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Heterosis and Combining Ability of CIMMYT's Subtropical and Temperate Early-Maturity Maize Germplasm

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ABSTRACT

Knowledge about the combining ability and heterotic patterns among CIMMYT's maize (*Zea mays* L.) germplasm is essential for hybrid development work at CIMMYT, as well as at other national research programs using CIMMYT germplasm. This study was conducted to determine the heterosis and combining ability among CIMMYT's subtropical and temperate early-maturity maize germplasm. A seven-parent diallel involving two populations and five gene pools was made. The parents and 21 crosses were evaluated in 17 temperate and 5 subtropical environments during 1985–1986. Average yield across temperate environments (4.35 Mg ha^{-1}) was comparable to that obtained in subtropical environments (4.59 Mg ha^{-1}). Highest yield in subtropical environments was recorded by Population 48 × Pool 27 (5.42 Mg ha^{-1}), with a high-parent heterosis of 9.9%. Maximum high-parent heterosis was observed in Population 46 × Pool 30 (13%), which yielded 5.17 Mg ha^{-1}. Under temperate environments, the highest-yielding combinations included Population 48 crossed with Population 46 and Pools 27, 28, and 30, although maximum heterosis (10.2%) was recorded for Pool 27 × Pool 40. General combining ability (GCA) effects for yield were significant in both sets of environments, while specific combining ability (SCA) effects were significant only in temperate environments. Highly significant positive GCA effects for yield were observed with Population 48 (0.43 Mg ha^{-1}) and Pool 30 (0.33 Mg ha^{-1}) under temperate conditions. Pools 40 and 42 were poor general combiners in both sets of environments. Significant positive SCA effects for yield were observed with Population 46 × Population 48 and Population 46 × Pool 30 crosses in temperate environments and the Population 48 × Pool 27 cross under subtropical environments. Population 48 and Pool 30 may hold potential for use as source germplasm for both temperate and subtropical maize breeding programs.

During the past 25 yr, CIMMYT's maize improvement program has developed an array of maize germplasm to meet the needs of farmers in developing countries. CIMMYT's maize germplasm has contributed to the release of >225 open-pollinated cultivars and hybrids by national programs and is estimated to be cultivated on >6 million ha in developing countries (Pandey et al., 1991). In recent years, several national programs and private seed companies in developing countries have shown an increased interest in hybrid-oriented products, which led to the creation of CIMMYT's hybrid maize program in 1985. The immediate task that faced the hybrid program was to gain information on the combining ability and heterotic patterns of the various gene pools and populations developed and improved over the years at CIMMYT.

Information on heterosis and combining ability of CIMMYT maize germplasm is limited and incomplete. Naspolini et al. (1981) conducted a diallel study using several of CIMMYT's tropical and subtropical pools and populations and found that Populations 42 and 33 had the highest GCA effects for grain yield. In a related study involving crosses of various CIMMYT materials with Tuxpeño Crema-1 P.B. C-17 (currently called Population 49) and ETO Blanco (Population 32), Johnson and Fisher (1981) identified a few crosses that exhibited high-parent heterosis >10%. Cortez et al. (1981), from a diallel study using CIMMYT's tropical germplasm, reported that Pool 20 × Population 49 cross exhibited highly significant heterosis for yield. Darrah et al. (1987) tested CIMMYT's tropical and subtropical pools and populations crossed to the two Corn-Belt inbreds B73 and Mo17. Their results, combined across four U.S. and two Mexican locations, revealed no significant differences between crosses to B73 and Mo17.

A more complete and systematic approach was followed by CIMMYT's hybrid program, soon after its initiation in 1985, to characterize all existing CIMMYT gene pools and populations for combining ability. A summary of the findings was reported by Vasal et al. (1986) and also discussed in the US–CIMMYT Combining Ability Workshop (1987). Results from these studies on the combining ability of tropical early- and intermediate-maturity maize germplasm were reported by Beck et al. (1990) and for tropical late-maturity yellow maize germplasm by Crossa et al. (1990). Combining ability among CIMMYT's subtropical and temperate intermediate-maturity germplasm based on trials conducted at 5 locations in Mexico and 11 in the USA has been reported by Beck et al. (1991). They observed highly significant, positive GCA effects for yield for Populations 42, 47, and 34 in Mexico and for Pool 41 in the USA. Although CIMMYT materials did not generally perform well in temperate environments, Pool 41 and Population 42 were identified as showing potential as exotic germplasm sources for temperate breeding programs.

The utility of CIMMYT's germplasm for hybrid development was demonstrated by Han et al. (1991), who identified several high-yielding hybrids from crosses involving S_3 lines derived from CIMMYT pools and populations. Many superior intrapopulation hybrids were identified in their study, in addition to interpopulation hybrids. CIMMYT's hybrid program has thus considered developing both inter- and intrapopulation hybrids, using inbred lines, in order to exploit the broad genetic variability available in its maize germplasm (Vasal and Srinivasan, 1991).

Our objectives were to (i) determine the heterotic patterns and combining ability among CIMMYT's subtropical and temperate early-maturity pools and populations and (ii) identify suitable germplasm for hybrid development work at CIMMYT and other breeding programs for subtropical areas. Because these germplasms may be of use and interest for maize breeders in temperate regions, they were evaluated

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Abbreviations: G × E, genotype × environment; GCA, general combining ability; SCA, specific combining ability; Pop., population.

Temperate environments

1. L'Assomption, Quebec
2. Brookings, SD
3. Arlington, WI
4. Ames, IA (2 locations)
5. Bloomington, IL
6. Champaign, IL (3 locations)
7. W. Lafayette, IN
8. Oxford, IN
9. University Park, PA
10. Rossville, KS
11. N. Lexington, KY
12. Raleigh, NC
13. Mississippi State, MS
14. Rock Springs, TX

Subtropical environments

15. Cd. Obregón, Mexico
16. Tlacamulco, Mexico
17. Silao, Mexico
18. Tlaltizapán, Mexico
19. Antalya, Turkey (not shown)

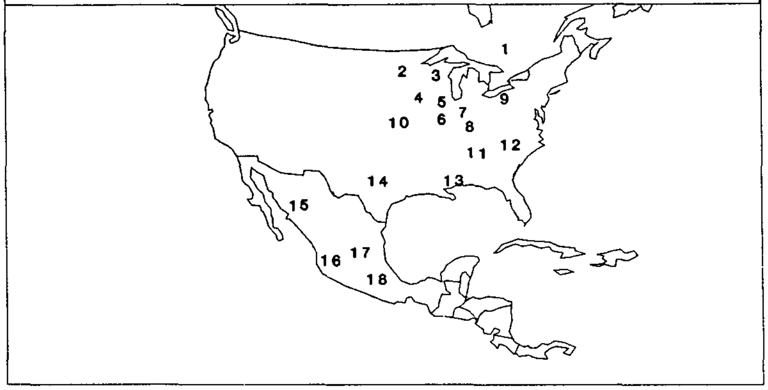

Fig. 1. Distribution of 17 temperate and 5 subtropical environments where CIMMYT's subtropical and temperate early-maturity germplasm was evaluated in 1985–1986.

extensively in temperate environments to identify useful exotic source germplasm.

MATERIALS AND METHODS

Two CIMMYT populations and five gene pools were chosen to form the diallel. Detailed descriptions of the germplasm are presented in Table 1. The populations and pools were of subtropical-to-temperate adaptation, with early maturity. A complete description of the germplasm and selection methods used to develop these materials can be found in various CIMMYT publications (CIMMYT, 1981, 1982, 1984; Vasal et al., 1982).

The diallel crosses were made at CIMMYT's experiment station in Tlaltizapán, Mexico, during the 1985 winter season. The latest cycles of selection of the seven parents 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. Seeds of each cross and its reciprocal were bulked for use in the trials. Seed increase of the parents was done simultaneously in the same season.

The seven parents and 21 crosses were evaluated in 22 temperate and subtropical environments (16 environments in the USA, 1 in Canada, 4 in Mexico, and 1 in Turkey) during 1985–1986. The different environments where the trials were evaluated are presented in Fig. 1. Since the environments tested were quite varied, resulting in a large genotype × environment interaction, it was necessary to stratify them in order to reduce the interaction. After careful consideration, it was decided to divide the environments into two groups, namely, temperate and subtropical. This classification also helped us to group the environments across geographical boundaries, made sense for discussion, and was consistent with the objectives of this study. Accordingly, all the environments in the USA and the one in Canada were classified as temperate. The subtropical group consisted of the four Mexican environments and the one in Antalya, Turkey. Although the Turkish environment could have been classified with the temperate environments, a careful examination of the data justified its inclusion with the subtropical environments.

The experimental design used was a randomized complete block with three replicates per environment. In subtropical environments, the experimental unit was two 5-m rows spaced 75 cm apart. Plots were overplanted and thinned to two plants per hill, with 50 cm between hills, to give a final plant density of 53 500 plants ha^{-1}. In temperate environments, plot size and plant density varied; at most sites, the experimental unit was two rows either 3.05 or 6.10 m in length, spaced either 76.2 or 91.4 cm apart. Final plant densities ranged from 53 000 to 87 700 plants ha^{-1}. Due to the differences in plant densities between some environments, it is possible that plant densities and environmental effects might be confounded.

For subtropical environments, data were recorded for days to silking (number of days from planting to 50% extruded silk), plant height (cm from soil surface to the point where tassel branching begins), field ear weight, and grain moisture at harvest. Plots were hand-harvested and grain yield (Mg ha^{-1}) was calculated using 80% shelling and adjusting to 155 g kg^{-1} moisture. At one environment (Silao, Mexico), plant height was not recorded. For all temperate environments, plots were machine-harvested and the shelled grain weight was adjusted to 155 g kg^{-1} moisture. Days to silking were recorded at eight environments (Mississippi State, MS; Raleigh, NC; West Lafayette, IN; Quebec, Canada; Ames, IA; Rock Springs, TX; and two locations at Champaign, IL)and plant height was measured at four environments (Raleigh, NC; Champaign, IL; Ames, IA; and Rock Springs, TX).

Statistical Analysis

Analyses of variance (ANOVA) using plot-mean data were conducted for grain yield, plant height, and days to silking. Each of the 22 environments was first analyzed

Table 1. Germplasm description of seven CIMMYT subtropical and temperate early-maturity maize gene pools and populations used in this study.

Population or pool number	Population or pool name	Germplasm description
Population 46	Templado Amarillo Cristalino	Represents superior fraction (240 half-sib families) of Pool 29 which is based on materials from Europe, Lebanon, U.S. Corn Belt, China, Indonesia, and South America. Yellow flint grain type. Selection cycle 1.
Population 48	Compuesto de Hungaria	Central U.S. Corn-Belt materials, Southern European materials, and 54 half-sib families from Pool 30. Yellow dent grain type, improved for stalk-rot resistance. Selection cycle 5.
Pool 27	Subtropical early white flint	Includes germplasm from the USA, China, Lebanon, Pakistan and several European countries. Selected for tolerance to high density and resistance to ear and stalk rots and leaf diseases. Selection cycle 20.
Pool 28	Subtropical early white dent	Based on white dent selections from crosses between white flint materials from Pakistan and yellow flint and dent materials from Europe, China, Lebanon, Mexico, Guatemala, and the U.S. Corn-Belt. Selection cycle 14.
Pool 30	Subtropical early yellow dent	Made up of materials from Europe, China, Lebanon, Mexico, South America, and the U.S. Corn-Belt. Improved for tolerance to high density and for resistance to ear and stalk rots and leaf diseases. Selection cycle 15.
Pool 40	Intermediate temperate range (ITR)	Based on materials from Bulgaria, Spain, Hungary, France, Turkey, Yugoslavia, Pakistan, Poland, and Germany. Designed for the intermediate temperate ranges and winter maize areas of the tropics and subtropics. Yellow grain color with mixed grain type. Selection cycle 12.
Pool 42	CIMMYT–German maize gene pool (NTR-2)	Designed to introduce tropical germplasm into temperate areas. Developed in cooperation with the University of Hohenheim, Germany, and is based on germplasm from Mexico, Peru, Bolivia, Pakistan, China, Hungary, the USA, and Yemen. Yellow grain color with mixed grain type. Selection cycle 12.

separately and then in a combined analysis (data not shown). As large genotype × environment interactions were observed in the combined analyses across all environments, analyses were then performed across temperate and subtropical environments separately. Environments were considered as random and genotypes as fixed effects. Analysis III of Gardner and Eberhart (1966) was used to obtain estimates of GCA and SCA. Entry sums of squares were partitioned into parents, crosses, and parents vs. 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 replicate, u is the overall mean, g_i and 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 to 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 (1966) Analysis III is considered superior to Griffing's (1956) Model 1, Method II analysis, especially when the parents are open-pollinated varieties or populations (Gardner and Eberhart, 1966; Singh, 1978).

Table 2. Partial analyses of variance of diallel crosses among subtropical and temperate early-maturity maize gene pools and populations for yield combined across five subtropical and 17 temperate environments during 1985–1986.

Source	Subtropical environments		Temperate environments	
	df	Mean squares	df	Mean squares
Entries	27	3.70**	27	10.98**
Parents	6	5.98**	6	18.71**
Parents vs. crosses	1	8.02**	1	23.40**
Crosses	20	2.80**	20	8.04**
GCA	6	8.55**	6	23.56**
SCA	14	0.34	14	1.38*
Environments (E) × entries	108	0.90**	432	0.96*
E × Parents	24	1.45**	96	1.11*
E × Parents vs. crosses	4	0.20	16	1.26
E × crosses	80	0.77**	320	0.90
E × GCA	24	1.74**	96	1.41**
E × SCA	56	0.34	224	0.69
Pooled error	270	0.35	918	0.79
Mean		4.59		4.35
CV, %		12.95		20.42

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

The F-tests for the ANOVA were calculated as follows. Main effects, such as entries and its partitions, were tested against their respective interaction with environment, and all the interaction terms were tested against the pooled error. For example, mean squares for GCA was tested against the mean squares for GCA × environments and that for SCA against SCA × environments. Heterosis (%) for yield was calculated over the high-parent values.

RESULTS AND DISCUSSION

Analysis of Variance

Combined ANOVA for grain yield showed a highly significant G × E interaction ($P < 0.01$) at subtropical environments and a significant interaction ($P < 0.05$) at temperate environments (Table 2). Significant G × E interactions observed were in line with expectations, considering the wide range of environments in which the materials were evaluated. At both environments, highly significant differences for grain yield were observed for parents, parents vs. crosses, crosses, and GCA. For SCA, a significant difference was observed only in temperate environments.

The highly significant variance due to parents vs. crosses, which is a measure of average heterosis, points to the importance of nonadditive genetic effects in determining yield in these germplasms; however, for lack of significant differences in SCA in subtropical environments, our results failed to support this conclusion. Partitioning of the sums of squares among crosses between GCA and SCA showed that 92 and

Table 3. Partial analyses of variance of diallel crosses among subtropical and temperate early-maturity CIMMYT maize germplasm for days to silking and plant height combined across five subtropical and 17 temperate environments during 1985–1986.

	Mean squares							
	Subtropical environments				Temperate environments			
Source	df	Days to silking	df	Plant height	df	Days to silking	df	Plant height
Entries	27	4.56	27	225.82*	27	102.37**	27	824.63**
Parents	6	5.78	6	478.55**	6	223.72**	6	1222.65**
Parents vs crosses	1	0.84	1	372.84	1	23.67*	1	146.11
Crosses	20	4.38	20	142.65	20	69.90**	20	739.15*
GCA	6	3.94	6	245.64	6	222.13**	6	1271.59*
SCA	14	4.57	14	98.50	14	4.67	14	510.96
Environments (E) × entries	108	5.45**	81	112.28	189	7.83**	81	344.59
E × Parents	24	4.13**	18	85.30	42	7.48**	18	258.51
E × Parents vs. crosses	4	2.94	3	125.67	7	3.73	3	21.67
E × crosses	80	5.97**	60	119.70	140	8.14**	60	386.56
E × GCA	24	5.21**	18	213.70	42	15.49**	18	333.83
E × SCA	56	6.28**	42	79.41	98	4.98*	42	409.15
Pooled error	270	2.02	216	175.26	432	3.78	216	348.06
Mean		54.34		181.03		71.58		199.55
CV, %		2.62		7.31		2.72		9.35

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

88% of the variation could be attributed to GCA in subtropical and temperate environments, respectively. These values clearly indicate the relative importance of additive genetic effects in controlling expression of yield in these germplasms. Similar results were reported in CIMMYT's tropical early- and intermediate-maturity germplasm (Beck et al., 1990) and in subtropical and temperate intermediate-maturity germplasm tested in Mexican and temperate environments (Beck et al., 1991).

The G × E interaction variance was reduced considerably because of grouping into temperate and subtropical environments; however, several interactions remained significant. The E × GCA interaction remained highly significant in both environments, whereas the E × SCA was nonsignificant. Considering the spread of the 17 temperate environments, ranging from Quebec in the north to Texas and Mississippi in the south and from North Carolina in the east to the Corn-Belt states of the Midwest, the significant interactions were not surprising. Mean grain yields were 4.59 Mg ha^{-1} and 4.35 Mg ha^{-1} in subtropical and temperate environments, respectively. The CV for yield was relatively high (20%) in temperate environments (Table 2).

Combined analyses of variance for days to silking showed no significant differences among entries and their partitionings at subtropical environments, whereas highly significant differences were observed in temperate environments (Table 3). Many of the interaction terms were significant in both environments for this trait. Mean days to silking were 71 and 54 d under temperate and subtropical environments, respectively. Among temperate environments, variation in days to silking was observed, with flowering in the southern environments coming much earlier than in some of the more northern locations.

Combined analyses for plant height (measured in four environments in each group) showed highly significant variation among parents (Table 3). Under temperate environments, a significant difference in GCA was observed, while the remaining terms were nonsignificant. All interaction terms with environments were nonsignificant. Mean plant height under temperate environments was slightly greater (+18 cm) than under subtropical environments. Results obtained by Beck et al. (1991) with subtropical intermediate-maturity material, however, showed much larger differences (50 cm) for plant height between temperate and subtropical environments.

Heterosis and Combining Ability

Temperate Environments

Mean yields for parents and their crosses were 4.13 and 4.43 Mg ha^{-1}, respectively. Among the parents, Pool 30 and Population 48 had the highest mean yields: 4.95 and 4.93 Mg ha^{-1}, respectively (Table 4). Both possess yellow dent grain type and include a significant portion of U.S. and European germplasm (Table 1). Pool 42 and Population 46 yielded the lowest (3.45 and 3.70 Mg ha^{-1}, respectively). Among the crosses, the mean yields ranged from 3.66 Mg ha^{-1} (Pool 40 × Pool 42) to 5.03 Mg ha^{-1} (Population 48 × Pool 28). High-parent heterosis ranged from −16.7% (Pool 30 × Pool 42) to 10.2% (Pool 27 × Pool 40) (Table 4). Nine crosses showed positive heterosis, but only four crosses exceeded 5%. Similar levels of high-parent heterosis 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 parent varieties. In previous studies of diallel crosses among CIMMYT's tropical and subtropical materials, low heterosis has been reported (Beck et al., 1990, 1991; Crossa et al., 1990). The low level of heterotic response observed was not unexpected, considering CIMMYT's emphasis on developing broad-based genetic pools and populations, with less importance given to keeping heterotic groups separate (Vasal et al., 1982).

Among parents, Pools 40 and 42 were the earliest to silk (68 d), while Pool 27 and Population 46 were the latest (75 d). Days to silking among crosses ranged from 68 (Pool 40 × Pool 42) to 75 d (Population 46 × Pool 27) (Table 4).

Table 4. Mean values for days to silking, plant height, and grain yield of seven CIMMYT maize gene pools and populations (Pop.) and their crosses evaluated in five subtropical and 17 temperate environments during 1985–1986.

	Subtropical environments					Temperate environments				
Pedigree	Time to silking	Plant height	Yield	Ranking for yield	Heterosis	Time to silking	Plant height	Yield	Ranking for yield	Heterosis
	d	cm	Mg ha^{-1}		%	d	cm	Mg ha^{-1}		%
					Crosses					
Pop. 46 × Pop. 48	55	185	4.89	9	4.1	73	218	4.98	2	1.1
Pop. 46 × Pool 27	55	182	4.82	10	−1.1	75	193	4.06	17	6.5
Pop. 46 × Pool 28	54	179	4.95	6	−0.8	74	200	4.28	11	−0.4
Pop. 46 × Pool 30	55	189	5.17	4	13.0	73	206	4.88	4	−1.3
Pop. 46 × Pool 40	53	181	4.33	17	−3.8	71	206	3.88	19	1.9
Pop. 46 × Pool 42	55	178	4.32	18	−4.0	71	199	3.90	18	5.3
Pop. 48 × Pool 27	54	186	5.42	1	9.9	73	200	4.82	5	−2.2
Pop. 48 × Pool 28	55	183	5.26	2	5.2	73	211	5.03	1	2.0
Pop. 48 × Pool 30	55	188	4.93	7	4.9	72	200	4.96	3	0.2
Pop. 48 × Pool 40	55	178	4.45	12	−5.4	70	196	4.56	8	−8.2
Pop. 48 × Pool 42	54	182	4.40	13	−6.6	70	197	4.38	10	−12.6
Pool 27 × Pool 28	54	182	4.92	8	−1.3	74	208	4.45	9	3.5
Pool 27 × Pool 30	55	179	5.18	3	5.8	72	202	4.70	7	−5.2
Pool 27 × Pool 40	54	180	4.25	19	−14.7	71	193	4.23	14	10.2
Pool 27 × Pool 42	53	182	4.37	16	−11.5	71	199	4.10	16	7.4
Pool 28 × Pool 30	55	179	5.15	5	3.2	71	206	4.71	6	−4.9
Pool 28 × Pool 40	55	179	4.18	20	−19.1	70	191	4.27	12	−0.6
Pool 28 × Pool 42	54	175	4.39	14	−2.4	70	186	4.17	15	−3.1
Pool 30 × Pool 40	54	184	4.46	11	1.2	70	201	4.70	7	−5.2
Pool 30 × Pool 42	54	183	4.38	15	−0.6	70	200	4.24	13	−16.7
Pool 40 × Pool 42	55	181	3.80	21	1.9	68	186	3.66	20	−3.8
Overall crosses	54.4	181.7	4.67			71.5	199.9	4.43		
					Parents					
Pop. 46	55	181	4.50	4	—	75	203	3.70	5	—
Pop. 48	55	187	4.69	3	—	73	203	4.93	2	—
Pool 27	54	179	4.88	2	—	75	196	3.80	4	—
Pool 28	54	183	4.99	1	—	74	207	4.30	3	—
Pool 30	54	183	4.41	5	—	71	209	4.95	1	—
Pool 40	54	170	3.73	6	—	68	181	3.80	4	—
Pool 42	54	171	3.26	7	—	68	190	3.45	6	—
Overall parents	54.3	179.1	4.35			72.0	198.4	4.13		
LSD (0.05)	1.0	10.6	0.42			1.1	14.9	0.34		—
CV, %	2.6	7.3	13.0		—	2.7	9.4	20.4		—

Estimates of GCA for grain yield, days to silking, and plant height for the seven parents used in this study are presented for both subtropical and temperate environments in Table 5. Highly significant GCA estimates for yield were recorded for Population 48 (0.43 Mg ha^{-1}) and Pool 30 (0.33 Mg ha^{-1}) on the positive side and by Pool 40 (−0.25 Mg ha^{-1}) and Pool 42 (−0.42 Mg ha^{-1}) on the negative side. Population 48 × Population 46 (0.24 Mg ha^{-1}), Population 46 × Pool 30 (0.24 Mg ha^{-1}) and Pool 30 × Pool 40 (0.20 Mg ha^{-1}) recorded significant positive SCA effects for yield, whereas Population 46 × Pool 27 (−0.21 Mg ha^{-1}) and Population 48 × Pool 30 (−.23 Mg ha^{-1}) had significant negative SCA effects (Table 6).

Subtropical Environments

Overall mean grain yield for parents and crosses was 4.35 and 4.67 Mg ha^{-1}, respectively (Table 4). Among the parents, Pool 28 had the highest mean yield (4.99

Table 5. Estimates of general combining ability (GCA) effects for seven CIMMYT subtropical and temperate early-maturity maize gene pools and populations for days to 50% silking and plant height.

	Subtropical environments			Temperate environments		
Parents	Grain Yield	Time to silking	Plant height	Grain Yield	Time to silking	Plant height
	Mg ha^{-1}	d	cm	Mg ha^{-1}	d	cm
Population 46	0.10	−0.03	0.56	−0.11	1.30**	4.65*
Population 48	0.27	0.36	2.66	0.43**	0.30	4.44
Pool 27	0.19	−0.22	0.31	−0.04	1.66**	−0.84
Pool 28	0.17	0.11	−2.45	0.07	0.53	0.52
Pool 30	0.25	0.19	2.31	0.33**	−0.26	3.30
Pool 40	−0.51*	−0.12	−1.43	−0.25**	−1.70**	−5.26*
Pool 42	−0.47**	−0.28	−1.95	−0.42**	−1.83**	−6.81**

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

Table 6. Estimates of specific combining ability (SCA) effects among seven CIMMYT subtropical and temperate early-maturity maize gene pools and populations (Pop.) for yield combined across subtropical (above diagonal) and temperate (below diagonal) environments.

Parents	Pop. 46	Pop. 48	Pool 27	Pool 28	Pool 30	Pool 40	Pool 42
	Mg ha^{-1}						
Pop. 46	—	−0.14	−0.13	−0.01	0.15	0.08	0.03
Pop. 48	0.24*	—	0.29*	0.16	−0.26*	0.02	−0.07
Pool 27	−0.21*	0.00	—	−0.11	0.07	−0.10	−0.02
Pool 28	−0.10	0.10	−0.01	—	0.06	−0.15	0.02
Pool 30	0.24*	−0.23*	−0.01	−0.11	—	0.05	−0.07
Pool 40	−0.18	−0.05	0.10	0.03	0.20*	—	0.11
Pool 42	0.01	−0.06	0.13	0.09	−0.09	−0.09	—

* Significant at the 0.05 probability level.

Mg ha^{-1}) followed by Pool 27 (4.88 Mg ha^{-1}). Lowest mean yield was recorded by Pool 42 (3.26 Mg ha^{-1}) and Pool 40 (3.73 Mg ha^{-1}), both of which are based on temperate germplasm. These two pools also had relatively shorter plant height. Similar findings were reported by Beck et al. (1991) with subtropical intermediate-maturity materials, where Pools 39 and 41, both of which were earlier and shorter compared to the rest of the materials, also yielded the least. Mean yield among the crosses ranged from a high of 5.42 Mg ha^{-1} (Population 48 × Pool 27) to a low of 3.80 Mg ha^{-1} (Pool 40 × Pool 42). Heterosis over the higher parent for yield ranged from 13.0% (Population 46 × Pool 28) to −19.1% (Pool 28 × Pool 40). Nine out of 21 crosses showed positive values for high-parent heterosis (Table 4).

Under subtropical conditions, unlike the temperate environments, the range for days to silking was narrow both for parents and crosses (53–55 d). Plant height also showed a similar narrow range, although both Pools 40 and 42 consistently possessed short plants under both temperate and subtropical environments.

Pool 40 and Pool 42 had significant negative GCA effects for yield, whereas the remaining five populations and pools had positive but nonsignificant GCA estimates (Table 5). Although the SCA effects were not statistically significant under subtropical environments, two crosses, Population 48 × Pool 27 (0.29 Mg ha^{-1}) and Population 48 × Pool 30 (−0.26 Mg ha^{-1}), were the best and poorest specific combiners, respectively.

Temperate vs. Subtropical Environments

Overall mean grain yield for parents and crosses were similar in subtropical and temperate environments (Table 4). This is in contrast to the performance of subtropical and temperate germplasm with intermediate-maturity maturity, as reported by Beck et al. (1991). In that study, the average yield in temperate environments (3.4 Mg ha^{-1}) was about half that obtained in Mexican environments (6.3 Mg ha^{-1}). It seems that CIMMYT's subtropical and temperate early-maturity germplasm are more favorably adapted to the temperate conditions in the USA and yield better than our intermediate-maturity germplasm. The mean yields of parents in both environments were consistent, except for Population 46, Pool 27, and Pool 28, which yielded better in subtropical environments, and Pool 30, which performed better in temperate environments. Crosses involving Population 48 with Pools 27, 28, and 30 were high-yielding in both environments. Crosses of Pool 27 with Pool 40 and Pool 42 showed negative heterosis in subtropical environments, while showing positive heterosis in temperate environments.

Based on SCA effects in the two environments, six crosses showed positive SCA, with an equal number showing negative SCA for yield in both temperate and subtropical environments (Table 6). The remaining nine crosses had contrasting SCA effects between the two environments. Population 46 × Pool 30 and Population 48 × Pool 28 had positive SCA effects, whereas Population 46 × Pool 27 and Population 48 × Pool 30 had negative SCA effects in both environments. Among crosses that showed mixed performances in the two environments, Population 46 × Population 48, which is a yellow flint × dent cross, did well in temperate environments and poorly in the subtropical environments (Table 6). Crosses between yellow dent × yellow flint grain types generally performed well in temperate environments. Although crosses involving white grain-color materials generally performed poorly in temperate environments, several crosses involving Pool 42 with Pool 27 (flint) and Pool 28 (dent) gave positive SCA effects for yield. Under subtropical environments, several of the crosses with positive SCA for yield were white × yellow crosses, such as Population 48 × Pool 27 and Population 48 × Pool 28.

For days to silking and plant height, GCA estimates were relatively low and nonsignificant in subtropical environments (Table 5). Under temperate environments, Population 46 and Pool 27 showed significant positive GCA effects and Pools 40 and 42 showed significant negative GCA effects for days to silking. For plant height, significant positive GCA effects were obtained for Population 46, while Pools 40 and 42 had significant negative GCA effects (Table 5).

Introduction of exotic germplasm into Corn-Belt germplasm has been demonstrated by Hallauer and Sears (1972), Lonnquist (1974), Brown (1975), and Crossa and Gardner (1987). Reporting on the heterosis and combining ability of CIMMYT's subtropical and temperate germplasm with intermediate maturity, Beck et al. (1991) emphasized their long-term potential as exotic source germplasm in spite of their relatively poor yield performance under temperate environments. Our current results from subtropical and temperate early-maturity germplasm are much more encouraging. Unlike our experience with intermediate-maturity materials, early germplasm yielded on a par in both temperate and subtropical environments. Under subtropical conditions, crosses involving Pool 30 with Population 46, Population 48, and Pool 27 showed considerable heterosis for yield and seem to hold potential for the subtropics. Population 48 and Pool 30 showed significantly positive GCA effect for yield under temperate environments. Although both sources were developed largely from U.S. and European germplasm, it is noteworthy that they have not been subjected to any selection pressure under temperate Corn-Belt conditions. Against this background, their performance seems encouraging, suggesting their potential use as source germplasm for the temperate maize breeding programs, especially for the U.S. Corn Belt.

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