best, Table 3.

Then the crosses between two regions generally showed high heterosis effect. The "*Italy* × *Asia*" cross exhibited the highest heterosis ratio, 190.69%, in contrast with the cross between "I × II" which has low heterosis ratio, 49.13%. Relatively high heterotic effect was considered in the between-region crosses of which one parent is derived from Italy.

The materials were also divided into three types as *Northern America*'s flint or "A", which consists of N 208, N 209, N 210, N 211, and N 146;

TABLE 3. Yield of line crosses averaged by regions in gram per plant and percent of mid parent.

	I	II	III	IV	V
I	118.51 8.92	157.54	163.33	200.50	171.84
II	49.81	101.85 —	138.10	173.29	136.53
III	70.13	49.13	83.36 —	186.67	126.47
IV	154.50	134.77	190.69	45.77 —	170.95
V	84.68	51.59	56.48	175.63	78.28 —

the upper triangle is F_1 performance
the under triangle is heterosis ratio
I: N208, N209, N210, N211 (*America*)
II: N56 (*Germany*)
III: N146 (*America*)
IV: T6 (*Italy*)
V: T113 (*Asia*: *Japan*)

TABLE 4. Yield of line crosses averaged by types in gram per plant and percent of mid parent.

	F_1 performances			heterosis ratio %		
	A	E	T	A	E	T
A	140.922	175.540	180.350	29.37	105.71	120.39
E		173.290	160.250		134.77	120.60 (115.60)
T			170.950			175.63

( ): indicates the value when T6 is excluded from E
A: N208, N209, N210, N211, N146
E: N56, T6 (or N56)
T: T6, T113

European type or "E" is of N56, T6; and finally, *Tropical flint* or "T" consists of T113 and T6, respectively. As for T6, it is actually a tropical flint but derived from a local variety of *Italy* and hence it may belong to either European type or tropical type (Table 4). The crosses within the type "A" have the lowest performances of yield for F_1 generation, and consequently, showing the smallest values of heterosis ratio as 29.37% per plant. The highest heterosis ratio is for the type "T" (including T6 and T113). The average of heterosis ratios of the within-type crosses is 113.25% in comparison with that of between-type crosses as 115.60%. There existed less heterotic effect in the crosses between the "A" and "E" types.

TABLE 5. Yield of grain (g/pl) of the three generations of synthetic varieties in respect to different levels of diversity of Syn. 0 and their relative heterosis ratio to mid parent and to high parent.

Diversity levels	I	II	III	IV	V	VI	VII
Syn. 0	95.797	89.423	85.174	79.862	63.900	70.301	63.927
F_1 or Syn. 1	118.318	140.370	150.307	157.600	158.609	162.311	155.501
F_2 or Syn. 2	112.837	130.180	139.451	147.883	144.908	146.972	132.607
F_1 vs. M. P.¥	22.82	62.44	76.88	107.50	128.22	138.47	153.84
F_1 vs. H. P.¥	13.81	41.57	57.56	73.97	88.65	98.80	109.31

¥ measured as percentage (%)

TABLE 6. Analysis of variance for general and specific combining ability at different diversity levels.

	Source	d. f.	Mean Square	a^2
I	G. C. A.	3	750.511**	0.415
	S. C. A.	2	311.891**	
	errors	10	37.606	
II	G. C. A.	4	2417.480**	0.347
	S. C. A.	5	839.081**	
	errors	18	79.497	
III	G. C. A.	5	2345.121**	0.389
	S. C. A.	9	921.587**	
	errors	28	119.008	
IV	G. C. A.	7	1982.938**	0.414
	S. C. A.	20	821.191**	
	errors	54	90.071	
V	G. C. A.	6	1306.002**	0.631
	S. C. A.	14	824.525**	
	errors	40	92.856	
VI	G. C. A.	5	982.108**	0.684
	S. C. A.	9	671.997**	
	errors	28	92.792	
VII	G. C. A.	3	648.075**	0.869
	S. C. A.	2	563.213**	
	errors	10	58.487	

*, **, indicate significant at the 5 and 1% levels, respectively.

Mean performances of F_1 (or Syn. 1), F_2 (or Syn. 2) and heterosis effect in reference to different levels of heterozygosity of parental population are summarized in Table 5. The level III was of the average of all in performances of F_1 as well as F_2; but the average of all in the "F_1 vs. M.P." and "F_2 vs. H.P." was close to the values of the level IV. The level VI showed the highest advantage in yield performances of Syn. 1 and Syn. 2. The consistent trend of heterosis appearance was considered that increasing with the number of unrelated genotypes in Syn. 0 and the level VII showed the best heterosis as 153.84 g/pl.

The variances for both general combining ability and specific combining ability were computed significantly at 1% of statistical probability (Table 6). The mean square values of the second effect became larger and larger with levels.

It is also clarified that partial dominant effect became greater and greater from the level I to the level VII, and in effect, the value of a^2 was the highest at the level VII as 0.869. The mean square values for error component were not so different between levels.

Estimates of gene effects, additive and non-additive effects, are shown in Table 7. The estimates of non-additive gene effect were consistently greater than those of additive gene effect throughout all levels. Then the large genetic variance of general combining ability noted in the above table 35 may be mainly due to the contribution of non-additive rather than additive portion. The ratio of either effect $(\sigma^2_s/(2\sigma^2_g+\sigma^2_s))$ and $(2\sigma^2_g/(2\sigma^2_g+\sigma^2_s))$ showed that of σ^2_g took greater proprtion from the level II, and in-

TABLE 7. Estimates of gene effects and their portion to the total variance of Syn. 1 at different diversity levels.

	Source	estimated values	%		Source	estimated values	%
I	σ^2_g	164.479	57.09#	V	σ^2_g	152.405	29.41
	σ^2_s	247.283	42.91		σ^2_s	731.671	70.59
II	σ^2_g	400.905	51.35	VI	σ^2_g	64.606	18.24
	σ^2_s	759.589	48.65		σ^2_s	579.205	81.76
III	σ^2_g	308.204	44.43	VII	σ^2_g	31.86	11.21
	σ^2_s	771.051	55.57		σ^2_s	504.725	88.79
IV	σ^2_g	169.421	31.67				
	σ^2_s	731.174	68.33				

computed as $\frac{2\sigma^2_g}{2\sigma^2_g+\sigma^2_s}$ and $\frac{\sigma^2_s}{2\sigma^2_g+\sigma^2_s}$

creasing to the best at the level VII where the parental population or Syn. 0 was consituted by 100% of unrelated genotypes, with 88.29%.

Discussion

The result obtained herein indicates that the crosses between sources (same and diverse origin) are always superior than those made from lines within source. This seems to be an additional evidence approving the association between diversity of parents and heterosis amount in hybrid which has been quoted by many previous workers (EAST and HAYES, 1912, EAST, 1936, HAYES and JOHNSON, 1939, WU, 1939, JOHNSON and HAYES, 1940, MOLL *et al.*, 1962, PATERNIANI and LONNQUIST, 1963, TIMOTHY, 1965, LONNQUIST and GARDNER, 1961, and so forth). Besides, it is more interest because the association was found not only from the data of single crosses as noted, but with the data of synthetic varieties.

The results of almost early works showed that F_1 never exceeded their parents over 50%, for example, 46% as the case of PATERNIANI *et al.* (1963); 47% according to Krug's result; 24% as reported by MOLL *et al.* (1962) in case of varietal crosses. While, the study shows the heterosis ratio is more than 100% for many crosses. The advantage of heterosis can be expected in line crosses rather than varietal crosses; and in crosses of unrelated plant rather than in those made from related plants, respectively.

If the assumption that inbred lines are genotypically copies of the ancestral varieties from which they are derived, is correct, genetic diversity between inbred lines should be reference to the relationship between their ancestral varieties. As can be seen from Table 4, the classification of used inbred lines in the study is not satisfied when the "type" is considered as the creterion, T6 probably belongs to either type "E" or type "T". The within-type crosses showed relatively high heterosis effect comparable with between-type crosses, and moreover, the best value is considered at the cross of within-type "C" as 175.63%. If T6 is excluded the value becomes smaller, 113.25%. Consequently, the classification is a good procedure of definiting diversity of parental lines.

On the other hand, the results of Tables 3, 5, and 7 state the more reasonable evidence on the geographical separation as indication of genetic divergence.

According to HO (1974), HO *et al.* (1973), the utilization of inbred lines of diverse origin is a requisite in breeding program of high yielding synthetic varieties of corn. Indeed, the increase of yield performances of

F_1 or Syn. 1 and Syn. 2 is relative to the proportion of the number of unrelated genotypes to the total genotypes used in Syn. 0. However, the quite divergent parental components are not always profitable to produce synthetic of high yield because the best synthetic varieties developed from the limited materials of the study are not those at the level VII, but at the level VI. Commonly, the best crosses are involved from their parents which show high stability to the environmental condition of testing, and by contrast it is rare to have favorable hybrid from unstable parents. The performance of Syn. 0 of the level VII is the lowest with 63.93 g/pl among seven levels, and the fact means that the parents may contain unfavorable lines. Thus, there may be unfavourable single crosses which made between unfavourable lines cause the decrease in yield performance of Syn. 1 at the level VII. CORKILL (1962) detected in addition that the use of so divergent parents of synthetic varieties of alfalfa is unfavourable for many cases since it is so heterogeneous for agronomic characters other than yield, being unsatisfied during seed increase from Syn. 2.

The gradual increase of estimates of gene effects in nonadditive way with the degree of diversity (Table 6, 7) is considered simultaneously with the increase of heterotic effect (Table 5). It can be interpreted that high heterotic effect is generally contributed by the gene which act in geometric way. Besides, the results state the association between the three phases: the degree of genetic diversity of components used in Syn. 0, heterosis appearance in Syn. 1 and Syn. 2, and the magnitude of non-additive gene effect.

It is commonly known that maximum heterotic response in corn results from crossing parental varieties of contrasting endosperm types (HAYES *et al.*, 1919 and RICHEY, 1922). But PATERNIANI and LONNQUIST (1963) proved that the better heterotic effect can be provided from crosses between varieties within endosperm if a sufficiently wide selection of parents is possible. Then, we can go on from the results obtained in this study the conclusion for the use of components of synthetic varieties as follows: The parents must be derived from distinguishable genetic base or different each other in genotype where the indicator of genetic diversity is based on the geographical separation, and the degree of diversity of components parents seems mostly profitable at about 70–80%, respectively.

Summary

Our objectives were to provide some evidences on the indicator of genetic diversity of inbred lines and to investigate the relationship between

different diversity levels of Syn. 0 and heterosis amount appeared in the Syn. 1 and Syn. 2 of corn, *Zea mays* L.

The diversity between inbred lines, components used in Syn. 0, is quite dependent on that of their ancestral varieties of which the diversity indicator can be considered as the geographical isolation between them. The association between the three phases, the degree of diversity of the component, heterosis in Syn. 1 and in Syn. 2, and the magnitude of non-additive gene effects, was considered that the heterotic effects were maximum when the inbred lines as parents were quite unrelated together in genotype or at the diversity level of 100%, and the highest estimates for non-additive gene effect were also obtained at the same level.

However, Syn. 1 and Syn. 2 performed best at the level where the component of synthetic varieties was constituted of inbred lines of which 70–80% were of diversely originated ones. The results sugguest that the component seemed to be mostly desirable for breeding synthetic varieties of high yield in corn.

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Literature cited

CORKILL, L. 1956. The basis of synthetic strains of crosspollinated grasses. Proc. 7th Inter. Grassl. Congr. pp. 427–438.

EAST, E. M. 1936. Heterosis. Genetics 21: 375–397.

EAST, E. M. and H. K. HAYES 1912. Heterozygosis in evolution and plant breeding. U.S.D.A. Bur. Plant Ind. Bul. No. 243: 1–58.

GILBERT, N. 1960. Quantitative inheritance in *Drosophila*. J. Genetics 57: 77–83.

GRIFFING, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. Jour. Biol. Sci. 9: 463–493.

HAYES, H. K. and P. J. OLSON 1919. First generation crosses between standard Minesota corn varieties. Univ. Minn. Tech. Bul. 183.

HAYES, H. K. and R. J. GARBER 1939. Synthetic production of high protein corn in relation to breeding. J. Amer. Soc. Agron. 11: 309–318.

HO, V. CH. and S. HOSOKAWA 1973. The stabilty of gene effects of parental lines used to produce a synthetic variety of high yield in maize, *Zea mays* L. J. Facul. Agr., Hokkaido Univ. 57: 132–140.

HO, V. CH. 1974. Breeding method of Synthetic Varieties of High Yield in corn, *Zea mays* L. Thesis of Doctor Degree.

HULL, F. H. 1948. Evidence of overdominance in yield of corn. Genetics 33: 110.

JOHNSON, I. J. and H. K. HAYES 1940. The value in hybrid combinations of inbred lines of corn selected from single crosses by the pedigree method of breeding. J. Amer. Soc. Agron. 32: 479-485.

LONNQUIST, J. H. and C. O. GARDNER 1961. Heterosis in intervarietal crosses in maize and its implication in breeding procedures. Crop Sci. 1: 179-183.

MOLL, R. H., W. S. SALHUANA and H. F. ROBINSON 1962. Heterosis and genetic diversity in variety crosses of maize. Crop Sci. 2: 197-198.

MOLL, R. H.; M. F. LINDSEY and H. F. ROBINSON 1964. Estimates of genetic variances and the level of dominance in maize. Genetics 49: 411-423.

PATERNIANI, E. and J. H. LONNQUIST 1963. Heterosis in interracial Crosses of corn (*Zea mays* L.). Crop Sci. 3: 263-266.

RICHEY, F. D. 1922. The experimental basis for the present status of corn breeding. J. Amer. Soc. Agron. 14: 1-17.

SENTZ, J. C., H. F. ROBINSON and R. E. COMSTOCK 1954. Relation between heterozygosis and performance in maize. Agron. J. 46: 514-520.

TIMOTHY, D. H. 1963. Genetic diversity, Heterosis, and Use of Exotic Stocks of Maize in Colombia. Statistcal Genetics and Plant Breeding. pp. 581-593.

WU, S. K. 1939. The relationship between the origin of selfed lines of corn and their value in hybrid combination. J. Amer. Soc. Agron. 31: 131-140.