

## Recurrent selection methods to improve germplasm in maize

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### Abstract

Recurrent selection (RS) schemes were introduced to increase the frequency of favorable alleles for quantitatively inherited traits. The main goal of RS was to genetically improve germplasm resources for breeding programs. Data were summarized for 14 intra-population and eight inter-population maize (*Zea mays* L) RS programs conducted in 17 genetically broad-based populations. The intra-population programs included evaluation of half-sib and full-sib families, either  $S_1$  or  $S_2$  inbred progenies, and a combination of  $S_1$  and  $S_2$  inbred progenies. The inter-population reciprocal RS programs were restricted to either half-sib or full-sib family selection. Grain yield was the primary trait considered in selection, but selection indices that include grain moisture at harvest and resistance to root and stalk lodging also were considered in making the selections that were intermated to form the next cycle population. Approximately, 10 to 20 selections were intermated for each cycle. Estimates of the genetic variation among progenies tested ( $\sigma_g^2$ ), interactions of progenies with environments ( $\sigma_{ge}^2$ ), and experimental error ( $\sigma^2$ ) were obtained from the combined analyses of variance for each cycle of selection and then averaged across cycles for each selection program. From the estimates of the components of variance, estimates of heritability ( $h^2$ ) on a progeny mean basis, the genetic coefficient of variation among progenies tested relative to their mean, (GCV), selection differentials (D), predicted genetic gains ( $\Delta_G$ ), and least significant differences (LSD) were calculated and averaged across cycles of selection. The average estimates of  $\sigma_g^2$  were largest for inbred progeny selection and smallest for half-sib family selection as expected. Averaged expected genetic gain across all intra-population selection programs was  $3.17 \text{ q ha}^{-1} \text{ yr}^{-1}$  vs  $2.32 \text{ q ha}^{-1} \text{ yr}^{-1}$  for inter-population reciprocal recurrent selection, or  $2.64 \text{ q ha}^{-1} \text{ yr}^{-1}$  across all methods. On a per cycle and per year basis the differences among types of progeny were relatively small, ranging from  $(3.57 \text{ q ha}^{-1} \text{ yr}^{-1}, 1.78 \text{ q ha}^{-1} \text{ cycle}^{-1})$  for half-sib family selection to  $(9.62 \text{ q ha}^{-1} \text{ yr}^{-1}, 3.21 \text{ q ha}^{-1} \text{ yr}^{-1})$  for  $S_2$  inbred progeny selection. Regression analyses of the square roots of  $\sigma_g^2$  with cycles of selection suggested that genetic variation was not reduced significantly with selection. Even though RS was used to determine the primary types of genetic effects that respond to selection and contribute the expression of heterosis and could ideally support basic association and genome selection studies, the principle goal of RS is to adapt and improve genetically broad-based germplasm sources for potential use in breeding programs. Few programs have integrated RS programs with development programs to isolate unique inbred lines that have potential either as parents of hybrids or use in elite line crosses to develop recycled lines. In the past 10 years North Dakota has released 18 (out of 28) derived from RS programs, six from the NDSU EarlyGEM program (also diverse), and four from elite x elite combinations. Based on the number of progenies evaluated (25,692) in the RS programs presented and the number of inbred lines (31) that met standards for a 'B' designation and release to other maize breeders, the frequency of released lines was 0.12% or 1.2 lines per 1000 tested. However, the value of each line is different. B73 is a successful example of integrating recurrent and pedigree selection programs in order to develop outstanding cultivars. These significant gains can be realized with long-term RS selection programs. National support for them is encouraged in order to develop the next generation of maize products.

**Keywords:** frequency of inbred lines, genetic variation, genetic gain, germplasm enhancement, heritability, intra- and inter-population selection, maize, recurrent selection

### Introduction

Use of cyclical selection methods is prevalent in plant breeding. There are two general types of cyclical selection methods, depending upon the primary goals of the breeding program. For breeding programs that emphasize development of improved maize (*Zea mays* L) inbred lines for hybrids, cyclical selection includes primarily selection within  $F_2$  populations from crosses of elite and normally related in-

bred lines belonging to the same heterotic group. The recycling of elite inbred lines has been used very effectively in maize breeding to develop recovered elite lines (Mikel, 2006). Although formal data are not available, it seems likely that more than 95% of the total maize breeding effort in the US is allocated to developing recycled inbred lines, especially in the private sector. The recent importance given to transgenic events is directed primarily to the insertion of specific

segments of DNA for specific herbicide or pest resistance traits, but the breeding methods of recovering the original inbred line with the inserted segment(s) of DNA are also cyclical and they are dependent on improved genetics by traditional breeding methods (Hallauer and Carena, 2009; Hallauer et al, 2010).

The other type of cyclical selection includes the genetic improvement or enhancement of genetically broad-based populations; this is usually referred to as recurrent selection (RS). Regardless of the types of germplasm undergoing cyclical selection, the primary goal, in all instances, is the same:

- 1) increase the frequency of all favorable alleles, especially the dominant ones;
- 2) maintain genetic variability.

Both types of cyclical selection methods are not exclusive. In fact, the Iowa State and North Dakota State University maize breeding programs have integrated, for a long time, germplasm improvement of genetically broad-based populations with inbred line development (Carena and Cross, 2003; Hallauer et al, 2010). In these cases, while recombination of top progenies is conducted to form improved populations, early generation progenies are also self-pollinated and testcrossed to initiate inbred line development of top progenies.

Cyclical selection methods were designed to ensure systematic, incremental genetic improvement (e.g., increase the frequency of favorable alleles) for important genetically complex traits, traits that are controlled by an unknown number of genes, each having a small effect that varies with environments. The effectiveness of cyclical selection methods differs for the two types of populations that undergo selection for either inbred lines or hybrids as their ultimate goal. Evidence of the effectiveness of cyclical selection to improve inbred line performance is mostly indirect evidence because of importance of inbred lines is their use as parents of hybrids. Genetic improvement of hybrid performance during the past 70 years has been reported in studies that made direct comparisons of hybrids used by the producers during the past decades in replicated yield trials conducted across environments (Duvick, 1977; Russell, 1974, 1986; Duvick et al, 2004). In all instances, more than 60% of the greater yields of the newer hybrids were because of the genetic improvements of the parental inbred lines and their hybrids. Duvick et al (2004) also reported that the methods designed to produce inbred lines improved the yield of the recycled inbred lines at a greater rate than their respective hybrids. Their data suggested that the level of heterosis was decreasing in the successive decades of the newer hybrids.

A greater number of direct estimates of response to cyclical (recurrent) selection have been reported for genetically broad-based populations (Hallauer and Carena, 2009; Hallauer et al, 2010). Rates of genetic gain for grain yield from RS usually ranged from 2 to

5% per cycle of selection. The levels of heterosis also increased at similar rates for populations undergoing intra- and inter-population improvement (Carena and Wicks III, 2006; Hallauer and Carena, 2009; Hallauer et al, 2010). Duvick (1977) reported a study that compared rates of genetic improvement for grain yield for cyclical selection via pedigree selection vs RS with populations; rates of genetic improvement on a per year basis were similar for the two methods.

RS programs in the public sector were originally initiated with different objectives: the concern for developing and improving germplasm resources for inbred line and hybrid development; the development of selection procedures for the improvement of quantitatively inherited traits; the comparison of the relative efficiency of different types of progenies evaluated for genetic improvement of genetically broad-based populations; and the relative importance of different types of genetic effects important in selection and the expression of heterosis. RS studies were actually initiated to determine what genetic effects were of greater importance for the response to selection, based on the suggestions by Jenkins (1940), Hull (1945), and Comstock et al (1949). Preliminary data and interpretations of RS programs have been summarized, and in most instances, additive genetic effects with partial to complete dominance were the more important gene effects affecting response to selection for grain yield (Hallauer et al, 2010). Most of the RS studies, however, were of limited duration because of limited resources to continue, change in research emphasis due to new personnel and interest, and greater emphasis on the potential benefits of molecular genetics (e.g., study at the genotypic level rather than at the phenotypic level).

The objective of this study is to summarize rates of genetic gain for different RS programs relative to responses to selection, genetic variations, heritability, and predicted responses to selection.

## Materials and Methods

### Genetic Materials

Different Iowa populations were used for different RS schemes (Table 1). Three examples are given below. Iowa Stiff Stalk synthetic (BSSS) was developed by intermating 16 inbred lines with above average stalk strength (Sprague, 1946). The initial crosses were made in 1932 at the US Department of Agriculture Research Farm at Arlington, VA. Intermatings were made to form BSSS that GF Sprague used to initiate half-sib selection in 1939. Similarly, when GF Sprague initiated a reciprocal RS program in 1949, BSSS and Iowa Corn Borer Synthetic No 1 (BSCB1) were his choice populations. BSCB1 was developed by intermating 12 inbred lines with above average resistance to first-generation feeding of the European Corn Borer (ECB) (*Ostrinia nubilalis* Hübner). Because improved stalk strength and increased resistance to feeding by first-generation ECB were serious con-

**Table 1** – Brief description and selected references for the maize populations included in the RS studies.

Population	Description	Reference
BSSS	BSSS is the designation for the Iowa Stiff Stalk Synthetic developed by intermating 16 inbred lines with above average stalk strength. The initial crosses were made by G.F. Sprague at Arlington Farms, VA in 1932. BSSS is the base population for two long-term selection programs: 1) BSSS(HT)Ci with Ia13 [(L317xBi349)(Bi345xMc401)] double-cross as tester and BS13Ci with inbred selection; and 2) BSSS(R)Ci of the reciprocal recurrent selection program with BSCB1(R)Ci as the tester. Inbred lines derived from BSSS have had a significant impact in breeding programs for the development of lines used in proprietary hybrids.	Sprague (1946) Hallauer et al (1983) Stucker and Hallauer (1992) Mikel and Dudley (2006)
BSSS(HT)	Half-sib recurrent selection in BSSS with Ia13 as tester was initiated in 1939. Seven cycles of half-sib intra-population recurrent selection was completed. BSSS(HT)Ci was the source population for B14 and B37 (cycle 0), B73 (cycle 5), B78 (cycle 6), and the progenitor population of BS13(S).	Hallauer et al (1983) Eberhart et al (1973)
BS13(S)	Following seven cycles of half-sib recurrent selection, BSSS(HT) was renamed BS13 and inbred progeny recurrent selection was initiated. Inbred lines B84, B104, B110, B119, B121, B127, and B128 were developed from BS13(S)Ci.	Hallauer and Smith (1979)
BSSS(R)	Reciprocal half-sib recurrent selection was initiated in 1949 with BSCB1(R)Ci as the tester. After eight cycles of half-sib selection, full-sib selection was used in later cycles. Inbred lines B89, B105, and B111 were developed from BSSS(R)Ci.	Hallauer et al (1983) Keeratinijakal and Lamkey (1993) Russell et al (1971)
BSSS2	BSSS2 was developed by intermating BSSS(HT)C6 and BSSS(R)C4. This population was used to determine the relative response to $S_1$ and $S_2$ recurrent selection on average yields and genetic variability.	
BSCB1(R)	Iowa Corn Borer Synthetic No 1 was the original designation of BSCB1. This population was developed by intermating 12 inbred lines with above average resistance to feeding by the first generation European Corn Borer (ECB) <i>Ostrinia nubilalis</i> Hübner. Reciprocal recurrent selection with BSSS(R)Ci as the tester was initiated in 1949. Inbred lines B54, B90, B95, B97, B99, and B120 were developed from BSCB1(R)Ci.	Hallauer et al (1974) Keeratinijakal and Lamkey (1993)
BS10(FR)	BS10 was originally released as Iowa Two-Ear Synthetic, which was developed by intermating 10 inbred lines that had a tendency for prolificacy (two-ear expression) and above average combining ability for grain yield. BS10(FR)Ci was the tester for BS11(FR)Ci in the reciprocal full-sib selection program initiated in 1964. B79 was developed from BS10(FR)Ci.	Russell et al (1971) Eyherabide and Hallauer (1991)
BS11(FR)	BS11 was originally released as Pioneer Two-Ear Synthetic No 1, developed by WL Brown of Pioneer Hi-Bred Int by crossing southern prolific materials with US Corn Belt dent lines followed by selection for prolificacy and temperate area maturity. BS11(FR)Ci was the tester for BS10(FR)Ci in the reciprocal full-sib selection program initiated in 1964. B77, B98, B113, and B115 were developed from BS11(FR)Ci. BS11 was also the source populations to evaluate response to evaluate the effects of population size on response to selection.	Hallauer et al (1974) Eyherabide and Hallauer (1991) Lamkey and Hallauer (1997) Weyhrich et al (1998a,b) Hallauer et al (1974)
BS12(HI)	BS12 is the designation for Alph, an open-pollinated cultivar grown by a farmer in southwest IA. The population has long ears, tendency to barrenness under stress, very poor root and stalk strengths, and was considered to be included in the non-BSSS heterotic group. Half-sib recurrent selection was initiated in 1950 with inbred B14 as the tester. Seven cycles were completed by 1975.	
BS16(S-HT)	ETO Composite was obtain from Medellin, Colombia in 1963. After six cycles of mass selection for earlier flowering, the populations was designated as BS16. Inbred and testcross hybrid selection were conducted to improve agronomic traits. BS16 includes 100% tropical germplasm that is adapted to the central US Corn Belt.	Hallauer and Sears (1972) Hallauer and Smith (1979)
BS21(R)	BS21 was developed by intermating BS5 and BS20, two early maturity synthetic IA cultivars. BS21 was included in two reciprocal half-sib recurrent selection programs: 1) half-sib inter-population selection with BS22(R)Ci as the tester; 2) half-sib intra-population selection with A632 inbred line as the tester. BS21 is included in the non-BSSS heterotic group.	Hallauer (1999) Menz et al (1999) Hallauer et al (2000)
BS22(R)	BS22 was developed by intermating 16 inbred lines of north-central Iowa maturity. BS22 was included in two reciprocal half-sib recurrent selection programs: 1) half-sib inter-population selection with BS21(R)Ci as the tester; 2) Half-sib intra-population selection with H99 inbred line as the tester. BS22 is included in the BSSS heterotic group.	Menz et al (1999) Hallauer et al (2000)
BS26(S)	BS26 is a synthetic cultivar developed by intermating Composite A and Composite B derived primarily from Lancaster Sure Crop germplasm. Three synthetic cultivars were crossed to 15 inbred lines and then intermated to form composite A. Composite B was formed by crossing six inbred lines with BS12(HI)C7, Nebraska Cattleman, and Composite A. Seed of Composites A and B were mixed, planted in isolation, and permitted to random mate by open pollination. From seed of the isolation intermating, 1036 $S_1$ progenies were evaluated <i>per se</i> and in testcrosses. Based on the overall evaluations, remnant seed of 50 $S_2$ early generation lines were intermated to form BS26. Inbred progeny recurrent selection was conducted for improved agronomic traits.	Hallauer (1986) Clucas and Hallauer (1986)
BS28(R)	Mass selection for earlier flowering was conducted within a composite of Tuxpeño germplasm to form BS28. Reciprocal half-sib recurrent selection for improved grain yield and agronomic traits was conducted with BS29(R)Ci as the tester.	Hallauer (1994, 1999)
BS29(R)	Mass selection for earlier flowering was conducted within Suwan-1(S)C6 germplasm to develop A strain of Suwan-1 designated as BS29. Reciprocal half-sib recurrent selection for improved grain yield and agronomic traits was conducted with BS28(R)Ci as the tester.	Hallauer (1994, 1999)
BS33(S-HI)	An accession of the Leaming open-pollinated cultivar was introduced to Iowa from Ohio as a possible alternative heterotic group in 1983. Three cycles of $S_1$ - $S_2$ progeny selection and two cycles of testcross hybrid selection (A632 and LH227 inbred lines as testers) were conducted for improved grain yield and agronomic traits to form BS33.	Kaufmann et al (1982) Carena and Hallauer (2001)
BS34(S-HI)	An accession of the Midland open-pollinated cultivar was introduced to Iowa from Kansas as a possible alternative heterotic group for the US Corn Belt in 1981. Four cycles of $S_1$ - $S_2$ progeny selection and one cycle of testcross hybrid selection (LH185 inbred line as tester) were conducted for improved grain yield and agronomic traits to form BS34.	Kaufmann et al (1982) Carena and Hallauer (2001)
BSK	BSK is a strain of the Krug Yellow Dent open-pollinated cultivar designated as Krug High1 Syn3. Selection in BSK was initiated in 1953 to compare relative rates of response to selection via half-sib and inbred progeny recurrent selection. The two selection studies were conducted to obtain empirical information relative to the importance of over-dominance vs partial dominance effects in maize. If over-dominance effects were of greater importance, response to half-sib selection would be expected to be greater than inbred selection, which would be due primarily to additive effects with partial to complete dominance.	Lonnquist (1949) Tanner and Smith (1987)
BSK(HI)	Half-sib family selection in BSK involved a series of different testers: double-cross hybrid Ia4652 [(WF9xW22)(B14xM14)] was the tester for the first three cycles; the two parental single crosses of Ia4652 were testers for cycles four and five; low yielding inbred line Krug755 was tester for the sixth cycle; an inbred line B73 was tester for cycles seven and eight. The choice of testers was based on increasing genetic variability among testcrosses. Reid Yellow Dent germplasm was included in BSK and the testers in varying amounts.	Tanner and Smith (1987)
BSK(S)	Inbred progeny selection in BSK involved $S_1$ progeny recurrent selection for cycles 0 through C5 and a combination of $S_1$ and $S_2$ inbred progeny recurrent selection was used for later cycles.	Tanner and Smith (1987)
BS2(S)	BS2 was developed by crossing six early maturity inbred lines (A251, A554, A575, A619, Mt42, and ND203) with ETO Composite (see BS16 above). The six inbred-ETO composite crosses were intermated to form BS2. Inbred progeny $S_1$ - $S_2$ recurrent selection was used to select for earlier maturity and improved agronomic traits to develop germplasm resources with tropical germplasm.	Eberhart (1971)
BSTL(S)	BSTL was derived by crossing Tuxpeño with Lancaster Sure Crop and backcrossing the cultivar cross to Lancaster Sure Crop. Therefore, BSTL includes 25% tropical germplasm. The backcross population was intermated before selection was initiated. A combination of $S_1$ - $S_2$ progeny selection conducted for improved grain yield and agronomic traits. Comparisons were to be made among BSTL, BS2, and BS16 having, respectively, 25, 50, and 100% tropical germplasm.	Eberhart (1971) Russell et al (1971)

cerns in the 1940s for developing improved parental lines for double-cross hybrids, BSSS and BSCB1 seemed logical choices as populations to test the effectiveness of reciprocal RS to improve germplasm resources for breeding purposes. BSK is an improved strain of the Krug open-pollinated cultivar that had exhibit good grain yield potential (Lonnquist, 1949). BSK, was considered a potentially useful source of germplasm for breeding purposes as well as for obtaining basic genetic information on the relative importance of genetic effects that respond to selection. Response to selection for grain yield was significant for both the testcross and inbred progeny RS (Tanner and Smith, 1987). But inbred lines that justified release have not been developed yet, perhaps, due to poor root [BSK(S)] and stalk [BSK(HI)] strength.

The selection studies included 17 genetically broad-based populations (Table 1), some with several RS programs. The BSSS germplasm, for instance, was included in five selection programs and contributed more useful inbred lines than any of the populations and/or selection programs. BSSS was one of the populations for two of the longer cycle RS programs conducted in the US: 1) the initial testcrosses for BSSS(HT) were made in 1939, and 2) the initial half-sib families for reciprocal recurrent selection (RRS) were made in 1949.

Both selection programs have been continued to the present time. Of the 17 populations included nine were considered synthetic cultivars, using the broad definition that synthetic cultivars are those formed by intermating selected genetic materials for a specific goal, such as stalk strength and pest resistance. Alph (BS12), Leaming (BS33), and Midland (BS34) are three US Corn Belt open-pollinated cultivars that have undergone selection in an effort to develop materials that could provide possible heterotic group alternatives to the Reid Yellow Dent (represented by BSSS) and Lancaster Sure Crop, which have been extensively used in the US Corn Belt and other important temperate maize production areas. This was an effort to broaden the US Corn Belt domestic germplasm base.

Because of the concern that only three of the approximately 250 races of maize have had significant use in US maize breeding programs, accessions of ETO composite, Tuxpeño composite, and Suwan-1(S)C6 were introduced to the Iowa breeding program in an effort to broaden even more the US germplasm base, following the suggestions of Brown (1953, 1975). Mass selection for earlier flowering and adaptation was practiced (Eno and Carena, 2008; Hallauer and Carena, 2009), within large sample isolation plantings, within each of the three tropical cultivars. After five to seven cycles of mass selection, ETO composite (BS16), Tuxpeño Composite (BS28), and Suwan-1(S)C6 (BS29) were adapted to central Iowa environments.  $S_1$  and testcross selection within BS16 and RRS involving BS28 and BS29 were con-

ducted to improve adaptation, grain yield, and root and stalk strength. Two populations (BSTL and BS2) that included 25 and 50% tropical germplasm were also developed to determine if response to selection would vary with different portions of tropical germplasm. Hence, a total of five populations that included different portions of tropical germplasm were included. Because of limited cycles of selection none of the five populations has provided any lines that have justified release for commercial or breeding purposes yet. Three of these populations have continued adaptation and selection in North Dakota environments. More details included in the recurrent selection studies are listed in Table 1.

#### Progeny production and recombination

The strategies used for conducting the different RS studies were similar except for developing the full-sib, half-sib, testcross, and inbred progenies used in the evaluation trials. All populations chosen for the selection studies had two or more generations of intermating before selection was initiated. Hand pollinations were used to produce all the progenies included in the evaluation trials except in the later cycles of the RRS programs conducted for BS21(R), BS22(R), BS28(R), and BS29(R). Isolation plantings of  $S_1$  progenies were conducted for each population. Progenies were planted ear-to-row and the ones acting as females were detasseled while the opposing population provided the pollen to produce the half-sib families used in the evaluation trials. The number of years and/or seasons varied during the cycles of selections. In earlier cycles, it usually required three years to complete each cycle. In later cycles, when off-season nurseries were available, intermating and production of  $S_1$  progenies were usually done in the off-season nurseries, which reduced the time-frame for completion of each cycle from three to two years per cycle. However,  $S_2$  inbred-progeny selection required a minimum of three years per cycle in all instances. It is encouraged to conduct progeny selection in one year per cycle if selection before flowering is possible either genetically (Hallauer et al, 2010) or phenotypically (Sezegen and Carena, 2009) or if winter nurseries and short-season germplasm are available (Carena et al, 2009b). Controlled winter nursery conditions for cold and drought tolerance allow four seasons per year.

The number of progenies evaluated and intermated for all intra-population selection programs were similar. Evaluation trials were mostly conducted at a minimum of three locations within one year, with two replications at each location. There were some variations, however, among cycles for the distribution of resources for data collection, which occurred primarily in the earlier selection cycles. The selection cycles  $C_0$  and  $C_1$  for BSK(S) and BSK(HI) included two replications at two locations, whereas in the  $C_2$  and  $C_3$  cycles data were obtained at four locations with two replications per location. The earlier cycles

Table 2 – Summary of the data averaged over selection cycles for each population included in the intra-population RS studies.

Population	Pro <sup>y</sup>	Cyc <sup>y</sup>	Env <sup>y</sup>	Rep <sup>y</sup>	Eval <sup>y</sup>	Sel <sup>y</sup>	Estimates of Components of Variance			GCV	h <sup>2</sup>	D	$\Delta_G$	LSD
							$\sigma_g^2$	$\sigma_{ge}^2$	$\sigma^2$					
							-----No.-----	-----q ha <sup>-1</sup> -----	-----%-----					
BS13(HT)la13	HS	7	2.2 <sup>†</sup>	2.8 <sup>†</sup>	105 <sup>†</sup>	10	6.88 (2.30) <sup>¶</sup>	7.16 (2.78)	35.58 (2.59)	4.24 [62.62-55.79]	58.2	6.83	3.97	6.5
BS13(S)	S <sub>1</sub>	9	3.0	2.0	117 <sup>†</sup>	20	42.22 (9.87)	32.02 (6.04)	52.20 (3.86)	9.80 [52.53-41.80]	69.8	10.73	7.40	9.8
BSK(HI)	HS	7	3.0 <sup>†</sup>	2.0	97 <sup>†</sup>	10	9.37 (3.05)	6.59 (5.44)	50.68 (4.26)	5.39 [69.34-62.20]	52.7	7.14	3.52	7.9
BSK(S)	S <sub>1</sub>	11	3.0	2.0	94 <sup>†</sup>	12 <sup>†</sup>	37.88 (7.48)	13.92 (4.21)	41.93 (4.03)	15.68 [53.00-43.90]	77.9	10.10	7.86	8.9
BS12(HI)	HS	8	2.5 <sup>†</sup>	2.0	89 <sup>†</sup>	10	15.46 (4.62)	13.03 (5.48)	69.02 (5.65)	6.28 [70.53-62.48]	59.6	8.05	4.64	7.8
BS16(HI)	HS	3	3.0	2.0	80 <sup>†</sup>	16 <sup>†</sup>	43.48 (7.78)	16.52 (4.67)	85.00 (5.88)	13.35 [69.20-55.90]	68.9	13.30	9.00	11.3
BS16(S)	S <sub>1-2</sub>	5	3.0	2.0	113 <sup>†</sup>	23 <sup>†</sup>	61.80 (9.83)	14.30 (3.78)	38.24 (3.96)	30.60 [36.82-26.30]	80.2	10.52	8.42	10.3
BSTL(S)	S <sub>1-2</sub>	6	3.0	2.0	112 <sup>†</sup>	18 <sup>†</sup>	53.42 (10.03)	15.67 (4.73)	55.01 (5.30)	27.00 [40.35-28.50]	72.7	11.85	8.52	12.0
BS2(S)	S <sub>1-2</sub>	5	3.0	2.0	115 <sup>†</sup>	20	58.50 (9.72)	12.08 (3.70)	41.22 (3.86)	34.60 [34.86-23.00]	80.7	11.90	9.54	11.8
BS26(S)	S <sub>1-2</sub>	4	3.0	2.0	130 <sup>†</sup>	25	68.46 (10.55)	17.35 (4.38)	52.35 (5.42)	16.62 [60.48-53.20]	81.9	7.28	3.92	11.3
BS33(S)	S <sub>1-2</sub>	5	3.0	1.5 <sup>†</sup>	78 <sup>†</sup>	32 <sup>†</sup>	39.67 (11.17)	7.24 (4.13)	73.08 (7.09)	16.84 [53.82-48.40]	58.7	5.42	3.92	11.3
BS34(S)	S <sub>1-2</sub>	5	2.2 <sup>†</sup>	1.0 <sup>†</sup>	114 <sup>†</sup>	35 <sup>†</sup>	67.90 (14.28)	8.89 (8.23)	57.15 (7.88)	30.18 [9.21]	75.5	12.2	9.23	12.2
BS2(S)	S <sub>1</sub>	3	3.0	2.0	115 <sup>†</sup>	10	38.16 (7.27)	14.72 (5.31)	66.33 (5.66)	13.20 [57.53-47.40]	67.8	10.13	7.50	10.8
BS2(S)	S <sub>2</sub>	2	3.0	2.0	100	10	60.94 (12.52)	40.52 (8.87)	73.96 (8.78)	19.60 [58.35-42.40]	71.8	15.95	11.30	14.0
$\bar{X}_{HS}$ (4)		2.7	2.2		92.8	11.5	18.80 (12.4)	10.82 (4.44)	60.07 (4.59)	7.32	59.8	8.83	5.28	8.4
$\bar{X}_{S_1}$ (3)		3.0	2.0		108.7	14.0	39.42 (12.9)	20.22 (8.21)	53.49 (5.19)	12.89	71.8	10.32	7.59	9.8
$\bar{X}_{S_{1-2}}$ (6)		2.9	1.9		108.0	18.6	58.29 (17.2)	12.59 (10.93)	52.84 (4.82)	25.97	75.0	9.87	7.58	11.3
$\bar{X}_{S_2}$ (1)		3.0	2.0		100	10	60.94 (10.0)	40.52 (12.52)	73.96 (8.78)	19.60	71.8	15.95	11.30	14.0
														[3.77] <sup>§</sup>

<sup>y</sup> Pro: types of progenies evaluated (HS for testcross and S<sub>1</sub> and S<sub>2</sub> for inbred progenies); Cyc: number of cycles; Env: number of environments; Rep: number of repeats; Eval: number of progenies evaluated; Sel: number of progenies intermated. GCV: genetic coefficients of variation; h: estimate of heritability; D: selection differential; LSD: least significant differences for the experimental trials. All estimates were obtained by the combined ANOVA.

<sup>†</sup>Harmonic means

<sup>‡</sup>Calculated from average estimates of h<sup>2</sup> times average estimate of D

<sup>§</sup> Average expected genetic gains per year

<sup>¶</sup> Standard errors

of half-sib selection within BS13(HT) also included ranges in testing with two locations and three replications for C0 conducted in 1940, one location with six replications in 1948, and two-to-four locations with two-to-three replications for selection cycles C<sub>2</sub> to C<sub>6</sub>. Similar allocation of resources were used for the RRS program of BSSS(R) and BSCB1(R) in the earlier cycles of selection. Part of the variation for the extent of testing was because of the number of progenies produced for testing and the availability of resources to conduct the trials during the course of the selection programs.

A minimum of 100 progenies were evaluated with a minimum effective population size of 10 early generation lines selected for intermating to form the next cycle population (Tables 2 and 3). In earlier cycles of selection, the diallel crossing scheme was used for intermating. However, the bulk-entry method of intermating was used in later cycles because a greater number of progenies were evaluated and selected. The bulk-entry method also reduced the number of nursery rows required to produce the crosses. If selecting before flowering an intra-diallel recombination method can be utilized (Sezegen and Carena, 2009). The number of ears pollinated by the bulk-entry method was counted and an equal number of kernels were randomly selected from each ear to form the 500-kernel bulk which represented the next cycle population. Selection intensities varied among the different selection programs and cycles, they were 10% or greater (Tables 2 and 3). For S<sub>1</sub>-S<sub>2</sub> inbred-progeny selection, the number of S<sub>2</sub> progenies tested was a sample from a larger sample of 200-300 S1 progenies (Table 2). A single replicate of S1 progenies was included in the breeding and pest nurseries; drought and cold screening and/or fast dry down nurseries can be added (Carena et al, 2009a; Yang et al, 2010). Based on ratings for insects and diseases in the pest nursery and agronomic traits and maturity in the breeding nursery, individual S<sub>1</sub> plants were self-pollinated and individual S<sub>2</sub> ears with adequate seed were harvested to include in evaluation trials. Hence the selection intensities for S<sub>1</sub>-S<sub>2</sub> inbred progeny selection programs are relative to the number of S<sub>2</sub> progenies tested and selected (Table 2).

The inter-population selection studies generally included a greater number of half-sib and full-sib families for evaluation except for the RRS program conducted for BSSS(R) and BSCB1(R) (Table 3). Average number of families evaluated was 163 for the RRS programs with an average selection intensity of 11.5%. Except for the RRS half-sib program for BSSS(R) and BSCB1(R), the number of selections intermated were usually 20. The same intermating methods described for the intra-population selection programs were used except there were two intermatings (one for each population) for each program. There was a difference in the number of testing trials between full-sib and half-sib RRS programs as full-

sib RRS required one evaluation trial instead of two which is a significant advantage.

#### Progeny testing

All evaluation trials for the 14 intra-population and eight inter-population RS programs were conducted at locations within Iowa. The only location common to all programs was the Agronomy Research Farm located near Ames, IA. The other locations were determined by the availability of land areas at either the branch research stations or private farmer cooperators. Husbandry practices conducted at each location were based on recommendations for high grain production for the specific location and, consequently, varied among locations within a year, among years at the same location, and among cycles of selection. Agronomic practices have significantly changed from the initial cycles of selection during the 1940s to the recent cycles. Deep fall plowing followed by spring disking was common until about 1970. In recent cycles, the land preparation could include only spring cultivation, minimum tillage, or no tillage. Even though tillage by population interactions would need to be tested, tillage by hybrid interactions were shown to not be significant (Carena et al, 2009c). Disease and insect pressures also changed among years, locations, and cycles which impacted grain yield levels and quality of data. Average fertilizer application changed ranging from 100 to 120 kg ha<sup>-1</sup> in early cycles to 180 kg ha<sup>-1</sup> by the 1970s, decreasing to 120 to 140 kg ha<sup>-1</sup> in more recent cycles.

Standard two-row plots that were 7.92 m long were used for testing in all instances. Distance between rows varied from 101 cm in earlier cycles to 76 cm for selection conducted after 1970. Therefore, the number of plots per hectare changed from 969 to 1,292, respectively, which is almost 30% more plots per hectare. The changes in agronomic practices during the different selection cycles were similar to those recommended for commercial maize production. With the changes in row widths, average plant densities per hectare increased from approximately 39,000 plants ha<sup>-1</sup> in 1950 to more than 69,000 plants ha<sup>-1</sup> in the past three decades, currently surpassing 80,000 plants ha<sup>-1</sup> increasing the selection pressure on genotypes as well as emphasizing yield hectare<sup>-1</sup> over yield plant<sup>-1</sup> (Carena and Cross, 2003; Hyrkas and Carena, 2005). Weed control was done via cultivation and hoeing before the development of commercial herbicides. The herbicides used also varied among locations within years, among years, and among cycles based on the recommended weed control for the specific locations.

Data were collected for all plots and included grain yield (q ha<sup>-1</sup>), grain moisture at harvest (%), number of plants root and stalk lodged relative to final stands (%), number of ears detached from plants relative to final stands (%), and final stand densities (thousands ha<sup>-1</sup>). Plant stands were recorded at flowering time. The number of dropped ears as well as root and stalk

Table 3 – Summary of the data averaged over selection cycles for each population included in the inter-population RS studies.

Population	Pro <sup>¥</sup>	Cyc <sup>¥</sup>	Env <sup>¥</sup>	Rep <sup>¥</sup>	Eval <sup>¥</sup>	Sel <sup>¥</sup>	Estimates of Components of Variance			GCV	h <sup>2</sup>	D	Δ <sub>G</sub>	LSD
							σ <sub>g</sub> <sup>2</sup>	σ <sub>ge</sub> <sup>2</sup>	σ <sup>2</sup>					
							-----No.-----	-----q ha <sup>-1</sup> -----	-----%-----					
BSSS(R)	HS	9	3.8†	2.4†	100	10	14.72 (3.79)§	8.05 (4.04)	54.02 (4.04)	5.20 [73.20-66.50]	51.1	6.70	3.58 [3.42]‡	8.4
BSCB1(R)	HS	9	3.2†	2.4†	101†	10	14.24 (3.96)	8.51 (4.33)	55.62 (4.07)	4.81 [73.22-65.77]	54.8	7.45	4.31 [4.09]‡	7.9
BSSS(R) x BSCB1(R)	FS	6	4.0	2.0	146†	20	12.54 (2.70)	7.34 (3.90)	62.40 (3.80)	4.81 [79.26-73.54]	55.9	5.72	3.3 [3.19]‡	7.7
BS10(FR) x BS11(FR)	FS	18	3.0	2.0	170†	20	32.65 (5.82)	12.18 (5.39)	87.17 (5.63)	8.44 [78.18-67.70]	61.6	10.48	6.40 [7.16]‡	11.2
BS21(R)	HS	10	3.0	2.0	197†	20	15.68 (2.55)	4.21 (2.75)	53.85 (3.28)	5.86 [75.83-69.36]	57.3	6.47	3.81 [3.70]‡	8.6
BS22(R)	HS	10	3.0	2.0	191†	20	19.21 (3.24)	6.43 (2.69)	50.60 (3.10)	6.31 [75.95-69.50]	61.1	6.45	4.05 [3.94]‡	8.2
BS21(HT-A632)	HS	6	3.0	2.0	211†	22	18.08 (3.07)	5.41 (3.34)	59.81 (6.20)	6.72 [70.62-63.30]	57.1	7.32	4.20 [4.17]‡	9.8
BS22(HT-H99)	HS	6	3.0	2.0	212†	22	12.19 (3.35)	5.20 (3.39)	57.39 (3.49)	4.38 [84.67-77.50]	48.7	7.17	3.68 [8.68]‡	10.3
BS28(R)	HS	5	3.2†	2.0	165†	18†	30.85 (4.82)	17.82 (3.56)	52.50 (3.12)	9.56 [69.30-59.00]	61.3	10.30	6.59 [6.31]‡	8.5
BS29(R)	HS	5	3.2†	2.0	165†	18†	21.56 (3.82)	11.49 (3.42)	55.94 (3.50)	8.38 [66.69-58.27]	58.6	8.42	4.98 [4.93]‡	8.6
̄X <sub>FS</sub> (2)		3.5	2.0	158.0	20.0 (4.26)	22.60 (4.64)	9.76 (4.72)	74.78		6.62	58.8	8.10	4.87 [2.44]‡	9.4
̄X <sub>HS</sub> (8)		3.2	2.1	168.0	17.5 (3.58)	18.32 (3.44)	8.39 (3.85)	54.97		6.40	56.3	7.54	4.40 [2.20]‡	8.9

¥ Pro: types of progenies evaluated (HS - half-sibs and FS - full-sibs); Cyc: number of cycles; Env: number of environments; Rep: number of repeats; Eval: number of progenies evaluated; Sel: number of progenies intermated. GCV: genetic coefficients of variation; h: estimate of heritability; D: selection differential; LSD: least significant differences for the experimental trials. All estimates were obtained by the combined ANOVA.

†Harmonic means

‡Average expected genetic gains per year

§Standard errors

lodging were recorded immediately before harvest. Data collection for grain yield and grain moisture at harvest changed during the mid-to late 1960s with the development of planters and combines, adapted to plant and harvest small experimental plots. Before the mid-1960s all plots were hand planted and hand harvested saving dropped ears and ears on lodged plants. Ear weights were recorded and a sample of kernels taken from 12 to 15 ears for determining grain moisture in the laboratory. Final grain yield were determined by adjustments for shelling percentage and grain moistures. With the introduction of combine harvesters, shelled grain weights and moisture percentages were determined electronically on data collectors on combines. Our definition for grain yield

gradually changed over selection cycles because of the advancements in handling small experimental plots: from retrieval of all hand-harvested ears to what the gathering chains of the combines pulled in for shelling. The change in harvest methods was more representative of those used by farmers. However, this change would impact the variation among the progenies being evaluated. If extensive lodging occurred because of local storm damage or susceptibility to a serious local pest problem, there would be differences in final yield for hand vs combine harvesting.

#### Data analyses

Incomplete block experimental designs were used in all instances. The arrangement of blocks within lat-

tice designs also changed with type of harvesting. Originally the blocks were arranged to account for any differences in possible soil types. With the introduction of mechanical harvesters, the blocks were arranged in the direction the plots were harvested to account for time of harvest, different operators, and the severity of root and stalk lodging that may have occurred.

Analyses of variance (ANOVA) of the lattice designs were conducted for each location-year combination (e.g., environment) and a combined ANOVA across all environments. Random effects were assumed for all sources of variation in the combined ANOVA. Detailed agronomic data for each entry at each environment and across environments were listed for each trait. From the combined ANOVA, estimates of the variation among the progenies tested ( $\sigma_g^2$ ), interaction of progenies by environment ( $\sigma_{ge}^2$ ), and experimental error ( $\sigma^2$ ) were estimated. Estimates of the components of variance were used to determine heritability ( $h^2$ ) on a plot mean basis [ $h^2 = 1/(\sigma^2/re + \sigma_{ge}^2/e + \sigma_g^2)$ ], the genetic coefficient of variation among progenies tested relative to their mean [ $GCV = (\sqrt{\sigma_g^2} / \bar{X} * 100)$ ], predicted genetic gain expected in next cycle of selection ( $\Delta_G = D * h^2$ ) where D is the selection differential for the selection means ( $\bar{X}_s$ ) minus the means of all progenies tested ( $\bar{X}$ ), and the least significant difference (LSD) as difference between means for the combined ANOVA. In most instances, the estimates of ( $\sigma_g^2$ ) from combined ANOVAs included data collected at three locations with two replications at each location. Harmonic means of the number of progenies evaluated and intermated for the environments and replications are listed in **Table 2** because there were some exceptions, primarily before 1965. Data used for making selections was usually based on a total of six observations. There were a few instances where one location was lost because of a local natural disaster. There were some minor deviations among populations and cycles depending on success rate of developing progenies in off-season nurseries.

Increased grain yield was the primary trait considered in all of the RS studies. But grain yield is a composite expression of all the traits that either directly or indirectly affect harvested grain yield. These traits include the number of ears, number of kernels per ear, root and stalk quality, tolerance to heat, drought, cold, salinity, and wind storms (e.g., lodging and green snap), and tolerance to disease, insect, and weed pressures during plant growth and development. Our definition of grain yield also changed from hand vs machine harvesting of the experimental plots. In the earlier selection cycles a rank-summation index was used which included grain yield, grain moisture at harvest, and percentage of root and stalk lodging primarily. But some adjustments were made, for example, if a progeny had very good yield but greater root lodging than the average as the increased lodg-

ing may have occurred because of severe lodging that occurred at one specific location. With hand-harvesting the ears on lodged plants, these ears were included in the yield measurements. These types of exceptions were reduced with the introduction of combine harvesting. Since 1976, selections were determined by a selection index (Smith et al, 1981) based on heritability estimates calculated from the combined ANOVA. The heritability estimates of the relative weights for grain yield (Y), grain moisture at harvest (M), and root (RL) and stalk lodging (SL) were used to construct the index [ $I = h_1^2(Y) - h_2^2(M) - h_3^2(RL) - h_4^2(SL)$ ]. Progenies selected included those with greatest grain yield and the least grain moisture at harvest and root and stalk lodging. The index reduced biases sometimes used in the past and the estimates of heritability provided relative weights for the four traits based on the actual variation among progenies during evaluation. The selection of the 10-20 progenies for intermating was based on the index values.

Genetic variation among progenies is essential if selection is to be effective during the course of the selection studies. To determine if genetic variation has either been maintained, reduced, or increased with continuous selection, a regression analysis including square roots of estimates of variation among progenies ( $\sigma_g^2$ ), the dependent variable, on the different cycles (Ci) of selection, the independent variable, was conducted for longest selection programs. Deviations from regression also were determined. The regression analyses would provide estimates of the trends of  $\sigma_g^2$  with continuous selection and the relative changes in the estimates of  $\sigma_g^2$  among cycles. Tests of significance were made for the estimates of the regression coefficients (b) and deviations from regression (Dev).

#### Comparing selection methods

Direct comparisons among the relative effectiveness of the different methods of progeny evaluations to increase expected genetic gain for grain yield are limited, in most instances, because different source populations were used to initiate selection. For intra-population RS, half-sib and inbred progeny selection in BSK provide the only direct comparisons for these two selection methods (Tanner and Smith, 1987). Half-sib and inbred progeny selection was conducted in BS13 but BS13(S) was initiated in BS13(HT)C<sub>6</sub>; the change in types of BS13 progenies evaluated was made subjectively because it seemed genetic variation was not adequate to permit continuous genetic progress. Inbred progeny selection was initiated in BS16, BS2, and BSTL; but different sources of exotic germplasm were used for the three populations. Inter-population RS was limited to either half-sib or full-sib family evaluation. Half-sib and full-sib family selection was conducted for BSSS(R) and BSCB1(R), but full-sib family selection was initiated after nine cycles of RRS. There were four RRS programs based

on half-sib family selection, but each program included two separate sets of populations (Table 3). Direct comparisons can be made for the two BS21 and BS22 RRS programs that included either genetically broad-based populations or inbred lines as testers (Menz et al, 1999). BS28 and BS29 included 100 % tropical germplasm previously selected for adaptation to the US Corn Belt. The effectiveness of half-sib family selection for expected genetic progress can be made for the three RRS programs but the initial source populations were different, consequently, the initial allele frequencies could be different to permit valid comparisons among the three RRS programs.

Weyhrich et al (1998a,b) reported on the responses to selection for six different types of progeny evaluations and four effective population sizes within the BS11 population (Table 4). The study was conducted for five or six cycles for all methods.  $S_1$  inbred progeny evaluations were used for the four different population sizes (25, 50, 100, and 150) evaluated with a selection intensity of 20% (5, 10, 20, and 30 selections intermated between selection cycles) used for each group of progenies evaluated. The experimental methods and ANOVA were similar to those described for the other selection programs (Tables 2 and 3).

## Results

### *Intra-population recurrent selection*

Estimates for the components of variance calculated from the combined ANOVA for each cycle, were averaged across cycles of selection (Table 2). BS13 estimates of  $\sigma_g^2$  averaged across seven cycles of half-sib family selection was  $6.88 \pm 2.30$  compared with the average estimate of  $42.22 \pm 9.87$  after nine cycles of  $S_1$  progeny selection. The average estimates of  $\sigma_g^2$  for the two selection programs conducted in BSK were  $9.37 \pm 3.05$  for half-sib family selection vs  $37.88 \pm 7.48$  for  $S_1$  progeny selection (Table 2). There was significant variation among cycles of selection for BS13 and BSK (data not shown). The estimates of  $\sigma_g^2$  among cycles of BS13(HT) ranged from  $-1.60 \pm 2.30$  for  $C_3$  (there was a severe drought in 1955) to  $10.30 \pm 2.30$  for  $C_5$  (1962) and  $12.90 \pm 3.30$  for  $C_0$  (1940). For BS13(S), the estimates  $\sigma_g^2$  of ranged from  $23.20 \pm 4.10$  for  $C_6$  (1990) to  $80.20 \pm 12.20$  for  $C_1$  (1975). Similar variations for the estimates of  $\sigma_g^2$  for individual cycles of selection were present for all of the different RS programs for the different populations (data not shown).

Because of the nature of the RS systems, progenies evaluated for each cycle of selection were exposed to year-location environments (drought, heat, pests, moisture, etc) that affect grain yields. Data for individual selection cycles do not permit evidence of the progress made in successive selection cycles, unless checks common in all cycles of selection are included which was not the case for any of the selection studies included in Table 2. It is only when all of the successive cycles of selection are evaluated in

the same replicated experiments that valid evidence of the effectiveness of selection can be determined; e.g. Smith (1983) for BSSS, Tanner and Smith (1987) for BSK.

Grain yield was the primary trait emphasized in the RS studies. But the goal of them also was to develop germplasm resources that could have potential value for the isolation of genetically broad-based inbred lines having potential use as parents (e.g., females or males) to produce hybrids. Single-trait selection has proven to be effective, but, in most instances, the selected populations usually have not been acceptable as germplasm resources for the development of useful inbred lines. The studies reported by Devey and Russell (1983) for greater stalk strength, Klenke et al (1986) for greater resistance to feeding by the European corn borer, Carena et al (1998) for greater prolificacy, and Hallauer et al (2004) for increased ear lengths demonstrated the effectiveness for the RS methods for the respective traits but in each of the four reports grain yield often decreased. Although selection for grain yield was emphasized in the populations included in Table 2, it was appreciated that perceptible levels of root and stalk strength and grain moisture at harvest for intensive maize production were necessary traits if the selected germplasm was to have any potential use for increasing the genetic base of breeding programs. The inclusion of additional traits in the selection of progenies for intermating does reduce the intensity of selection for grain yield (Lerner, 1958). Across all studies (Table 2), average selection intensity was 13.2%, but with the inclusion of the other three traits, selection intensity for grain yield per se may have exceeded 30%. Selection based solely on grain yield in temperate areas usually results in taller plants and later maturity with greater incidence of lodging.

Intra-population RS emphasizes selection primarily for additive effects. The relative magnitude of the  $\sigma_g^2$  estimates averaged across cycles of selection tends to agree with the expected coefficient of the additive genetic variance component  $\sigma_A^2$  for the different types of progenies evaluated. The coefficients of  $\sigma_A^2$  for half-sibs,  $S_1$  progenies, and  $S_2$  progenies are 0.25, 1.00, and 1.50, respectively. Therefore, the variance among  $S_1$  progenies would theoretically be four times greater than the variance among half-sib families. The only direct comparison available for these two types of progenies was for BSK; the average estimate of  $\sigma_g^2$  for  $S_1$  progeny selection ( $37.88 \pm 7.48$ ) was 4.04 times greater than the average estimate of  $\sigma_g^2$  for half-sib family selection ( $9.37 \pm 3.05$ ); which agrees with the theoretical expectations. Another possible comparison is between the average estimates of  $\sigma_g^2$  for seven cycles of half-sib selection and nine cycles of  $S_1$  progeny selection within BS13. Average estimate of  $\sigma_g^2$  across seven cycles of half-sib family selection was  $6.88 \pm 2.30$  vs  $42.22 \pm 9.87$  across nine cycles of  $S_1$  progeny selection (Table 2).

The average estimate of  $\sigma_g^2$  for  $S_1$  progeny selection was 6.14 times greater than the average estimate of  $\sigma_g^2$  for half-sib family selection.  $S_1$  progeny selection, however, was initiated in BS13(HT)C<sub>6</sub> population. The type of progeny used in selection within BS13(HT) was changed because it seemed genetic variation was not adequate to permit continued effective selection based on half-sib family selection. The seven cycles of half-sib family selection, with Ia13 double-cross the common tester, may have altered the genetic architecture of BSSS by increasing the level of heterogeneity at some important loci for grain yield. Self-pollination would increase the genetic variance expressed among  $S_1$  progenies. Estimates of  $\sigma_g^2$  among  $S_1$  progenies decreased significantly in continued  $S_1$  progeny selection. The estimate of  $\sigma_g^2$  for BS13(S)C<sub>0</sub> was  $58.9 \pm 10.4$  vs  $27.1 \pm 4.20$ , the average for the last three cycles of  $S_1$  progeny selection (data not shown). The only direct comparison for estimates of  $\sigma_g^2$  for  $S_1$  and  $S_2$  progeny selections was for BSSS2 (Table 2). Only three cycles of  $S_1$  progeny and two cycles of  $S_2$  progeny selection were completed: the average estimate of  $\sigma_g^2$  for  $S_2$  progeny selection ( $60.94 \pm 12.52$ ) was 1.6 times greater than the average estimate of  $\sigma_g^2$  for  $S_1$  progeny selection, which is similar to the theoretical expectation of 1.5. Most of the evidence for intra-population RS suggests that they were effective for additive genetic effects.

Inbred progeny selection was conducted sequentially at the  $S_1$  and  $S_2$  generations of inbreeding for six populations (Table 2). Three populations (BSSL, BS2, and BS16) included different portions of tropical germplasm and three populations (BS26, BS33, and BS34) were representative of open-pollinated cultivars of the US Corn Belt that were unrelated to BSSS (Table 1). The primary goal of selection was to reduce the frequency of deleterious alleles for agronomic and pest traits. The averages of the  $\sigma_g^2$  estimates for the six populations that included  $S_1$  and  $S_2$  selection (58.29) was greater than the average estimate of  $\sigma_g^2$  for  $S_1$  (39.42) selection and similar to the one estimate for  $S_2$  (60.94) selection, which should be expected because estimates of  $\sigma_g^2$  were obtained from the  $S_2$  progeny trials. The screening among the 200-300  $S_1$  progenies in the pest and breeding nurseries did not include any yield measurements, which were made only in the  $S_2$  replicated trials. The average estimates of  $\sigma_g^2$  for the three populations (BSSL, BS2, and BS16) with 25, 50, and 100 % tropical germplasm were not significantly different, based on their respective standard errors.

As stated before, the estimates of  $\sigma_g^2$  have a direct effect of the estimates of genetic coefficient of variation (GCV) as well as on other important genetic parameters. GCVs were all greater for inbred progeny testing because, however, of lower grain yields. The estimates of heritability are also greater when inbred progenies are evaluated and were similar to those reported by Lamkey and Hallauer (1987). Expected

genetic gain per cycle of selection also was greater with inbred progeny selection. On a per year basis average expected genetic gains for  $S_1$  ( $3.72 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) and  $S_2$  ( $3.77 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) progeny selection were similar and greater than half-sib family ( $2.64 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) and  $S_1$ - $S_2$  progeny ( $2.54 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) selection (Table 2). Average expected genetic gain across all selection methods and all populations was  $3.17 \text{ q ha}^{-1} \text{ yr}^{-1}$ .

#### Inter-population recurrent selection

Four pairs of populations have been included in RRS programs (Table 3). BS21 and BS22 were included in two separate programs. The one set was not technically a RRS by its usual definition because an inbred parent was used as the tester rather than the opposite population. It was included in Table 3 because the two selection programs provide information relative to Comstock's (1979) discussion on use of inbred lines vs. populations as testers in RRS.

RRS procedures were designed to select for both additive and non-additive genetic effects. Two populations that are considered representative of important heterotic groups are usually the choices to include in RRS. Because the progenies evaluated are crosses of individuals between two populations, the types of progenies evaluated are restricted to half-sib and full-sib families. It is often assumed that RRS methods are more complex than intra-population RS methods, but RRS are similar to half-sib family and testcross methods of intra-population recurrent selection, except two populations rather than one are included in selection. The four pairs of populations included in this RRS summary are considered to be either in the BSSS (BS10, BS22, and BS28) or in the non-BSSS (BSCB1, BS11, BS21, and BS29) heterotic groups. Estimates of  $\sigma_g^2$  averaged across cycles of selection for each population were similar even across methods (Table 3) except for full-sib family selection for BS10(FR) and BS11(FR) ( $32.65 \pm 5.82$ ) and for half-sib family selection for BS28(R) ( $30.85 \pm 4.82$ ). The average estimates of  $\sigma_g^2$  were very similar for BSSS(R) ( $14.72 \pm 3.79$ ), BSCB1(R) ( $14.24 \pm 3.96$ ), and BSSS(R) x BSCB1(R) ( $12.54 \pm 2.70$ ). The change from half-sib to full-sib family selection did not increase  $\sigma_g^2$ , although a greater number of full-sib families were evaluated.

The BS10(FR) x BS11(FR) RRS program has been under continuous full-sib family selection for 18 cycles, and the average estimate of  $\sigma_g^2$  ( $32.65 \pm 5.82$ ) was significantly greater than for six cycles of full-sib family selection for BSSS(R) x BSCB1(R). The nine cycles of half-sib family selection within BSSS(R) and BSCB1(R) had similar estimates of  $\sigma_g^2$  for each population and previous selection with the use of full-sib family selection. For both half-sib and full-sib selection programs in BSSS(R) and BSCB1(R), there were no trends in the estimates of  $\sigma_g^2$  for individual cycles (data not shown). For BS10(FR) x BS11(FR), there also was not a significant trend that the estimates of  $\sigma_g^2$  had changed significantly from C<sub>0</sub> ( $35.3 \pm 5.18$ )

**Table 4** – Summary of the data averaged over selection cycles for six methods of progeny evaluation and four effective population sizes conducted in BS11 by the Cooperative Federal-State Maize Breeding Program, Ames, IA.

Population	Pro <sup>†</sup>	Cyc <sup>†</sup>	Env <sup>†</sup>	Rep <sup>†</sup>	Eval <sup>†</sup>	Sel <sup>†</sup>	Estimates of Components of Variance			GCV	h <sup>2</sup>	D	LSD				
							Components of Variance										
							No. q ha <sup>-1</sup> %										
BS11(FS)	FS	5	3.0	2.0	100	20	26.60 (6.30)	22.90 (5.20)	48.20 (4.00)	7.80 [71.60-65.70]	62.9	5.90 [3.71] <sup>‡</sup>	3.71 11.0				
BS11(HT)-B79	HS	5	3.0	2.0	100	20	19.46 (6.08)	17.38 (7.44)	68.70 (6.24)	6.34 [75.00-68.54]	51.1	6.46 [3.30] <sup>‡</sup>	3.35 10.2				
BS11(MER)	HS	7	3.0	2.0	100	20	21.46 (5.78)	9.36 (6.95)	73.30 (6.36)	8.10 [64.08-57.32]	55.9	6.76 [3.78] <sup>‡</sup>	3.78 10.0				
BS11(FR)	FS	6	3.0	2.0	178 <sup>†</sup>	20	34.48 (6.00)	11.58 (6.02)	95.88 (6.07)	10.47 [73.84-63.02]	63.2	10.82 [6.84] <sup>‡</sup>	6.60 12.2				
BS11(5-S1)	S <sub>1</sub>	6	2.6 <sup>†</sup>	2.0	25	5	50.82 (12.93)	14.82 (7.12)	51.70 (6.37)	22.10 [44.26-34.48]	75.3	9.78 [7.37] <sup>‡</sup>	7.24 11.3				
BS11(10-S1)	S <sub>1</sub>	6	2.6 <sup>†</sup>	2.0	50	10	40.55 (7.95)	9.16 (5.66)	52.05 (5.23)	16.28 [44.67-36.80]	68.9	7.87 [5.42] <sup>‡</sup>	5.58 10.8				
BS11(20-S1)	S <sub>1</sub>	6	3.0	2.0	100	20	28.58 (5.83)	10.35 (4.20)	46.85 (3.97)	15.88 [43.84-36.67]	70.4	7.17 [5.05] <sup>‡</sup>	5.21 8.8				
BS11(30-S1)	S <sub>1</sub>	6	2.6 <sup>†</sup>	2.0	150	30	41.70 (6.18)	16.81 (4.16)	57.03 (4.33)	16.22 [47.02-38.46]	67.6	8.55 [5.78] <sup>‡</sup>	5.78 11.5				
BS11(S)	S <sub>2</sub>	5	3.0	2.0	100	20	81.48 (13.80)	15.10 (4.74)	38.50 (3.60)	29.42 [42.76-31.46]	84.7	11.30 [9.57] <sup>‡</sup>	9.62 9.2				
	$\bar{X}_{FS}$ (2)						30.54 (6.15)	17.24 (5.61)	72.04 (5.04)	9.14	63.0	8.36 [2.60] <sup>‡</sup>	5.20 11.6				
	$\bar{X}_{HS}$ (2)						20.46 (5.93)	13.37 (7.20)	71.00 (6.30)	7.22	53.5	6.61 [1.78] <sup>‡</sup>	3.57 10.1				
	$\bar{X}_{S_1}$ (4)						40.41 (8.22)	12.78 (5.28)	51.91 (4.98)	17.62	70.6	8.34 [2.98] <sup>‡</sup>	5.95 10.6				
	$\bar{X}_{S_2}$ (1)						81.48 (13.80)	15.10 (4.74)	38.50 (3.60)	29.42	84.7	11.30 [3.21] <sup>‡</sup>	9.62 9.2				

† Pro: types of progenies evaluated (HS - half-sibs, FS - full-sibs, and S<sub>1</sub> - inbreds); Cyc: number of cycles; Env: number of environments; Rep: number of repeats; Eval: number of progenies evaluated; Sel: number of progenies intermated. GCV: genetic coefficients of variation; h: estimate of heritability; D: selection differential; LSD: least significant differences for the experimental trials. All estimates were obtained by the combined ANOVA.

<sup>†</sup>Harmonic means

<sup>‡</sup>Average expected genetic gains per year

to the average of the last three cycles ( $51.4 \pm 9.34$ ).

The two parallel selection programs conducted with BS21 and BS22 were conducted in order to obtain information on the relative efficacy of the use of either the populations as testers or an elite inbred line from the opposing population heterotic group as tester. The estimates of  $\sigma_g^2$  averaged across selection cycles do not provide any clear evidence for the choice of testers to produce half-sib families. Comstock (1979) emphasized that the choice of either inbred lines or populations depended on the relative allele frequencies of the respective testers and that the use of populations as testers was a safer option.

The average estimates of for the four populations utilized were not significantly different for the limited number of cycles completed (Table 3).

RRS was initiated in two strains of tropical germplasm that had previously been selected for adaptation to temperate environments (Hallauer, 1994). BS28 (a selected strain of Tuxpeño) and BS29 [a selected strain of Suwan-1(S)C<sub>6</sub>] represent a heterotic pattern for the tropical maize growing areas. Because BS28 and BS29 were adapted to the central US Corn Belt, the decision was made to conduct RRS in order to develop an alternative heterotic pattern to increase

the germplasm base of breeding programs. The average estimates of  $\sigma_g^2$  across five cycles of RRS for BS28 ( $30.85 \pm 4.82$ ) and BS29 ( $21.56 \pm 3.86$ ) do not differ significantly from the estimates for half-sib family selection.

The average estimate of GCV for BS10(FR) x BS11(FR), BS28(R), and BS29(R) tend to be greater than the other populations. The estimate was larger for BS10(FR) x BS11(FR) because of a larger estimate of  $\sigma_g^2$ . For BS28(R) and BS29(R), the GCVs were larger because of not only larger estimates of  $\sigma_g^2$  but also due to lower grain yields. Similar estimates of heritability were obtained in all selection experiments, averaging 58.8 and 56.3% for full-sib and half-sib selection, respectively. Average predicted genetic gain was greatest for BS10(R) x BS11(R) ( $6.40 \text{ q ha}^{-1}$ ) and BS28(R) ( $6.59 \text{ q ha}^{-1}$ ) (Table 3). Average predicted gain across all populations on a per year basis was  $2.44 \text{ q ha}^{-1}$  for full-sib family selection vs  $2.20 \text{ q ha}^{-1}$  for half-sib family selection. The un-weighted average predicted genetic gain ( $2.32 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) for inter-population recurrent selection was  $0.85 \text{ q ha}^{-1} \text{ yr}^{-1}$  less than the un-weighted average for intra-population recurrent selection ( $3.17 \text{ q ha}^{-1} \text{ yr}^{-1}$ ).

One of the major concerns of conducting RS programs is the expected short- and long-term response to selection. Rawlings (1970) addressed some of the issues related to RS, and one important aspect was the number of individuals that are intermated to maintain genetic variation for continued response to selection. The data for six types of progenies evaluating four different effective population sizes are summarized in Table 4. Selection intensity was 20% for all selection programs except for the reciprocal full-sib RS program for BS10(FR) x BS11(FR) which averaged 11.8%. The data for the first six cycles of BS10(FR) x BS11(FR) were used for comparison, using the same data included in Table 3. The number of individuals intermated (5, 10, 20, and 30) was only for the  $S_1$  progeny selection program. The experimental procedures and analyses of data were similar to those used for the populations included in Tables 2 and 3. The average parameter estimates were again across cycles of selection. The average estimates of  $\sigma_g^2$  ranged from  $19.46 \pm 6.08$  for BS11(HT-B79) to  $81.48 \pm 13.80$  for  $S_2$  progeny selection. B79 was a released line developed from BS10C<sub>0</sub> and may have masked the genetic variation among the testcrosses. The two smallest average estimates of  $\sigma_g^2$  were for the two half-sib selection methods. The two average estimates of  $\sigma_g^2$  for full-sib family selection were intermediate to the estimates for half-sib family and inbred progeny selection. The average of the four estimates for  $S_1$  progeny selection was  $40.41 \pm 8.22$  vs  $81.48 \pm 6.18$  for  $S_2$  progeny selection. BS11 is a heterogeneous population that included southern US and US Corn Belt germplasms (Hallauer, 1973). Consequently, inbreeding exposed deleterious alleles that affected grain yield. Average yield of the four half-

sib and full-sib selection programs was  $71.10 \text{ q ha}^{-1}$  vs  $40.10 \text{ q ha}^{-1}$  for the five inbred progeny selection programs, 37% lower yield for the inbred progenies. Among the four  $S_1$  progeny selection programs, intermating of 20 individuals had the lowest average estimate of  $\sigma_g^2$  ( $28.58 \pm 5.83$ ), but based on the standard errors of the  $\sigma_g^2$ , estimates were not significantly different. The estimates of other parameters were similar to the estimates reported in Tables 2 and 3. The GCVs ranged from 6.34 for BS11(HT-B79) to 29.42 for BS11( $S_2$ ) from a lower estimate of  $\sigma_g^2$  for BS11(HT-B79) to the largest estimate of  $\sigma_g^2$  for BS11( $S_2$ ). The average heritability estimates and predicted genetic gain from selection also was a reflection of the genetic variability among progenies and their respective heritability estimates. Average expected genetic gain was greatest for  $S_2$  progeny selection ( $9.62 \text{ q ha}^{-1} \text{ cycle}^{-1}$ ) and the least for half-sib family selection ( $3.57 \text{ q ha}^{-1} \text{ cycle}^{-1}$ ). On a per year basis, the average expected genetic gain across all methods and cycles was  $2.64 \text{ q ha}^{-1} \text{ yr}^{-1}$ , which was intermediate to the expected gains for intra-population ( $3.17 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) and inter-population ( $2.32 \text{ q ha}^{-1} \text{ yr}^{-1}$ ) RS, on average.

To avoid tests for heterogeneity of variance components (e.g., large and not very meaningful variances of variances) regressions of the square roots of estimates of variation among progenies for each cycle as the dependable variable on cycles of selection were calculated to determine if any significant changes of genetic variance were present among cycles of selection for longest RS programs (Table 5). A positive trend was present for BSK(HI) while a negative trend was shown for BS21(R). BS13 showed a negative trend after changing from half-sib selection to inbred progeny selection. Average across intra-population RS programs was 0.09 while average across inter-population RS programs was 0.01.

## Discussion

A major transition in maize breeding and selection occurred when Shull (1910) and others introduced the use of hybridization methods and the inbred-hybrid concept in maize. The transition from mass selection within open-pollinated cultivars to the isolation of inbred lines from open-pollinating cultivars for use as parents of hybrids had a profound effect on the future of maize breeding. Initially, the inbred-hybrid concept had limited acceptance, but during the following 30 years, breeding, selection, and production were developed to provide double-cross hybrid seed for the producers. By 1950, nearly 100% of the US central Corn Belt maize production area was planted with seed of double-cross hybrids. Although the concept had become a reality, there were concerns relative to the germplasm resources needed to sustain progress made in maize yields and the genetic basis for heterosis expressed in hybrids. The development and use of hybrids had significantly increased grain yields since their introduction in the 1930s (see Table 12.1,

**Table 5** – Estimates of linear regression and deviations from regression for selection programs with seven or more cycles of selection determined by the regression of the square roots of estimates of genetic variation among progenies ( $\sigma_g^2$ ) for each cycle as the dependent variable on cycles of selection ( $C_i$ ) as the independent variable to determine if any significant changes of  $\sigma_g^2$  were obtained with cycles of selection.

Populations improved	Cycles of selection (n°)	Estimates of regression (q $ha^{-1}$ )	Deviations from regression (q $ha^{-1}$ )
Intra-population selection			
BS13(HT) –BS13(S)	16	-0.33	0.18
BSK(HI) <sup>†</sup>	7	0.11*	0.03
BSK(S)	11	0.28	0.15
BS12(HI)	8	0.30	0.21
Average		0.09	0.14
Inter-population selection			
BSSS((R)	9	0.10	0.09
BSCB1(R)	9	0.02	0.07
BS10(FR) x BS11(FR)	18	0.01	0.05
BS21(R)	10	-0.24*	0.06
BS22(R)	10	0.07	0.11
Average		0.01	0.08

<sup>†</sup>This population had the only quadratic significant coefficient.

[Hallauer et al, 2010](#)). During the 70 years from 1865 to 1935, average US maize yields were less than 18.8 q  $ha^{-1}$ , using open-pollinated cultivars developed with mass selection methods. Grain yield of maize has always been the primary economic trait in maize production. Research during the 1920s and 1930s had shown that grain yield was a complex trait whose expression was affected by several plant and ear traits, each with relative low associations with yield; also that grain yield was affected by the environmental effects experienced across space and time; and that the grain yields of inbred lines was not a good prediction of their hybrid yields ([Hallauer et al, 2010](#)). Breeding and selection methods, therefore, were needed that were amenable for the improvement of quantitatively inherited traits, such as grain yield. RS methods seemed appropriate for the systematic genetic improvement of germplasm resources in order to significantly sustain significant yield improvements.

The original intent of RS was directed at improving grain yields relative to the hypotheses proposed for the expression of heterosis and the primary gene effects affected by selection. [Jenkins \(1940\)](#) suggested a method that emphasized selection of additive gene effects for improvement of cultivars for use in marginal production environments where use of hybrids may not be justified. The method proposed by [Jenkins \(1940\)](#) is usually referred to as selection for general combining ability (GCA). [Hull \(1945\)](#) supported the hypothesis that over-dominant gene effects were of primary importance for the expression of heterosis, and that selection for non-additive effects should be emphasized. [Hull \(1945\)](#) proposed that RS with an inbred line as tester, and inbred progeny RS be conducted in parallel fashion for the same population to obtain empirical evidence of the relative importance of additive and non-additive effects

in response to selection. The proposal of [Hull \(1945\)](#) is usually referred to as selection for specific combining ability (SCA) when an inbred tester is used. Because there was no general consensus among maize breeders and geneticists on the predominant type(s) of genetic effects important in selection and heterosis, [Comstock et al \(1949\)](#) proposed a scheme they designated RRS that would capitalize both GCA (primarily additive effects) and SCA (primarily non-additive genetic effects). The proposal of [Comstock et al \(1949\)](#) also had the advantage that selection between two populations that represented popular heterotic patterns would enhance the heterosis of the population cross if RRS was effective for non-additive genetic effects.

The concerns, discussions, suggestions, and proposals put forth during the 1940s for the systematic improvement of maize germplasm for grain yields stimulated the initiation of RS programs nationwide, especially the ones conducted by the Cooperative Federal-State Corn Breeding Project, Ames, IA. The major goals of the programs were to determine their relative efficiencies to enhance grain yields. An important corollary of the selection programs was to gain knowledge of the types of genetic effects of greater importance in selection for increased grain yields. Later, exotic germplasm sources were introduced, adapted, and selected in an attempt to broaden the genetic base of US maize breeding programs ([Anonymous, 1972](#); [Brown, 1975](#); [Goodman, 1999](#); [Hallauer and Carena, 2009](#); [Sharma and Carena, 2012](#)).

The summaries in [Tables 2, 3, and 4](#) are the expected genetic gains averaged across cycles of selection. Realized gains from the selection programs at various stages of selection were reported for most studies (e.g., [Smith, 1983](#); [Tanner and Smith, 1987](#); [Eyherabide and Hallauer, 1991](#); [Keeratinijakal and](#)

**Table 6** – Summary of average expected gain per cycle and per year for grain yield ( $q \text{ ha}^{-1}$ ) for intra-population RS, inter-population reciprocal RS, and different RS programs conducted within BS11.

Progeny types	Intra-population	Inter-population	BS11	Average
(q $\text{ha}^{-1}$ )				
Half-sibs				
Per cycle	5.28	4.40	3.57	4.42
Per year	2.64	2.20	1.78	2.21
Full-sibs				
Per cycle	---	4.87	5.20	5.04
Per year	---	2.44	2.60	2.52
$S_{1s}$				
Per cycle	7.59	---	5.95	6.77
Per year	3.79	---	2.98	3.38
$S_1$ - $S_{2s}$				
Per cycle	7.58	---	---	7.58
Per year	2.53	---	---	2.53
$S_{2s}$				
Per cycle	11.30	---	9.62	10.46
Per year	3.77	---	3.21	3.49
Average				
Per cycle	7.93	4.64	6.08	6.22
Per year	3.18	2.32	2.64	2.71

Lamkey, 1993; Menz et al, 1999; Carena and Hallauer, 2001; Hallauer et al, 2010, etc). The realized gains were, in most instances, similar to the expected gains when averaged across cycles. The average expected and realized responses suggest that the additive genetic effects had a greater effect on selection than non-additive genetic effects (Hallauer and Carena, 2009; Hallauer et al, 2010). For the inter-population RS, the expected genetic gain averaged less than for intra-population RS. However, estimates of the components of variance for inbred progeny selection may be biased upward based on a prediction model on three populations (Wardyn et al, 2009). Perhaps, inter-population RS requires more cycles of selection to increase the divergence of allele frequencies of populations under selection. Eyherabide and Hallauer (1991) and Keeratinijakal and Lamkey (1993) did report that heterosis had increased from the  $C_0$  to later cycles of selection for BS10(FR) x BS11(FR) and BSSS(R) x BSCB1(R).

A brief summary of the un-weighted average expected gains for the different RS methods are listed in Table 6. Average expected genetic gain per year across methods was 3.18, 2.32, 2.64  $q \text{ ha}^{-1}$  for intra-population, inter-population, and BS11, respectively or 2.71  $q \text{ ha}^{-1}$  for all populations and progeny types. RRS had the least expected genetic gain of 2.32  $q \text{ ha}^{-1} \text{ yr}^{-1}$ . The average expected genetic gains for the different selection programs with a common source population were similar to those involving different source populations. On a per year basis the expected genetic gain for BS11 (2.64  $q \text{ ha}^{-1} \text{ yr}^{-1}$ ) was similar to the average for intra- and inter-population RS programs (2.75  $q \text{ ha}^{-1} \text{ yr}^{-1}$ ).

RS programs are a minor importance to maize

breeding programs dedicated to developing improved inbred lines to produce and sell competitive hybrids in the marketplace. Major emphasis is given to pedigree selection within  $F_2$  populations of elite and related inbred line crosses. Although the methods used in pedigree breeding are not commonly referred as RS, the same principles (e.g., develop progenies, evaluate progenies in replicated trials, and intermate or cross newer lines to create genetic variability for future selection) are similar to those used in RS (Weatherspoon, 1973; Hallauer, 1992; Carena and Wicks III, 2006). One major distinction between the RS studies listed in Tables 2, 3, and 4 was they were closed populations; i.e., no new germplasm was introduced during selection, whereas newer lines are introduced as they become available in breeding emphasizing pedigree selection within  $F_2$  populations (e.g., see Figure 1.6, Hallauer et al, 2010).

The significance of RS programs can only be realized if the selected populations can contribute useful germplasm to the cultivar development. In the Iowa RS programs, the 10 to 20 progenies intermated to form the next cycle population also were included in the breeding and testcross nurseries for further inbreeding, evaluation of testcrosses in replicated trials, and continued selection for other agronomic traits. Nearly 100% of the selections were discarded. The estimates included in Tables 2, 3, and 4 were derived from data collected for an estimated 25,692 progenies evaluated in 168,797 test plots in replicated trials conducted across Iowa environments.

There were 31 inbred lines that were given a 'B' designation and released for used either directly or indirectly in either public or private breeding programs. The two RS programs in BSSS [BS13(HT),

BS13(S), and BSSS(R)] were the germplasm sources for 17 of the 31 released lines. BSSS seems unique relative to the other populations because the total genetic variance  $\sigma_g^2$  within BSSS has equal portions of additive genetic ( $\sigma_A^2$ ) and variance due to dominant deviations ( $\sigma_D^2$ ) compared with other populations having two to four times greater estimates of  $\sigma_A^2$  compared with the estimates of  $\sigma_D^2$  (Silva and Hallauer, 1975; Stucker and Hallauer, 1992; Hallauer et al, 2010). BSSS also was the source population for B67 and B69 developed by Chase (1952) for doubled haploids, and B101 with above average methionine content (Hallauer and Wright, 1995). Inbred lines originating from BSSS have had persistent use in recycling programs via pedigree selection; Mikel and Dudley (2006) concluded that BSSS germplasm was included in the lineage of 63% of the proprietary inbred lines protected either by the US patent or US Plant Variety Protection Act (PVPA). BSCB1 was the source of seven inbred lines released; BS11 was the sources of four released lines; and one line was released each from BS10, BS22, and BS26. Relative to the number of progenies (25,692) tested for only one year at two to four locations, the success rate for inbred lines that merited release on the basis of further inbreeding, testing, and selection, was 0.121% of the original progenies tested, or 1.21 per 1,000 original progenies tested. This seems a low success rate, but inbred lines developed from genetically broad-based populations would be unique genetically and have potential value as new sources of genetic variation if used as one of the parents to produce  $F_2$  populations for recycling widely used elite inbred lines (Hallauer and Carena, 2009; Carena et al, 2010). Except for Lindstrom's (1939) survey, no known information is available on the relative frequencies of success in pedigree selection programs. It seems logical to assume the success rate would be greater within  $F_2$  populations derived from planned crosses with known diversity estimates. Lindstrom (1939) concluded that only 2.4% useful lines were identified, presumably from open-pollinated varieties. Nevertheless, even within those percentages certain lines (e.g., B73) have been extremely successful and have been an example to using genetically broad-based germplasm sources in order to achieve significant genetic gains (Carena, 2011).

RS programs are long-term breeding programs with no definitive end-point. Intermating between cycles of selection is a unique feature to RS and generates genetic variation. For most cases, it seems genetic variation is persistent over cycles of selection even though only one cycle of recombination was often conducted (Table 5) which agrees with the changes seen in the molecular studies done in populations improved by RS. Moreover, SEs decreased with selection. The decrease in the SEs for GxE was probably because of improved adaptation over cycles of selection. However, it may have occurred because

of improved experimental methods, choice of environments, and more consistent husbandry practices across locations. Producing more seed per progeny for multi-location testing of populations can lower SEs and further intermating between cycles of selection may be preferable, especially for BS21(R), but this would reduce genetic progress on a yearly basis (Eberhart, 1970). It seems more cycles of selection were preferable to more generations of intermating between cycles.

RS programs should be an integral part of maize breeding rather than a separate entity. Ideally, breeders should have germplasm enhancement programs linked to product development. If the RS programs are an integral part of the mainstream breeding for inbred line development, the breeder will have first-hand knowledge of what is required in the populations under selection. The populations could be open-ended with newer materials added to maintain genetic variability with better man performance. Limited success can be made if wrong choices of germplasm are made to initiate selection. BS12(HT) is an example (Table 1). BS12 was an open-pollinated variety with good ear length but very weak root and stalk strength. Expected response to selection for greater grain yield ( $4.64 \text{ q ha}^{-1}$ ) was similar to other programs but continued poor root and stalk lodging continued to be a problem. Selection was discontinued after eight cycles of half-sib family selection because it seemed BS12(HI) would not become a likely source of germplasm useful to breeders. What the future of the populations that include adapted tropical germplasm (BS16, BS2, BSTL, BS28, and BS29) may be is not clear. ETO composite (BS16), Tuxpeño (BS28), and Suwan-1 (BS29) were considered important germplasm sources in tropical breeding programs. But additional selection pressures for better root and stalk strength, lower grain moisture at harvest, and greater grain yields for temperate environments are needed to meet current standards in temperate breeding programs. A complementary strategy could be to continue inbreeding and selection of selected progenies from the latest cycles that could be used in pedigree selection from  $F_2$  populations of tropical by temperate or early by late maturing inbred lines, following the breeding methods used by Goodman (1999) and Sharma and Carena (2012).

Genetic responses within all the populations included in Tables 2, 3, and 4 can be expected. The choices of populations to include and the progenies tested are dependent on the goals of individual breeding programs. Response to inbred progeny selection in maize, has seemed to plateau after two to four cycles of selection [e.g., Tanner and Smith (1987) for BSK and BS13(S)] but Weyhrich et al (1998a,b) reported that inbred progeny selection was as effective as the other methods in BS11. Perhaps, previous selection in the development of Krug open-pollinated variety and the genetic variability within BSSS (Silva

and Hallauer, 1975) were affected in the response to inbred progeny selection. Depending on the goals of the maize breeder, it seems progress can be expected with any of the RS methods. If one particular type of progeny selection does not seem effective, changes can be made either for the types of progenies being evaluated or additional carefully selected germplasm can be intermated with the latest cycle population. One does not desire to lose the progress previously made. RS methods will never replace the pedigree selection methods often used in cultivar development programs. But RS programs do have the potential to develop alternative germplasm sources and, unique, unrelated inbred lines that could provide additional useful alleles in pedigree selection program increasing their potential to provide unique genetic products (Carena, 2012a,b) or create alternative heterotic patterns (Carena, 2005; Carena and Wicks III, 2006; Jumbo and Carena, 2007; Hallauer and Carena, 2009; Hallauer et al, 2010).

If RS is to have relevance we should emphasize they should be included as a component of breeding programs. In the past, many RS programs were seen as isolated projects that were expensive and time consuming, with no contribution to maize breeding. Iowa and North Dakota were and still are few of the programs still combining RS with applied breeding developing inbred lines with value for either hybrids or to use in pedigree breeding (Hallauer and Carena, 2009; Hallauer et al, 2010).

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