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Abstract

Relative success of maize (*Zea mays* L.) breeding programs depends on the proper choice of parental germplasm and the recognition and the use of heterotic groups. Our objective was to identify maize populations with exotic germplasm that would be potentially useful germplasm sources in temperate area maize breeding programs. A factorial mating design was used to produce 35 crosses between seven Iowa Stiff Stalk Synthetic and five non-Iowa Stiff Stalk Synthetic populations. The 12 parental populations and their 35 population crosses also were selfed to produce F2 generation. The two sets of genetic materials were evaluated at five Iowa locations for two years. Estimates of general combining ability (GCA) for each parental population and specific combining ability (SCA), heterosis (H) and inbreeding depression (ID) for each population cross were determined for grain yield. The population cross, BS10(FR)C14 by BS29(R)C3, had the greatest significant estimate of SCA (0.55^* t ha^{-1}), the greatest grain yield at the F1 (8.30 t ha^{-1}) and F2 (6.71 t ha^{-1}) generations, the lowest estimate of ID (1.59 t ha^{-1}), but the estimate of H (1.90 t ha^{-1}) was similar to the average estimate of H (1.74 t ha^{-1}) for all crosses. BS10(FR)C14 is a selected strain within the Iowa Stiff Stalk Synthetic heterotic group, whereas BS29(R)C3 is an adapted strain of Suwan-1 a tropical cultivar that originated in Thailand. BSSS(R)C14 (0.63^* t ha^{-1}) and BS13(S)C9 (0.54^* t ha^{-1}), both selected strains of Iowa Stiff Stalk Synthetic, had the greatest estimates of GCA of all parental populations; BS10(FR)C14 had a significantly positive GCA estimate (0.25^* t ha^{-1}), which was similar in magnitude to the GCA estimates for BS11(FR)C14, BS29(R)C3, and BSCB1(R)C14 of the non-Iowa Stiff Stalk Synthetic heterotic group. The data provide information on the relative performance of the populations assigned to the respective heterotic groups of the U.S. Corn Belt, and that BS29(R)C3 includes germplasm that could enhance the genetic variation of the non-Iowa Stiff Stalk Synthetic heterotic group.

Keywords

Zea mays L., Corn, Heterosis, Inbreeding depression, Heterotic groups

Disciplines

Agricultural Science | Agriculture | Agronomy and Crop Sciences | Genetics | Plant Breeding and Genetics

Comments

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ESTIMATES OF HETEROSIS AND INBREEDING DEPRESSION FOR CROSSES OF IOWA MAIZE POPULATIONS¹

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ABSTRACT - Relative success of maize (*Zea mays* L.) breeding programs depends on the proper choice of parental germplasm and the recognition and the use of heterotic groups. Our objective was to identify maize populations with exotic germplasm that would be potentially useful germplasm sources in temperate area maize breeding programs. A factorial mating design was used to produce 35 crosses between seven Iowa Stiff Stalk Synthetic and five non-Iowa Stiff Stalk Synthetic populations. The 12 parental populations and their 35 population crosses also were selfed to produce F₂ generation. The two sets of genetic materials were evaluated at five Iowa locations for two years. Estimates of general combining ability (GCA) for each parental population and specific combining ability (SCA), heterosis (H) and inbreeding depression (ID) for each population cross were determined for grain yield. The population cross, BS10(FR)C14 by BS29(R)C3, had the greatest significant estimate of SCA (0.55* t ha⁻¹), the greatest grain yield at the F₁ (8.30 t ha⁻¹) and F₂ (6.71 t ha⁻¹) generations, the lowest estimate of ID (1.59 t ha⁻¹), but the estimate of H (1.90 t ha⁻¹) was similar to the average estimate of H (1.74 t ha⁻¹) for all crosses. BS10(FR)C14 is a selected strain within the Iowa Stiff Stalk Synthetic heterotic group, whereas BS29(R)C3 is an adapted strain of Suwan-1 a tropical cultivar that originated in Thailand. BSSS(R)C14 (0.63* t ha⁻¹) and BS13(S)C9 (0.54* t ha⁻¹), both selected strains of Iowa Stiff Stalk Synthetic, had the greatest estimates of GCA of all parental populations; BS10(FR)C14 had a significantly positive GCA estimate (0.25* t ha⁻¹), which was similar in magnitude to the GCA estimates for BS11(FR)C14, BS29(R)C3, and BSCB1(R)C14 of the non-Iowa Stiff Stalk Synthetic heterotic group. The data provide information on the relative performance of the populations assigned to the re-

spective heterotic groups of the U.S. Corn Belt, and that BS29(R)C3 includes germplasm that could enhance the genetic variation of the non-Iowa Stiff Stalk Synthetic heterotic group.

KEY WORDS: *Zea mays* L.; Corn; Heterosis; Inbreeding depression; Heterotic groups.

INTRODUCTION

The identification and enhancement of elite germplasm are essential for the ultimate success of plant breeding efforts. The sequence of germplasm for maize breeders has evolved from sampling within popular, open-pollinated cultivars for development of inbred lines for the production of double-cross hybrids to inbreeding within F₂ populations of elite line crosses within the same heterotic group to develop inbred lines for use in single-cross hybrids. The evolution of germplasm sources available to maize breeders was a function of germplasm available to the breeders, information generated from genetic studies, and the development of selection and breeding methods after SHULL (1910) suggested the inbred-hybrid concept for the improvement of maize.

The inbred-hybrid concept for maize improvement is considered one of the greatest plant breeding achievements during the twentieth century. The success of the inbred-hybrid concept is predicated on the development of inbred lines that have the greatest expression of heterosis in their crosses, or hybrids. Initially, inbred lines were developed from popular open-pollinated cultivars, crosses made among inbred lines, and replicated yield trials conducted to determine the superior hybrid, which was reproduced and made available to the producers (JENKINS, 1936). Because information was lacking on

¹ The authors dedicate this paper to Professor Heinz Saedler who dedicated his MPI laboratory to explore the molecular aspects of the corn genome.

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which germplasm sources would produce better hybrids, the crosses were made between different sources in more-or-less haphazard manner. Theoretical and empirical genetic information became available which led to the concept of heterotic patterns (HALLAUER *et al.*, 1988; HALLAUER, 1999). It was found empirically that the crosses of inbred lines derived from specific sets of germplasm sources were generally greater yielding, on the average, than crosses of inbred lines derived from either the same germplasm source or from other germplasm sources. Evidence, both theoretical and empirical, has shown that the level of heterosis in crosses depends on the differences in allele frequencies of the parents and nonadditive genetic effects, such as overdominance, pseudo-overdominance, and epistasis (COORS and PANDEY, 1999). Within the U.S. Corn Belt, crosses of inbred lines between the open-pollinated cultivars Reid Yellow Dent and Lancaster Sure Crop were identified by the 1940s (TROYER, 1999). Since the 1940s, inbred lines developed from the open-pollinated cultivars were recycled to improve vigor and tolerance to pests and environmental effects; synthetic cultivars were produced by intermating inbred lines for specific traits; development of inbred lines from the synthetic cultivars; recycling of synthetic cultivars to increase frequency of favorable alleles for yield and tolerance to pests and environmental effects; continued recycling of the best performing inbred lines; and finally molecular insertion of specific genes for pest tolerance in the recycled inbred lines. Genetic improvement of inbred lines and hybrids has been effective. DUVICK (1992), for example, estimated that 50 to 60% of the yield improvement of hybrids since their introduction in the 1930s was because of better genetics. Average U.S. maize yields from 1865 to 1935 averaged 1.88 t ha⁻¹ (30 bu acre⁻¹) or less, whereas since 2000 average U.S. grain yields has been 9.16 t ha⁻¹ (146.5 bu acre⁻¹).

The widely used heterotic pattern currently used in the U.S. Corn Belt is generally designated as the Iowa Stiff Stalk Synthetic (BSSS) and the non-BSSS germplasm sources. BSSS germplasm is primarily of the Reid Yellow Dent and the non-BSSS includes germplasm not related to Reid Yellow Dent, such as Lancaster Sure Crop, Iodent, Midland, etc. BSSS was developed by intermating 16 inbred lines with above average stalk strength (SPRAGUE, 1946). BSSS has been under continuous selection since 1939, and different strains of BSSS have been important contributors of inbred lines useful as female parents

in commercial hybrids. MIKEL and DUDLEY (2006) reported that of the inbred lines granted patents and PVPs since 1980 that 63% included varying amounts of BSSS germplasm.

GOODMAN (1985) reported that U.S. maize breeders have included only 2 to 3% of the maize germplasm available in the world in their breeding programs. Because of the concerns of possible genetic vulnerability to important pests of maize and the potential of identifying useful genes for yield, pest resistance, and drought tolerance in germplasm sources outside the U.S. Corn Belt, the potential benefits from use of exotic germplasm to increase the genetic variability within U.S. maize breeding programs seems desirable. Maize originated more than 8,000 years ago in the tropical highlands of southern Mexico and Guatemala (GALINAT, 1988). Hence, maize originated in the tropics, and before tropical germplasm sources can be used effectively in temperate areas, photoperiod effects have to be mediated. Maize breeding programs in North Carolina and Iowa have been introducing and adapting tropical germplasm for possible use in temperate area maize breeding programs. The two programs used different sources of tropical germplasm. The North Carolina program introduced tropical inbred lines and hybrids, and by selfing, testcrossing, and evaluating hybrids developed inbred lines adapted to southern U.S. In contrast, the Iowa program introduced genetically broad-based tropical cultivars and by phenotypic mass selection procedures for earlier flowering for 6 to 8 years developed tropical cultivars adapted to temperate environments.

The objectives of our study were to determine 1) the heterosis expressed in crosses between two groups of cultivars, 2) the inbreeding depression expressed in the parent cultivars and their crosses, and 3) what the relation was between our estimates of heterosis and inbreeding depression. The study included 12 cultivars, with seven assigned to the BSSS heterotic group and five assigned to the non-BSSS heterotic group. Four of the 12 parental cultivars were introductions that originally were not adapted for use in U.S. Corn Belt breeding programs. Information was desired to determine how the adapted introductions would perform in crosses with the temperate cultivars. The basis for assigning the 12 parental cultivars to the respective heterotic groups was based on previous breeding information in both temperate and tropical area breeding programs.

MATERIALS AND METHODS

The 12 synthetic cultivars, herein designated as populations, have been under recurrent selection to improve grain yield, tolerance to pests, root and stalk strength, and have acceptable levels of maturity for Iowa. The 12 parental populations were assigned to two heterotic groups (BSSS and non-BSSS) based on previous breeding information. Four of the populations (BS16, BS28, BS29, and BS34) were introduced to the U.S. Corn Belt. Previous selection at Ames, IA had been completed to adapt the populations to central Iowa environments. The four populations selected for adaptation were assigned to the two heterotic groups based on previous information (KAUFFMANN *et al.*, 1982; VASAL *et al.*, 1999). Seven of the populations were included in BSSS heterotic group and five to the non-BSSS heterotic group. A brief description of the 12 populations is as follows.

BSSS Heterotic Group

- BS13(S)C9 – A strain of BSSS developed after seven cycles of half-sib and 9 cycles of S_2 recurrent selection. Selection started in 1939.
- BSSS(R)C14 – A strain of BSSS developed after 14 cycles of reciprocal recurrent selection with BSCB1 as the tester. Selection started in 1949.
- BSK(S)C11 – A strain of Krug High 1 Syn. 3 developed after 11 cycles of S_1 and S_2 recurrent selection. Krug High 1 Syn. 3 is a strain of Krug Yellow Dent. Selection started in 1953.
- BSK(H)C11 – A strain of Krug High 1 Syn. 3 developed after 11 cycles of half-sib recurrent with inbred lines and single-cross hybrids used as the testers. Selection also was initiated in 1953.
- BS10(FR)C14 – A strain of Iowa Two-ear Synthetic developed after 14 cycles of full-sib selection with BS11 as the tester. Selection was initiated in 1963.
- BS28(R)C3 – A strain developed from Tuxpeno Composite germplasm from the tropical lowlands of Mexico (HALLAUER, 1994). BS28(R)C3 was after five cycles of phenotypic selection for earlier maturity and three cycles of reciprocal half-sib recurrent selection with BS29 as the tester parent. Selection for earlier flowering was initiated in 1985 and half-sib selection started in 1992.
- BS34(S)C4 – A strain of Midland open-pollinated cultivar developed in southeastern Kansas and introduced to Iowa in 1980. S_1 and S_2 recurrent selection for adaptation, greater root and stalk strength, and improved resistance to feeding by the 1st generation European corn borer (*Ostrinia nubilalis* Hubner) was initiated in 1980.

Non-BSSS Heterotic Group

- BSCB1(R)C14 – A strain of Iowa Corn Borer Synthetic No. 1 developed after 14 cycles of reciprocal half-sib recurrent selection with BSSS as the tester. Selection started in 1949.
- BS11(FR)C14 – A strain of Pioneer Two-Ear Synthetic developed after 14 cycles of reciprocal full-sib recurrent selection with BS10 as the tester. Selection started in 1963.
- BS16(S)C2 – A strain of ETO Composite tropical cultivar obtained from Medini, Colombia, SA in 1963. After six cycles of selection for earliness, S_1 and S_2 selection were initiated in 1970s for agronomic traits and tolerance to pests.
- BS26(S)C4 – A strain of Lancaster Sure Crop Composite developed after four cycles of S_1 and S_2 recurrent selection. Selection was initiated in 1980.

BS29(R)C3 – A strain of Suwan-1, a tropical strain that originated in Thailand (HALLAUER, 1994). BS29(R)C3 was developed after five cycles of phenotypic selection for earlier maturity and three cycles of reciprocal half-sib recurrent selection with BS28 as the tester. Selection for earlier maturity was started in 1986 with half-sib selection started in 1992.

Additional information for the 12 populations was given by RASMUSSEN and HALLAUER (2006).

Seed of the parental populations and the population crosses was produced the same year to reduce possible bias due to seed age and quality. The parental populations were increased by cross-pollination among 100 plants for each population. A factorial mating design was used to produce the 35 population crosses (7 BSSS x 5 Non-BSSS) between 100 plants of each population used to make the crosses. Reciprocal crosses were made between the two parental populations for each cross. No tassel of either parent was used to make more than two crosses to increase sampling of plants within each population. A minimum of 80 pollinated ears were harvested for each population and population cross. The harvested ears were dried, and 100 kernels taken from each ear were bulked to form the seed composite for each of the 12 populations and 35 population crosses. Similar procedures were used to produce the F_2 generation of the parental populations and population crosses except all plants were self-pollinated.

Two experiments were conducted at five Iowa locations (Lewis, Carroll, Ames, Ankeny, and Crawfordsville) in 2003 and 2004. The first experiment (F_1 experiment) included 60 entries: 12 parental populations, 35 population crosses, and 13 check populations. The second experiment (F_2 experiment) included 50 entries: 12 parental populations that had been self-pollinated, 35 population crosses that had been self-pollinated, and three checks. The experimental design for each experiment at each location-year combination was a randomized complete block design with three replications. Each plot in each experiment included two rows that were 5.45 m (18 feet) long with 75 cm (30 inches) between rows. Plots were overplanted and thinned to 56 plants plot⁻¹ for a final stand of 66,974 plants ha⁻¹ (27,104 plants acre⁻¹). Plots were thinned shortly after emergence. Tillage, fertilization, and weed control were representative of those recommended for high maize productivity at each location. All plots were planted with 4-row planters adapted for small experimental plots.

Data were collected from all plots at all 10 environments (5 locations x 2 years) for grain yield (t ha⁻¹), grain moisture (%), stand density (number plants ha⁻¹), and root and stalk lodging (% of final stand). Plant and ear height (cm) data on 10 unselected plants plot⁻¹ were taken at Ames, Carroll, and Crawfordsville. Grain yield data were the total weight of shelled grain that was harvested with a combine adapted to harvest small experimental plots. The harvested grain in each plot was adjusted to 15.5% grain moisture and converted to t ha⁻¹. Grain moisture was measured by a moisture meter onboard the plot combine. Stand was recorded before anthesis for each plot and converted to plants ha⁻¹. Plant and ear height (cm) were recorded after the completion of flowering. Plant height was the average height of 10 unselected plants in a plot measured from ground level to the base of the tassel. Ear height was the average height of 10 unselected plants in a plot measured from ground level to the primary ear node. Root and stalk lodging data were recorded immediately before harvest. Root lodging (%) was the number of plants in plot that leaned more than 30% from vertical at ground level di-

TABLE 1 - Average grain yield (t ha⁻¹) for 35 crosses and 12 parental cultivars in each experiment combined across five locations for each year and across years for each location.

	Crosses		F ₁ vs. F ₂	
	F ₁ Experiment t ha ⁻¹	Crosses selfed F ₂ Experiment t ha ⁻¹	(F ₁ - F ₂) t ha ⁻¹	[(F ₁ -F ₂)/F ₁] x 100 %
Year -				
2003	5.80	3.82	1.98	-34.1
2004	8.69	5.97	2.72	-31.1
Location -				
Ames	8.70	6.17	2.53	-29.1
Ankeny	7.28	4.46	2.82	-38.7
Carroll	6.81	4.43	2.38	-34.9
Crawfordsville	7.80	5.95	1.95	-25.0
Lewis	5.58	3.46	2.12	-38.0
Average	7.23	4.90	2.33	-31.9
C.V. %	7.1	12.0	----	----

vided by the total number of plants. Stalk lodging (%) was the number of plants broken at or below the top ear node divided by total number of plants in a plot.

Individual analyses of variance were conducted for each trait at each location for the two years to examine trends across locations and years (Table 1). A combined analyses was conducted across the 10 year-location combinations (i.e., environments) for each trait. In the combined analyses, the environments and entry x environment interaction were considered random sources of variation and entries were considered as fixed sources of variation. SAS GLM was used to perform the analyses of variance for both experiments (SAS INSTITUTE, 1990). Tests of significance were done for entries and entry x environment sources of variation in both experiments. LSDs were calculated by use of the entry x environment mean square. Estimates of general (GCA) and specific (SCA) combining abilities were calculated from the factorial model analyses of the population crosses. Heterosis (H) was calculated as midparent (MP) heterosis for the crosses (F₁): H = F₁ - MP. Inbreeding depression (ID) was calculated by subtracting the mean of traits at the F₂ level from the F₁ values. Both H and ID are expressed in absolute units. All estimates were calculated from combined means across the 10 environments for each entry for each trait. Product-moment correlations between F₁ traits, between F₂ traits, and between F₁ and F₂ traits were calculated by the covariance of the two traits divided by the product of their standard deviations to determine the linear association between traits.

RESULTS AND DISCUSSION

The productivity levels of the two growing seasons were significantly different (Table 1). The 2003 growing season was drier than normal, particularly for the western locations (Lewis and Carroll), whereas 2004 was excellent for maize production

with record yields for the state. Grain yield for the F₁ experiment was 49.8% greater in 2004 compared with 2003, and for the F₂ experiment grain yields were 56.3% greater in 2004 compared with 2003. Among locations grain yield of the 35 crosses varied from 5.58 t ha⁻¹ at Lewis to 8.70 t ha⁻¹ at Ames. For the F₂ experiment, grain yield ranged from 3.46 t ha⁻¹ at Lewis to 6.17 t ha⁻¹ at Ames (Table 1). The grain yield differences among locations were greater for the three eastern locations because they were not affected as much by the drought conditions that were experienced for the two western locations in 2003. The average grain yield difference between the noninbred (F₁) and inbred (F₂) populations was 2.33 t ha⁻¹ or the F₂ generation averaged 31.9% less yield than the F₁ generation.

Populations and population crosses (F₁ experiment)

Population cross grain yields across environments ranged from 8.30 t ha⁻¹ for [BS10(FR)C14 x BS29(R)C3] to a low grain yield of 6.12 t ha⁻¹ for [BS34(S)C4 x BS16(S)C2] (Table 2). Both of the parental populations for the lowest yielding cross were introductions selected for adaptation to central Iowa and have had limited selection compared with, for example, BS10(FR)C14, which has been under continuous selection since 1963. BS29(R)C3 is a tropical cultivar adapted to central Iowa, which also has had less selection than BS10(FR)C14. But BS29(R)C3 exhibited good performance itself (6.22

TABLE 2 - Estimates of grain yield (t ha⁻¹) for 12 parent cultivars and their 35 cultivar crosses, estimates of general combining ability (GCA) for 12 parents, and estimates of specific combining ability (SCA) and heterosis for 35 cultivar crosses evaluated in three replications at five Iowa locations for two years.

Non-BSSS heterotic group	BSSS heterotic group							Average of crosses t ha ⁻¹	GCA t ha ⁻¹	Parent per se t ha ⁻¹	Average heterosis t ha ⁻¹
	BS13(S)C9 t ha ⁻¹	BSSS(R)C14 t ha ⁻¹	BSK(S)11 t ha ⁻¹	BSK(HI)C11 t ha ⁻¹	BS10(FR)C14 t ha ⁻¹	BS28(R)C3 t ha ⁻¹	BS34(S)C4 t ha ⁻¹				
BSCB1(R)C14:											
Yield	8.14	8.21	6.95	7.76	7.83	7.42	7.02	7.62	0.22*	4.72	
SCA	-0.28	0.05	-0.31	0.12	0.03	0.25	0.13	----	----	----	
Heterosis	2.94	3.31	1.80	2.46	1.89	2.22	2.12	----	----	----	2.39
BS11(FR)C14:											
Yield	8.24	7.92	7.15	7.86	7.30	7.40	7.18	7.58	0.22*	6.58	
SCA	0.16	-0.27	-0.10	0.22	-0.54*	0.22	0.31	----	----	----	
Heterosis	2.09	2.07	1.05	1.61	0.41	1.25	1.33	----	----	----	1.40
BS16(S)C2:											
Yield	7.45	7.72	6.93	7.06	7.07	6.46	6.12	6.97	-0.43*	5.41	
SCA	-0.03	0.17	0.31	0.01	-0.14	-0.13	-0.18	----	----	----	
Heterosis	1.90	2.47	1.43	1.37	0.78	0.91	0.87	----	----	----	1.39
BS26(S)C4:											
Yield	7.90	7.82	6.95	7.01	7.50	6.73	6.31	7.17	-0.21*	5.50	
SCA	0.24	0.06	0.12	-0.26	0.10	-0.07	-0.19	----	----	----	
Heterosis	2.30	2.52	1.40	1.31	1.16	1.13	1.01	----	----	----	1.55
BS291(R)C3:											
Yield	7.98	8.12	7.21	7.54	8.30	6.91	6.81	7.55	0.20*	6.22	
SCA	-0.09	-0.02	-0.01	-0.09	0.55*	-0.27	-0.06	----	----	----	
Heterosis	2.03	2.47	1.31	2.65	1.61	0.96	1.16	----	----	----	1.74
Average of crosses	7.74	7.96	7.04	7.45	7.60	6.98	6.69	7.38	----	5.75	
GCA	0.54*	0.63*	-0.36*	0.08	0.25*	-0.41*	-0.73*	----	----	----	----
Parent per se	5.65	5.14	5.56	5.88	7.18	5.70	5.12	5.69	----	5.72	----
Average heterosis	2.25	2.57	1.40	1.88	1.17	1.29	1.30	----	----	----	1.69

LSD (0.05) for each cross = 0.51.

LSD (0.05) for GCA estimates of BSSS populations = 0.18.

LSD (0.05) for GCA estimates of non-BSSS populations = 0.15.

LSD (0.05) for SCA estimates = 0.40.

t ha⁻¹) as well as averaged across all crosses (7.55 t ha⁻¹) (Table 2). Other population crosses whose grain yields were not significantly different from [BS10(FR)C14 x BS29(R)C3] included: [BS13(S)C9 x BS11(FR)C14] (8.24 t ha⁻¹); [BSSS(R)C14 x BSCB1(R)C14] (8.21 t ha⁻¹); [BS13(S)C9 x BSCB1(R)C14] (8.14 t ha⁻¹); [BSSS(R)C14 x BS29(R)C3] (8.12 t ha⁻¹); and [BS13(S)C9 x BS29(R)C3] (7.98 t ha⁻¹). The greater yielding crosses included parents [e.g., BS13(S)C9, BSSS(R)C14, BSCB1(R)C14, BS10(FR)C14, and BS11(FR)C14] that have been included in long-term selection programs in Iowa, and, based on previous data (EYHERABIDE and HAL-

LAUER, 1991; KEERATINIJAKAL and LAMKEY, 1993) would be expected to contribute to greater yielding crosses. [BSSS(R)C14 x BSCB1(R)C14] has been under selection for cross-performance and had one of the greater grain yields (8.21 t ha⁻¹), but [BS10(FR)C14 x BS11(FR)C14] that has been under similar selection pressure had less grain yield (7.30 t ha⁻¹) than expected. The two lesser yielding crosses [BS34(S)C4 x BS16(S)C2] (6.12 t ha⁻¹) and [BS34(S)C4 x BS26(S)C4] (6.30 t ha⁻¹) include parental populations with less selection for grain yield but also tended to exhibit greater grain moistures and greater incidence of root and stalk lodging (data not included).

Estimates of GCA were significantly positive for BSCB1(R)C14, BS11(FR)C14, and BS29(R)C3 and significantly negative for BS16(S)C2 and BS26(S)C4 for the non-BSSS heterotic group (Table 2). BS29(R)C4 seems to include germplasm that can contribute positive alleles for grain yield in temperate area maize breeding programs. For the BSSS heterotic group, BS13(S)C9 and BS10(FR)C14 had significantly positive estimates of GCA, whereas BS28(R)C3 and BS34(S)C4 had significantly negative estimates of GCA; the estimates of GCA for these four populations are indicative of their average grain yield in their crosses (Table 2). BSK(S)C11 was the only population that did not have an estimate of GCA that differed from zero. BSCB1(R)C14 had one of the greatest yields (8.21 t ha^{-1}) with its tester population BSSS(R)C14 and with BS13(S)C9 (8.14 t ha^{-1}), but BSCB1(R)C14 did not have good cross performance with the other parental populations of the BSSS heterotic group. Only two estimates of SCA were significantly different from zero and both estimates were not expected; significantly negative (-0.54) for [BS10(FR)C14 x BS11(FR)C14] and significantly positive (0.55) for [BS10(FR)C14 x BS29(R)C3].

Populations and crosses selfed (F₂ experiment)

The 12 parental populations and the 35 population crosses were evaluated in a comparative experiment to obtain estimates of inbreeding depression (ID) when compared with the noninbred populations and their population crosses. Inbreeding in maize causes reduction in vigor, stature, and productivity. Inbreeding results in the decrease of heterozygous genotypes with a corresponding increase of homozygous genotypes. Inbreeding depression occurs, therefore, with the changes of genotypic frequencies rather than allele frequencies because allele frequencies do not change with inbreeding (FALCONER, 1960). All of the populations have been under selection, some more than others. The goal of the selection programs has been to increase the frequency of the more favorable alleles for the traits under selection. If selection has been effective for increasing the frequency of the desirable alleles, it is expected that ID will be reduced. Desirable alleles of genes at intermediate frequencies will have greater impact on the changes of means than alleles at either higher or lower allele frequencies (FALCONER, 1960). Hence, the relative size of the estimates of ID for the populations and their crosses provide

some guide on the relative frequencies of the heterozygous and homozygous genotypes within the populations and their crosses. For the pairs of populations included in reciprocal recurrent selection program, it seems a priori that ID would decrease in the populations per se but increase in the population crosses.

Averaged for all populations and population crosses, the F₂ generation was 2.33 t ha^{-1} (31.9%) less yielding compared with the noninbred (F₁) materials (Table 1). The average estimate of ID for the 35 populations was 2.46 t ha^{-1} compared with ID estimates of 1.31 t ha^{-1} for BSSS population parents and 1.53 t ha^{-1} for the non-BSSS population parents (Table 3). As expected, the frequency of heterozygous genotypes was greater in the population crosses than in the parental populations. The estimates of ID for individual population crosses ranged from 1.59 t ha^{-1} for [BS10(FR)C14 x BS29(R)C3] to 3.16 t ha^{-1} for [BSSS(R)C14 x BS26(S)C4]. BSSS(R)C14 includes primarily Reid Yellow Dent germplasm and BS26(S)C4 includes Lancaster Sure Crop germplasm, and this diversity of germplasm was reflected in the greater estimate of ID (3.16 t ha^{-1}). Greater estimates of ID also were obtained for the crosses [BSSS(R)C14 x BSCB1(R)C14] and [BS13(S)C9 x BSCB1(R)C14], which have been under long-term selection for greater yield. For the populations themselves, the smaller estimates of ID were for BS13(S)C9, BSSS(R)C14, and BSCB1(R)C14, suggesting an increased fixation of favorable grain yield alleles within these populations. BS10(FR)C14, BS11(FR)C14, and BS28(R)C3 had estimates of ID greater than 2.00 t ha^{-1} . There was no consistent relation among the ID estimates for adapted populations of exotic germplasm vs. domestic populations; BS29(R)C3, for example, had one of the smaller estimates (1.54 t ha^{-1}), whereas BS28(R)C3 had one of the greater estimates (2.16 t ha^{-1}).

The selfed generation (F₂s) of the populations had significantly less grain yield than the noninbred populations: 7.38 t ha^{-1} (Table 2) vs. 4.90 t ha^{-1} (Table 3). The average yield of the seven populations within the BSSS heterotic group was 4.44 t ha^{-1} vs. 4.16 t ha^{-1} for the five populations within the non-BSSS heterotic group. BS29(S)C3, an adapted strain of the tropical cultivar Suwan-1, had the greatest yield (4.68 t ha^{-1}) at the F₂ generation of the five populations included in the non-BSSS heterotic groups. BS10(FR)C14 (5.09 t ha^{-1}) and BS13(S)C9 (5.04 t ha^{-1}) had the best yields of the seven BSSS heterotic group populations. The poor-

TABLE 3 - Estimates of grain yield ($t\ ha^{-1}$) for the F_2 generation of 12 parent cultivars and their 35 cultivar crosses, estimates of inbreeding depression (ID) for the 12 parent cultivars and 35 cultivar crosses, and estimates of deviations from linearity of parents, F_1 s, and F_2 s of entries evaluated in three replications at five locations for two years.

Non-BSSS heterotic group		BSSS heterotic group						Average of crosses $t\ ha^{-1}$	Parents per se $t\ ha^{-1}$	
		BS13(S)C9 $t\ ha^{-1}$	BSSS(R)C14 $t\ ha^{-1}$	BSK(S)C11 $t\ ha^{-1}$	BSK(HD)C11 $t\ ha^{-1}$	BS10(FR)C14 $t\ ha^{-1}$	BS28(R)C3 $t\ ha^{-1}$			BS34(S)C4 $t\ ha^{-1}$
BSCB1(R)C14:	Yield	5.08	5.16	4.76	4.66	5.28	4.34	4.75	4.86	3.62
	ID	3.06	3.05	2.18	3.10	2.56	3.08	2.27	2.76	1.10
	Dev.-1‡	3.17*	2.82	2.57	3.74*	3.22*	3.95*	2.34	3.10	---
	Dev.-2#	0.11	0.27	0.38	0.64	0.67	0.87	0.20	0.45	---
BS11(FR)C14:	Yield	5.52	5.02	4.41	5.06	4.89	4.80	4.69	4.91	4.54
	ID	2.71	2.89	2.74	2.80	2.41	2.61	2.49	2.66	2.05
	Dev.-1	3.32*	3.74*	4.40*	3.97*	4.40*	3.94*	3.65*	3.92	---
	Dev.-2	0.60	0.84	1.66*	1.17	1.99*	1.34	1.16	1.25	---
BS16(S)C2:	Yield	5.33	4.65	4.91	4.59	5.10	4.33	4.42	4.76	4.03
	ID	2.12	3.07	2.02	1.80	1.97	2.13	1.70	2.12	1.38
	Dev.-1	2.32	3.70*	2.59	3.52*	3.17*	3.36*	2.54	3.03	---
	Dev.-2	0.20	0.63	0.57	1.05	1.20	1.23	0.84	0.82	---
BS26(S)C4:	Yield	5.07	4.66	4.66	4.77	5.29	4.50	3.89	4.69	3.93
	ID	2.83	3.16	2.29	2.25	2.21	2.23	2.42	2.48	1.58
	Dev.-1	3.34*	3.82*	3.16*	3.16*	3.26*	3.33*	3.84*	3.42	---
	Dev.-2	0.51	0.66	0.87	0.92	1.05	1.10	1.42	0.93	---
BS29(R)C3:	Yield	5.74	5.72	5.30	4.89	6.71	4.33	4.37	5.29	4.68
	ID	2.24	2.40	1.90	2.65	1.59	2.58	2.44	2.26	1.54
	Dev.-1	2.44	2.36	2.50	3.81*	1.58	4.21*	3.74	2.95	---
	Dev.-2	-0.20	0.04	-0.59	-1.16	0.01	-1.63	-1.30	-0.69	---
Avg. crosses:	Yield	5.35	5.04	4.81	4.79	5.45	4.46	4.42	4.90	---
	ID	2.59	3.11	2.23	2.52	2.15	2.53	2.26	2.46	---
	Dev.-1	2.92	3.29	3.04	3.64	3.13	3.76	3.22	3.28	---
	Dev.-2	0.24	0.49	0.58	0.52	0.98	0.58	0.46	0.55	---
Parents per se:	Yield	5.04	4.44	4.29	4.50	5.09	3.53	4.17	4.44†	4.16§
	ID	0.61	0.70	1.28	1.38	2.09	2.16	0.95	1.31†	1.53§

LSD (0.05) for each cultivar yield is 0.50.

LSD (0.05) for estimates of inbreeding depression is 0.40.

† 4.44 and 1.31 are the average estimates of BSSS parents for F_2 grain yield and inbreeding depression (ID), respectively.

§ 4.16 and 1.53 are the average estimates of non-BSSS parents for F_2 grain yield and inbreeding depression (ID), respectively.

‡ Deviation-1 (Dev.-1) calculated as $[(P_1 + P_2)/2 + F_1 - 2F_2]$ with standard error (SE) of $1.42\ t\ ha^{-1}$.

* indicates estimates are greater than two SEs.

Deviation-2 (Dev.-2) calculated as $(MP - F_2)$ with standard error (SE) of $0.80\ t\ ha^{-1}$; * indicates estimates are greater than two SEs.

est yielding F_2 population was BS28(R)C3, an adapted strain of the tropical Tuxpeno Composite cultivar, suggesting a greater level of heterozygosity in BS28(R)C3 population compared with the BS29(R)C8 population; the estimates of ID were $2.16\ t\ ha^{-1}$ for BS28(R)C8 vs. $1.54\ t\ ha^{-1}$ for BS29(R)C3. Similar to the F_1 population data, the data for the F_2 generation of BS16(S)C2, BS28(R)C3, BS29(R)C3, and BS34(S)C4 suggest that BS29(R)C3

would be the superior choice of the four populations having exotic germplasm. [BS10(FR)C14 x BS29(S)C3] was the greatest yielding cross ($6.71\ t\ ha^{-1}$) for the F_2 generation crosses (Table 3), and this cross was also the greatest yielding cross ($8.30\ t\ ha^{-1}$) at the non-inbred level. The estimate of ID ($1.59\ t\ ha^{-1}$) for [BS10(FR)C14 x BS29(R)C3] also was the lowest value for the 35 population crosses.

Two estimates were calculated to determine the

TABLE 4 - Estimate of correlations between F_1 and F_2 generations of 35 cultivar crosses and correlations of grain yield at the F_1 and F_2 generations for grain yield, heterosis (H), midparent (MP), specific combining ability (SCA), and inbreeding depression (ID) and estimates and correlations between F_1 and F_2 generations of 35 cultivar crosses between grain yield, moisture, root and stalk lodging and plant and ear heights from data collected in three replications at five locations for two years.

Parameters	Parameters				
	Yield	Heterosis	Midparent	SCA	ID
F_1 vs. F_2 -					
Yield	0.52	0.32	0.26	0.05	0.22
Heterosis	0.09	0.22	0.00	0.03	0.37
Midparent	0.26	0.00	0.49	0.00	0.03
SCA	0.12	0.23	0.00	0.39	0.00
ID	0.07	0.05	0.03	0.16	---†
F_1 Yield vs. parameter -					
Yield	---	0.51	0.04	0.12	0.22
Heterosis	---	---	0.29	0.09	0.37
Midparent	---	---	---	0.00	0.09
SCA	---	---	---	---	0.00
F_2 Yield vs. parameter -					
Yield	---	0.63	0.49	0.30	0.07
Heterosis	---	---	0.01	0.58	0.05
Midparent	---	---	---	0.00	0.03
SCA	---	---	---	---	0.16

† Data did not permit estimation.

nonlinearity among the generations (parents, F_1 s, and F_2 s), based on their genetic expectations (Table 3). The estimates of nonlinearity (Dev.-1) that included all generations were larger and positive compared with estimates (Dev.-2) that included the parents and F_2 s. Significant departures from linearity suggest that epistatic effects were important in the expression of heterosis. The frequency of significant estimates of Dev.-1 was greater than for Dev.-2 estimates. Two tropical populations [BS28(R)C3 and BS29(R)C3] adapted to Iowa, had the largest average Dev.-1 [3.76 t ha⁻¹ for BS28(R)C3] and smallest average Dev.-1 [2.95 t ha⁻¹ for BS29(R)C3] (Table 3), and the population cross had the largest, significant Dev.-1 estimate (4.21 t ha⁻¹). The cross also had one of the larger Dev.-2 estimates (-1.63 t ha⁻¹).

Phenotypic correlations

Associations between traits were calculated between F_1 and F_2 traits and within the F_1 and F_2 generations (Table 4). The greatest correlation ($r = 0.52$) was between the F_1 and F_2 population crosses for grain yield, and this correlation was similar to the

midparent heterosis ($r = 0.49$) between the F_1 and F_2 population crosses. The correlations between midparent and grain yield for F_1 , F_2 , and F_1 vs. F_2 were 0.26, 0.04, and 0.49, respectively, and between heterosis and grain yield, the correlations were 0.32, 0.51, and 0.63, respectively. The correlations between grain yield and heterosis were consistently larger than between grain yield and midparent yield. The correlations between the F_1 and F_2 generation traits were 0.87 for grain moisture, 0.80 for plant height, 0.63 for ear height, 0.01 for root lodging, and 0.19 for stalk lodging (data not shown). The correlation ($r = 0.37$) between midparent heterosis and ID for the F_1 vs. F_2 generations was too small to have predictive value for either generation. For the parameters midparent heterosis and SCA, $r = 0.58$ for the F_2 generation, but $r = 0.09$ for the F_1 generation and $r = 0.03$ for the F_1 vs. F_2 generations. The differences between the correlation estimates may have occurred because of either different ranges in expression for the different generations or experimental errors for the two experiments.

CONCLUSIONS

The experiments included 12 parental populations that were assigned to either the BSSS or the non-BSSS heterotic groups, which are the principle heterotic groups of the U.S. Corn Belt. Four of the parental populations were adapted strains of cultivars introduced from areas outside the U.S. Corn Belt to provide additional sources of germplasm for U.S. Corn Belt breeding programs. The major goals of the study were to determine the heterosis expressed in population crosses and how the estimates of heterosis are related, or unrelated, to the estimates of inbreeding depression. Both heterosis [$X_{F_1} - MP$] = Sy^2d where $y = p-p$ and d is level of dominance] and inbreeding depression [$F_1 - F_2 = S(1/2)y^2d$] depend on the gene frequencies and some level of dominance. RASMUSSEN and HALLAUER (2006) had evaluated previously the parental populations and their 35 population crosses; average midparent heterosis for the present study (1.66 t ha⁻¹ or 34.4%) was similar to their estimates (1.78 t ha⁻¹ or 34.4%). Average inbreeding depression of the 35 population crosses was 2.46 t ha⁻¹ vs. 1.31 and 1.53 t ha⁻¹ for the BSSS and non-BSSS populations themselves. The relation between the estimates of heterosis and inbreeding depression, however, was only $r = 0.37$.

The parental populations that have been under long-term selection in Iowa tended to have the better yields per se and in crosses, smaller estimates of inbreeding depression, and positive estimates of general combining ability. The populations that included exotic germplasm performed as well in population crosses in comparison with the U.S. Corn Belt domestic germplasm populations. Two of the best five grain yielding population crosses included exotic germplasm: [BS10(FR)C14 x BS29(R)C3] (8.30 t ha⁻¹) and [BSSS(R)C14 x BS29(R)C3] (8.12 t ha⁻¹). The genetic load of deleterious recessive alleles also was not consistently greater for the populations with exotic germplasm than for the domestic U.S. Corn Belt populations. Estimates of inbreeding depression for BS29(R)C3 (1.54 t ha⁻¹) and BS16(S)C2 (1.38 t ha⁻¹) were significantly less than for BS11(FR)C14 (2.05 t ha⁻¹) and BS10(FR)C14 (2.09 t ha⁻¹). The population cross [BS10(FR)C14 x BS29(R)C3] was the greatest yielding population cross at both the F₁ and F₂ generations, and the estimates of heterosis (1.61 t ha⁻¹) and inbreeding depression (1.59 t ha⁻¹) were similar. Evidence from the present study and from RASMUSSEN and HALLAUER (2006) support the potential of BS29(R)C3

germplasm to contribute useful alleles to U.S. Corn Belt maize breeding program for grain yield. Breeders would need, however, to monitor grain maturity at harvest because BS29(R)C3 was 3.6% wetter than average of other populations and 1.7% greater grain moisture than average of other crosses (data not shown). BS29(R)C3 was equivalent to the other populations for root and stalk strength. Additionally, BS29(R)C3 had a significantly positive estimate (0.20 t ha⁻¹) of GCA with the seven populations included in the BSSS heterotic group. Because BS29(S)C3 is included in the non-BSSS heterotic group, it may be an advantage of BS29(S)C3 to develop new, unique male parents for possible use in newer hybrids.

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