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RESEARCH

Combining Ability of Yellow Lines Derived from CIMMYT Populations for Use in Subtropical and Tropical Midaltitude Maize Production Environments

Xing-Ming Fan,* Yu-Dong Zhang, D .P. Jeffers, Ya-Qi Bi, M. S. Kang, and Xing-Fu Yin

ABSTRACT

The introduction and utilization of new maize (*Zea mays* L.) germplasm from sources, such as the International Maize and Wheat Improvement Center (CIMMYT), can be valuable for broadening the genetic base of breeding populations through the introgression of new alleles. Twenty-five inbred lines, derived from CIMMYT breeding populations, were selected on the basis of grain color, resistance to turcicum leaf blight, and per se line performance in Yunnan. To use the lines effectively, information on their performance in hybrid combinations and on general combining ability (GCA) and specific combining ability (SCA) needed to be obtained. The objectives of this study were (i) to evaluate these lines for grain yield (GY) in hybrid combinations and determine GCA of parental lines and SCA of crosses between the 25 introduced lines and six testers using North Carolina Design II; and (ii) to classify the lines into different maize heterotic groups. The field testing at three locations identified crosses with lines from Cateto and Population 147 (P147) as having significantly higher GY than those from SA3 and other introduced populations, and the high GY was largely attributable to their high positive GCA effects. Lines from the same population were not necessarily classified into same maize heterotic group. Lines selected at S_4 or a later generation would be expected to have more stable GCA effects than lines selected in earlier generations.

X.M. Fan, Y.D. Zhang, Y.-Q. Bi, and X.-F. Yin, Institute of Food Crops, Yunnan Academy of Agricultural Sciences, No. 2238, Beijing Rd., Kunming 650200, Yunnan Province, China; D.P. Jeffers, CIMMYT Yunnan Office/Institute of Food Crops, Yunnan Academy of Agricultural Sciences; M.S. Kang, Dep. of Plant Pathology, Kansas State Univ., Manhattan, KS 66506-5502. Received 13 May 2017. Accepted 5 Sept. 2017. *Corresponding author (xingmingfan@163.com). Assigned to Associate Editor David Fang.

Abbreviations: GCA general combining ability; GEM, Germplasm Enhancement of Maize; GY, grain yield; NCII, North Carolina Design II; SCA, specific combining ability; SNP, single-nucleotide polymorphism.

INTRODUCTION and utilization of exotic germplasm in local breeding programs is a highly effective way of broadening the maize (*Zea mays* L.) genetic base (Crossa et al., 1987; Hallauer and Miranda, 1988; Holland and Goodman, 1995; Reif et al., 2010; Fan et al., 2015). A narrow genetic base can render maize vulnerable to attacks by insects and pathogens, leading to severe yield losses. A case in point is the southern corn leaf blight epiphytotic of 1970, caused by *Bipolaris maydis* (Y. Nisik. & C. Miyake) Shoemaker, 1959, which affected maize hybrids containing the Texas type (T) cytoplasm in the US Cornbelt, leading to the loss of billions of dollars (Gregory et al., 1978).

For decades, maize germplasm developed by CIMMYT have been used globally for increasing maize yields in nontemperate environments (López-Pereira and Morris, 1994; Gerpacio, 2001; Morris, 2002; Menkir et al., 2004; Goodman, 2005; Reif et al., 2010; Fan et al., 2008b, 2015). A large amount of germplasm from CIMMYT and other sources has been introduced into China and intensively studied (Fan et al., 2002, 2005; Tan et al., 2002; Sun et al., 2007; Wu et al., 2007; Chen et al., 2011). The major exotic tropical and subtropical germplasm being used in China includes

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Suwan 1, Suwan 2, ETO, Tuxpeño, and Cuban Flint (Li et al., 2001; Fan et al., 2002). Recently, an open-source, collaborative breeding program based in Yunnan has introduced a large set of new germplasm for evaluating its adaptation and utilization in subtropical regions of China and in similar environments globally. Twenty-five inbred lines with dark orange grain color and possessing resistance to turcicum leaf blight, caused by *Setosphaeria turcica* Luttrell [anamorph *Exserohilum turcicum* (Pass) K.J. Leonard and E.G. Suggs], and desirable agronomic characteristics were selected for crossing with locally adapted inbreds to determine their heterotic group and general combining ability (GCA) effects, as well as specific combining ability (SCA) effects of crosses. Included in this set were several lines representing the landrace Cateto, SA3 (a tropical, acid-soil-tolerant CIMMYT population), and the tropical, early-maturity CIMMYT population 147 (P147). The specific lines from Cateto were derived from crosses of CIMMYT inbreds to lines derived from a double-cross hybrid donated to CIMMYT by Cargill International in the early 1990s. The CIMMYT populations SA3 and P147 possess desirable agronomic traits and resistance to foliar diseases for use in nontemperate environments (CIMMYT, 1998). The Cateto germplasm has been used for improving performance under acid-soil conditions in the tropical lowlands (Magnavaca, 1982; Pandey et al., 2007; Guimaraes et al., 2014) and has also been included in the formation of Thai Composite #1, from which Suwan-1 and Suwan-2 were derived (Sriwatanapongse et al., 1993). The CIMMYT acid-soil-tolerant population SA3 also has 14 Cateto landrace collections included in its original formation (CIMMYT, 1998; Pandey et al., 2007). P147 is a tropical, early-maturity flint and dent population formed from a broad germplasm base, including sources of resistance or tolerance to turcicum leaf blight, tarspot complex (caused by *Phyllachora maydis* Maubl. in combination with *Monographella maydis* E. Müller), downy mildew (caused by several *Peronosclerospora* spp.), *Maize streak virus*, and drought. Lines derived from Suwan 2 are also a component of P147 (CIMMYT, 1998).

Germplasm derived from the Cateto landrace from South America has been studied by several researchers for use in tropical and temperate environments (Magnavaca, 1982; Hameed, 1991; Holland and Goodman, 1995; Taba, 1999; Santos et al., 2001; Salhuana and Pollak, 2006; Subedi, 2015). Hameed (1991) studied important agronomic traits for use in temperate US maize and found the Cateto accessions to increase test weight and decrease kernel moisture when crossed with temperate US inbreds. Santos et al. (2001) and Salhuana and Pollak (2006) found that the Cateto accessions PE001 and PE011, included in the Latin American Maize Project, had high yield potential in multilocation evaluations in the tropical lowlands when crossed with the Brazilian Suwan and Tuxpeño testers, respectively. Subedi (2015) studied maize diseases and their management in Nepal and found that lines developed from Cateto and P147, introduced from the Yunnan collaborative Yunnan Academy of Agricultural Sciences–CIMMYT breeding program as hybrids (Daniel Jeffers, personal communication, 2015), had high levels of resistance to turcicum leaf blight (also referred to as northern leaf blight). Recently, Fan et al. (2016) reported hybrids formed with Cateto and P147 to have 10% higher grain yield (GY) than the check.

Proper heterotic group classification improves breeding efficiency (Hallauer and Miranda, 1988; Fan et al., 2014). A method based on combined information on SCA and GY (SCA_GY) is widely used for assigning lines to maize heterotic groups (Crossa et al., 1987; Hallauer and Miranda, 1988; Barata and Carena, 2006; Fan et al., 2009, 2015). Diallel analysis and North Carolina Design II (NCII) are two frequently used methods for determining combining ability (Hallauer and Miranda, 1988; Barata and Carena, 2006; Fan et al., 2002, 2016). Fan et al. (2002) reported the results from an NCII design trial wherein 25 tropical inbred lines from five tropical populations were crossed to four testers representing four temperate heterotic patterns in China. They found that heterotic groups Suwan1 and ETO were close to Luda Red Cob, a local maize heterotic group in China; Antigua and Tuxpeño were close to Reid; and POP28 was close to Tangsipingtou, another local maize heterotic group in China. Fan et al. (2003) classified 29 temperate and tropical maize inbred lines into four heterotic groups and also classified 18 quality protein maize lines, which included CIMMYT germplasm, into five heterotic groups. Wu et al. (2007) studied combining ability of 24 quality protein maize inbred lines from CIMMYT and classified them into four widely accepted heterotic groups in China. Fan et al. (2008a) identified Suwan1 as a new heterotic group, which was different from Reid and non-Reid heterotic groups, establishing a triheterotic pattern to simplify breeding.

The ultimate goal of introducing exotic germplasm is to improve local elite maize lines and to develop high-yielding hybrids. To know which CIMMYT populations possessed the highest potential and where the introduced germplasm fit, the 25 selected inbred lines, including the lines derived from Cateto, P147, and SA3, were crossed to six testers from three maize heterotic groups according to NCII mating design. Breeding theory and practice have shown the necessity of both assigning new lines to proper heterotic groups and obtaining combining ability information on the introduced lines prior to their effective utilization in a breeding program (Hallauer and Miranda, 1988; Goodman, 2005; Fan et al., 2008b, 2009, 2015). Therefore, the objectives of this study were (i) to determine GY, GCA effects of parental lines, and SCA effects for GY of the resulting 150 crosses (25 lines × six testers); and (ii) to assign the 25 lines developed from CIMMYT germplasm to appropriate heterotic groups.

MATERIALS AND METHODS

Germplasm Used

Twenty-five inbred lines, from CIMMYT populations or "breeding starts," were crossed to six testers (two testers each from Suwan1, Reid, and non-Reid heterotic groups). The term "breeding starts" is defined as a new source germplasm from the crosses of Cateto × CML lines or P147 × P45 or P33 lines to introduce new genetic variability into a breeding program by providing traits complementary to the existing germplasm base. The source and ecological type of the inbred lines are listed in Table 1. The 25 lines include 16 sister lines obtained from three different common ancestors. Among the 16 sister lines, nine lines (L3, L4, L5, L6, L7, L8, L9, L17, and L18) involved CIMMYT germplasm of Cuban Flint (Cateto) descent; two lines (L13 and L22) involved SA3, and five lines (L1, L10, L20, L21, and L23) P147 (Table 1). North Carolina mating design II was used to generate 150 testcrosses (25 lines × 6 testers) in summer 2013. The 150 crosses and a commercial check, Yunrui 999, were planted at Kunming (25°02′ N, 120°45′ E; 1960 m asl), Wenshan (23°19′ N, 104°45′ E; 1540 m asl), and Dehong (24°26′ N, 98°35′ E; 913.8 m asl). Each single-row plot was 4 m long. Inter-row spacing was 0.7 m, whereas spacing between plants within a row was 0.25 m. Plant density was ~55,300 plants ha^{-1}. Compound fertilizer (N–P_2O_5–K_2O = 28–6–6) was applied at the rate of 1050 kg ha^{-1}. Plots were irrigated once a week during the dry season, and no irrigation was applied or needed during the rainy season. Sulfur was applied at a rate of 17 kg ha^{-1}. Plots were harvested after black-layer formation, and GY per plant was recorded after adjusting the kernel moisture content to 130 g kg^{-1}.

Statistical Model and Data Analysis

Data analyses were conducted with SAS 9.1.3 (SAS Institute, 2005). The ANOVA was done according to the following statistical model:

$$Y_{ijkl} = \mu + \alpha_l + b(a)_{kl} + \upsilon_{ij} + (\alpha\upsilon)_{ijl} + e_{ijkl}$$

where Y_{ijkl} = observed value from each experimental unit; μ = population mean; α_l = location effect; $b(a)_{kl}$ = replication effect within each location; υ_{ij} = F_1 hybrid effect = $l_i + t_j + lt_{ij}$ (where l_i = ith exotic line effect; t_j = jth tester effect; lt_{ij} = interaction

Table 1. Population source and ecological type of the 31 inbred lines.

Line	Population source	Ecological type	Generations†	Group‡
L1	(P147-F2-102-S6/P33-C3-64-S4)-F2-B-24-1-1	Mixed tropical/subtropical		P147
L2	(CML329/CML20)-F2-47-2-B-4	Mixed subtropical/tropical		Other
L3	[CML226/(CATETO DC1276/7619)]B-B -5-1-1	Mixed tropical/subtropical	S_2	Cateto
L4	[CML226/(CATETO DC1276/7619)]B-B-25-1-1	Mixed tropical/subtropical	$S_4(S_2)$	Cateto
L5	[CML226/(CATETO DC1276/7619)]B-B-25-1-3	Mixed tropical/subtropical	$S_4(S_2)$	Cateto
L6	[CML226/(CATETO DC1276/7619)]B-B-38-3-1	Mixed tropical/subtropical	$S_4(S_2)$	Cateto
L7	[CML226/(CATETO DC1276/7619)]B-B-38-3-2	Mixed tropical/subtropical	$S_4(S_2)$	Cateto
L8	[CML226/(CATETO DC1276/7619)]B-B-38-3-3	Mixed tropical/subtropical	$S_4(S_2)$	Cateto
L9	(CML226/CATETO//CML323/CATETO)-F2-B-2-1-B	Mixed tropical/subtropical		Cateto
L10	(P147-F2-152-S7/P45-C8-76-S9)-F2-B-13-1-1	Mixed tropical/subtropical		P147
L11	GLSIY01HGA-B-8–1-1-B	Subtropical		Other
L12	FS8BT-278-B-6-1-4-2-2-3-1-B/MD37)-8-B-32-1-B*3-3-B	Mixed Temperate/subtropical		Other
L13	CLA155 = SA3-C4-FS(16/25)-2-4-3-1-4-5-2	Tropical	S_4	SA3
L14	CLA161 = SA4-C2-FS(21/26)-1-2-2-2-2-1-2	Tropical		Other
L15	CL-RCY023 = (CL-02439/CML-286)-B-1-2-2-B*8	Tropical		Other
L16	GLSIY01HGB-27-1-2-B	Subtropical		Other
L17	CML323/(CATETO DC1276/7619)-F2-42-2-B	Mixed subtropical/tropical		Cateto
L18	(CML226/CATETO)-F2-B-1-2-B	Mixed tropical/subtropical		Cateto
L19	P45-C6-FS40-1-1-1-B-1-1-3-2-1-1-2-B	Subtropical		Other
L20	P147-F2-114-S7/P45- C8-76-S9)-F2-B-2-1-1	Mixed tropical/subtropical		P147
L21	(P147-F2–136-S7/P45-C8–76-S9)B-B-B-15–1-3	Mixed tropical/subtropical	S_4	P147
L22	CLA44 = SA3-C4-FS(16/25)-2–4-3–6-B	Tropical	S_4	SA3
L23	(P147-F2–136-S7/P45-C8–76-S9)B-B-B-15–2-1	Mixed tropical/subtropical	S_4	P147
L24	P45-C8–164–1-1–2-8-B	Subtropical		Other
L25	DTPY-C9-F74–1-1–1-1-B	Tropical		Other
T1		Temperate		
T2		Temperate		
T3		Temperate		
T4		Temperate		
T5		Tropical		
T6		Tropical		

† S_x, refers to the line to be selected at generation x; $S_x(S_y)$ refers to the line was selected at S_y first, then selected again at S_x. A bulk of selfs is signified by B.

‡ When a line was selected from a cross with Cateto, P147, and SA3 as one of the parents, the line was assigned to the Cateto, P147, and SA3 group, respectively.

effect between ith exotic line and jth tester); $(\alpha\upsilon)_{ijl}$ = interaction effect between ijth F_1 hybrid and lth location; and e_{ijkl} = residual effect.

Percent check heterosis (CH%) for each cross was calculated as follows:

$$\text{CH\%} = [(\text{cross value} - \text{check value}) \times 100]/\text{check value}$$

Because the three locations selected for this experiment were not a random sample of all possible locations within Yunnan province, we treated location as a fixed factor. Hybrid or cross effect and, consequently, line and tester effects were also regarded as fixed effects. Only replication was considered a random factor. Therefore, significance of location variance was tested against a replication-within-location [Replication(location)] entity (Table 2). Combining ability analysis was conducted on the basis of the model and method used by Fan et al. (2009).

RESULTS AND DISCUSSION

ANOVA for Grain Yield and Mean Grain Yield between Sister and Non-Sister Lines

Analysis of variance for GY across locations is given in Table 2. All the sources of variation were statistically significant (α = 0.05), except line × tester × location interaction. Variances attributable to lines and testers represent GCA variances, whereas the variance attributable to line × tester interaction represents SCA variance. The GCA variances for lines and testers were significant, and SCA variance was also significant (Table 2).

Mean GY of the crosses with lines from P147, Cateto, SA3, and the other CIMMYT maize populations or breeding starts are shown in Fig. 1. Duncan's multiple range tests (α = 0.01) showed that GY of the crosses with lines from P147 and Cateto populations was statistically significantly higher than GY of crosses with lines from SA3 and other CIMMYT genetic backgrounds. These results suggested that CIMMYT populations or breeding starts derived from Cateto and P147 were useful for breeding programs aimed at improving GY in Southwestern China, as well as in similar subtropical regions (e.g., Nepal; Subedi, 2015). The CIMMYT populations could also be potentially useful for breeding programs in other areas (e.g., temperate North America), as the testers used in this study were developed with materials from the United States (Fan et al., 2002, 2003, 2005).

GCA of the Lines from Different CIMMYT Maize Populations or Breeding Starts

Mean GY and GCA effects of the 25 inbred lines are listed in Table 3. The lines were ordered from highest to lowest according to mean GY (Table 3). The results revealed several interesting points. First, the GCA effects were highly correlated with mean GY of the individual lines ($P < 0.001$, with R^2 close to 1). To compare differences relative to GCA effects of the lines from different populations, the GCA effects of the 25 inbred lines were plotted (Fig. 2). All the lines from P147 had positive GCA effects, five out of nine lines from Cateto and other populations had positive GCA effects, and the two lines from SA3 had negative GCA effects. The number of lines with positive GCA effects from the three populations (P147, Cateto, and SA3) corresponded well with mean GYs of the three populations (Fig. 1). Mean GCA effects for the lines from three CIMMYT populations or breeding starts (P147, Cateto, and SA3) and other populations were 4.5, 2.8, −8.82, and −3.3, respectively. These results strongly suggested that high GY of lines developed from P147 and Cateto was mainly attributable to their GCA effects (Fig. 2, Table 3).

Introduced tropical maize germplasm has played an important role in nontemperate breeding programs globally and has been shown to enhance genetic diversity of temperate maize (López-Pereira and Morris, 1994; Gerpacio, 2001; Morris, 2002; Goodman, 2005; Reif et al., 2010; Fan et al., 2015). However, lines with genetic backgrounds related to Cateto and P147 have not been widely reported on so far. This may be because only limited information is available on the use of the Cateto landrace or CIMMYT populations that contain Cateto as a component (Hameed, 1991; Holland and Goodman, 1995; Santos et al., 2001; Salhuana and Pollak, 2006; Subedi, 2015; Fan. et al., 2016); information on P147 is also lacking. In this study, we focused on GY performance and

Table 2. Analysis of variance for grain yield of 150 testcrosses evaluated at three locations.

Source	df	Sum of squares	Mean squares	*F*-value	Prob*F*
Location	2	37,765.89	18,882.94	31.85	<0.0001
Replication(location)	6	22,242.51	3,707.09	6.25	<0.0001
Crosses	149	453,421.75	3,043.10	5.13	<0.0001
Lines	24	112,545.29	4,689.39	7.64	<0.0001
Testers	5	173,654.90	34,730.98	56.6	<0.0001
Lines × testers	120	167,221.56	1,393.51	2.27	<0.0001
Crosses × location	298	341,348.61	1,145.47	1.93	<0.0001
Lines × location	48	152,673.07	3,180.69	5.18	<0.0001
Testers × location	10	16,863.81	1,686.3809	2.75	0.0024
Lines × tester × location	240	171,811.73	715.88	1.17	0.0616
Error	894	530,001.73	592.84		

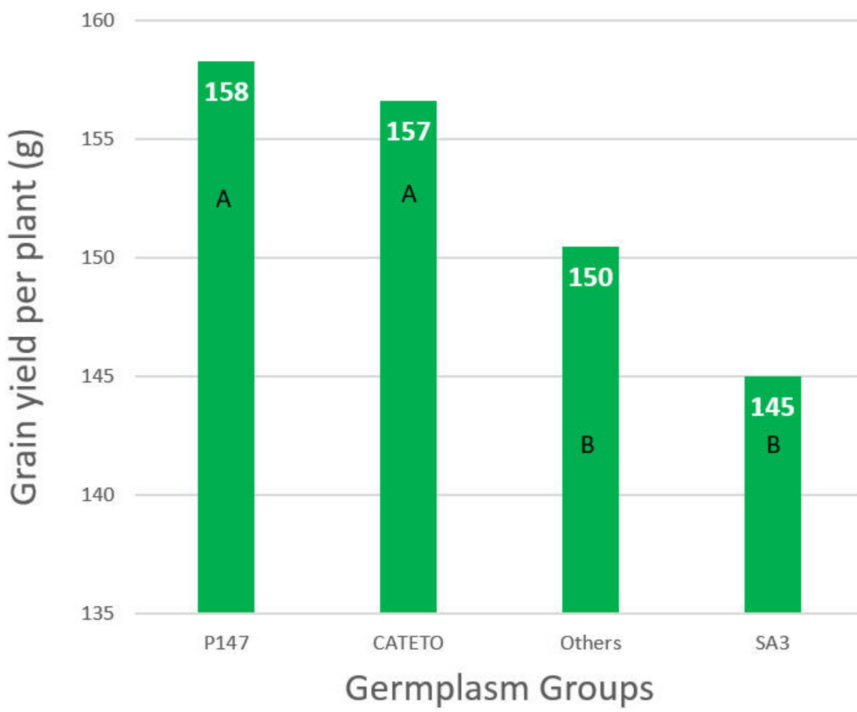

Fig. 1. Mean grain yield (g) per plant from of the crosses with lines from different CIMMYT germplasm or populations.

GCA effects of the lines from Cateto, P147, SA3, and other populations to obtain valuable information that can be used in global maize breeding programs. Hartkamp et al. (2000) used climatic data, daylength during the maize growing season, and geospatial analysis to classify nontemperate global maize production areas into 12 mega-environments. Under this classification, Yunnan, where the introduced lines were tested, was classified as temperate to subtropical warm. Based on mean temperature during the growing season, presence of similar biotic stresses affecting maize production, and preference for yellow or orange grain color, globally, there are >7 million ha across Asia, Africa, and South and North America in the subtropics and tropical midaltitude areas. The findings with the Cateto and P147 germplasm could at least be applied to maize breeding programs in these areas. In addition, in temperate maize areas, these inbred lines could be used via their introgression into temperate backgrounds to introduce new genetic diversity, as has already been done with other sources of Cateto germplasm in the 14 lines released in the US Germplasm Enhancement of Maize (GEM) project between 2003 and 2013 (GEM Project, 2017). The development of introgression lines could be especially valuable in China, where there is a concern for the lack of genetic diversity in temperate maize (Liu et al., 1997; Wang et al., 1997; Zhang et al., 2000).

During the past few years, we have successfully developed a few hybrids containing Cateto and P147 lines that have the potential for commercial release on account of their high GY in Southwestern China. These hybrids not only possessed higher GY and test weights than the commercial checks, but the grain from the hybrids of Cateto and P147 also had a shiny reddish-yellow color that is

Table 3. Mean grain yield and general combining ability (GCA) effects of 25 lines for grain yield.

Line (L) or tester (T)	Mean yield per plant	GCA effect	Populations
	g		
L24	170.60	16.78	Other
L15	167.50	13.68	Other
L3	162.96	9.14	Cateto
L6	162.01	8.19	Cateto
L9	161.69	7.87	Cateto
L1	161.06	7.25	P147
L2	159.57	5.76	Other
L21	159.55	5.73	P147
L7	158.78	4.96	Cateto
L23	157.97	4.15	P147
L10	157.14	3.32	P147
L8	156.38	2.56	Cateto
L11	155.79	1.97	Other
L20	155.74	1.92	P147
L17	154.54	0.72	Cateto
L4	152.73	–1.09	Cateto
L18	150.90	–2.92	Cateto
L5	149.55	–4.27	Cateto
L13	145.22	–8.59	SA3
L22	144.77	–9.05	SA3
L12	144.55	–9.27	Other
L19	143.32	–10.5	Other
L14	143.03	–10.79	Other
L25	138.05	–15.77	Other
L16	132.09	–21.73	Other
T1	144.47	–9.35	
T2	139.13	–14.69	
T3	162.24	8.42	
T4	169.37	15.55	
T5	162.67	8.85	
T6	145.03	–8.79	

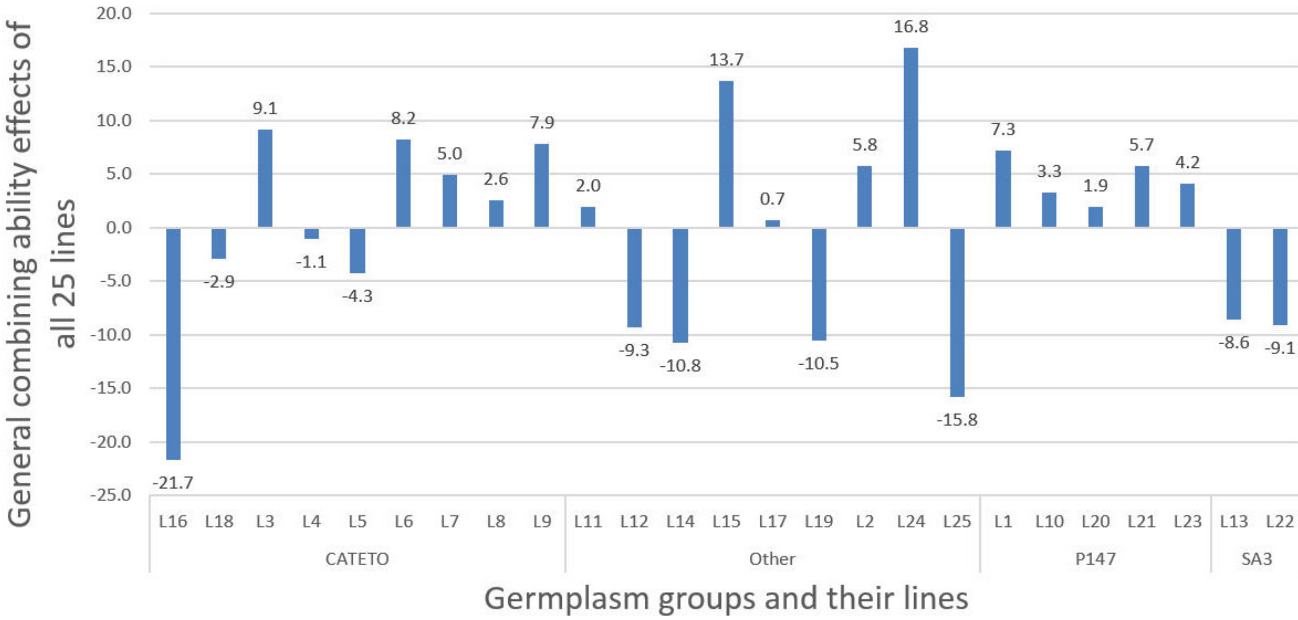

Fig. 2. General combining ability (GCA) effects of the 25 lines from different germplasm groups. The SEs for testing the GCA effects being different from zero and for testing GCA differences between lines are 3.31 and 4.69, respectively, at the $\alpha = 0.05$ level.

attractive to many farmers (Fig. 3). In addition, hybrids developed by the use of Cateto and P147 lines carried high levels of resistance to leaf blights and gray leaf spot (caused by *Cercospora zeina* Crous & U. Braun).

Information on nine key agronomic traits for the crosses derived from Cateto, P147, SA3, and other CIMMYT populations is presented in Fig. 4, where the relative value for mean of the crosses in each category is compared against the highest value among all the crosses. A population with 100% is the best population for that trait and can be used in either inbred or hybrid development programs. The results showed that of the nine selected traits, eight traits gave the highest values (i.e., 100%) for the crosses made with lines including either Cateto or P147, and only one trait (i.e., shelling percentage) had the highest value for crosses of lines from the SA3 population. These data further reflected the breeding value of the Cateto and P147 populations. In addition to Cateto and P147, the CIMMYT subtropical dent population P45 was a component of four of the five P147 inbreds (L10, L19, L20, and L21), and a line derived directly from this population L24 was the top performer in mean GY when crossed to the six testers and had the highest GCA (Table 3) and SCA for the lines evaluated (Supplemental Table S1). Line 15, of tropical origin, had the second highest mean GY in crosses to the testers, the second highest GCA (Table 3), and the second highest SCA of the lines evaluated (Supplemental Table S1). Line 15 is the only representative line from its genetic background included in this study, and it comes from a CIMMYT tropical P24 including Tuxpeno, and Antigua Group 2 germplasm that is a source of resistance to fall armyworm (*Spodoptera frugiperda* Smith). Evaluation of more P24 lines might be needed and could provide other useful inbreds for Southwestern China. Thus, these lines may also be useful in maize breeding programs.

Fig. 3. Ears of Cateto (left) and P147 (right) showing the reddish yellow grain color.

Differences Relative to GCA Effects among Lines Developed at S_3, S_4, and S_5 from the Same CIMMYT Population or Breeding Start

The GCA effects seemed to be related to generations in which selection was started. We found the GCA effects to be more stable for lines developed at the S_4 or later generations than for lines selected before the S_4 generation. For example, GCA effects of L3, L4, L5, L6, L7, and L8

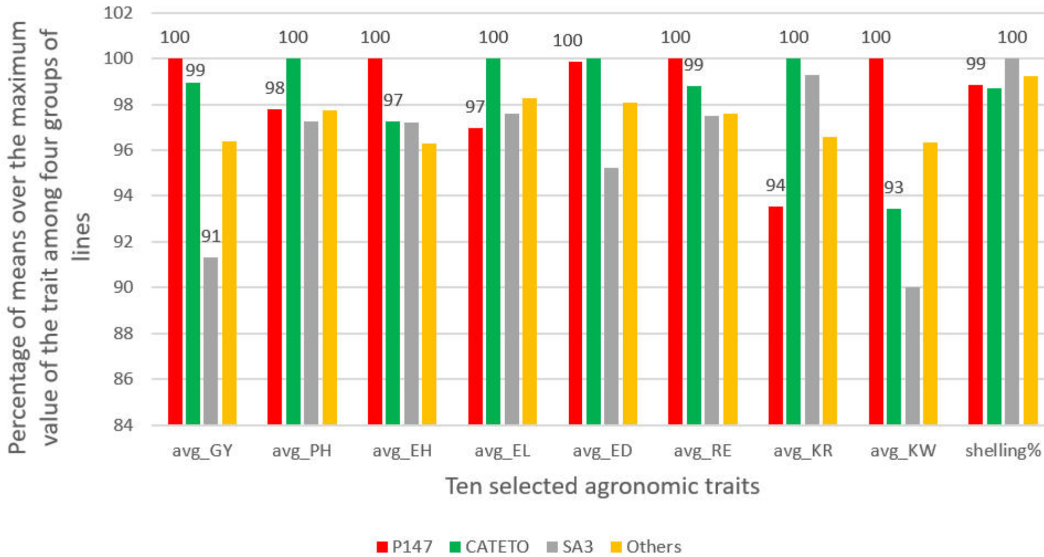

Fig. 4. Percentage of a trait value of the crosses with lines from four different CIMMYT populations divided by maximum trait value of the crosses with lines from a CIMMYT population (mean of a trait in a population × 100/maximum mean of the trait in four populations). The maximum trait values are always 100% . GY, grain yield; PH, plant height; EH, ear height; EL, ear length; ED, ear diameter; RE, number of rows of kernels per ear; KR, kernel number per row; KW, 100-kernel weight.

lines, which were developed from a common CIMMYT breeding population (Cateto), were 9.14, −1.09, −4.27, 8.19, 4.96, 2.56, respectively (Table 3). An examination of the generations in which these lines were selected (see Table 1) revealed that (i) L4 (GCA = −1.09) and L5 (GCA = −4.27) were selected in the S_4 generation (population source in Table 1); and (ii) L6 (GCA = 8.19), L7 (GCA = 4.96), and L8 (GCA = 2.56) were also selected in S_4 generation. The GCA effects for the lines selected at S_4 seemed quite stable (small variation among GCA effects). Lines L3, (L4, L5), and (L6, L7, and L8) were differentiated at S_2 (Table 1). The GCA effects of lines selected at S_2 varied more than those of lines that were selected at S_4. To confirm this finding, we examined the GCA effects of L13 (−8.95) and L22 (−9.05) developed at S_4 from SA3 population and found that these GCA effects were almost equal in magnitude. Furthermore, L21 and L23 were also selected at S_4 from a common breeding population (P147), and their GCA effects were 5.73 and 4.15, respectively. These results further suggested that GCA effects were more stable for lines developed at the S_4 or later generations than for lines selected before the S_4 generation.

Typical breeding methods used for developing inbred lines are pedigree breeding, backcrossing, bulk breeding, single-seed descent, doubled haploid, etc. Among these methods, pedigree breeding is the most widely used method to develop maize inbred lines (Bauman, 1981; Hallauer and Miranda, 1988). Selection is usually applied among progeny rows and among plants within S_1 families in pedigree breeding. This process of selfing and selection is repeated in successive generations (i.e., S_2, S_3, S_4, S_5, …, S_n) until homozygous elite inbred lines are developed (Bauman, 1981; Hallauer and Miranda, 1988). Selection for high-performing lines can begin in the S_2 generation or later (S_3, S_4, S_5, or even later generations). Bauman (1981) surveyed 130 maize breeders and found that breeders started inbred testing in S_2 (18%), S_3 (33%), S_4 (27%), S_5 (9%), or later generations (13%). The majority of breeders (33 + 27 = 60%) started testing inbred lines in S_3 or S_4 generations. This result corresponded with the proposal of Jenkins (1935), who suggested decades ago that, because combining ability of a line was established in early generations of inbreeding and remained relatively stable in successive generations, inbred lines should be tested in S_3 or S_4 generation to cull out lines showing poor combining ability. Early testing (i.e., S_2 to S_3) was questioned by Richey (1945), as he found a lack of correspondence between early and late (i.e., S_6 to S_8) testing relative to yield, thus concluding that early selection based on topcross performance would be both a waste of time and detrimental to the breeding program, as potentially high-yielding segregants might be discarded after early testing.

The current study shows that the GCA effects of lines selected at S_4 or later generations were more consistent and stable than the GCA effects of lines selected before S_4. Although this experiment was not designed specifically to identify the generation in which to start selection to obtain stable GCA effects, the results from this study corroborate the findings of Chen et al. (1994), who reported that when a parental line in a hybrid was substituted by a sister line selected at S_2 (or S_3) generation, the hybrid could have large variation in GY (i.e., 60–130% GY of the original hybrid). However, when one of the parental lines in the hybrid was substituted with a sister line selected at S_4 (or S_5), the hybrid GY increased only by ~5% and showed very little variation. Li et al. (2006) studied the combining ability of 38 sister lines developed from five different generations and found that the sister lines selected at S_2 and S_3 stages showed larger variation in GY than the sister lines selected at the S_4 or later generations. The results from the current study strongly support that the breeding practice of substituting a sister line as a parent in a commercial hybrid when inbreeding causes large decreases in hybrid seed production. Thus, although additional largescale experimental confirmation is needed, we conclude that if a sister line is used for hybrid parent line substitution, the substituted sister line should be developed at S_4 or a later generation to keep original hybrid performance stable.

Heterotic Groups of the 25 Exotic Lines from Different CIMMYT Populations

The SCA and the check heterosis (CH%) for the 150 crosses are given in Supplemental Table S1. The SCA_GY method was used to classify the 25 lines into three maize heterotic groups. The basic procedure was as follows: if a cross from a line with a tester of known heterotic group had a significant negative SCA effect, the line was assigned to the heterotic group to which the tester belonged. Further, if a line was assigned to more than one heterotic group, the line would be assigned to the heterotic group of the tester if the tester × line cross had the lowest GY. If no crosses between a line and any of the six testers had significant negative SCA effects, the line was assigned to the heterotic group of the tester in the cross with lowest GY and/or lowest SCA effect to avoid missing a cross with high GY potential.

According to the above procedure, the 25 lines were successfully assigned on the basis of SCA and GY to the three heterotic groups (i.e., Suwan1, Reid, and non-Reid, Table 4, Supplemental Table S1). The results in Table 4 and information in Table 1 revealed that all the lines originating from a specific cross from a CIMMYT breeding population might not be assigned to a single heterotic group. For example, although six lines (L3–L8) were developed from one specific cross (Table 1), five lines (L3–L7) were assigned to the Suwan1 heterotic group, but one line (L8) was assigned to the Reid heterotic group. Lines L13 and L22 from the SA3 population were assigned to the non-Reid and Reid heterotic groups, respectively. These results suggest that original CIMMYT populations or breeding starts might be genetically diverse. Research reports have shown that the CIMMYT populations were mostly grouped on the basis of agronomic trait performance, and not on the basis of heterotic groups (Vasal et al., 1992a, 1992b, 1992c). Our results confirm that the genetic base of a CIMMYT population might be quite diverse, and lines selected from a population or same breeding starts could be assigned to different maize heterotic groups.

Table 4. Heterotic groups of each of the 25 lines based on specific combining ability effects and grain yield of the 150 crosses between the 25 lines and six testers with known heterotic groups.†

Line	Population	Reid‡	Non-Reid	Suwan1	Heterotic group
L1	P147			L1	Suwan1
L2	Other	L2			Reid
L3	Cateto			L3	Suwan1
L4	Cateto			L4	Suwan1
L5	Cateto		**L5**	L5	Suwan1
L6	Cateto		**L6**	L6	Suwan1
L7	Cateto		**L7**	L7	Suwan1
L8	Cateto		**L8**	L8	Suwan1
L9	Cateto	L9			Reid
L10	P147		**L10**	L10	Suwan1
L11	Other	L11	**L11**		Reid
L12	Other	L12		**L12**	Reid
L13	SA3		L13		non-Reid
L14	Other	L14			Reid
L15	Other	**L15**		L15	Suwan1
L16	Other	L16	**L16**		Reid
L17	Cateto		**L17**	L17	Suwan1
L18	Cateto	**L18**		L18	Suwan1
L19	Other	**L19**	L19		non-Reid
L20	P147		L20		non-Reid
L21	P147	L21			Reid
L22	SA3	L22		**L22**	Reid
L23	P147	L23	**L23**	**L23**	Reid
L24	Other	L24			Reid
L25	Other	L25	**L25**		Reid

† L1–L25 are the 25 lines. If a line in a test-cross has significant negative specific combining ability (SCA) effect with a tester of known heterotic group, the line will be assigned to the same heterotic group as the tester. If a line is assigned to more than one heterotic groups, and the line will be assigned to the heterotic group of the tester in the cross between the line and the tester having the lowest grain yield. For example, for L5, when the line crosses with non-Reid and Suwan1, we found SCA = −10.40 and −12.61, respectively (Supplemental Table S1). Both SCA effects are statistically significant. Since the grain yield of the crosses with non-Reid is 147.57 and with Suwan1 is 145.78, we assigned the L5 into Suwan1, since it has lower grain yield.

‡ The heterotic groups of the lines labeled with unbolded characters are the final heterotic groups of these 25 lines.

The finding that different lines developed from a specific cross could belong to different heterotic groups might be attributable to the fact that the components of the CIMMYT maize populations were selected on the basis of agronomic trait similarities, most often from open-pollinated landraces, not on the basis of any other factor (Vasal et al., 1982). In addition, some of the breeding starts selected for inclusion in this study were derived from genetically diverse, tropical-based populations that were developed to provide improved yield, biotic stress resistance, and abiotic stress tolerance. This could explain why the lines developed from these backgrounds exhibited large genetic variation, which sometimes even caused them to be classified into different heterotic groups.

Suwan1, another tropical population, has been studied intensively in China (Fan et al., 2002, 2009, 2014; Yang et al., 2006). Research has revealed that the lines developed from Suwan1 had consistently high GY when crossed with typical local testers used in China (Fan et al., 2009, 2014). Sister lines developed from Suwan1 generally were classified into the Suwan1 heterotic group. The origin of the Suwan1 population is germplasm that was improved via recurrent S_1 selection from Thai Composite #1 of a broad genetic base that included both dent and flint germplasm (Sriwatanapongse et al., 1993). Another well-known base population is Iowa Stiff Stalk Synthetic, which was established by intermating 16 lines primarily belonging to the Reid Yellow Dent background, with above-average stalk quality. According to a molecular marker analysis, Romay et al. (2013) found the Iowa Stiff Stalk Synthetic to be well separated from other base populations. Wen et al. (2012) analyzed 94 CIMMYT lines and 54 lines developed in the US GEM project by examining 1266 single-nucleotide polymorphisms (SNPs). Principal component analysis showed that the GEM introgression lines clustered with those corresponding to the "Stiff Stalk" and "non-Stiff Stalk" heterotic grouping, whereas the CIMMYT lines were quite distinct with no obvious clusters. Further, simple sequence repeat (SSR) analysis of CIMMYT inbred lines showed no clustering of heterotic groups (Xia et al., 2005). Wu et al. (2016) found via genotyping-by-sequencing of SNPs that heterotic classification of CIMMYT maize inbred lines did not always agree with heterotic grouping based on combining ability tests and pedigree information; they further suggested that, in the future, both combining ability tests and genetic relatedness inferred from molecular marker analyses should be used for defining heterotic groups for CIMMYT germplasm.

The results for heterotic group classifications of the lines from CIMMYT, US Stiff Stalk, non-Stiff Stalk, and Suwan1 populations highlighted the fact that during the establishment of a maize breeding population, agronomic traits, genetic base, and heterotic grouping of the lines should be considered. This population-building method should help improve breeding efficiency by avoiding heterotic group reclassification of the sister lines developed from the same base population, since they would have a high chance of belonging to the same heterotic group to which the base population belonged. When genetically diverse germplasm sources are used in population improvement, segregation for heterotic grouping may occur.

CONCLUSIONS

The two CIMMYT source populations, Cateto and P147, were exceptional in performance, produced more hybrids with higher levels of GY, and possessed more favorable key agronomic traits when compared with SA3 and other genetic backgrounds included in this study. The GY advantage was mainly attributable to the fact that lines developed from Cateto and P147 populations or breeding starts had high positive GCA effects. Thus, Cateto and P147 should be explored further in global subtropical, midaltitude tropical, and temperate maize breeding programs requiring yellow or orange germplasm to broaden the genetic base while providing new alleles for exploitation, as seen in the Nepal study reported by Subedi (2015). P45 and the tropical line CL-RCY023 also provided higher yield potential than the commercial check and could be used directly or in line recycling activities for maize breeding for the same target environments.

Lines developed from a population may not necessarily be classified into a single (same) maize heterotic group. Thus, classification of lines into heterotic groups from many CIMMYT populations or breeding starts should be a necessary step in local maize breeding programs, even if different lines used in the program came from the same population. Lines selected at S_4 or a later generation from a cross would be expected to have more stable GCA effects than lines selected in earlier generations.

Conflict of Interest

The authors declare that there is no conflict of interest.

Supplemental Material Available

Supplemental material for this article is available online.

Acknowledgments

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