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EVALUATION OF COMBINING ABILITY OF QUALITY PROTEIN MAIZE DERIVED FROM U.S. PUBLIC INBRED LINES

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ABSTRACT - Quality Protein Maize (QPM) has improved nutritional quality due to the *opaque2* mutation as well as hard endosperm conferred by uncharacterized modifier genes. We have developed a series of QPM inbred lines based on crosses between public U.S. Corn Belt-adapted lines with QPM lines developed at the International Wheat and Maize Improvement Center (CIMMYT). The resulting inbred lines exhibit characteristics of other QPM germplasm including translucent endosperm and elevated concentration of the essential amino acids lysine and tryptophan. We characterized the genetic mechanisms controlling yield of hybrids made from the QPM inbreds. For machine harvestable grain yield, specific combining ability was significant, while general combining ability was significant only for the inbreds designated as males in the study, suggesting both additive and non-additive genetic effects were important for determining yield of these temperate QPM hybrids. Hybrids produced from different QPM donor lines on average had higher yields than hybrids produced in from the same donor lines, suggesting the combining ability of the QPM donor may contribute to the performance of these hybrids.

KEY WORDS: *Opaque2*; Nutritional quality; Combining ability; Hybrid.

INTRODUCTION

Maize (*Zea mays* L.) is an important source of food and feed, but its nutritional value is limited by its low concentration of protein and the poor quality of this protein. One reason the quality of maize grain protein is low is essential amino acids lysine and tryptophan are deficient relative to the dietary requirements of monogastric animals, including humans. In animal feed, these deficiencies are corrected by addition of supplements that add to the feed cost. Genetic improvements to the amino acid balance of maize grain would reduce the need for supplementation, reducing the cost of animal feed.

Several approaches have been used to improve the amino acid balance of maize grain. Recurrent selection for amino acid concentration has been shown to be effective (Choe *et al.*, 1976; Scott *et al.*, 2008). Several transgenic approaches have been shown to be effective as well (Lai and Messing, 2002; Huang *et al.*, 2004, Huang *et al.*, 2005; Houmard *et al.*, 2007; Bicar *et al.*, 2008; Frizzi *et al.*, 2008). Naturally occurring mutations have been used as well. The approach most commonly used relies on *opaque2 (o2)*, a recessive mutation that increases the levels of tryptophan and lysine in the grain (Mertz *et al.*, 1964). The *opaque2* mutation has a number of pleiotropic effects, including soft kernels that are prone to insect attack and fungal infections, resulting in reduced germination rate and yield. Thus, much of the effort when working with *opaque2* involves overcoming these pleiotropic effects to improve the seed quality and agronomic characteristics. Several groups of researchers have independently succeeded in producing *o2/o2* germplasm with acceptable agronomic characteristics and seed quality, and have designated this germplasm Quality Protein Maize (QPM) (Prasanna *et al.*, 2001; Gevers and Lake, 1992; Vasal *et al.*, 2004). QPM is potentially valuable for feed and food, but little if any QPM germplasm is adapted to the U.S. Corn Belt. Using QPM germplasm as starting material, additional QPM varieties adapted to Canada (Zarkadas *et al.*, 2000), Brazil, Southern U.S. (Bhatnager *et al.*, 2004), and Kenya and Rwanda (Ngaboyisonga *et al.*, 2009) have been developed.

The objectives of this study were to characterize a set of QPM inbred lines derived from U.S. public inbred lines. First, we sought to establish that the lines are QPM by evaluating amino acid content and

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grain translucence. We then sought to determine repeatability and general and specific combining ability (SPRAGUE and TATUM, 1941) of agronomic traits (yield, grain moisture content, root lodging and stalk lodging) of a set of hybrids with these QPM inbred lines as parents. Because the choice of the direction of cross can be important for production of hybrid seed, we sought to determine if reciprocal crosses were different than direct crosses for the agronomic traits we evaluated. These data suggest strategies for obtaining optimal performance from these inbred lines and for development of new QPM inbred lines for use in hybrid maize production.

MATERIALS AND METHODS

Temperate QPM inbred lines were derived from crosses between two CIMMYT QPM donor lines (CLRQ00502 and CLQ06901) and recurrent parent inbred lines released from Iowa State University (Table 1). F1 and BC1 lines were produced in Mexico by CIMMYT. The Iowa QPM lines were developed from the BC1 generation by three generations of pedigree selection for agronomically desirable individuals. Selected plants were self-pollinated and kernels of each selected ear were planted ear-to-row in the next season for continued inbreeding and selection. Kernels of selected ears had opacity scores of two or lower on a scale of 1 to 5, similar to elite inbred lines used in Iowa (Fig. 1). The presence of the *opaque2* gene was confirmed in these inbreds by molecular genotyping (BABU *et al.*, 2005). In some years, selection was based on tryptophan, methionine and lysine concentration evaluated using microbial amino acid analysis methods (SCOTT *et al.*, 2004) in addition to agronomic properties and grain opacity.

The grain amino acid concentration from the inbred lines used in this study was evaluated using AOAC standard method at the University of Missouri Experiment Station Chemistry Laboratory (Method 982.30 E(a,b,c), AOAC INTERNATIONAL, 2006). Crude protein was determined by combustion analysis (Method 990.03, AOAC INTERNATIONAL, 2006) using the formula crude protein = N x 6.25. ANOVA was used to identify significant variation for each amino acid and crude protein. Where significant variation was found, means of the QPM genotypes were compared to the means of two representative non-QPM genotypes using a Student's t-test to determine the probability the observed differences in the means of the two groups are due to chance.

Hybrids were produced using a North Carolina design II mating design (COMSTOCK and ROBINSON, 1952), which is a modified diallel in which parents are assigned to either the male or female group and all possible female by male crosses are made (Table 1). When inbred lines are classified into heterotic groups, this design offers the advantage of requiring fewer crosses than a complete diallel because crosses are not made between members of the same heterotic groups. This design allows estimation of general and specific combining ability. In addition, we examined reciprocal effects by making all crosses in the reverse direction as well. Experimental entries were grown from seed produced in the same environment in two-row plots in a randomized complete block design near Crawfordsville and Carroll Iowa in 2007 and near Ames, Crawfordsville, and Carroll, Iowa in 2008, with each location serving as a replication. Planting dates for these locations were May 2, May 14, May 12, May 6 and May 10, respectively. Plant densities were similar to what is used in this region for commercial corn production (approximately 65,000 plants per hectare), and fertilization was carried out according to recommendations for commercial corn production. Immediately prior to harvest, plots were visually scored for root lodging (percentage of leaning plants) or stalk lodging (percentage of plants broken below the ear). At grain maturity, plots were harvested with a plot combine equipped with a weigh bucket and moisture meter. Average moisture content at each location varied from 13.7 to 23.6%. These data were used to calculate yield at 15.5% moisture.

Statistical procedures

To gain an overview of the data with respect to the significance of genotype effects, environmental effects, and the direction in which crosses were made in production of the hybrids, trait data were initially subjected to ANOVA using the following linear model in which all terms in the model were considered fixed effects:

TABLE 1 - *Iowa QPM inbred lines, source QPM lines from CIMMYT, source germplasm of the Iowa lines and gender designation for the design II mating design.*

QPM line	Recurrent Parent	Source of QPM[1]	Origin	Designated Gender
BQPM1	B97	CLQ06901	Iowa Corn Borer Synthetic No. 1 (R) C9	Male
BQPM2	B98	CLQ06901	Pioneer two-ear Composite (FR) C5	Male
BQPM3	B99	CLRQ00502	Iowa Corn Borer Synthetic No.1 (R) C10	Male
BQPM4	B100	CLRQ00502	(B85 x H99)H99	Male
BQPM5	B113	CLQ06901	Pioneer two-ear Composite (FR) C9	Male
BQPM6	B104	CLQ06901	Iowa Stiff Stalk Synthetic [BS13(S)C5]	Female
BQPM7	B109	CLRQ00502	(B73 x BS20)B73	Female
BQPM8	B110	CLQ06901	Iowa Stiff Stalk Synthetic [BS13(S)C5]	Female

[1] CLQ06901 is a direct derivative of QPM population 69 (Templado Amarillo QPM). It has intermediate maturity and a yellow flint grain type. CLRQ00502 is a recycled QPM line representing subtropical population 502. There is little genetic relationship between the two lines.

$$Y = \text{mean} + \text{Year} + \text{Loc[Year]} + \text{Dir/Rec} + \text{Genotype[Dir/Rec]} + \text{Year x Dir/Rec} + \text{Loc[Year]} \times \text{Dir/Rec} + \text{error}$$

Where

Y	=	the observed value
Mean	=	the overall mean value of the experiment
Year	=	the effect of the year of the yield trial (2007 or 2008)
Loc[Year]	=	the effect of the location(Ames, Carroll or Crawfordsville) nested within Year
Dir/Rec	=	whether the parents of the hybrid were crossed as designated in Table 1 (direct) or with the male and female designations reversed (reciprocal)
Genotype[Dir/Rec]	=	the effect of genotype nested within Dir/Rec

Fixed effects were used because our inference space is limited to this set of observations.

No more than 1% of the observations made for each trait were removed as outliers. Repeatability was calculated by dividing variance of the Genotype[Dir/Rec] by the total variance. For yield, contrasts between the direct and reciprocal version of individual hybrids were examined for statistical significance.

To obtain information about the combining abilities of the parental lines, we next carried out ANOVA with the year and location effects combined to represent an effect called "environment". Since the direct/reciprocal effect was not significant in the previous analysis, we combined these observations for this analysis. The genetic effects divided into Parent 1 (those lines designated as males), Parent 2 (those lines designated as females) and Parent 1 x Parent 2 interaction effects. The model used was:

$$Y = \text{mean} + \text{Loc} + \text{Parent 1} + \text{Parent 2} + (\text{P1} \times \text{P2}) + (\text{Loc} \times \text{P1}) + (\text{Loc} \times \text{P2}) + \text{error}$$

Where:

Y	=	the observed value
Mean	=	the overall mean value of the experiment
Environment	=	the effect of the environment
Parent 1 or P1	=	the effect of the parent of the hybrid from the "male" group
Parent 2 or P2	=	the effect of the parent of the hybrid from the "female" group

As before, all effects were fixed, limiting the inference space to this set of observations.

To determine if the combining ability of the QPM donor line impacted the yields of our hybrids, one-way ANOVA and Student's t-test were carried out to compare means of hybrids produced with the same QPM donor to the means of hybrids produced with different QPM donors.

RESULTS AND DISCUSSION

We initiated a program to develop U.S. Corn Belt-adapted QPM hybrids. Our approach was to carry out four generations of pedigree selection in populations derived from crosses between inbred lines released by Iowa State University and CIMMYT QPM lines (Table 1, see Materials and Methods for

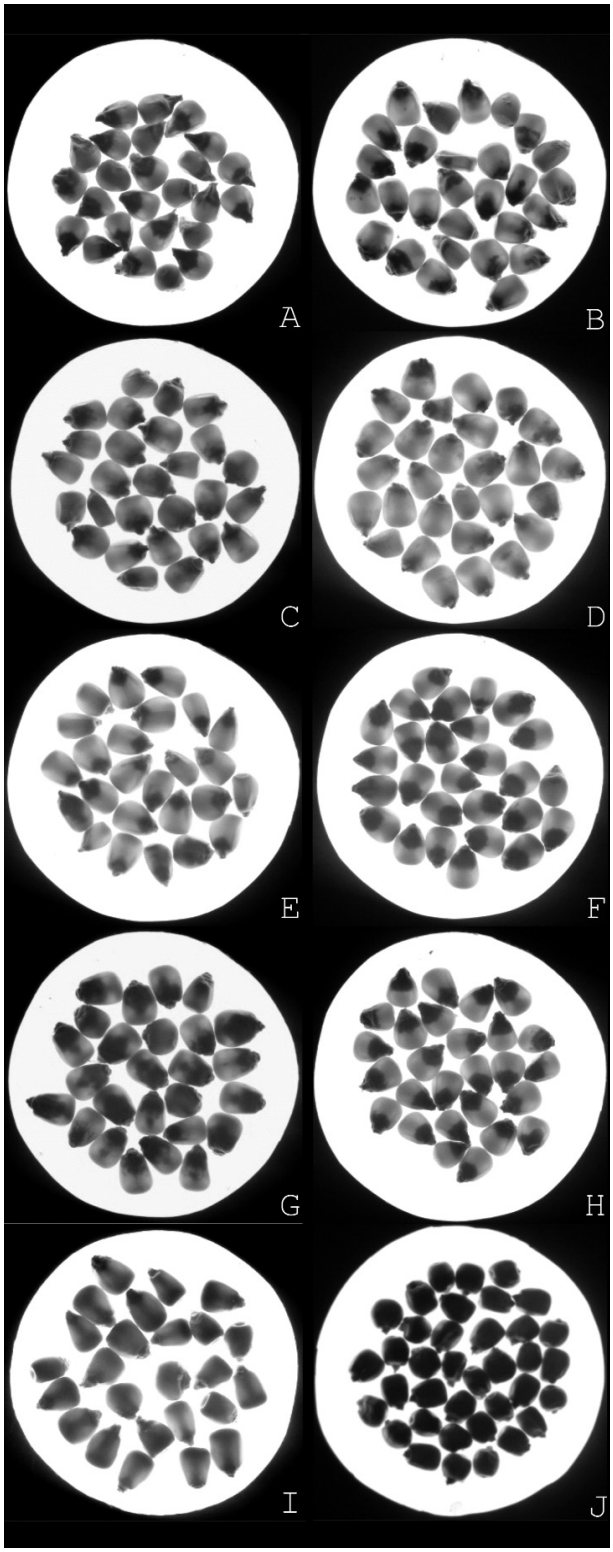

FIGURE 1 - Photograph of the abaxial side of back-lit kernels of the 8 inbred lines used in this study. A. BQPM1, B. BQPM2, C. BQPM3, D. BQPM4, E. BQPM6, F. BQPM7,G. BQPM8, H. BQPM5, I. B110, J. *o2/o2*.

TABLE 2 - *Amino acid concentration of eight QPM inbred lines used in this study and representative normal inbreds B110 and B97.*

Amino acid	BQPM1	BQPM2	BQPM3	BQPM4	BQPM5	BQPM6	BQPM7	BQPM8	B110	B97	QPM vs. w.t.[b]
Asp	0.76[a]	1.11	0.87	0.71	0.79	0.69	0.87	0.85	0.52	0.68	
Thr	0.33	0.38	0.32	0.34	0.30	0.33	0.35	0.37	0.27	0.35	
Ser	0.33	0.38	0.32	0.31	0.28	0.35	0.34	0.40	0.33	0.38	
Glu	1.43	1.70	1.39	1.51	1.24	1.56	1.66	1.94	1.45	1.82	
Pro	0.81	0.98	0.86	1.02	0.71	0.94	0.91	1.00	0.64	0.91	
Gly	0.46	0.50	0.41	0.45	0.41	0.45	0.48	0.48	0.31	0.37	**
Ala	0.55	0.66	0.53	0.55	0.48	0.60	0.62	0.75	0.61	0.74	
Cys	0.25	0.30	0.23	0.28	0.23	0.26	0.27	0.29	0.17	0.22	*
Val	0.53	0.60	0.50	0.55	0.45	0.53	0.57	0.60	0.39	0.52	
Met	0.16	0.18	0.14	0.17	0.16	0.19	0.17	0.18	0.16	0.18	
Ile	0.30	0.36	0.29	0.31	0.27	0.32	0.33	0.39	0.30	0.36	
Leu	0.80	0.99	0.82	0.84	0.71	0.93	0.82	1.09	1.04	1.30	*
Tyr	0.25	0.29	0.25	0.25	0.22	0.26	0.29	0.33	0.26	0.31	
Phe	0.37	0.44	0.36	0.35	0.32	0.39	0.37	0.46	0.41	0.49	
Lys	0.43	0.51	0.39	0.43	0.39	0.42	0.44	0.47	0.29	0.33	**
His	0.39	0.44	0.36	0.41	0.31	0.38	0.40	0.39	0.23	0.33	*
Arg	0.61	0.71	0.51	0.57	0.51	0.62	0.59	0.67	0.39	0.43	**
Trp	0.09	0.09	0.08	0.09	0.08	0.09	0.09	0.09	0.06	0.06	**
Asp/pn	0.085	0.097	0.094	0.074	0.094	0.07	0.084	0.074	0.064	0.069	
Thr/pn	0.037	0.033	0.034	0.035	0.036	0.034	0.034	0.032	0.033	0.036	
Ser/pn	0.037	0.033	0.034	0.032	0.033	0.036	0.033	0.035	0.041	0.039	**
Glu/pn	0.159	0.148	0.150	0.156	0.147	0.159	0.161	0.168	0.180	0.186	**
Pro/pn	0.090	0.086	0.093	0.106	0.084	0.096	0.088	0.087	0.079	0.093	
Gly/pn	0.051	0.044	0.044	0.047	0.049	0.046	0.047	0.042	0.038	0.038	**
Ala/pn	0.061	0.058	0.057	0.057	0.057	0.061	0.060	0.065	0.076	0.076	**
Cys/pn	0.028	0.026	0.025	0.029	0.027	0.027	0.026	0.025	0.021	0.022	**
Val/pn	0.059	0.052	0.054	0.057	0.053	0.054	0.055	0.052	0.048	0.053	
Met/pn	0.018	0.016	0.015	0.018	0.019	0.019	0.016	0.016	0.020	0.018	
Ile/pn	0.033	0.031	0.031	0.032	0.032	0.033	0.032	0.034	0.037	0.037	**
Leu/pn	0.089	0.086	0.088	0.087	0.084	0.095	0.080	0.095	0.129	0.133	**
Tyr/pn	0.028	0.025	0.027	0.026	0.026	0.027	0.028	0.029	0.032	0.032	**
Phe/pn	0.041	0.038	0.039	0.036	0.038	0.040	0.036	0.040	0.051	0.050	**
Lys/pn	0.048	0.045	0.042	0.045	0.046	0.043	0.043	0.041	0.036	0.034	**
His/pn	0.043	0.038	0.039	0.042	0.037	0.039	0.039	0.034	0.029	0.034	*
Arg/pn	0.068	0.062	0.055	0.059	0.060	0.063	0.057	0.058	0.048	0.044	**
Trp/pn	0.010	0.008	0.009	0.009	0.009	0.009	0.009	0.008	0.007	0.006	*
Crude Protein	8.97	11.46	9.28	9.65	8.43	9.80	10.31	11.53	8.07	9.80	

[a] Values are g amino acid/100 g grain or g amino acid/(100 g grain x % protein).

[b] t-test results for comparison between the QPM and normal inbreds. * and ** indicate the probability of a greater value of t due to chance is less than 0.05 or 0.01, respectively.

details). It is surprising we were able to develop modified endosperm *o2/o2* lines in so few generations. One possible explanation for this observation is in the development of QPM, modifier genes were assembled into linkage blocks that were largely inherited intact in our selection program. A second possibility is the modified endosperm trait is conditioned by a few major alleles. In addition, the rapid conversion suggests the endosperm modification trait has a high heritability.

TABLE 3 - *Mean squares resulting from ANOVA of four agronomic traits for 30 crosses evaluated in five environments.*

Effect [a]	Df	Yield (Mg/Ha)	Moisture (%)	RtLdg[b] (plants/plot)	Skldg[c] (plants /plot)
Year	1	9.0 *	101.9 **	95.4 **	61.8 **
Loc[Year]	3	73.6 **	777.0 **	126.5 **	34.1**
Dir/Rec	1	0.0 n.s.	5.1 n.s.	0.9 n.s.	1.0 n.s.
Genotype[Dir/Rec]	28	3.3 **	15.1 **	10.4 *	6.6 n.s.
Year x Dir/Rec	1	0.1 n.s.	1.5 n.s.	7.3 n.s.	9.5 n.s.
Loc[Year] x Dir/Rec	3	0.2 n.s.	3.2 n.s.	2.9 n.s.	9.9 n.s.
Error	127	1.6	3.4	6.6	6.7
Repeatability[d]		0.17	0.13	0.18	0.15
Model R^2		0.61	0.87	0.50	0.32

* Probability of greater F <0.05. ** Probability of greater F<0.01. n.s., not significant.
[a] The effect abbreviations are: Loc, location; Dir/Rec, Direct crosses (i.e. plants in the male group (Table 1) were used as males) vs. reciprocal crosses (i.e., plants in the male group were used as females).
[b] Root lodging.
[c] Stalk lodging.
[d] Repeatability = Variance of Genotype [Dir/Rec] effect / Total variance.

TABLE 4 - *Mean squares resulting from ANOVA of four agronomic traits of 15 direct and reciprocal crosses.*

Effect [a]	Df	Grain Yield (Mg/Ha)	Grain Moisture (%)	RtLdg[b] (plants/plot)	Skldg[c] (plants /plot)
Environment	4	56.7 **	523.6 **	177.8 **	40.9 **
Parent 1 (GCA)	4	7.4 **	36.6 **	34.5 **	16.8 *
Parent 2 (GCA)	2	0.0 n.s.	13.4 n.s.	55.4 **	1.9 n.s.
P1 x P2 (SCA)	8	5.6 **	16.6 *	6.7 n.s.	3.7 n.s.
Env x Parent 1	16	2.1 *	9.9 n.s.	21.1 **	8.8 n.s.
Env x Parent 2	8	2.8 **	3.7 n.s.	26.7 **	12.9 *
Env x P1 x P2	32	1.5 n.s.	4.8 n.s.	8.2 n.s.	5.6 n.s.
Error	90	1.2	7.5	5.6	6.0
Model R^2		0.80	0.82	0.79	0.57

* Probability of greater F <0.05. ** Probability of greater F<0.01. n.s., not significant.
[a] The effect abbreviations are: Environment or Env, location combined with year; Parent 1, the effect of inbreds designated as males with direct and reciprocal crosses combined (a measure of GCA the effect of inbreds designated as females with direct and reciprocal crosses combined (a measure of GCA); P1 x P2, the interaction of the Parent 1 and Parent 2 main effects (a measure of SCA).
[b] Root lodging.
[c] Stalk lodging.

Kernels of the inbred lines used in this study were more vitreous than a typical *o2/o2* grain sample (Fig. 1), presumably due to selection for modifier genes most likely donated by the CIMMYT inbred lines. In order to verify our inbred lines had the desired improvements in amino acid balance, we determined the amino acid balance of these lines (Table 2). Comparison of the mean of QPM inbreds with the mean of two representative non-QPM inbreds gave results typical of other QPMs, with Lysine and Tryptophan showing significant increases of 40 and 46%, respectively, over the two non-QPM inbreds evaluated. Since crude protein was not significantly different between these two groups, this change in amino acid concentration represents redistribution of amino acids. A significant reduction in leucine in part balances the increase in other amino acids. Evaluation of the methionine concentration of germplasm in another QPM breeding program identified a reduction in

methionine concentration in *o2/o2* germplasm (SCOTT *et al.*, 2004), however we did not see a significant difference in methionine concentration between QPM and the two wild-type lines in this study.

The inbreds in this study were evaluated in hybrid combinations using a North Carolina Design II diallel mating design (COMSTOCK and ROBINSON, 1952) with reciprocal crosses. Yield, moisture, and root and stalk lodging were evaluated. To get an overview of the data, we first set out to identify the impact of environments, genotypes and the direction of crossing the hybrid parents on the traits examined using ANOVA (Table 3). The production environment effects (year and location within year) were significant for all traits. The mean of the crosses made in the direction designated in Table 1 was not significantly different than the mean of the crosses made in the reciprocal direction for any of the traits examined, as evidenced by the Dir/Rec effect in Table 3. Further, comparison of the yields individual hybrids in the direct and reciprocal direction showed no significant differences. The genotype effects within the direction the crosses were made were significant for yield and moisture, but not for root or stalk lodging, although repeatabilities were relatively low, ranging from 0.13 to 0.17.

One of our goals was to characterize the combining ability of the inbred lines. One advantage of the North Carolina Design II mating design is ANOVA can be conducted using a linear model in which the parameters are related to general and specific combining ability (GCA and SCA) and, therefore, can be tested for significance. Thus, the male and female effects reflect general combining ability of individual lines, while the male x female interaction reflects the specific combining ability of a cross. Since no significant difference was found between direct and reciprocal crosses, these data were combined. Thus, the lines designated as Males in Table 1 were designated as Parent 1 and the lines designated as Females were designated as Parent 2 and these effects were used for determination of GCA (Tables 4 and 5) while crosses were designated as the interaction of these parents and used for determination of SCA. For grain yield, the effect of Parent 1 was significant while the effect of Parent 2 was not. Grain moisture and Stalk lodging gave similar results, while the effects of both parents were significant in Root lodging. This suggests that GCA has an effect on the agronomic traits measured, at least for some inbreds. The interaction of the Parent 1 and Parent 2 effects was significant for Grain yield and Grain moisture, but not for Root lodging or Stalk Lodging. These significant effects are an indication of the importance of specific combining ability. Because of the significance of this effect for yield, we examined it in more detail by examining the least squares mean yields for each cross. These estimates are presented in Table 5. The significance of the overall Parent 1 x Parent 2 interaction effect is emphasized by a high yield value for BQPM8 x BQPM4 (7.4 Mg/ha**) and low yield values for BQPM6 x BQPM5 (4.7 Mg/ha**). The significant GCA for Parent 1 is driven by a high value for BQPM4 (6.5 Mg/ha**) and a low value for BQPM2 (5.2 Mg/ha**).

Because two QPM donors were used, it is possible that yields are explained in part by residual combining characteristics carried forward from these two QPM donors. This is reasonable because only two backcrosses were made to the recurrent parent prior to initiating pedigree selection. This means on average, the inbreds tested in this study

TABLE 5 - *Least squares means of yield (Mg/ha, ± standard error) for five lines designated as males, three lines designated as females and their crosses with data from direct and reciprocal crosses combined.*

		Parent 2			
		BQPM6	BQPM7	BQPM8	Mean
Parent 1	BQPM1	5.9 ± 0.3	6.4 ± 0.3*	5.5± 0.3	5.9 ± 0.2
	BQPM2	5.4 ± 0.3	5.3 ± 0.3	5.0 ±0.4	5.2 ± 0.2**
	BQPM3	6.5 ± 0.3*	5.2 ± 0.3*	6.1 ± 0.4	6.0 ± 0.2
	BQPM4	6.6 ± 0.3	5.6 ± 0.4**	7.4 ± 0.4**	6.5 ± 0.2**
	BQPM5	4.7 ± 0.3**	5.1 ± 0.4**	5.1 ± 0.4	5.4 ± 0.2*
	Mean	5.8 ± 0.1	5.8 ± 0.1	5.8 ± 0.2	5.8 ± 0.1**

* Probability of greater t <0.05 in a test of a null hypothesis that each parameter estimate equals zero.

** Probability of greater t <0.01 in a test of a null hypothesis that each parameter estimate equals zero.

contain one-fourth of the genomic complement of the QPM donor by decent. Examination of the data in Tables 5 reveals that hybrids made between inbreds derived from different QPM donors did in fact tend to have higher yields than hybrids made between inbreds with the same QPM donor. To examine this in more detail we compared the means of crosses made between lines derived from different QPM donors and lines derived from the same QPM donors and found crosses made between lines derived from different QPM donors to be significantly (Probability of $> t < 0.001$) higher (6.34 vs. 5.3 Mg/ha). This observation suggests the heterotic group and possibly the combining ability of the QPM donor should be considered when initiating a bacrossing program. Inbreds intended for use as females may best made from QPM donors that are good female parents, while inbreds intended for use as male parents may best be made from QPM donors that are good male parents.

To characterize combining abilities of the lines in this study, a potentially better comparison would be among hybrids made between inbreds derived from the same QPM donor. When grain yields of the subset of lines made with QPM donor CLQ06901 was examined using the same model that was used for the full study, no significant GCA or SCA effects were found. This observation lends support to the hypothesis that the combining abilities of the QPM donor parents are contributing to the combining abilities of the BQPM lines.

The significance of general and specific combining ability has important implications for designing a breeding strategy. General combining ability is attributed primarily to additive gene effects, while specific combining ability is attributed to non-additive gene effects (dominance and epistasis). When improving traits such as grain yield, where specific combining ability is important, testing a larger number of hybrids may allow identification of combinations that are significantly better than others. Alternatively, for traits in which general combining ability is important, such as root lodging in this study, it may be most efficient to test more lines in fewer hybrid combinations.

A number of previous studies have examined GCA and SCA in QPM with mixed results. A study of inbreds with subtropical or southern U.S. adaptation found no significant GCA for grain yield, but significant SCA for this trait (Bhatnagar *et al.,* 2004), similar to our results. Conversely, a study of subtropical QPMs found significant GCA and no significant SCA (Vasal *et al.*, 1992). A study of tropical QPMs found both significant GCA and SCA for grain yield (Pixley and Bjarnason, 1993), in partial agreement with the other studies. This variation in results makes it difficult to draw general conclusions about optimal breeding approaches.

One of the main impediments to commercial use of QPM is that it frequently has low yields relative to non-QPM hybrids. While we did not include commercial check hybrids in this study, our yields were generally lower than commercial hybrids grown in similar growing conditions. It will therefore be important in future studies to compare the yield of these QPM hybrids to normal maize hybrids to determine their value for commercial use.

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