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HETEROSIS AND COMBINING ABILITY OF CIMMYT'S TROPICAL EARLY AND INTERMEDIATE MATURITY MAIZE *(ZEA MAYS* L.) GERMPLASM

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ABSTRACT - A 10 parent diallel was formed to determine combining ability and heterotic patterns among CIMMYT'S tropically adapted, early and intermediate maturity maize *(Zea mays* L.) gene pools and populations. The parents and their crosses were evaluated for yield (t/ha), plant and ear height (cm), and days to silk at five locations in México, and one each in Colombia, Ecuador, India and Thailand. The test for average heterosis, parents vs. crosses, was significant for grain yield, and plant and ear height in the combined analysis of variance. General combining ability (GCA) was significant for all traits. Specific combining ability (SCA) was significant only for ear height. Although yield heterosis over the better parent was low in most crosses, moderate levels were observed in the Population 49 x Population 26 cross (9.6%). Population 26 also combined well with Pool 21 yielding 6.05 t/ha with 7.3% heterosis over the better parent. Pool 22 had the highest GCA effect for yield (0.37 t/ha), and was a parent in three of the five top yielding crosses. High yielding combinations included Pool 22 with Pool 20 (6.33 t/ha), Population 23 (6.24 t/ha), and Population 26 (6.23 t/ha). However, maximum heterosis over the better parent was only 3.2% in these crosses. The only cross with a significant positive SCA effect for yield was Population 23 x Pool 20 yielding 6.13 t/ha with 6.7% heterosis. Heterosis for plant and ear height, and days to silk were generally low. Based on our study, the best choices for initiating hybrid work among white grain materials are Population 23 and Pool 20, and among yellow grain materials Population 26, Pool 21, and Pool 22.

KEY WORDS: *Zea mays* L.; Heterosis; Combining ability.

INTRODUCTION

Since CIMMYT'S initiation, the maize *(Zea mays* L.) improvement program has placed emphasis on the development of open-pollinated products tailored largely to the needs of developing countries. However, over the past decade, some national programs have become interested in hybrid oriented products, opening up a whole range of new possibilities in the use of CIMMYT'S gene pools and populations.

Knowledge about the combining ability and heterotic patterns among CIMMYT'S maize germplasm is essential in order to maximize its use for hybrid development. Currently, limited information is available for CIMMYT'S tropically adapted, early and intermediate maturity gene pools and populations.

JOHNSON and FISCHER (1981) evaluated the performance of various CIMMYT materials in crosses with Tuxpeño Crema-1 P.B. C-17 (currently called Population 49) and ETO Blanco (Population 32), representing two widely known heterotic groups in the tropics. Results for the tropical, early and intermediate maturity materials tested in 3 Mexican environments showed that some of the crosses exhibited high parent heterosis in excess of 10%, however none of these crosses could be used directly in hybrid work because of differences in grain color.

CORTEZ *et al.* (1985) made diallel crosses among several of CIMMYT'S tropically adapted, white grained, intermediate and late maturity pools and populations. In crosses among the intermediate maturity materials, the Pool 20 x Population 49 cross exhibited highly significant heterotic effects. DARRAH *et al.* (1987) top crossed CIMMYT tropical pools and populations with the inbreds B73 and Mo17, representing the major heterotic groups in U.S. maize production. Combined results from four U.S. and two Mexican locations showed no significant differences when comparing crosses of early and intermediate maturity CIMMYT materials to B73 versus the same crosses to Mo17.

The objective of this study was to generate additional information on the combining ability and heterotic patterns of CIMMYT'S tropically adapted, early and intermediate maturity gene pools and populations by using a ten parent diallel including five pools and five populations.

MATERIALS AND METHODS

Five CIMMYT gene pools and five populations were chosen to form the diallel (Table 1). More detailed descriptions of the germplasm makeup and the selection methods used to develop these materials are described in various CIMMYT publications (CIMMYT, 1981, 1982, 1984; VASAL *et al.*, 1982). The pools and populations included most of CIMMYT's tropically adapted materials of early and intermediate maturity. When a given maturity-grain color-grain texture combination was available as both a pool and population, and the materials happened to be genetically similar, only one was chosen for inclusion in the diallel.

The diallel crosses were made at Poza Rica, Mexico in the 1985 winter cycle by planting each parent in six 5 m rows for each combination of crosses. The crosses were made in both directions using bulk pollen from a minimum of 100 plants representing each parent. Bulked seed of each cross and its reciprocal were used in the trials.

The parent and their crosses were evaluated at five locations in México, and one each in Colombia, Ecuador, India, and Thailand. The experimental design was a randomized complete block with three replications per location. The experimental units was two 5 m rows spaced 75 cm apart. Plots were overplanted, then thinned to two plants per hill, with 50 cm between hills for a final plant density of 53,333 plants/ha. Data were recorded for days to silk (number of days from planting to 50% extruded silks), plant height (cm from soil surface to the point where tassel branching begins), ear height (cm from soil surface to the node with the primary ear), grain yield, and percent grain moisture at harvest. Grain yield (t/ha) was calculated at 80% shelling and adjusted to 15.5% moisture for all plots. Data for days to silk, plant height, and yield were obtained from all locations. Ear height data was obtained from all locations except Colombia.

STATISTICAL ANALYSIS

Analysis of variance were conducted for the four plant traits using the plot means. The nine locations were initially analyzed separately (data not shown) and then in a combined analysis of variance. Locations were considered random and genotypes were considered fixed effects. Analysis III of GARDNER and EBERHART (1966) was used to obtain estimates of general (GCA) and specific combining ability (SCA) among crosses, and general and specific effects for each parent and their crosses, respectively. Orthogonal partitioning of the total entry variance by least squares was used to estimate the single df comparison of parents vs. crosses, which is a test of average heterosis.

RESULTS AND DISCUSSION

Entry by environment interactions were significant for grain yield, days to silk, and plant and ear height (Table 2). Partitioning of these interactions revealed that the crosses by environment mean squares were highly significant for all traits except ear height. Further partitioning showed highly significant GCA by environment interactions for each trait. These interactions may not be surprising considering the wide range of environments in which these materials were grown. However, examination of individual GCA effects by location (data not shown) revealed no clear trends. Therefore, further discussion will focus on the combined results.

Combined analysis of variance for grain yield showed highly significant differences for parents, parents vs. crosses, crosses, and GCA (Table 2). The parents vs. crosses comparison represents the average heterosis contributed by the particular set of parents used in the crosses and is attributable to nonadditive genetic effects. However, comparison of variation due to GCA and SCA revealed that 91.5% of the total sums of squares among crosses could be explained by GCA whereas only 8.5% was explained by SCA indicating the relative importance of additive genetic effects to nonadditive genetic effects for this trait.

Mean yield for crosses and parents, and percent heterosis over the best parent are presented in Table 3. Yields of the parents showed large differences ranging from 4.44 t/ha for Pool 18 to 6.13 t/ha for Pool 22. Yields of the crosses ranged from 4.75 t/ha to 6.33 t/ha.

Parents demonstrating highly significant, positive GCA effects for yield included Pool 22 (0.37 t/ha), Population 23 (0.27 t/ha), Population 26 (0.20 t/ha), Population 49 (0.17 t/ha), and Pool 21 (0.17 t/ha) (Table 4). All early maturing parents had highly significant, negative GCA effects for yield.

Best high parent heterosis was manifest in the Population 49 x Population 26 cross. JOHNSON and FISCHER (1981) also found best high parent heterosis with this cross, although the 18% heterosis was higher than the 9.6% heterosis observed in our study. Population 26 also combined well with Pool 21 yielding 6.05 t/ha with 7.3% heterosis over the better parent.

Three of the top five yielding crosses contained Pool 22 as one of the parents. High yielding combinations included Pool 22 with Pool 20 (6.33 t/ha), Population 23 (6.24 t/ha), and Population 26 (6.23 t/ha). However, maximum heterosis over the better parent, Pool 22 (6.13 t/ha), was only 3.2% in these crosses.

Another high yielding cross was Population 23 x

TABLE 1 - *Germplasm description of the ten* CIMMYT *tropical maize gene pools and populations.*

Pool or Population	Population Name	Germplasm description
Population 30	Blanco Cristalino-2	White, semiflint to flint grain, and early maturity. Constituted primarily from Pool 15 and white segregates from Seleccion compuesto precoz.
Population 31	Amarillo Cristalino-2	Yellow, semiflint to flint grain, and early maturity. Consists largely of materials from Seleccion compuesto precoz and Pool 17.
Population 49	Blanco Dentado-2	White, dent grain and intermediate maturity. Derived from the 17th cycle of short plant selection of Tuxpeño Crema-1.
Population 23	Blanco Cristalino-1	White, flint grain and intermediate maturity. Mostly derived from Pool 19 which includes Antigua, Cuban Flints, ETO, Tuxpeño, Suwan-1, Pfister hybrids, and early selections from a Phillipine composite.
Population 26	Mezcla Amarilla	Yellow, semiflint grain, and intermediate maturity. Includes Tuxpeño, Cuban Flints, Antigua, ETO amarillo, and some U.S. Corn Belt germplasm, and families from Pool 21.
Pool 16	Early white dent pool	Based on a large number of early and late white dent materials from Mexico, El Salvador, Guatemala, Nicaragua, Venezuela, Zaire, Indonesia, and the Carribean area.
Pool 18	Early yellow dent pool	Includes yellow dent materials from Mexico, El Salvador, Guatemala, Nicaragua, Venezuela, Zaire, Indonesia, and the Carribean area.
Pool 20	Intermediate white dent pool	Based mainly on materials from the Phillipines, India, and Southeast Asia. A smaller fraction of the germplasm comes from Tuxpeño, ETO, Cuban Flints, Suwan-1, and U.S. Corn Belt materials.
Pool 21	Intermediate yellow flint pool	Includes ETO, Suwan-1, Thai Composite, Cuban Flints, Antigua, and other materials from the Carribean, Central and South America, and India.
Pool 22	Intermediate yellow dent pool	Includes Antigua, ETO, Cuban Flints, Tuxpeño, Suwan-1, Corn Belt materials, and other germplasm from the Carribean, Central and South America, and India.

Pool 20 (6.28 t/ha, with 6.7% high parent heterosis). This was the only cross with a significant, positive SCA effect for yield (data not shown).

Analysis of variance for plant and ear height showed significant differences for parents, parents vs. crosses, crosses and GCA. SCA was significant only for ear height. A comparison of GCA sums of squares to SCA sums of squares revealed a predominance of additive genetic effects for both plant and ear height.

Plant and ear height varied greatly among parents. Plant height ranged from 167 cm in Population 49 to 206 cm in Pool 22 (Table 3). Ear height ranged from 82 cm in Population 49 to 106 cm in Pool 22. Plant height among crosses varied from 184 to 208 cm while ear height varied from 89 to 106 cm.

Populations 31 and 49, and Pools 16 and 18 had significantly negative GCA effects for both plant and ear height, indicating that these parents contributed reduced height in their crosses. The height reductions were accompained by yield reductions in both pools and Population 31, as indicated by their highly significant negative GCA effects for yield. However, Population 49 had a significantly positive GCA effect for yield. Populations 23 and 26, and Pools 21, and 22 showed significant positive GCA effects for both plant and ear height.

In general, heterosis over the higher parent was small for both plant and ear height. Only one cross, Population 23 x Pool 18, had significantly positive SCA effects for plant height (data not shown). Crosses with significant positive SCA effects for ear height included Population 31 x Pool 21, Pool 18 x Population 23, and Pool 18 x Population 26.

Analysis of variance for days to silk showed highly significant differences for parents, crosses, and GCA. SCA and the test for average heterosis, parents vs. crosses, were non significant. These tests, along with a comparison of GCA to SCA sums of squares clearly indicate the predominance of additive genetic effects for day to silk.

Parental means for days to silk ranged from 56 days in Pools 16 and 18 to 63 days for Pool 22. Flowering dates among crosses varied similarily from 56 to 62 days. These values may appear high considering the maturity of the germplasm included in this study. However, the flowering date means were inflated due to an unusually long vegetative growth phase in two Mexican locations (data not shown). Highly significant, negative GCA effects were observed for Populations 30 and 31, and Pools 16 and 18, indicating that these parents contributed earliness in their cros-

TABLE 2 - *Analysis of variance of diallel crosses among tropical early and intermediate maturity gene pools and populations for yield, days to silk, plant height, and ear height evaluated at nine environments in 1985 and 1986.*

Source	df@	Yield (t/ha)	Mean Squares for: Days to Silk (days)	Plant Height (cm)	df	Ear height (cm)
Site	8	407.97**	14,614.71**	184,317.38**	7	44,485.70
Replication/Site	18	4.53	17.38	3,250.67	16	528.13
Entry	54	5.31**	81.23**	1,491.91**	54	727.99**
Parents	9	8.95**	171.81**	3,978.22**	9	1,661.58**
Parents vs Crosses	1	22.71**	0.37	3,760.84**	1	1,670.84*
Crosses (C)	44	4.17**	64.54**	931.78**	44	515.60**
GCA	9	18.66**	298.34**	3,394.43**	9	1,948.28**
SCA	35	0.45	4.42	298.53	35	147.19*
Entry x Site	432	0.47**	3.49**	278.83**	378	110.49*
Parents x Site	72	0.50**	3.82**	302.34*	63	140.51*
Parents vs C x Site	8	0.64	2.72	302.20	7	166.35
Crosses x Site	352	0.46**	3.44**	273.49**	308	103.08
GCA x Site	72	0.78**	5.04**	327.60**	63	168.77**
SCA x Site	280	0.38	3.04	259.57*	245	86.20
Error	972	0.33	2.36	206.21	864	92.54
Mean		5.60	59.56	196.21		98.56
CV%		10.32	2.58	7.32		9.76

@, df for yield, days to silk, and plant height.

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

ses. However, the earliness was accompanied by an undesirable response in grain yield as suggested by the GCA effects for yield. Populations 23, 26, 49, and Pools 20, 21, and 22 showed highly significant, positive GCA effects for days to silk. This response in flowering dates was accompained by a desirable response in grain yield, i.e. all GCA effects for yield were positive and significant for these parents.

High parent heterosis for grain yield among crosses in this study ranged from –11.2% to 9.6%. Heterosis averaged over all crosses was approximately 0%. This value was less than that calculated by HALLAUER and MIRANDA (1981) in their summary of 47 independent reports including 1,394 variety crosses involving 611 parent varieties. For plant and ear height, high parent heterosis averaged –1.4% and –1.8%, respectively. High parent heterosis of –2.4% was observed for days to silk. Although these levels of heterotic response are low, other researchers have reported similar results (BARRIGA and VENCOVSKY, 1973; CASTRO *et al.*, 1968; EL ROUBY and GALAL, 1972; LONNQUIST and GARDNER, 1961; PATERNIANI, 1970, 1977).

The low level of heterotic response for yield among the crosses of CIMMYT pools and populations was not unexpected considering the emphasis in their development on establishing heterosis within each pool or population (VASAL *et al.*, 1982). However, several materials demonstrated reasonable levels of heterosis in crosses and may be good starting materials for initiating hybrid work.

A majority of the superior hybrid combinations occurred between materials of different grain type, i.e. flint x dent and/or yellow x white. CORTEZ *et al.* (1985) found among crosses of CIMMYT tropical, intermediate and late maturity pools and populations with white grain type, that the dent x flint combinations were often superior to the dent x dent and flint x flint crosses.

The Population 49 x Population 26 cross exhibited maximum heterosis in our study. Similar results were obtained by JOHNSON and FISCHER (1981). Population 49 consists largely of Tuxpeño germplasm (Table 1), whereas Population 26 is a mixture of numerous materials such as the Cuban Flints, Carribean Flints, ETO and Tuxpeño. However, these populations would probably not be used directly as opposing populations for hybrid development because of their differing grain colors.

Based on our study, the best choices for initiating hybrid work among CIMMYT tropical, early and intermediate maturity pools and populations with white grain type are Population 23 and Pool 20. Among the materials with yellow grain type, Population 26, Pool 21, and Pool 22 would be the best choices. Some of

TABLE 3 - *Means of ten tropical early and intermediate maturity gene pools and populations and their crosses and high parent heterosis (Het %) for yield, days to silk, plant height and ear height combined over nine environments in 1985 and 1986.*

Pedigree	Yield (t/ha)		Days to Silk (days)		Plant Height (cm)		Ear Height (cm)	
	Mean	Het%	Mean	Het%	Mean	Het%	Mean	Het%
Pop 30 x Pop 31	5.07	–1.7	57	–2.0	193	–1.5	97	–2.1
Pop 30 x Pop 49	5.51	2.1	60	–2.3	192	–2.3	95	–4.4
Pop 30 x Pop 23	5.68	–3.4	60	–1.9	203	–0.6	104	1.5
Pop 30 x Pop 26	5.48	–2.3	59	–3.1	199	–1.9	101	–3.5
Pop 30 x Pool 16	5.17	0.2	58	–1.5	194	–1.1	95	–4.3
Pop 30 x Pool 18	5.02	–2.6	58	–1.6	195	–0.8	96	–3.0
Pop 30 x Pool 20	5.47	–5.0	59	–2.8	199	–1.9	101	–0.2
Pop 30 x Pool 21	5.59	–0.7	59	–2.2	201	2.7	103	3.9
Pop 30 x Pool 22	5.81	–5.2	61	–3.6	206	–0.2	105	–0.3
Pop 31 x Pop 49	5.56	3.0	59	–3.9	187	–1.0	89	–0.3
Pop 31 x Pop 23	5.55	–5.6	59	–2.7	199	–2.7	99	–3.5
Pop 31 x Pop 26	5.46	–2.5	59	–4.1	192	–5.4	100	–4.6
Pop 31 x Pool 16	4.93	4.3	56	–0.8	194	2.4	91	2.3
Pop 31 x Pool 18	5.05	6.7	56	–0.3	184	–2.6	91	2.0
Pop 31 x Pool 20	5.55	–3.6	59	–3.7	196	–3.3	97	–4.6
Pop 31 x Pool 21	5.59	–0.8	59	–3.8	200	4.8	103	4.4
Pop 31 x Pool 22	5.86	–4.4	59	–6.5	200	–3.0	98	-7.4
Pop 49 x Pop 23	5.86	–0.5	61	0.3	195	-4.5	95	-7.3
Pop 49 x Pop 26	6.14	9.6	61	–0.6	194	–4.4	100	–4.7
Pop 49 x Pool 16	5.59	3.6	59	–3.4	186	1.1	93	4.5
Pop 49 x Pool 18	5.48	1.5	59	–3.9	188	1.8	91	2.3
Pop 49 x Pool 20	5.83	1.3	61	0.3	194	–4.3	97	–4.7
Pop 49 x Pool 21	6.13	8.8	61	–0.5	198	3.5	99	0.7
Pop 49 x Pool 22	6.11	–0.3	61	–3.0	195	–5.2	97	–8.2
Pop 23 x Pop 26	6.24	6.0	60	–0.9	199	–2.3	99	–5.8
Pop 23 x Pool 16	5.43	–7.8	59	–3.5	198	–3.0	101	–2.0
Pop 23 x Pool 18	5.70	–3.1	59	–2.8	204	–0.6	103	0.4
Pop 23 x Pool 20	6.28	6.7	61	–0.7	203	–0.7	105	2.7
Pop 23 x Pool 21	6.08	3.3	61	–0.5	203	–0.4	105	1.8
Pop 23 x Pool 22	6.24	1.8	62	–1.6	204	–0.8	101	–4.7
Pop 26 x Pool 16	5.64	0.6	58	–4.5	196	–3.4	98	–6.5
Pop 26 x Pool 18	5.39	–3.9	58	–4.2	198	–2.1	103	–2.1
Pop 26 x Pool 20	5.89	2.3	61	0.1	204	0.3	103	–2.1
Pop 26 x Pool 21	6.05	7.3	62	0.8	204	0.8	102	–2.4
Pop 26 x Pool 22	6.23	1.6	62	–1.7	208	1.2	106	0.7
Pool 16 x Pool 18	4.75	2.7	57	0.5	185	0.4	89	–0.6
Pool 16 x Pool 20	5.21	–9.4	59	–3.9	188	–7.1	93	–8.1
Pool 16 x Pool 21	5.55	–1.5	59	–2.9	195	1.9	98	–0.8
Pool 16 x Pool 22	5.70	–7.0	59	–7.5	201	–2.4	101	–4.4
Pool 18 x Pool 20	5.55	–3.6	59	–2.9	200	–1.4	101	–1.0
Pool 18 x Pool 21	5.23	–7.2	59	–3.2	190	–0.5	97	–1.7
Pool 18 x Pool 22	5.44	–11.2	61	–4.1	194	–5.9	102	–3.3
Pool 20 x Pool 21	5.89	2.3	61	–0.4	201	–1.0	105	2.9
Pool 20 x Pool 22	6.33	3.2	61	–3.0	204	–0.9	103	–2.6
Pool 21 x Pool 22	6.13	0.0	62	–1.8	199	–3.4	105	–0.5
Pop 30	5.15	–	58	–	196	–	100	–
Pop 31	4.73	–	56	–	189	–	89	–
Pop 49	5.40	–	61	–	167	–	82	–
Pop 23	5.86	–	61	–	204	–	103	–
Pop 26	5.60	–	61	–	203	–	105	–

TABLE 3 - Continued

Pedigree	Yield (t/ha)		Days to Silk (days)		Plant Height (cm)		Ear Height (cm)	
	Mean	Het%	Mean	Het%	Mean	Het%	Mean	Het%
Pool 16	4.63	–	56	–	184	–	89	–
Pool 18	4.44	–	56	–	184	–	89	–
Pool 20	5.76	–	61	–	203	–	102	–
Pool 21	5.63	–	61	–	191	–	99	–
Pool 22	6.13	–	63	–	206	–	106	–
LSD (0.05)	0.37		1		9		6	

TABLE 4 - *Estimates of general combining ability effects among tropical early and intermediate maturity gene pools and populations for yield, days to silk, plant height, and ear height combined over nine environments in 1985 and 1986.*

Parents	Yield (t/ha)	Days to Silk (days)	Plant Ht (cm)	Ear Ht (cm)
Population 30	–0.26**	–0.63**	1.17	0.98
Population 31	–0.28**	–1.64**	–3.48**	–3.29**
Population 49	0.17**	0.70**	–5.43**	–4.45**
Population 23	0.27**	0.82**	4.34**	2.48**
Population 26	0.20**	0.57**	2.68*	2.54**
Pool 16	–0.36**	–1.64**	–4.41**	–4.16**
Pool 18	–0.41**	–1.25**	–4.32**	–2.33*
Pool 20	0.14*	0.75**	2.01	1.64
Pool 21	0.17**	0.75**	2.57*	3.17**
Pool 22	0.37**	1.57**	4.87**	3.41**

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

the suggested white and yellow materials have good possibilities for use in cross combination with national program materials (MIRANDA and VENCOVSKY, 1984; NASPOLINI *et al.*, 1981).

In light of the good performing intrapopulation hybrids developed from Suwan-1 (CHUTKAEW *et al.*, 1985), and Iowa Stiff Stalk Synthetic (HALLAUER and MIRANDA, 1981), and due to the way the CIMMYT materials in our study were developed and improved, consideration should also be given to the development of hybrids from lines derived from the same pool or population. HAN *et al.* (1990) identified several high-yielding intrapopulation hybrids consisting or S_3 lines derived from CIMMYT pools and populations, although in general, the interpopulation hybrids showed superior performance.

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