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Potential of tropical maize populations for improving an elite maize hybrid

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Abstract

Identifying exotic maize (Zea mays L) populations possessing favorable new alleles lacking in local elite hybrids is an important strategy for improving maize hybrids. Selection of an appropriate breeding method will increase the chance of successfully transferring these favorable new alleles into elite inbred lines of local hybrids. The objectives of this study were to: (i) evaluate 14 maize populations from CIMMYT and identify those containing favorable alleles for grain yield, ear length, ear diameter, kernel length, plant height, and ear height that are lacking in a local super hybrid [Jidan261 (W9706 × Ji853)], and to (ii) determine which inbred parent should be improved. These results showed that the populations Pob43, Pob501, and La Posta had positive and significant numbers of favorable alleles not found in hybrid W9706 × Ji853 that could be used for simultaneous improvement of its grain yield, ear length, and kernel length, and that population QPM-Y was also a good donor for improvement of ear diameter and kernel length in the hybrid. Based on allele frequencies in the two inbred lines and the donor population, when the populations Pob43, La Posta, Pob501, and QPM-Y were used as donors, inbred line W9706 would be improved by selfing the F, of the cross W9706 × donor population. These results suggested that CIMMYT germplasm has potential to improve temperate elite hybrids. The relationship between GCA and SCA from a previous study and the parameters obtained from the Dudley method are discussed. The results showed that the values of $Lpl\mu$ estimates obtained by applying the Dudley method had the same trend as GCA effects for grain yield but a less clear trend for ear length, while the trends in the relationship value were reversed for SCA between these populations and Lancaster-derived lines.

Keywords: Zea mays L, maize germplasm, favorable alleles, elite hybrid

Introduction

Recycling of elite inbreds used for breeding has led to narrowing of the genetic basis of Chinese maize (Zea mays L) germplasm (Zhang et al, 2000). Among the maize inbred lines currently used in breeding programs in China, most were derived from only five inbreds: Mo17, Dan340, Ye478, Huangzao4 and E28 (Peng and Zhang, 1994). The limited diversity within current maize germplasm can lead to genetic vulnerability to many abiotic and biotic stresses and is likely to limit future yield gains due to selection (Tallury and Goodman, 1999; Zhang et al, 2000). Introgression of exotic maize germplasm into adapted local germplasm was widely considered as an effective means of increasing favorable alleles for desirable characteristics not present in local elite germplasm, and for enhancing resistance to unpredictable biological and environmental stresses (Tallury and Goodman, 1999; Zhang et al, 2000). Previous studies suggested that maize yield in China increased by 0.01 t ha-1 and 0.025 t ha-1 with each 1% increment in genetic contribution from U.S. and CGIAR (Consultative Group on International Agricultural Research) germplasm, respectively (Li et al, 2006).

Dudley (1984, 1987) presented an innovative method for identifying populations carrying favorable dominant alleles not present in an elite hybrid, and proposed a statistic (Lplµ') to measure the relative number of favorable alleles lacking in the inbred lines used to develop an elite hybrid. Many authors had previously identified the best populations with favorable alleles for improving elite hybrids for grain yield and other traits using the Dudley theory (Dudley, 1988; Bernardo, 1990; Hogan and Dudley, 1991; Pfarr and Lamkey, 1992; Stojsin and Kannenberg, 1995; Dudley et al, 1996; Kraja et al, 2000a, b; Trifunovic et al, 2001; Taller and Bernardo, 2004; Rodriguez et al, 2007). Furthermore, the hybrids that included new inbred lines selected by the Dudley (1987) method were superior to the old hybrids (Zanoni and Dudley, 1989; Hogan and Dudley, 1991). All these results suggested that the Dudley method was an effective breeding strategy to further improve quantitative traits in contemporary elite hybrids.

Tropical and subtropical maize germplasms have valuable traits that differ from those found in temperate germplasm, such as strong roots, or disease or in-

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Name	Origin	Description					
Pob21	CIMMYT	Tropical, late maturing, white dent, Tuxpeno-based material, improved since 1977 for resis- tance to fall armyworm.					
Pob28	CIMMYT	Tropical, late maturing, yellow dent. Includes some material from Mexico and Colombia, 4 cycles of improvement through IPTTs, has undergone selection for downy mildew resistance.					
Pob32	CIMMYT	Tropical-subtropical, intermediate- to late-maturing, ETO-based material. Emphasis on ear rot resistance. Its excellent combining ability with Tuxpeno has long been recognized.					
Pob43	CIMMYT	Tropical, late maturing, white dent. La Posta-based material, Emphasis on streak resistance.					
Pob49	CIMMYT	Tropical and subtropical with white dent grain, intermediate maturity. Has undergone selec- tion for plant height.					
Pob445	CIMMYT	Heterotic to Early Yellow Heterotic Group "B". Formed by recombining S2 lines that per- formed well in testcrosses with Pool 29.					
Pob446	CIMMYT	Heterotic to Early Yellow Heterotic Group "A". Formed by recombining S2 lines that per- formed well in testcrosses with Pool 30.					
Pob501	CIMMYT	Subtropical/mid-altitude white semi-dent population. Heterotic to Population 502. Selection has emphasized yield, agronomic performance, and resistance to E. turcicum and root and stalk lodging.					
Pool 26	CIMMYT	Lowland tropical, intermediate/late maturity, yellow dent. Selected for drought tolerance.					
SG-Y	CIMMYT	Late-maturing, tall, yellow dent, good yield potential. A tendency to stay green, even at har vest time.					
QPM-Y	CIMMYT	Lowland tropical/subtropical, late in maturity, yellow dent kernel. Has 60 to 70% more lysine and tryptophan than normal maize populations.					
Suwan-1	CIMMYT	Tropical, intermediate maturing, yellow flint, 36 diverse germplasm sources and two sources of downy mildew resistance with high yield, Philippine DMR 1 and 5 (Sriwatanapongse et al 1993).					
La Posta	CIMMYT	Lowland tropical, late-maturing, white dent. Selected for drought tolerance. Relatively tall with high yield potential. Six cycles of improvement completed and inbred lines developed.					
Tuxpeno	CIMMYT	Lowland tropical, late-maturing, white dent population. Selected for drought tolerance. Relatively short with moderate-to-high yield potential. Ten cycles of selection for drought tolerance completed.					
Jidan261 (H	lybrid)	China, W9706 × Ji853					
Ji853 (Inbre	d line)	China, Huangzao4-derived line					
W9706 (Inbr	red line)	China, (Mo17 \times U8112) \times Mo17					

Table 1 - Description of the maize germplasm used in this study.

sect pest resistance (Goodman, 1999; Li et al, 2000). Materials from CIMMYT have widely been used as exotic germplasm for improving local populations or inbred lines across the world (Holland and Goodman, 1995; Goodman, 1999; Tallury and Goodman, 1999; Kraja et al, 2000a, b; Li et al, 2000, 2001; Mickelson et al, 2001; Goodman, 2004; Yang et al, 2006; Nelson and Goodman, 2008). In addition, improved tropical and subtropical maize germplasm reportedly has a high frequency of elite alleles and very good general combining ability with temperate germplasm (Holland and Goodman, 1995). Therefore, tropical and subtropical maize germplasm are often used to broaden the temperate maize germplasm base (Ron Parra and Hallauer, 1997; Fan et al, 2010). In China, 14 tropical and subtropical populations introduced from CIM-MYT since 1996 were improved for adaptation to temperate regions, and had high general combining ability for grain yield and resistance traits (Li et al, 2001; Yang et al, 2006). One of the challenges for Chinese maize researchers is to determine the best way to exploit these populations in maize breeding programs in China.

Because little research has been done to evaluate tropical populations from CIMMYT for contributions

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to elite temperate germplasm in China, this study will provide valuable information to private and public breeders for future improvement of temperate maize inbreds. The objectives of this experiment were to: (i) identify CIMMYT populations with favorable alleles as donors for improvement of yield and yield components of an elite hybrid (W9706 × Ji853) that is widely grown in northern China; and to (ii) determine which inbred parent should be improved and whether a backcross or selfing of the F_1 would be the best method for improving a targeted inbred line.

Materials and Methods

Plant Materials

Fourteen CIMMYT populations (Table 1) were chosen for analysis to identify favorable alleles not present in the elite hybrid Jidan261 (W9706 × Ji853). The elite hybrid Jidan261 exhibits the heterotic pattern of Lancaster × Sipingtou and is well adapted to northeastern China. Inbred lines Ji853 and W9706 were developed by the Jilin Academy of Agricultural Sciences and represented elite germplasm of SPT (Sipingtou, a Chinese landrace and its derivatives) and Lancaster (Lancaster Sure Crop) (Xia et al, 2006), respectively.

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Case	Estimator	Bias
\overline{q}_{j0} . \overline{q}_{kl}	$1/4[(I_1 \times P_y) + (I_2 \times P_y) - (I_1 \times I_2) - I_1]$	$1/2(k\overline{p}_k-j\overline{q}_j)\mu$
$\overline{q}_{j_0},\overline{q}_{j_l}$	$1/2(I_2 \times P_y) - 1/4[(I_1 \times I_2) + I_2]$	$1/2j(\overline{p}_j - \overline{q}_j)\mu$
$\overline{q}_{j1.} \overline{q}_{k0}$	$1/4[(I_1 \times P_y) + (I_2 \times P_y) - (I_1 \times I_2) - I_2]$	$1/2(j\overline{p}_j - k\overline{q}_k)\mu$
$\overline{q}_{k1.}$ \overline{q}_{k0}	$1/2(I_1 \times P_y)-1/4[(I_1 \times I_2)+I_1]$	$1/2k(\overline{p}_{k}, \overline{q}_{k})\mu$

Table 2 - Estimators for $Lpl\mu$ ' for different combinations of and (Dudley, 1987)	Table 2 - Estimators	for Lplu' for diffe	erent combinations of	and	(Dudlev.	1987)
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Field experiments

The crosses W9706 \times Ji853, W9706 \times P, and Ji853 × P, were made at the Hainan experiment station of the Chinese Academy of Agricultural Sciences (CAAS) during the 2008 winter season. Bulk pollen from a minimum of 100 plants was collected and used to pollinate at least 100 female plants. Seed bulks from the W9706 \times P crosses and the Ji853 \times P crosses were obtained for use in field experiments. The W9706 \times P $_{_{\rm V}}$ crosses, the Ji853 \times P $_{_{\rm V}}$ crosses, W9706 \times Ji853, and one commercial check (Xianyu335) were evaluated in a generalized lattice design with five blocks of six entries and three replications in each of three locations. Replicates were planted at the Gongzhuling experiment station of the CAAS (43°31'51.11"N, 124°47'53.43"E, 265 m altitude), at the Shenyang experiment station of the Liaoning Academy of Agricultural Sciences (41°48'2.38"N, 123°30'3.67"E, 58.2 m), and at the Shunyi experiment station of the CAAS in Beijing (40°13'29.57", 116°34'3.19", 49 m) in both 2009 and 2010. The inbred lines Ji853 and W9706 were grown in a randomized block design with 10 replications adjacent to the cross experiment in the same three locations.

The entries were grown in two-row plots in 5 m rows with spacing of 0.6 m in all three locations. The population densities were 45,000 plants ha⁻¹ at Gongzhuling and Shenyang, and 52,500 plants ha⁻¹ at Shunyi. Common agronomic practices for maize production were applied at all locations. Field data at Shunyi in 2009 was removed from this analysis due to the occurrence of a windstorm during the growing season.

Planting and harvesting were done by hand. Grain yield measured for each plot was converted to Mg/ha and was adjusted to 155 g kg⁻¹ moisture. Five traits including grain yield (GY), ear length (EL), ear diameter (ED), kernel length (KL), plant height (PH), and ear height (EH) were analyzed in this study. These traits were measured on 10 plants per entry from each rep-

Table 3 - Mean grain yield (GY), ear length (EL), ear diameter (ED), kernel length (KL), plant height (PH), and ear height (EH) of inbred lines, hybrids, and inbred × population crosses in 3 environments, combined.

Population	GY(M	GY(Mg/ha)		EL(cm)		ED(cm)		KL(cm)		PH(cm)		EH(cm)	
	I,	I ₂	I ₁	I ₂	I,	I ₂	I,	I_2	l,	I ₂	I,	I ₂	
Pob21	6.95	6.92	16.93	18.98	4.68	4.31	0.80	0.81	325.71	313.71	172.13	150.57	
Pob28	7.58	6.82	16.82	18.29	4.80	4.34	0.93	0.87	279.40	269.76	137.43	117.32	
Pob32	7.68	7.83	16.93	19.04	4.91	4.51	0.89	0.89	302.39	301.14	153.18	144.18	
Pob43	7.96	7.95	17.66	19.74	4.86	4.46	0.93	0.89	306.03	302.53	154.73	140.77	
Pob49	6.34	7.21	17.07	19.37	4.78	4.39	0.87	0.84	312.88	317.95	161.87	152.67	
Pob445	6.52	5.56	15.36	17.13	4.72	4.19	0.88	0.81	267.56	258.71	115.89	100.06	
Pob446	6.57	5.89	16.09	17.08	4.64	4.12	0.85	0.80	278.16	269.24	132.11	112.43	
Pob501	7.90	7.30	17.22	19.88	4.92	4.50	0.92	0.93	305.19	295.68	156.33	137.05	
Pool 26	7.29	7.14	16.73	19.53	4.87	4.44	0.89	0.86	303.74	293.51	153.50	137.90	
SG-Y	6.46	7.30	17.22	20.26	4.66	4.39	0.80	0.85	304.92	301.22	155.14	136.83	
QPM-Y	7.02	6.26	16.06	17.52	4.97	4.44	0.98	0.84	277.79	261.83	131.86	111.25	
Suwan-1	7.50	7.22	16.50	17.60	5.01	4.57	0.91	0.90	291.92	289.48	148.98	137.98	
La Posta	7.73	7.88	17.02	19.34	4.89	4.44	0.95	0.91	311.50	305.37	156.48	139.91	
Tuxpeno	7.04	7.01	17.01	18.48	4.54	4.15	0.78	0.79	298.09	281.74	151.21	130.45	
Mean	7.18	7.02	16.76	18.73	4.80	4.38	0.88	0.86	297.52	290.13	148.63	132.10	
SE†	0.	36	0.9	94	0.1	1	0.0)5	13	.95	15	5.45	
Jidan 261	7.	58	17.:	21	4.7	74	0.9	94	270	.20	114	1.51	
Ji853	3.	87	12.	75	4.5	53	0.7	70	190	.41	78	3.32	
W9706	4.	36	15.	82	3.7	' 9	0.6	69	202	.64	69	9.32	
SE‡	0.	72	0.	58	0.0)6	0.0)4	13	.49	13	3.68	

† Standard error of a population $\times I_1$, or I_2 mean.

‡ Standard error of inbred means.

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Table 4 - Estimates of $Lp|\mu'$ and their rank in 14 populations analyzed for improvement of target hybrid W9706 \times Ji853 for grain yield and ear length.

Population	Grain	yield (Mg/ha)	Ear length (cm)		
	Lplµ'	Lplμ'-(Jqjμ or Kqkμ)	Lplµ'	Lplµ'-(Jqjµ or Kqkµ)	
Pob21	0.49	-0.31	1.23‡	0.89	
Pob28	0.62	0.00	0.89	0.54	
Pob32	0.93‡	0.05	1.26‡	-0.14	
Pob43	0.99‡	0.19	1.62‡	1.27*	
Pob49	0.53	-0.18	1.43‡	1.08*	
Pob445	0.03	-0.53*	0.31	0.04	
Pob446	0.13	-0.50*	0.28	0.56	
Pob501	0.82‡	0.16	1.68‡	1.34*	
Pool 26	0.63	-0.14	1.51‡	1.16*	
SG-Y	0.58	-0.14	1.87‡	1.53*	
QPM-Y	0.34	-0.28	0.51	-0.57	
Suwan-1	0.70	-0.04	0.54	0.20	
La Posta	0.95‡	0.08	1.42‡	1.07*	
Tuxpeno	0.53	-0.27	0.98	0.63	

 \ddagger Greater than 2 \times SE

*Significantly different from zero at the 0.05 level of probability

lication.

Statistical Analysis

Analysis of variance for each trait was performed using PROC GLM (SAS Institute, 2009) and PROC MIXED (Littell et al, 1996) in SAS software. Years and locations were treated as random effects and hybrids were treated as fixed effects. Replications were treated as random effects and were nested in year × location combinations. Blocks were nested in replications × year × location. PROC MIXED in SAS software was used to estimate fixed effects and error variances. Adjusted means across years and locations were output by PROC MIXED and LSMEANS in SAS software for estimating parameters (Federer and

Wolfinger, 1998).

The statistic $Lpl\mu'$ proposed by Dudley (1987) was used to identify populations with favorable alleles not present in an elite hybrid. It can be calculated from four different equations based on the frequency of recessive alleles at locus classes j and k in the donor population. Dudley (1987) described the criteria for obtaining the appropriate $Lpl\mu'$ in selected cases by estimating upper and lower limits of qj and qk (Table 2).

According to Dudley (1987), relationship values are derived from the equation $(I_2 \times P_y) - (I_1 \times P_y) + 0.5 (I_1 - I_2)$, which estimates $(J\mu pj + K\mu qk) - (J\mu qj + K\mu pk)$. If the relationship is positive and significant,

Table 5 - Relative frequency of favorable alleles ($Lp|\mu'$) and differences $Lp|\mu'-(Jqj\mu \text{ or } Kqk\mu)$ of 14 CIMMYT maize populations for ear diameter and kernel length.

Population	Ear dia	ameter (cm)	Kernel length (cm)		
	Lplµ'	Lplµ'-(Jqjµ or Kqkµ)	Lplµ'	Lplµ'-(Jqjµ or Kqkµ)	
Pob21	0.02	-0.22*	-0.01	-0.07*	
Pob28	0.08	-0.20*	0.04	-0.01	
Pob32	0.14	0.08	0.03	-0.02	
Pob43	0.11	0.06	0.05‡	0.00	
Pob49	0.07	0.02	0.02	-0.05	
Pob445	0.04	0.01	0.01	-0.03	
Pob446	0	0.05	0.01	-0.05	
Pob501	0.14	-0.12	0.05‡	-0.01	
Pool 26	0.12	-0.15	0.03	-0.02	
SG-Y	0.01	-0.17	0	-0.05	
QPM-Y	0.17‡	0.11	0.05‡	0.02	
Suwan-1	0.19‡	-0.09	0.05‡	-0.01	
La Posta	0.13	-0.15	0.06‡	0.01	
Tuxpeno	0.05	-0.30	-0.02	-0.08*	

 \ddagger Greater than 2 \times SE

*Significantly different from zero at the 0.05 level of probability

Table 6 - Relative frequency of favorable alleles ($Lpl\mu$ ') and differences ($Jqj\mu$ or $Kqk\mu$) - $Lpl\mu$ ' of 14 CIMMYT maize populations for plant height and ear height.

Population	Plant h	neight (cm)	Ear height (cm)		
	Lplµ'	Lplµ'-(Jqjµ or Kqkµ)	Lplµ'	Lplµ'-(Jqjµ or Kqkµ)	
Pob21	41.65‡	-21.76*	34.72‡	-18.03*	
Pob28	19.08‡	0.22	17.73‡	-1.40	
Pob32	32.67‡	-16.10*	28.38‡	-19.34*	
Pob43	33.93‡	-17.92*	27.92‡	-20.11*	
Pob49	40.77‡	-21.34*	32.68‡	-23.68*	
Pob445	13.36‡	1.32	8.03‡	-0.69	
Pob446	18.64‡	-3.98	15.18‡	-8.80	
Pob501	32.01‡	-12.74*	27.39‡	-11.27*	
Pool 26	31.10‡	-11.66*	26.89‡	-11.70*	
SG-Y	33.33‡	-15.51*	27.04‡	-11.16*	
QPM-Y	16.70‡	-3.80	14.82‡	-8.68	
Suwan-1	27.14‡	-9.64	25.78‡	-11.74*	
La Posta	36.01‡	-17.59*	28.14‡	-12.70*	
Tuxpeno	26.75‡	-5.77	24.46‡	-7.97	

 \ddagger Greater than 2 \times SE

*Significantly different from zero at the 0.05 level of probability

then P_y is more closely related to I_1 than to I_2 ; if it is negative and significant, P_y is more closely related to I_2 . The difference between $Lpl\mu'$ and $Jqj\mu$ or $Kqk\mu$ (dependent upon the relationship of P_y to I_1 or I_2) is used as an indicator of whether to self the F_1 generation of the inbred × donor population directly, or to backcross the donor population to the inbred line prior to selfing. Selfing is recommended if the relative number of favorable alleles is significantly higher than the relative number of unfavorable alleles, otherwise backcrossing should be considered. The standard errors of estimators were calculated as the square root of the variance of the linear function associated with each estimator. Estimators were considered different from zero if they exceeded twice their standard error.

Results

Significant differences were found for grain yield, ear length, ear diameter, kernel length, plant height, and ear height among all inbred × population crosses, hybrids and inbreds, but not for kernel length (KL) in inbreds (ANOVA table not shown). Hybrid Jidan261 showed a significant heterosis advantage over inbred W9706 and Ji853 for all traits (Table 3). Grain yield, ear length, and plant height were significantly greater in the inbred W9706 than in Ji853, while ear diameter and ear height were significantly greater in Ji853 than in W9706.

Grain yield

Grain yield of the hybrid W9706 \times Ji853 showed significant heterosis over the inbreds W9706 and Ji853, which indicated the presence of positive and dominant alleles considered favorable for improving the target hybrid (Dudley, 1988; Trifunovic et al, 2001). On average, the grain yields of population \times inbred crosses varied from 5.56 to 7.95 Mg/ha. Yields

of Ji853 × donor population crosses were significantly higher than those of the W9706 × donor population crosses. Some crosses between Ji853 or W9706 and the donor population, including Ji853 × Pob28, Ji853 × Pob32, Ji853 × Pob43, Ji853 × Pob501, Ji853 × La Posta, W9706 × Pob32, W9706 × Pob43, and W9706 × La Posta, outvielded the W9706 × Ji853 target hybrid (Table 3). Four populations (Pob43, La Posta, Pob32, and Pob501), had positive and significant estimates of Lplµ', and their relationship values showed that these populations were more closely related to the Lancaster inbred W9706 than to the Sipingtou inbred Ji853 (Figure 2). Therefore, Pob43, La Posta, Pob32, and Pob501 may be used to improve the target hybrid W9706 \times Ji853 from the $\rm F_{1}$ of W9706 \times donor population by selfing. However, no significant difference between Lplµ' and Jqjµ was found (Table **4**).

Ear length

For ear length, the hybrid W9706 × Ji853 showed significant heterosis over inbreds W9706 and Ji853, therefore dominant alleles considered favorable for improving the target hybrid (Trifunovic et al, 2001) were present. Ear lengths in W9706 × donor population crosses were significantly longer than in Ji853 × donor population crosses, and varied from 15.36 to 20.26 cm (Table 3). Of eight populations with positive and significant Lplµ' estimates, SG-Y, Pob501, Pob43, Pob49, and La Posta had the highest values for new favorable alleles for ear length. SG-Y and Pob49 may be used as donors to improve ear length of the target hybrid W9706 × Ji853 by selfing the F, of Ji853 × donor populations, because these populations were more closely related to Sipingtou inbred Ji853 than to Lancaster inbred W9706, as shown by their relationship values (Figure 2), for which Lplµ' was

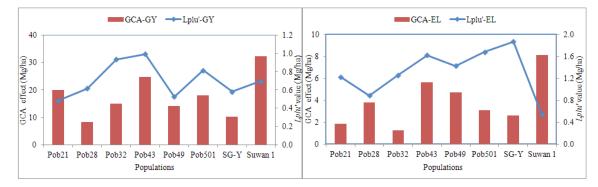


Figure 1 - Lplu' based on Dudley (1987) in this study, and GCA of eight of 14 tropical maize populations for grain yield (GY), ear length (EL) from Yang et al (2006).

significantly lower than $Jqj\mu$. Populations Pob501, Pob43, and La Posta were more closely related to W9706 than to Ji853, and may be used for improving the target hybrid W9706 × Ji853 by selfing from the F₁, because estimates for $Jqj\mu$ in those populations are significantly lower than for $Lpl\mu'$ (Table 4).

Ear diameter

For ear diameter, the hybrid W9706 × Ji853 showed significant heterosis over inbreds W9706 and Ji853: ear diameters in Ji853 × population crosses were significantly higher than in W9706 \times population crosses, and varied from 4.12 to 5.05 cm (Table 3). Therefore, dominant alleles favorable for improving the target hybrid were present. All populations tested, with the exception of Pob446, contained favorable alleles not present in parental inbreds. But only two populations, Suwan-1 and QPM-Y, had significant Lplµ' estimates; these two populations were shown to be closer to the Lancaster inbred W9706 than to the Sipingtou inbred Ji853 (Figure 2). Therefore, Suwan-1 and QPM-Y may be used as donors to improve ear diameter of the target hybrid by backcrossing from the F_1 (W9706 × Suwan-1) to W9706 prior to selfing, or by selfing from the F1 (W9706 \times QPM-Y) (Table 5).

Kernel length

Kernel length was selected as a trait for analysis because of the trend in modern maize breeding towards the development of long kernels to improve yield, and due to the potential for further improving kernel length in hybrids by utilization of CIMMYT germplasm. For this trait, the hybrid W9706 × Ji853 showed significant heterosis over inbreds W9706 and Ji853, therefore dominant alleles considered favorable for improving kernel length in the target hybrid were present. On average, kernel lengths in Ji853 \times donor population crosses were significantly longer than in W9706 × donor population crosses, and varied from 0.78 to 0.98 cm (Table 3). All of the populations tested had positive Lplu' estimates, except for Pob21 and Tuxpeno. Pob43, Pob501, QPM-Y, Suwan-1, and La Posta had significant high Lplu' estimates for kernel length. Their relationship values revealed they were closer to the Lancaster inbred W9706 (Figure 2).

Therefore, Pob43, Pob501, La Posta, Suwan-1, and QPM-Y may be used as donors to improve kernel length of the target hybrid W9706 × Ji853 by selfing from the F₁ (W9706 × Pob43, La Posta, or QPM-Y), or by backcrossing from the F1 (W9706 × Pob501, or Suwan-1) to W9706 prior to selfing. However, no statistically significant difference between $Lpl\mu$ ' and $Jqj\mu$ estimators was detected (Table 5).

Plant height and Ear height

Plant and ear height were chosen for analysis because the introduction of tropical germplasm usually results in taller plants that are more susceptible to lodging (Goodman, 1999). Favorable alleles for shorter plants and lower ear height are usually recessive (Dudley, 1988; Dudley et al, 1996; Kraja and Dudley, 2000a). Therefore, the selection of accessions with high frequencies of favorable recessive alleles for plant or ear height depends on the difference between $Jq\mu$ or $Kqk\mu$ (based on whether inbred line I, or I_2 is to be improved) and Lplµ' (Dudley et al, 1996). For the target hybrid W9706 × Ji853, only Pob28 and Pob445 had more favorable recessives alleles than unfavorable dominant alleles for plant height, and none of the populations tested had significant positive values for ear height (Table 6).

Discussion

In a previous study by Yang et al (2006), the same eight populations included in our materials were evaluated for general combining ability for grain yield, ear length, and ear diameter, and specific combining ability with Chinese maize germplasm. Histograms between Dudley parameters estimates and GCA effects in Figure 1 show grain yield and ear length. The values of Lplu' estimates and GCA effects showed the same trends for grain yield but a less clear trend for ear length. The relationship values derived from application of the Dudley (1987) method and SCA effects are both shown in Figure 2. The trends of the relationship values were opposite to those for SCA between the donor populations and the Lancaster lines. Because the GCA and SCA effects were obtained from other studies with different sets of maize

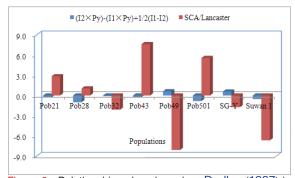


Figure 2 - Relationship values based on Dudley (1987) in this study, and SCA with Lancaster for grain yield of eight of 14 tropical maize populations from Yang et al (2006). Note: If $(I_2 \times P_y) - (I_1 \times P_y) + 1/2 (I_1 - I_2) > 0$ or SCA>0, then P_y is more closely related to Ji853 than to W9706; if $(I_2 \times P_y) - (I_1 \times P_y) + 1/2 (I_1 - I_2) < 0$ or SCA<0, then P_y is more closely

related to W9706 than to Ji853.

materials, these relationships certainly need to be confirmed by well-designed experiments for calculating $Lp|\mu'$ estimates and GCA/SCA effects from the same experimental data.

The 14 CIMMYT populations described here were evaluated to improve the elite hybrid Jidan 261. This elite hybrid was adopted by farmers in northeastern China and has been used as a check in maize variety trials at the national level (Xia et al, 2006). Therefore, Jidan 261 should have more favorable alleles for adaptation to local growing regions. However, it has performed poorly for grain yield and resistance to lodging in recent years. If donors with favorable alleles not present in the hybrid Jidan261 can be explored, a new hybrid with better performance for all traits may be developed. The results of this study showed that most of the CIMMYT populations tested are potential donors of favorable alleles for improving the yield components of an elite hybrid (W9706 × Ji853) by successful application of the Dudley method. Additionally, the populations Pob43, Pob32, and Pob501, with the highest values of favorable alleles for grain yield, also had better general combining ability effects for grain yield and related traits, except for plant height and ear height (Li et al, 2001; Yang et al, 2002). However, if tropical maize germplasm is used to improve temperate germplasm, traits with unfavorable dominant alleles should be monitored carefully (Kraia and Dudley, 2000a; Tallury and Goodman, 1999). In our results, all of the populations tested did not possess significantly more favorable recessive alleles than unfavorable dominant ones for both plant and ear height. Therefore, populations should be monitored carefully for plant and ear height in temperate maize breeding programs. Furthermore, the hybrid W9706 × Ji853 was representative of the Lancaster × Sipingtou heterotic pattern widely used in the northeastern China, and the results of this study will further contribute to improvement of hybrids from the Lancaster × Sipingtou heterotic group or inbred lines.

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References

- Bernardo R, 1990. Identifying populations useful for improving parents of a single cross based on net transfer of alleles. Theor Appl Genet 80: 349-352
- Cai Z, Liu YC, Xu MX, Zhang ZQ, 2010. Research on breeding and application of maize inbred line Ji853. J Maize Sci 18: 1-5 (in Chinese with English abstract)
- Dudley JW, 1984. A method for identifying populations containing favorable alleles not present in elite germplasm. Crop Sci 24: 1053-1054
- Dudley JW, 1987. Modification of methods for identifying populations to be used for improving parents of elite single crosses. Crop Sci 27: 940-943
- Dudley JW, 1988. Evaluation of maize populations as sources of favorable alleles. Crop Sci 28: 486-491
- Dudley JW, Lamkey KR, Geadelmann JL, 1996. Evaluation of populations for their potential to improve three maize hybrids. Crop Sci 36: 1553-1559
- Fan XM, Zhang YD, Liu L, Chen HM, Yao WH, Kang MS, Yang JY, 2010. Improving grain yield and yield components of temperate maize using tropical germplasm. J New Seeds 11: 28-39
- Federer WT, Wolfinger RD, 1998. SAS code for recovering intereffect information in experiments with incomplete block and lattice rectangle designs. Agro J 90: 545-551
- Goodman MM, Castillo F, Moreno J, 1990. Choosing and using exotic maize germplasm, pp. 148-171. In: 26th Annual Illinois Corn Breeders' School. Univ of Illinois
- Goodman MM, 1999. Broadening the genetic diversity in maize breeding by use of exotic germplasm, pp139-148. In: The Genetics and Exploitation of Heterosis in Crops. Coors JG, Pandey S eds. ASA-CSSA-SSSA, Madison, WI
- Goodman MM, 2004. Developing temperate inbreds using tropical maize germplasm: Rationale, results, conclusions. Maydica 49: 209-219
- Hogan RM, Dudley JW, 1991. Evaluation of a method for identifying sources of favorable alleles to improve an elite single cross. Crop Sci 31: 700-704
- Holland JB, Goodman MM, 1995. Combining ability of tropical maize accessions with US germplasm. Crop Sci 35:767-773
- Kraja A, Dudley JW, 2000a. Identification of tropical and temperate maize populations having favorable alleles for yield and other phenotypic traits. Crop Sci 40: 941-947

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- Kraja A, Dudley JW, White DG, 2000b. Identification of tropical and temperate maize populations having favorable alleles for disease resistance. Crop Sci 40: 948-954
- Li HM, Hu RF, Zhang SH, 2006. The impact of U.S. and CGIAR germplasm on maize production in China. Agri Sci in China 5: 563-571
- Li MS, Li XH, Deng LW, Zhang DG, Bai L, Zhang SH, 2007. Comparisons of four testers in evaluating 27 CIMMYT and Chinese maize populations. Maydica 52: 173-179
- Li XH, Li MS, Yuan LX, Zhang SH, 2000. Research on improvement and utilization of tropical and subtropical maize germplasm. Scientia Agricultura Sinica 33(Suppl.): 20-26 (in Chinese with English abstract)
- Li XH, Xu SZ, Li JS, Liu JL, 2001. Heterosis among CIMMYT populations and Chinese key inbred lines in maize. Acta Agro Sin 27: 575-581 (in Chinese with English abstract)
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, 1996. SAS system for mixed models. SAS Institute, Cary, NC
- Mickelson HR, Cordova H, Pixley KV, Bjarnason MS, 2001. Heterotic relationships among nine temperate and subtropical maize populations. Crop Sci 41:1012-1020
- Nelson PT, Goodman MM, 2008. Evaluation of elite exotic maize inbreds for use in temperate breeding. Crop Sci 48: 85-92
- Peng ZB, Zhang SH, 1994. Development of maize hybrids in China. TAMNET 1: 3
- Pfarr DG, Lamkey KR, 1992. Evaluation of theory for identifying populations for genetic improvement of maize hybrids. Crop Sci 32: 663-669
- Rodriguez VM, Malvar RA, Butron A, 2007. Maize populations as sources of favorable alleles to improve cold-tolerant hybrids. Crop Sci 47: 1779-1786
- Ron Parra J, Hallauer AR, 1997. Utilization of exotic maize germplasm. Plant Breeding Review 14: 165-187

- SAS Institute, 2009. SAS system for Windows. Version 9.1.3. SAS Institute, Cary, NC
- Sriwatanapongse S, Jinahyon S, Vasal SK, 1993. Suwan-1: Maize from Thailand to the World. CIM-MYT, Mexico
- Stojsin D, Kannenberg LW, 1995. Evaluation of maize populations as sources of favorable alleles for improvement of two single cross hybrids. Crop Sci 35: 1353-1359
- Stuber CW, 1978. Exotic sources for broadening genetic diversity in corn breeding programs. Proc Annu Corn Sorghum Ind Res Conf 33: 34-47
- Taller JM, Bernardo R, 2004. Diverse adapted populations for improving northern maize inbreds. Crop Sci 44: 1441-1449
- Tallury SP, Goodman MM, 1999. Experimental evaluation of the potential of tropical germplasm for temperate maize improvement. Theor Appl Genet 98: 54- 61
- Trifunovic S, Husic I, Rosulj M, Stojsin R, 2001. Evaluation of U.S. and Yugoslavian maize populations as sources of favorable alleles. Crop Sci 41: 302-308
- Xia YF, Xu MX, Liu YC, Yu MY, Dai XY, Liu AH, 2006. The breeding of maize hybrid Jidan 261. J Maize Sci 14: 87-89, 91 (in Chinese with English abstract)
- Yang AG, Zhang SH, Li MS, Rong YZ, Pan GT, 2006. Combining ability and heterosis of 14 CIMMYT and 13 domestic maize populations in an NC mating design. Acta Agro Sin 32: 1329-1337 (in Chinese with English abstract)
- Zanoni U, Dudley JW, 1989. Comparison of different methods of identifying inbreds useful for improving elite maize hybrids. Crop Sci 29: 577-582
- Zhang SH, Peng ZB, Li XH, 2000. Heterosis and germplasm enhancement, improvement and development of maize. Scientia Agricultura Sinica 33(Suppl.): 34-39 (in Chinese with English abstract)