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HETEROSIS AND COMBINING ABILITY OF CIMMYT'S TROPICAL LATE WHITE MAIZE GERMPLASM

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ABSTRACT - Seven tropically adapted, late maturity maize gene pools and populations (Populations 21, 22, 25, 29, 32 and 43, and Pool 24) developed and improved at CIMMYT were crossed in a 7 x 7 diallel mating system. The parent and 21 crosses were evaluated for grain yield, days to silk and plant height at five locations in México, and one each in Colombia and Thailand. The objectives of the study were to determine the heterosis and combining ability among these materials and to identify appropriate germplasm suitable for hybrid development work. The combined analysis of variance for all three traits measured showed no significant genotype x environment (G x E) interaction. Genotypes themselves showed significant differences for all three traits, as did their partitions into parents and crosses. General combining ability (GCA) was significant for all traits whereas specific combining ability (SCA) was not significant for any of the traits. Mean grain yield for the trial was 6.98 t/ha. The highest yielding combination was Population 21 x Population 43 (7.83 t/ha) followed by crosses of Population 22 with Population 32 and 43 (7.55 t/ha). Population 29 x Population 32 (dent x flint) yielded 7.36 t/ha while exhibiting the maximum high-parent heterosis (12.7%) for yield. Population 43 (La Posta) was the tallest and latest parent and produced high yields in crosses with other populations. All crosses to Population 43 were shorter and earlier than Population 43 per se. Population 21 (0.24 t/ha), Population 22 (0.15 t/ha) and Population 43 (0.23 t/ha) possessed significant positive GCA for yield. Populations 21 and 43 also showed significant positive GCA for days to silk while only Population 43 showed positive GCA for plant height. Significant ($P \leq 0.05$) positive SCA effects for yield were observed in two crosses involving Population 32 with Population 22 and 29 (flint x dent). Based on our study the best choices for initiating hybrid work are Populations 21, 22, 29 and 43. Many of the Tuxpeño based populations are ideal candidates for interpopulation improvement using Population 32 (ETO Blanco) as heterotic partner.

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

INTRODUCTION

Since its inception, CIMMYT's maize program has emphasized population improvement and cultivar development as a way to meet the needs of resource-poor farmers in the developing world. A large number of maize gene pools and populations were thus developed and have been widely used by national programs. It is estimated that more than 225 open-pollinated cultivars and hybrids released in developing countries contain CIMMYT germplasm, and are grown on more than 6 million ha (PANDEY *et al.*, 1991). However, during the past decade there has been an increasing interest in using hybrid oriented germplasm by national programs and private seed companies in the developing world, which led to the development of CIMMYT's hybrid maize sub-program in 1985.

Combining ability studies involving some of CIMMYT's maize gene pools, populations and experimental varieties have been reported (CORTEZ *et al.*, 1981; NASPOLINI FILHO *et al.*, 1981; MIRANDA FILHO and VENCOVSKY, 1984; OYERVIDES-GARCIA *et al.*, 1985). JOHNSON and FISCHER (1981) evaluated the performance of various CIMMYT materials in crosses with Tuxpeño Crema-1 P.B. C-17 (Population 49) and ETO Blanco (Population 32) wherein some of the crosses exhibited high-parent heterosis in excess of 10%.

Determining the heterotic behavior and combining ability patterns among CIMMYT's maize germplasm is essential for its utilization in hybrid research. For this purpose all of CIMMYT's maize germplasm were grouped according to adaptation, grain color, and maturity. Information on the combining ability of germplasm within each group was obtained through multilocation testing of the diallel crosses during 1985-86 and salient features were summarized (VASAL *et al.*, 1986; US-CIMMYT combining ability workshop, 1987). Results from the tropical early and

TABLE 1 - *Description of seven CIMMYT tropical late maize germplasm used in this study.*

Population/ Pool Number	Population/ Pool Name	Germplasm description
Population 21	Tuxpeño-1	Made up of seven Tuxpeño race collections plus some families from Pool 24. White dent grain type, excellent standability. Improved for shorter plant height. Selection Cycle 5.
Population 22	Mezcla Tropical Blanc	Broad genetic base including Tuxpeño, ETO Blanco, Antigua and Central American germplasm. White dent-semident grain type. Improved for downy mildew resistance in Thailand and the Philippines. Selection Cycle 6.
Population 25	Blanco-Cristalino-3	Derived from tropical late white flint Pool 23. Composed of white flint selections from crosses among materials from México, Colombia, the Caribbean, Central America, India, Thailand and the Philippines. White flint grain type. Currently being improved for husk cover and resistance to ear and stalk rots. Selection Cycle 0.
Population 29	Tuxpeño Caribe	Broad genetic base that includes Tuxpeño, Cuban flints and ETO. White dent grain type. Being improved for reduced plant height, stalk and root lodging, and husk cover. Selection Cycle 5.
Population 32	ETO Blanco	Developed in Colombia and includes germplasm from South America, Cuba, México, and U.S. corn belt. White flint grain type. Improved for shorter plant type at CIMMYT. Selection Cycle 5.
Population 43	La Posta	Tuxpeño synthetic composed of 16 S1 lines. White dent grain type. Improved for resistance to streak virus in Nigeria. Selection Cycle 5.
Pool 24	Tropical Late White Dent	Mainly based on Tuxpeño germplasm but also includes some materials from Central America, Caribbean and Zaire. White dent grain type. Tolerant to ear and stalk rots and is being selected for resistance to fall armyworm. Selection Cycle 21.

intermediate maturity germplasm showed that Population 23 and Pool 20 among white grain materials and Population 26 and Pool 22 among yellow grain materials were the best general combiners for yield (BECK *et al.*, 1990). Among tropical late maturity yellow germplasm, Population 24 and 36 were found to be good general combiners and also showed high specific heterosis (CROSSA *et al.*, 1990). Results from subtropical and temperate intermediate maturity germplasm evaluated in various environments in Mexico and the USA showed positive GCA effects for yield for Populations 34, 42 and 47 in the Mexican environments and Pool 41 in the U.S. environments (BECK *et al.*, 1991). Among CIMMYT's subtropical and temperate early maturity germplasm Population 48 and Pool 30 were identified as the best general combiners for yield (VASAL *et al.*, 1986).

HAN *et al.* (1991) evaluated the combining ability of 58 S3 lines from 11 CIMMYT populations and pools grouped into six diallel sets. The results showed that lines derived from Population 21 combined well with lines from Population 32 and Pool 23. Many superior intrapopulation interline crosses were also identified. Breeding strategies in hybrid development should consider the use of both inter- and intrapopulation interline crosses to exploit the broad genetic variability found in CIMMYT germplasm (VASAL and SRINIVASAN, 1991).

The objectives of the study were to determine the combining ability and heterotic patterns among CIMMYT's tropically adapted, late maturity germplasm with white grain type, and to identify appropriate germplasm for use in hybrid development programs.

MATERIALS AND METHODS

Six maize populations and one gene pool developed by CIMMYT and possessing tropical adaptation, late maturity, and white grain color were chosen to form the diallel. Detailed description of the germplasm is presented in Table 1. Further information on germplasm makeup and selection methods used to develop these materials can be found in various CIMMYT publications (CIMMYT, 1981, 1982, 1984; VASAL *et al.*, 1982; PANDEY *et al.*, 1986).

The seven parents were crossed in a diallel fashion at Poza Rica, México, in the 1985 winter cycle. Seeds from the latest cycles of selection available at the time of the study were planted in six paired rows of 5-m length for each cross combination. All possible 21 crosses were made in both directions using bulk pollen of each parent. Seeds from each cross and its reciprocal were bulked to represent a particular cross. Seed increase of parents was done simultaneously by sibbing.

The parents and their crosses, totaling 28 entries, were plant-

TABLE 2 - *Analyses of variance of diallel crosses among seven CIMMYT tropical late white maize germplasm for yield, days to silk, and plant height evaluated at seven locations during 1985 and 1986.*

Source	df	Mean squares		
		Yield (t/ha)	Time to Silk (days)	Plant height (cm)
Environment (E)	6	338.73**	7056.3**	120493.0**
Replication/E	14	3.07	23.9	289.3
Genotype	27	3.67**	27.2**	1021.1**
Parents	6	3.56**	39.6**	2151.0**
Parents vs. Crosses	1	33.56**	29.0	529.0
Crosses (C)	20	2.21**	23.3**	706.7**
GCA	6	4.90**	65.8**	1843.5**
SCA	14	1.06	5.2	219.5
Genotype x E	162	0.67	6.9	245.5
Parents x E	36	0.84	3.6	227.2
Parents vs C x E	6	0.73	6.2	427.2
Crosses x E	120	0.62	7.9*	241.8
GCA x E	36	0.64	8.2*	382.1**
SCA x E	84	0.62	7.8*	181.7
Error	378	0.65	5.7	211.2
Mean		6.98	68.1	217.3
CV%		11.56	3.5	6.7

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

ed at seven locations (Tlaltizapán, Poza Rica, Silao, Tlacomulco and Cd. Obregón in México, Palmira in Colombia and Nakornsawan in Thailand) during 1985-86. The experimental design was a randomized complete block with three replications at each location. The experimental unit consisted of two 5 m rows spaced 75 cm. Plots were overplanted and thinned to two plants per hill, with 50 cm between hills for a final plant density of approximately 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 weight (kg), and percent grain moisture at harvest. Grain yield (t/ha) was calculated using ear weight at harvest assuming 80% shelling and adjusted to 15.5% moisture.

Statistical Analysis

Analyses of variance was conducted for grain yield, days to silk, and plant height using plot data for each location separately (data not shown) and then in a combined analysis of variance. Environments were considered random and genotypes as fixed effects. Analysis III of GARDNER and EBERHART (1966) was used to obtain estimates of GCA and SCA for parents and their crosses.

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. Variation among crosses was further subdivided into that due to GCA and SCA. The GARDNER and EBERHART (1966) model for the combining ability analysis is as follows:

$$x_{ijk} = u + g_i + g_j + s_{ij} + e_{ijk}$$

where x_{ijk} is the performance of the cross between the ith and jth genotypes in the kth replication, u is the overall mean, $\hat{g}_i$ and $\hat{g}_j$ are GCA effects for the ith and jth parents respectively, s_{ij} is the SCA effect for the cross between the ith and jth genotypes, and the e_{ijk} is the error effect associated with the ijkth observation. This model is similar to the one adopted by LONNQUIST and GARDNER (1961) to calculate combining ability estimates in intervarietal crosses in maize. GARDNER and EBERHART'S Analysis III is considered superior to GRIFFING'S (1956) model 1, method 2 analysis especially when the parents are open pollinated varieties or populations (GARDNER and EBERHART, 1966; SINGH, 1978).

The F-tests for the ANOVA were calculated as follows. Main effects such as entries and its partitions, were tested against their respective interactions with environment and all the remaining interaction terms were tested against the pooled error. For example, mean squares for GCA was tested against the mean squares for GCA X environments and that for SCA against SCA X environments and so on. Percent heterosis for grain yield was calculated over the better parent values. The better parent used in calculating heterosis for days to silking was the later parent and for plant height the taller parent.

RESULTS AND DISCUSSION

Highly significant (P ≤ 0.01) differences were observed among genotype means and among parents and crosses in the combined analysis of variance for all three characters (Table 2). The parents vs crosses comparison, which is a measure of average heterosis and attributable to non-additive genetic effects, was significant only for grain yield. Partitioning of the variance due to crosses revealed highly significant differences for GCA and nonsignificant differences for SCA for all three traits. Similar results were obtained with CIMMYT's tropical early and intermediate materials (BECK *et al.*, 1990). However, in tropical late yellow materials, GCA and SCA effects were both found to be highly significant (CROSSA *et al.*, 1990).

The relative contribution of GCA and SCA to the total sums of squares revealed that for grain yield GCA accounted for 67% of the variation among crosses and SCA accounted for 33%. For days to silk and plant height, however, sums of squares for GCA accounted for a larger share (85% and 78%, respectively) of the variation among crosses. This suggests that although additive genetic effects were more important than non-additive genetic effects in determining all three characters, it was more pronounced for days to silk and plant height. This was similar to our observations in tropical late yellow and tropical early and intermediate germplasm, although in the case of the latter additive gene effects were more important in determining grain yield with the GCA sum of squares accounting for 91.5% of the total sums of squares (CROSSA *et al.*, 1990; BECK *et al.*, 1990).

Combined analyses of variance did not reveal any significant genotype x environment (G x E) interactions for grain yield, days to silk, and plant height (Table 2). Further partitioning of G x E mean squares showed a significant ($P \leq 0.05$) crosses x environment interaction for days to silk. GCA and SCA interactions with environment also were significant for days to silk. For plant height, GCA x environment variance was the only significant interaction.

Even though the materials were evaluated in a wide range of environments, the nonsignificant G x E interaction for grain yield suggests that the genotypes tested possessed broad adaptability and good stability. Tropical late white germplasm continues to receive high priority in CIMMYT's research efforts due to the large area under cultivation in developing countries. Most of the germplasm used in this study has undergone population improvement at CIMMYT using international testing which could have contributed to the broad adaptability of these materials over various environments. Similar results were reported by PANDEY *et al.* (1986, 1987) based on cycles of selection studies conducted on eight late and four intermediate maturity tropical maize populations developed by CIMMYT. The populations studied possess a fairly high level of genetic heterogeneity. Therefore, due to population buffering, smaller G x E interactions are expected for populations that are mixtures of genotypes (SPRAGUE and EBERHART, 1977; WRIGHT *et al.*, 1971).

On the other hand, our results with both tropical late yellow and tropical early and intermediate germplasm evaluated under very similar environments revealed highly significant G x E interactions for grain yield, days to silk and plant height (CROSSA *et al.*, 1990; BECK *et al.*, 1990). Based on a more comprehensive review of CIMMYT's international testing trials, GARDNER *et al.* (1990) suggested that there is no evidence that CIMMYT's populations selected over a broad spectrum of environments have become more stable. Any apparent increase in stability observed in these materials seems to be because of elimination of deleterious genes, shorter plant height, and increases in favorable genes controlling disease and insect pests than from an increase in frequency of genes contributing directly to yield in the absence of these stresses.

Means of crosses and parents and the percent heterosis over the better parent combined across all environments are presented in Table 3 for grain yield, days to silk, and plant height. Yields of the parents ranged from 7.12 t/ha for Population 22 to 5.96 t/ha for Population 32. Yields of the crosses ranged from 7.83 t/ha (Population 21 x Population 43) to 6.56 t/ha (Population 32 x Pool 24). Maximum better parent heterosis for yield was observed in the Population 29 x Population 32 cross (12.7%) although it was not the top-yielding cross. Two other crosses showing moderate heterosis for yield were Population 21 crossed with Population 25 and Population 43. Over 85% of the crosses showed favorable heterosis for yield. Only three crosses showed marginally negative heterosis, and the crosses had either Population 22 or Population 43 as one of their parents, both of which were high yielders per-se. This contrasts with our experience with tropical early and intermediate materials where the maximum heterosis obtained was 9.6% and 25 out of 45 crosses showed neutral or negative heterosis (BECK *et al.*, 1990). With tropical late yellow germplasm, however, heterosis in excess of 10% was observed for grain yield in six out of 21 crosses tested. Most crosses involving CIMMYT germplasm with Suwan-1 exhibited a high level of heterosis (CROSSA *et al.*, 1990). Similar levels of heterosis for yield in maize have been reported by other researchers. HALLAUER and MIRANDA (1981) summarized 47 independent reports and found the mean high parent heterosis for yield to be 8.2% from 1394 variety crosses involving 611 parental varieties.

TABLE 3 - *Means of seven CIMMYT tropical late white maize germplasm and their crosses and high parent heterosis (Het %) for yield, days to silk and plant height combined across seven environments during 1985 and 1986.*

Pedigree	Yield (t/ha)		Time to silk (days)		Plant Height (cm)	
	Mean	Het%	Mean	Het%	Mean	Het%
Pop. 21 x Pop. 22	7.34	3.1	68.2	−2.3	219.6	0.8
Pop. 21 x Pop. 25	7.40	11.1	67.7	−3.0	216.7	−0.6
Pop. 21 x Pop. 29	6.98	4.8	69.4	−0.6	210.8	−3.3
Pop. 21 x Pop. 32	7.15	7.4	68.8	−1.4	223.8	2.7
Pop. 21 x Pop. 43	7.83	10.9	68.9	−2.1	226.8	−3.4
Pop. 21 x Pool 24	7.22	8.4	69.4	−0.6	224.9	3.2
Pop. 22 x Pop. 25	6.92	−2.8	66.3	−1.6	208.3	−2.2
Pop. 22 x Pop. 29	7.21	1.3	66.4	−2.8	212.1	−0.4
Pop. 22 x Pop. 32	7.55	6.0	67.1	−2.9	216.3	−0.4
Pop. 22 x Pop. 43	7.55	6.0	67.1	−4.7	216.7	−7.7
Pop. 22 x Pool 24	6.90	−3.1	67.3	−1.0	217.2	0.1
Pop. 25 x Pop. 29	6.78	4.1	66.5	−2.6	215.1	4.5
Pop. 25 x Pop. 32	6.68	5.9	66.9	−3.2	213.0	−1.9
Pop. 25 x Pop. 43	7.07	0.3	67.9	−3.6	220.8	−6.0
Pop. 25 x Pool 24	6.80	6.9	67.9	−0.1	216.6	−0.2
Pop. 29 x Pop. 32	7.34	12.7	68.0	−1.6	211.2	−2.7
Pop. 29 x Pop. 43	7.06	0.1	69.2	−1.7	216.9	−7.7
Pop. 29 x Pool 24	6.78	4.1	68.0	−0.4	213.9	−1.4
Pop. 32 x Pop. 43	7.40	5.0	68.9	−2.1	229.6	−2.3
Pop. 32 x Pool 24	6.56	3.1	67.8	−1.9	218.5	0.6
Pop. 43 x Pool 24	6.98	−1.0	69.8	−0.9	227.1	−3.3
Pop. 21	6.66	–	69.8	–	217.9	–
Pop. 22	7.12	–	67.4	–	212.9	–
Pop. 25	6.31	–	66.4	–	205.9	–
Pop. 29	6.51	–	68.3	–	204.1	–
Pop. 32	5.96	–	69.1	–	217.1	–
Pop. 43	7.05	–	70.4	–	234.9	–
Pool 24	6.36	–	68.0	–	217.0	–
LSD (0.05)	0.49		1.4		8.8	

Days to silking among parents ranged from 70.4 in Population 43 to 66.4 in Population 25 (Table 3). All the crosses flowered earlier than their later parent. Earliness relative to the parents was more pronounced in crosses involving Population 43 (the latest parent). Population 43 also was the tallest while Population 29 was the shortest parent. Fifteen of 21 crosses recorded negative heterosis for plant height over the taller parent. As with days to silk, crosses involving Population 43 showed a greater magnitude of negative heterosis for plant height. Both for plant height and days to silking, negative heterosis (as calculated in this study) is a desirable attribute for tropical materials.

Estimates of general combining ability effects for yield, days to silk and plant height are presented in Table 4. Population 21 (0.24 t/ha), Population 22 (0.15 t/ha), and Population 43 (0.23 t/ha) recorded significant positive GCA effects for grain yield, while Population 25 (−0.21 t/ha) and Pool 24 (−0.30 t/ha) highly significant negative GCA effects. Although days to silking and yield followed similar trends in GCA there were a few exceptions. Population 22 which had a highly significant negative GCA for days to silk (−1.09 days) showed significant positive GCA for grain yield (0.15 t/ha) which is more desirable. The only parent showing significant negative GCA for plant height was Population 29 (−5.48 cm).

Estimates of specific combining ability effects for the 21 crosses tested based on grain yield data combined over the seven environments are presented in Table 5. Population 32 x Population 22 (0.28 t/ha) and Population 32 x Population 29 (0.34 t/ha) showed the highest SCA effects for grain yield. Crosses involving Population 21 with Population 25 and

TABLE 4 - *Estimates of general combining ability effects among seven CIMMYT tropical late white germplasm for yield, days to silk and plant height combined across seven environments during 1985 and 1986.*

Parents	Yield (t/ha)	Time to silk (days)	Plant Height (cm)
Pop. 21	0.24**	0.92**	3.03
Pop. 22	0.15*	−1.09**	−3.44
Pop. 25	−0.21**	−0.95**	−3.38
Pop. 29	−0.11	−0.05	−5.48**
Pop. 32	−0.01	−0.08	1.01
Pop. 43	0.23**	0.78**	6.10**
Pool 24	−0.30**	0.46	2.15

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

TABLE 5 - *Estimates of specific combining ability effects among crosses involving seven CIMMYT tropical late white germplasm for yield (t/ha) combined over seven environments during 1985 and 1986.*

Parents	Pop. 22	Pop. 25	Pop. 29	Pop. 32	Pop. 43	Pool 24
Pop. 21	−0.17	0.25	−0.26	−0.20	0.23	0.15
Pop. 22		−0.14	0.05	0.28	0.05	−0.07
Pop. 25			−0.01	−0.22	−0.07	0.19
Pop. 29				0.34	−0.18	0.07
Pop. 32					0.05	−0.25
Pop. 43						−0.08

43 also showed positive SCA for yield eventhough statistically nonsignificant. Population 21 x Population 43, had a relatively lower SCA for yield (0.23 t/ha) although it was the highest yielding cross (7.83 t/ha). Of the four crosses that showed positive SCA for yield greater than 0.2 t/ha, three were dent x flint crosses while Population 21 x Population 43 was a dent x dent combination. CORTEZ *et al.* (1981) found that among CIMMYT's tropical, intermediate, and late maturity pools and populations with white grain type, the dent x flint combinations were often superior to the dent x dent and flint x flint crosses.

JOHNSON and FISHER (1981) obtained similar results in their testcross studies of CIMMYT's tropical late maturity germplasm with testers from ETO Blanco (Population 32) and Tuxpeño C17 (Population 49). In their study, crosses of Population 43 with Population 32 gave the highest yields (6.5 t/ha) with high parent heterosis of 10%. In the current study we observed high yields (7.4 t/ha) with Population 43 x Population 32 cross although the heterosis observed was rather low (5%). Population 29 x Population 32, which was not very promising in their study, showed the highest SCA effect for yield in our study. Combining ability studies involving lines derived from some of these populations confirm the heterotic patterns observed at the population level (HAN *et al.*, 1991).

Results from this study have provided valuable information on the heterotic patterns and combining abilities of the seven populations and pools evaluated. The yield levels obtained for the crosses were reasonably high (6.6-7.8 t/ha) compared with the parents (6.0-7.1 t/ha). The more than 10% heterosis in three crosses suggest their suitability for further improvement in hybrid development. Two Tuxpeño based populations (Population 21 and 43) were not only the best general combiners for yield but also produced the highest yielding cross between them. Population 32 and 25, both flint parents, produced some of the highest yielding crosses with the dent parents. Population 43, which was tall and late, also contributed to high yield in its crosses with all the other parents except Pool 24. Population 32 crossed well with Population 22 and Population 29, both of which include Tuxpeño germplasm, confirming the widely known heterotic pattern existing between ETO and Tuxpeño material (WELLHAUSEN, 1978). Interpopulation improvement scheme could be applied to many of the Tuxpeño based populations in combination with ETO based germplasms.

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