Theor Appl Genet (1987) 73:445–450

Heterosis among populations of maize (*Zea mays* L.) with different levels of exotic germplasm*

J. Crossa[1], **C. O. Gardner**[2] **and R. F. Mumm**[3]

[1] International Center for Maize and Wheat Improvement (CIMMYT), Apartado Postal 6-641, 006600 Mexico DF, Mexico
[2] Department of Agronomy, University of Nebraska, Lincoln, NE 68583, USA
[3] Biometrics and Information Systems Center, University of Nebraska, Lincoln, NE 68583, USA

Received May 20, 1986; Accepted June 27, 1986
Communicated by A. R. Hallauer

Summary. Thirteen maize (*Zea mays* L.) populations including five adapted, five adapted × exotic, two composites of adapted and exotic, and one exotic selected for adaptability were crossed in a diallel mating system. The parents and 78 crosses and nine check hybrids were evaluated for grain yield and plant height in five environments. The Gardner-Eberhart model Analysis II indicated that additive and nonadditive gene effects accounted for 60 and 40% of the total variation among populations, respectively, for grain yield and 86% and 14% of the total variation, respectively, for plant height. Components of heterosis were significant in the combined analysis for both traits. Adapted Corn Belt populations tended to have higher performance in crosses and greater values of variety heterosis than 50% adapted populations. 'Nebraska Elite Composite', 'Corn Belt' × 'Mexican', and 'Corn Belt' × 'Brazilian' showed high mean yields in crosses, however, they were not among those with high estimates of variety heterosis. One exotic population ('Tuxpeno' × 'Antigua Grupo 2') and three adapted populations ['307 Composite', 'NB(S_1)C-3', and 'NK(S_1)C-3'] might be combined together to form a high-yielding population. It may be possible to synthesize two useful populations for reciprocal recurrent selection by grouping 'Tuxpeno' × 'Antiqua Grupo 2', 'NB(S_1)C-3', and 'NS(FS)LFW-8' into one population and 'NK(S_1)C-3', 'Krug' × 'Tabloncillo', and '307 Composite' in the other one.

Key words: Unadapted germplasm – Adapted germplasm – Heterotic patterns – Gardner-Eberhart model – Composites

Introduction

Much has been written about the narrowness of the germplasm base and its potential effect on the vulnerability of U.S. maize (*Zea mays* L.) production. One way to increase genetic variation is to introduce exotic germplasm. Often exotic material is unadapted, and when it is introduced, many problems are encountered in making crosses, generating recombinations, and extracting useful alleles.

It is important to identify superior resources among available exotic germplasm and then find the most efficient way to incorporate such germplasm to well adapted maize populations. Studies conducted at the University of Nebraska-Lincoln (Chopra 1964; Romero-Franco 1965; Shauman 1971; Subandi 1972), with exotic and exotic × adapted populations, indicate that useful genes in exotic populations can be used to improve adapted maize breeding populations.

Researchers have reported an increase in yield when crossing exotic with adapted populations, which is caused by heterotic effects resulting from the genetic diversity of the two parental populations. However, some reports indicate that no immediate positive effects are obtained when crossing exotic with adapted germplasm (Kramer and Ullstrup 1959; Efron and Everett 1969; Lonnquist 1974). Therefore, the determination of (a) what exotic population will provide the desired characteristics and (b) which exotic × adapted crossed population will produce a high heterosis effect becomes very imporant issues in the introgression of exotic germplasm for improving maize breeding populations.

The diallel cross is used as a mating system for determining cumulative gene effects of breeding populations (Hayman 1954a, b, 1957, 1958; Griffing 1956). A general model for estimating genetic effects was proposed which includes additive × additive epistasis and can be applied to both inbred parents and noninbred parents (varieties and/or populations) (Gardner 1965; Gardner and Eberhart 1966; Eberhart and Gardner 1966). Heterosis effects serve as a guide to genetic diversity and provide a basis for the formation of genetic pools and for choosing two germplasm pools to be used in reciprocal recurrent selection programs (Gardner 1982).

---

* Contribution from the Department of Agronomy, University of Nebraska, Lincoln, NE 68583. Published as Paper No. 8011. Journal Series, Nebr. Agric. Exp. Station. Research was conducted under Project 12-049

The main objectives of this study were to identify superior exotic and exotic × adapted populations for use in maize population improvement and to determine heterotic patterns among adapted, exotic, and adapted × exotic populations.

Materials and methods

A 13-population diallel cross was developed in the summer of 1981 at the University of Nebraska-Lincoln. The populations included five adapted populations, five adapted × exotic populations, two composites of adapted and exotic material, and one exotic population selected for adaptability (Table 1).

The population TA (selected for adaptability) was derived as follows: 1,000 seeds from a "Composite L(Me)C_2 ('Tuxpeno' × 'Antigua')" obtained from CIMMYT (International Maize and Wheat Improvement Center), were irradiated (x-ray). One thousand S_1 progeny rows were grown at Lincoln, Nebraska. A set of selfed lines were developed and testcrossed. The top 20 lines were recombined to form the population (TA) used in this study.

The population NSY was formed from a diallel cross made in 1977 among 18 lines and hybrids from the USA, Canada, France, and Yugoslavia.

To make the crosses, paired rows of parents (with enough seed to have 30 plants per row) were planted for each cross. This was repeated in two planting dates. All possible crosses between corresponding paired rows were made. The male inflorescence was used only once, and the ears of each cross collected over the two diallels were shelled in bulk and mixed.

In the summer of 1982, the 13 populations with their $n(n-1)/2$ crosses and nine checks were planted at three locations (Lincoln, Mead, and Clay Center, Nebraska). A randomized complete block design with two replications was used at each location. The plot (3.81 m x 1.52 m) consisted of two rows of five hills each. Four kernels were hand-planted in each hill and stand was subsequently adjusted to three plants per hill (51, 802 plants/ha). In the summer of 1983 the test was planted at two locations (Lincoln, and Mead, Nebraska) using the same procedure. The following data were recorded: plant height, missing hills, grain yield, and percent grain moisture at harvest.

Table 1. Populations, pedigree citation, and code letters

Population and pedigree citation	Code letters
Adapted	
Nebraska Elite Composite (Crossa 1984)	EC
NS(FS)LFW-8 (Gardner et al. 1982)	NS
NB(S_1)C-3 (West et al. 1980)	NB
307 Composite (Johnson 1974)	307C
NK(S_1)C-3 (West et al. 1980)	NK
Adapted × Exotic	
Corn Belt × Mexican (Compton et al. 1979)	CM
Corn Belt × Caribbean (Compton et al. 1979)	CC
Corn Belt × Brazilian (Compton et al. 1979)	CB
Krug × Tabloncillo (Chopra 1964, Shauman 1971)	KT
Illinois × Eto (Pixley 1984)	IE
Exotic	
Tuxpeno × Antigua Grupo 2 (see text)	TA
Adapted-exotic composites	
Novi Sad Yugoslavia Composite (see text)	NSY
Alaquat (Compton, personal communication)	AL

Statistical analyses

Analyses of variance for plant height and for grain yield at 15.5% moisture adjusted for stand were performed on data from each of the five environments. A combined analysis of variance of the five environments was also computed.

As described by Gardner (1967), a variety effect (v_j) is the difference between the mean of a parent per se and the mean of all parents. The average heterosis ($\bar{h}$) contributed by the particular set of parents used in crosses is the difference between the mean of all crosses ands the mean of all parents. The variety heterosis (h_j) is the contribution of heterosis by variety j in its crosses measured as a deviation from average heterosis. It is calculated as a function of the difference between the mean of a parent in crosses and the average of all crosses and the difference between a parent mean and the average of all parents. The specific heterosis ($s_{jj'}$) that occurs when varieties j and j′ are mated measures the deviation between the observed performance of the specific cross and its expected performance based on variety effect (v_j), average heterosis ($\bar{h}$), and variety heterosis (h_j); it is calculated as a function of the sum between the mean of a cross and the average of all crosses and the sum of the mean of all crosses of varieties j and j′.

The Gardner and Eberhart (1966) Analysis II (diallel cross and parents) was used to estimate the genetic effects. The analyses were performed using a FORTRAN program developed by J. J. Hammond, R. F. Mumm, and Leo Roth and revised by Carl W. Johnson (1974) at the University of Nebraska-Lincoln.

Results and discussion

The 100% exotic population, TA, performed well as a parent per se and in crosses (Table 2); it ranks second in mean cross performance (7,101 kg/ha) and first as a parent per se (7,005 kg/ha). The 100% Corn Belt population, NB, had the highest yield in crosses (7,571 kg/ha), but it yielded poorly as a parent per se (5,610 kg/ha). NSY yielded poorly both as a parent per se and in crosses. The AL population, developed with considerable genetic diversity, had a low yield performance in crosses (6,122 kg/ha).

Variety effect (v_j) was significant for both traits in all environments. Variety heterosis (h_j) was significant in four environments for grain yield, and in one environment for plant height. Although specific heterosis ($s_{jj'}$) accounted for a sizeable portion of the total sum of squares due to generation means (13 to 47% for grain yield and 10 to 27% for plant height), significance was detected in only one environment for plant height and in no environments for grain yield (data not presented). The combined analyses of variance over the five environments (Table 3) shows that for grain yield, 60% of the total sum of squares due to differences among generation means could be explained by variety effects (v_j) and 40% could be

Table 2. Grain yield means (kg/ha) of 13 parents per se and the 78 F_1's derived from all possible crosses among them, calculated over five environments

	F_1 mean													Mean performance	
	EC	NS	NB	307C	NK	CM	CC	CB	KT	IE	TA	NSY	AL	in crosses	per se
EC		6,464	7,477	6,813	6,899	6,731	7,118	7,116	7,241	7,176	7,073	5,180	6,528	6,818	6,539
NS			7,840	6,265	6,823	6,662	7,293	7,028	7,524	6,684	7,485	4,956	6,342	6,781	5,400
NB				8,005	8,058	7,342	7,979	7,343	7,898	7,845	7,740	6,472	6,847	7,571	5,610
307C					7,139	6,872	6,999	6,423	7,229	6,947	7,415	6,013	6,631	6,896	6,662
NK						6,583	6,774	6,459	7,112	6,765	8,001	5,569	6,368	6,879	5,157
CM							6,817	6,561	6,331	6,697	7,120	5,321	6,043	6,590	6,254
CC								6,319	5,992	6,560	7,239	5,485	5,925	6,708	6,019
CB									6,427	6,925	7,764	5,807	6,011	6,682	6,218
KT										6,626	6,904	5,414	5,992	6,724	5,380
IE											6,576	5,984	5,834	6,718	4,966
TA												5,684	6,207	7,101	7,005
NSY													4,743	5,552	3,921
AL														6,122	5,274

The L.S.D. (0.05) for parents is 1,494 kg/ha; the L.S.D. (0.05) for crosses is 791 kg/ha

Table 3. Combined analysis of variance of grain yield (q/ha) and plant height (m) for 13 maize populations and their diallel crosses evaluated in five environments

Source of variation	df	Yield (q/ha)		Plant height (m)	
		% Among pop. SS	MS	% Among pop. SS	MS
Among populations	90	100.00	681.81**	100.00	0.227**
Varieties (v_j)	12	60.12	3,074.18**	85.96	1.469**
Heterosis ($h_{jj'}$)	78	39.88	313.75**	14.04	0.036**
Average heterosis ($\bar{h}$)	1	17.45	10,698.98**	3.60	1.035**
Variety heterosis (h_j)	12	10.57	540.88**	2.88	0.074**
Specific heterosis ($s_{jj'}$)	65	11.86	112.04*	7.56	0.014**
E×among populations	360	–	107.58**	–	0.012**
E×v_j	48	–	276.32**	–	0.026**
E×$h_{jj'}$	312	–	81.62**	–	0.011**
E×h	4	–	61.79	–	0.008
E×h_j	48	–	72.83	–	0.011
E×$s_{jj'}$	260	–	83.55**	–	0.009
Error	495	–	76.25	–	0.010
CV%			13.24		3.81

*, ** Significant at 0.05 and 0.01 probability level, respectively

explained by nonadditive genetic effects ($h_{jj'}$). Even though average heterosis was the most important of the three subdivisions of the $h_{jj'}$, specific heterosis ($s_{jj'}$) accounted for 12% of the total sum of squares and was significant at the 5% level. For plant height, 86% of the total sum of squares due to differences among generation means could be attributed to variety effects, and only 14% could be attributed to heterosis effects. As in the case of yield, average heterosis was more important than variety heterosis. Specific heterosis accounted for 8% of the total sum of square and was highly significant.

Similar results were reported by Miranda Filho and Vencovsky (1984) who considered two sets of diallel crosses. In the case of plant height in one set, variety effects and heterosis effects accounted for 86% and 14% of the total sum of squares, respectively, and for yield in the other set, variety effects and heterosis effects accounted for 58% and 42% of the total sum of squares, respectively.

The data suggest that both additive and nonadditive effects are involved in the expression of both traits. However, additive effects were relatively more important than nonadditive effects in determining both traits. Nonadditive genetic effects appeared to be more important in controlling yield than in controlling plant

Table 4. Estimates of variety effects, v_j, from Gardner-Eberhart model (Analysis II) and their ranks for grain yield (kg/ha) in five environments and combined over environments

Population	Lincoln 1981		Mead 1981		Clay Center 1981		Lincoln 1982		Mead 1982		Combined	
	v_j	Rank[a]	v_j	Rank	v_j	Rank	v_j	Rank	v_j	Rank	v_j	Rank
EC	545*	5	411*	5	824*	3	455*	6	1,842*	2	815*	3
NS	139*	8	-207*	8	-797*	11	-821*	11	71	7	-323*	8
NB	58	9	1,043*	2	942*	2	-756*	10	-1,854*	13	-113*	7
307C	902*	3	973*	3	1,357*	1	1,095*	2	365*	4	938*	2
NK	-504*	10	-3	6	-858*	12	-80*	7	-1,385*	12	-566*	11
CM	187*	7	809*	4	90*	7	1,233*	1	332*	5	530*	4
CC	355*	6	-98*	7	809*	4	459*	5	-48	8	296*	6
CB	1,041*	2	-413*	9	214*	6	1,095*	3	535*	3	494*	5
KT	746*	4	-1,229*	12	-304*	8	-182*	9	-746*	10	-343*	9
IE	-1,054*	12	-709*	10	-736*	10	-1,571*	12	283*	6	-757*	12
TA	1,179*	1	1,253*	1	787*	5	1,067*	4	2,120*	1	1,281*	1
NSY	-2,615*	13	-1,741*	13	-1,625*	13	-1,910*	13	-1,122*	11	-1,803*	13
AL	-978*	11	-88*	11	-702*	9	-85*	8	-393*	9	-450*	10
Std. error	32		27		31		36		52		7	

[a] 1 corresponds to the highest estimate of v_j; 13 corresponds to the lowest estimate of v_j

* Significantly different from zero at the 5% level

height. In this study generations × environment interactions were detected for both traits; v_j × environments and $h_{jj'}$ × environments interactions were significant. The $s_{jj'}$ × environments interaction was significant for yield only. The ranks of the v_j effects for grain yield vary among environments (Table 4). TA had the highest estimate of v_j in three environments and in the combined data. EC, 307C, and CM also had high and fairly stable estimates of v_j. NSY had a consistently low estimate. IE ranked 6th at Mead in 1982, but it was consistently lower in the other four environments. NK was variable, but overall it ranked 11th. AL was consistently ranked in the 8th to 11th range and overall ranked 10th. The other five populations had combined v_j values in the intermediate range. NB was most variable with ranks of 9, 2, 2, 10, and 13. In general, completely adapted populations showed higher values of v_j than 50% adapted populations. This indicates that additive gene effects are more important in populations with no introgression of exotic germplasm. The high values of $h_{j'}$ for NB for the five environments (Table 5) indicates that it has excellent general combining ability and its genetic makeup differs from that of the other populations. NK, IE, NS, and KT ranked consistently high. AL, NSY, CM, CB, and EC, derived by combining germplasms, had good heterosis with each other, exhibited low variety heterosis, and did not have good combining ability. The high variety heterosis showed by three adapted populations (NB, NS, and NK) indicate differences in frequencies of dominant alleles between them and the other populations. Only one 50% adapted population, (IE), showed high values of variety heterosis.

In the absence of epistasis, the Gardner-Eberhart model is used to explain heterosis in terms of dominance and the square of the difference in gene frequency between parents. Such a parameter provides an estimate of genetic variability which is an important consideration in choosing germplasm pools to be used in recurrent selection programs.

Estimates of heterosis effects ($h_{jj'}$) for grain yield over five environments were positive for all crosses except for EC × NSY (−49), 307C × CB (−17), TA × AL (−326), and NSY × AL (−248). High values of $h_{jj'}$ were found for NS × NB (2,335 kg/ha), NS × KT (2,134 kg/ha), NB × NK (2,674 kg/ha), NB × CB (2,165 kg/ha), NB × KT (2,402 kg/ha), and NB × IE (2,557 kg/ha).

The 100% adapted population, NB, showed consistently high heterosis effects when combined with all others; its values of $h_{jj'}$ expressed as a percentage of the highest-yielding parent are also consistently high for all crosses (Table 6). The good performance of NB in crosses is due in part to the high variety heterosis shown in combined analyses ($h_j = 1{,}003$ kg/ha).

IE presented fairly high values of $h_{jj'}$ in most of its crosses, but IE does not combine well with TA or with AL. Low values of $h_{jj'}$ expressed as a percentage of the highest-yielding parent were found for IE crossed with TA and AL (8.4 and 13.5, respectively). This is partly due to: (a) the negative specific heterosis found in this population when crossed with TA (−577 kg/ha) and AL (−252 kg/ha) and (b) to the negative heterosis effects of TA (−207 kg/ha) and AL (−409 kg/ha).

TA combined well with three of the adapted (NS, NB and NK) and with only one of the semi-exotic

Table 5. Estimates of variety heterosis, h_j, from Gardner-Eberhart model (Analysis II) and their ranks for grain yield (kg/ha) in five environments and combined over environments

Population	Lincoln 1981		Mead 1981		Clay Center 1981		Lincoln 1982		Mead 1982		Combined	
	h_j	Rank[a]	h_j	Rank	h_j	Rank	h_j	Rank	h_j	Rank	h_j	Rank
EC	-192*	9	31*	5	-313*	9	-114*	7	-825*	13	-282*	10
NS	-4	7	18	6	587*	2	154*	5	475*	3	246*	4
NB	697*	2	700*	1	977*	1	979*	1	1,666*	1	1,003*	1
307C	-437*	11	-89*	9	-355*	11	-578*	12	163*	6	-259*	8
NK	857*	1	-27*	8	552*	3	475*	3	517*	2	475*	2
CM	-141*	8	-432*	13	72*	7	-684*	13	-758*	12	-389*	12
CC	253*	4	-19	7	-1,055*	13	167*	4	-57*	7	-142*	6
CB	-640*	12	195*	4	-329*	10	-132*	8	-445*	9	-270*	9
KT	125*	6	227*	3	203*	4	33*	6	383*	4	194*	5
IE	689*	3	241*	2	82*	6	765*	2	198*	5	395*	3
TA	227*	5	-231*	10	147*	5	-476*	11	-702*	11	-207*	7
NSY	-1,102*	13	-266*	11	-48*	8	-239*	9	-115*	8	-354*	11
AL	-332*	10	-349*	12	-349*	12	-521*	10	-494*	10	-409*	13
Std. error	16		13		15		18		25		4	

[a] 1 corresponds to the highest estimate of h_j, 13 corresponds to the lowest estimate of h_j

* Significantly different from zero at the 5% level

Table 6. Estimates of heterosis effects, $h_{jj'}$, as % of the highest-yielding parent (above diagonal) and specific heterosis, $s_{jj'}$ (below diagonal) for grain yield (kg/ha) of 78 F_1's derived from all possible crosses among parents calculated over 5 environments

	EC	NS	NB	307C	NK	CM	CC	CB	KT	IE	TA	NSY	AL
EC		7.6	2.14	3.2	16.1	5.1	12.8	11.3	19.6	21.8	4.3	0.0	9.5
NS	-449*		41.6	3.5	28.6	13.3	26.3	19.6	39.5	27.8	18.3	5.5	18.7
NB	-197*	106*		28.0	47.7	22.5	36.1	23.1	42.9	45.6	20.4	30.4	25.0
307C	-226*	-732*	145*		18.4	6.2	9.9	0.0	18.1	17.0	8.3	10.8	9.9
NK	-121*	-157*	217*	34*		14.0	19.7	12.4	34.2	33.0	27.4	20.1	21.8
CM	26*	-2	-128*	82*	-189*		10.9	5.2	8.2	17.4	7.0	3.7	4.5
CC	285*	500*	325*	80*	-127*	232*		3.2	4.8	17.8	10.4	8.5	4.6
CB	311*	264*	-283*	-413*	-413*	5	-367*		10.1	21.4	16.4	11.9	4.2
KT	390*	714*	225*	292*	195*	-272*	-740*	-276*		27.0	10.1	14.2	12.4
IE	331*	-120*	179*	17*	-146*	101*	-165*	229*	-116*		8.4	31.0	13.5
TA	-189*	264*	-343*	68*	672*	107*	96*	650	-256*	-577*		8.8	0.0
NSY	-393*	-576*	78*	355*	-71*	-3	31*	382*	-56*	520*	197*		0.0
AL	333*	188*	-169*	351*	106*	97*	-150*	-36*	-110*	-252*	-690*	-464*	
Std. error			6										

* Significantly different from zero at the 5% level

populations (CB). It exhibited a high negative value of $h_{jj'}$ (-326 kg/ha) in its cross with AL.

NSY and AL exhibited low heterosis values in most of their crosses.

The lack of heterosis for some crosses between exotic and adapted materials was anticipated and is in agreement with Efron and Everett (1969), Kramer and Ullstrup (1959), Lonnquist (1974), Chopra (1964), and Crossa (1984). Comparisons among sets of populations with different levels of exotic germplasm showed that adapted Corn Belt populations have higher performance in crosses and greater values of variety heterosis than 50% adapted populations. Comparisons among populations with similar levels of exotic germplasm indicate that several of them, with high mean performance in crosses, were not among those with high variety heterosis; this is the case for EC within the set of adapted populations and for CM and CB in the 50% adapted group. TA has performed well in crosses but shows intermediate values of variety heterosis.

Use of exotic material for maize improvement is promising, but it is essential to examine relationships and heterotic patterns among populations in order to identify and separate heterotic groups for (1) deciding which germplasms will form populations suitable for reciprocal recurrent selection and (2) maximizing heterosis in crosses of lines extracted from those groups.

To form a single high-yielding population for use in a recurrent selection program from the populations evaluated herein, one might choose TA, 307C, NB, and NK. All of them had high mean performance in crosses; the high values of variety effects noted for the first two might allow plant breeders to make considerable gains when selecting superior genotypes. Populations NB and NK performed very well when crossed and either performs well when combined with 307C, and TA.

In forming two populations for reciprocal recurrent selection, one might choose to combine TA, NB, and NS into one population and NK, KT, and 307C in the other. The three 100% adapted populations NB, NS, and NK as well as the 50% adapted population KT have shown good general combining ability and high mean performance in crosses. TA has the second highest mean performance in crosses and does well when crossed with NK showing the highest specific heterosis value (672 kg/ha). Population 307C ranks third in mean cross performance (6,896 kg/ha); it combines particularly well with NB (8,005 kg/ha) with a specific heterosis value of 145 kg/ha.

Our results indicate that several populations, with high mean performance in crosses and derived by compositing germplasms that show considerable heterosis, were not among those with high variety heterosis. In choosing parents for composites to be used in recurrent selection programs (particularly those incorporating exotic germplasm), it is important to examine relationships among populations and their heterotic patterns.

References

Chopra KR (1964) Characterization of genetic variability in an adapted and exotic variety of corn (*Zea mays* L.) and in the cross derived from them. PhD Dissertation, University of Nebraska

Compton WA, Mumm R, Mathema B (1979) Progress from adaptive mass selection in incompletely adapted maize populations. Crop Sci 19: 531–533

Crossa J (1984) Introgression of exotic germplasm for improving maize (*Zea mays* L.) breeding populations. PhD Dissertation, University of Nebraska

Eberhart SA, Gardner CO (1966) A general model for genetic effects. Biometrics 22: 864–881

Efron Y, Everett HL (1969) Evaluation of exotic germplasm for corn hibrids in northern United States. Crop Sci 9: 44–47

Gardner CO (1965) Teoria genetica estadistica aplicable a las medias de variedades, sus cruces y poblaciones afines. Fitotec Latinoam 1:11–22

Gardner CO, Eberhart SA (1966) Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439–452

Gardner CO (1967) Simplified methods for estimating constants and computing sum of squares for diallel cross analysis. Fitotec Latinoam 4:1–12

Gardner CO (1982) Genetic information from the Gardner-Eberhart model for generation means. SOMEFI Saltillo, Coahuila, Mexico

Gardner CO, Schuster ML, Hall DT (1982) Registration of NS(FS)LFW-8 and NB(FS)LFW-8 maize germplasm. Crop Sci 22:451

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9:463–493

Hayman BI (1954a) The analysis of variance of diallel tables. Biometrics 10:235–244

Hayman BI (1954b) The theory and analysis of diallel crosses. Genetics 39:789–809

Hayman BI (1957) Interaction, heterosis and diallel crosses. Genetics 42:336–355

Hayman BI (1958) The theory and analysis of diallel crosses, 2. Genetics 43:63–85

Johnson CW (1974) Estimation of genetic parameters from generation means and their use in prediction of hybrid performance in *Zea mays* L. PhD Dissertation, University of Nebraska

Kramer HH, Ullstrup AJ (1959) Preliminary evaluation of exotic maize germplasm. Agron J 51:687–689

Lonnquist JH (1974) Considerations and experiences with recombination of exotic and Corn Belt maize germplasm. In: 29th Annu Corn Sorghum Res Conf, pp 60–100

Miranda Filho JB, Vencovsky R (1984) Analysis of diallel crosses among open-pollinated varieties of maize. Maydica 29:217–234

Pixley-Sinclair AL (1984) Evaluation of cycles of improvement of an exotic adapted maize (*Zea mays* L.) population. MS Thesis, University of Nebraska

Romero-Franco J (1965) The use of exotic germplasm for the development and improvement of maize hybrids. MS Thesis, University of Nebraska

Shauman WL (1971) Effect of incorporation of exotic germplasm on the genetic variance components of an adapted, open-pollinated corn variety at two plant population densities. PhD Dissertation, University of Nebraska

Subandi L (1972) Estimates of genetic parameters in a exotic population of corn (*Zea mays* L.) grown under different plant population densities. PhD Dissertation, University of Nebraska

West DR, Compton WA, Thomas MA (1980) A comparison of replicated S_1 per se vs. reciprocal full-sib index selection in corn. 1. Indirect response to population densities. Crop Sci 20:35–42