Quantitative Analysis of Iowa Stiff Stalk Synthetic

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SUMMARY

Stiff Stalk Synthetic is a synthetic variety that was deloped in the early 1930's by recombining 16 inbred lines that were considered to be above average for stalk quality. Because of the origin of the lines included in Stiff Stalk Synthetic, it is usually considered a Reid's Yellow Dent type. Stiff Stalk Synthetic (BSSS) has been used extensively in the cooperative federal-state corn breeding project at Ames, Iowa. BSSS has proved to be a good source of lines that have above average combining ability and stalk quality. BSSS was the source population for initiating half-sib recurrent selection in 1939 and one of the populations used for initiating reciprocal recurrent selection in 1949. Both selection programs have been continued to the present time. In addition, BSSS was included in basic research studies to determine the relative importance of different types of genetic effects and to estimate inbreeding depression for several quantitative traits. Results of these studies for BSSS were summarized and compared with data obtained from other corn populations.

BSSS per se tended to yield below average, but it was above average for combining ability in crosses with other varieties. BSSS performed as a Reid's Yellow Dent type because heterosis was greater in variety crosses with Lancaster Sure Crop types than in variety crosses with Reid's Yellow Dent types. Regardless of the particular variety included in crosses, however, BSSS tended to make a positive contribution to the variety cross. Because nearly all variety cross trials were machine harvested with no gleaning, the above average stalk quality of BSSS may have been a contributing factor in the performance of BSSS in variety crosses.

Quantitative genetic studies suggested BSSS has less genetic variability than many of the other corn varieties for yield. Whereas estimates of additive genetic variance in other *corn populations were, on the average, 1.6 times greater than the variance due to dominance effects, the estimates of additive genetic variance for BSSS were similar to the variance for dominance effects. Estimates of inbreeding depression for yield, however, tended to be smaller for BSSS than for other varieties. Performance of BSSS per se, less additive genetic variance, and smaller inbreeding effects suggests that BSSS may have a higher frequency of favorable alleles than for other varieties. BSSS may be in the homozygous condition for some important loci. Gene frequencies of favorable alleles greater than 0.5 would reduce the relative proportion of the additive genetic variance to the variance due to dominance effects and reduce the effects of inbreeding. Also, fixation of favorable alleles would affect variety performance per se and contribute to improved combining ability. It seems the main features that distinguish BSSS from other corn varieties are better-than-average stalk quality, source of lines with above average combining ability that have adaptation over wide areas, and frequencies of favorable alleles greater than 0.5. A wise choice of lines used to form BSSS and continued selection pressure for the past 40 years have developed improved strains of BSSS that have played an important role in continued genetic progress of hybrid corn.*

INTRODUCTION

'Stiff Stalk Synthetic' is a corn (*Zea mays* L.) variety that was developed by intermating 16 inbred lines in 1933 and 1934 (SPRAGUE 1946). The 16 lines were selected by different corn breeders for having acceptable stalk quality. Although the exact origins of the 16 lines included in Stiff Stalk Synthetic are not certain in all instances, most lines were derived from sources that included 'Reid's Yellow Dent' germplasm (Table 1). Empirical data obtained for crosses of Stiff Stalk Synthetic with populations that include 'Lancaster Sure Crop' germplasm and lines extracted from Stiff Stalk Synthetic and Lancaster Sure Crop show good heterosis. Hence, Stiff Stalk Synthetic is considered a Reid's Yellow Dent type.

Stiff Stalk Synthetic became an important germplasm source in the cooperative federal-state corn breeding program at Ames, Iowa, when G. F. Sprague initiated selection experiments in 1939 and 1949. Because Stiff Stalk Synthetic has had extensive study in Iowa, this particular strain was designated as 'Iowa Stiff Stalk Synthetic' (BSSS). BSSS has been the source population used in several selection, quantitative genetic, and breeding methods studies conducted in Iowa. Along with 'Burr's White' at the University of Illinois, 'Jarvis' and 'Indian Chief' at North Carolina State University and 'Hays Golden' at the University of Nebraska, BSSS has been one of the more intensively studied varieties.

Although BSSS has been studied primarily in Iowa, it also has had an impact in other areas, both as a breeding population for extraction of lines and use in developing recycled lines. Surveys have been conducted under the auspices of the American

Table 1. Lines included in the synthesis of Stiff Stalk Synthetic and the putative source of the lines.

Lines	Source
IaI159	Iodent - a strain of Reid Yellow Dent
IaI224	Iodent - a strain of Reid Yellow Dent
IaOs420	Osterland - a strain of Reid Yellow Dent
IaWD456	Walden Dent - a strain of Reid Yellow Dent
Ind. 461-3	Reid Medium (Duddleston No. 461)
Ill. 12E	†
CI617	Funks 176A - a strain of Reid Yellow Dent
CI540	Illinois Two-ear
Ill. Hy	Illinois High-yield
Oh3167B	Echelberger Clarage
Ind. AH83	Funks 176A - a strain of Reid Yellow Dent
Ind. Tr 9-1-1-6	Reid Early Dent (Troyer strain)
F_1B_1-7-1	(Fe x B2): Fe - Reid Early; B2 - Reid Yellow Dent
A3G-3-1-3	†
CI187-2	Krug - Nebraska Reid strain x Iowa Gold Mine
LE23	Illinois Low Ear

†Source of lines was not determined.

Seed Trade Association (ASTA) to determine the extent of use of publicly developed lines in production of commercial hybrids. Lines originating from BSSS were prominent in all surveys (Table 2). Three lines (B14, B37, and B73) were widely used in the production of commercial hybrids during the 24 years covered by the survey. In 1979, for example, B73 was used as one parent in the production of 81 million kilograms of hybrid seed corn, which was 16.1% of the total seed requirements. ZUBER & DARRAH (1980) summarized the lines that were either Lancaster Sure Crop related or Reid's Yellow Dent related for the 1979 U.S. hybrid seed corn production; they estimated 39.2% of the lines were related to Lancaster Sure Crop, 42.4% were related to Reid's Yellow Dent, and 18.4% were from other sources. The Reid's Yellow Dent related lines were primarily from BSSS (B14, B37, B73, and B84).

In addition to the direct use of B14 and B37 for the production of commercial hybrids, they also have been used extensively in pedigree selection programs for developing widely used recycled lines. The versatility of BSSS lines is evident from the direct use of the lines in hybrids grown throughout the United States, Europe, and Asia and for developing recycled lines adapted to areas other than the main corn growing areas. B73 is used in hybrids grown throughout the United States, Europe, and Asia. B14 has been used in pedigree selection programs to develop early lines with improved stalk quality for Canada, norther U.S. Corn Belt, and Europe; e.g., CM105, A632, A634, A635, A640, and A641. Presently, there are 71 recycled lines that include B14 germplasm, 27 that include B37, and 14 that include B73 (ANONYMOUS

Table 2. Percentage use of the five most widely used publicly developed lines in each of the five ASTA surveys.

Lines	Source	Commercial use as a percentage of the total seed requirements for each year of survey†				
		1957	1964	1971	1975	1980
C103	Lancaster‡	7.4¶	11.9¶	4.2	0.3	<0.1
Oh43	(Oh40B x W8)‡	5.2¶	15.7¶	11.7¶	0.9	0.1
B14	BSSS§	2.5¶	8.2¶	8.6¶	1.6	0.2
R61	Lancaster‡	1.6¶	1.0	0.0	0.0	0.0
P8	Reid Yellow Dent§	1.6¶	0.2	0.0	0.0	0.0
Oh41	($L317^2$ x K166)‡	1.6¶	1.8¶	0.0	0.0	0.0
B37	BSSS§	0.0	2.0¶	25.7¶	6.8¶	2.4¶
W64A	(WF9 x 187-2)§	0.0	0.9	13.0¶	1.5	0.6
A632	(Mt42 x $B14^4$)§	0.0	0.0	7.4¶	15.2¶	9.7¶
Mo17	(187-2 x C103)‡	0.0	0.0	1.7	7.0¶	12.2¶
A619	(A171 x $Oh43^2$)‡	0.0	0.0	3.4	4.2¶	0.9
B73	BSSS§	0.0	0.0	0.0	3.1¶	16.1¶
A634	(Mt42 x $B14^4$)§	0.0	0.0	0.4	0.6	3.0¶
B84	BSSS§	0.0	0.0	0.0	0.0	0.3

†Surveys were reported by JENKINS (1957), SPRAGUE (1964, 1971), ZUBER (1975), and ZUBER & DARRAH (1980), respectively.

‡Lines developed from Lancaster Sure Crop or by pedigree selection from crosses of lines that included Lancaster Sure Crop germplasm; Mo17 was derived from a cross of two lines in which one (187-2) also included Reid Yellow Dent germplasm.

§Lines that included Reid's Yellow Dent germplasm.

¶Five most widely used lines for each year of survey.

1981). These are recycled lines available for public use; there may be even a greater number of proprietary recoveries of these lines. B14, for example, was included in only 0.17% of the hybrids produced for use in 1980 (Table 2). Although B14 per se ranked only 32nd (0.17%) in use, it was one of the parents of five (A632, A634, A635, B64, and B68) of the top 10 most widely used lines (ZUBER & DARRAH 1980). These five B14 recoveries were used in production of 15.4% of the 1980 hybrid seed corn. Other recoveries of B14 (CM105, H100, B14A, and A665) were used for another 1.1% of the total seed needs. Hence, lines developed from BSSS have proven useful in: 1) direct use as parent seed stocks in the production of commercial hybrid seed and 2) as breeding germplasm in the development of recycled lines, which were used in the production of commercial hybrid seed.

Data on the performance of BSSS will be presented for: 1) performance per se and in crosses with other synthetic varieties; 2) recurrent selection studies that have been conducted since 1939 and 1949; and 3) quantitative genetic studies that have provided estimates on the relative importance of additive and nonadditive genetic variances and inbreeding depression. Most of the data have been reported for individual studies. Our main objective will be to summarize the information from several studies and to determine how BSSS differs from, or is similar to, other synthetic varieties of similar maturity.

PERFORMANCE IN VARIETY CROSSES

Since 1963, five sets of diallel crosses among synthetic varieties have been tested in Iowa to determine the relative heterosis expressed in the variety crosses; BSSS was included as one of the parent varieties in each set of diallel crosses (HALLAUER et al. 1966, 1968, 1972, 1976). Yield data for BSSS per se and in crosses with other varieties for five sets of diallel crosses are shown in Table 3. The 30 synthetic varieties included in the five sets of diallel crosses depended on their performance in previous crosses with BSSS and were included to determine how BSSS performed in crosses with other varieties that were available in the breeding program. For example, PaSI, BSLE and BS10; BSCB2 and BS20; and BS12 were included in 4, 3, and 2 sets of diallel crosses, respectively. Most of the varieties crossed with BSSS included either none or limited amounts of BSSS germplasm. BSSS5, BSSS2, BSBB, BS6, BS10, and BS17, however, either included lines from BSSS or were strains of BSSS improved by recurrent selection. Each diallel included nine parental varieties except the 1976 diallel, which included only seven varieties.

Table 3. Performance of BSSS per se and in crosses with other synthetic varieties for five series of diallel crosses for grain yield (q/ha).

Year	BSSS per se	BSSS crosses†									Avg. of crosses	Avg. heterosis‡
		BSCB1	BSCB2	BSCB3	BSSS2	BSLE	HSA	HSB	PaSI			
1966	61(6)§	69	68	71	68	71	69	68	73		70(2)¶	10
		(11.3)	(11.0)	(7.2)	(5.8)	(3.1)	(13.5)	(12.0)	(16.8)			
		BSAA	BSBB	BSCB3	BS10	BSLE	BS11	HSMJ	PaSI			
1968	51(8)	65	60	66	63	67	62	63	71		65(1)	11
		(5.0)	(-3.2)	(14.7)	(1.4)	(18.2)	(7.4)	(23.2)	(24.9)			
		BSSS2	BSCB9	BS2	BS10	BSLE	BSTL	BS6	PaSI			
1972	52(9)	66	72	67	69	68	64	68	72		68(8)	9
		(8.5)	(9.1)	(24.0)	(0.1)	(9.1)	(5.1)	(2.4)	(11.1)			
		BSK	---	BS5	BS10	BS20	BS23	BS12	PaSI#			
1976	55(3)	62	---	54	61	68	67	57	64		62(4)	7
		(11.9)	---	(-2.4)	(0.0)	(5.8)	(21.0)	(3.8)	---			
		BS1	BS9	BS16	BS17	BS20	BS18	BS12	BSL	BS13		
1981	49(9)	71	66	61	60	57	70	77	63	65	66(9)	13
		(18.4)	(21.5)	(-1.0)	(-10.0)	(7.3)	(15.4)	(25.3)	(48.0)	(-4.7)		

†BSSS was one of the parents included in diallel series of crosses with the other varieties shown. Only the crosses that included BSSS are listed. High parent heterosis is in parenthesis.

‡Average heterosis relative to the high parent for all crosses that included BSSS as one of the parents (%).

§Numbers in parenthesis indicate relative rank of varieties per se.

¶Numbers in parenthesis indicate relative rank of average of crosses.

#Not included in diallel but variety cross included as check.

BSSS per se was usually one of the lower yielding varieties (Table 3). BSSS ranked 3rd of seven varieties in the 1976 diallel, which included two unimproved varieties (BSK and BS12), one unadapted early variety (BS5), and one variety developed from introgression of teosinte in Corn Belt germplasm

(BS23). Only BS10 and BS23 were greater yielding than BSSS per se in the 1976 diallel. In the other four diallels, BSSS per se was below average in yield compared to the other synthetic varieties (Table 3).

High-parent heterosis of the crosses that included BSSS as one of the parents ranged from 7% for the 1976 diallel crosses of unimproved varieties to 13% for the 1981 diallel; average high-parent heterosis for the five sets of diallel crosses was higher in the 1966, 1968, and 1981 diallels than in the 1972 and 1976 diallels. But the 1972 (BSSS2, BS6, and BS10) and 1976 (BS10 and BS20) diallels included varieties with BSSS germplasm that had been under previous selection for yield improvement. In most instances, high-parent heterosis of the crosses that included varieties with BSSS germplasm was lower: BSSS2 (8.5%), BS6 (2.4%), and BS10 (0.1%) for the 1972 diallel and BS17 (-10.0%) and BS13 (-4.7%) for the 1981 diallel. Other instances of lower high-parent heterosis were evident in 1968 for BSBB (-3.2%) and BS10 (1.4%) and in 1976 for BS10 (0.0%), which also included germplasm related to BSSS. Crosses of BSSS with varieties that included Lancaster Sure Crop germplasm tended to express greater high-parent heterosis; e.g., BS2, HSA, BSAA, and PaSI. The diallel crosses also identified varieties that exhibited either good or poor heterosis in crosses with BSSS. BS16 was developed by mass selection for adaptability in Iowa from ETO Composite (HALLAUER & SEARS 1972); no heterosis was expressed in the BSSS x BS16 cross (1981 diallel, Table 3). BS18 was developed from the cross of two strains of BSK (BURTON et al. 1971), and BS12 is an improved strain of the open-pollinated variety 'Alph'; both BS18 (15.4%) and BS12 (25.3%) exhibited good heterosis in crosses with BSSS (1981 diallel, Table 3).

It was speculated that the relative performance of BSSS per se and in crosses may have been affected by the methods of reproduction used to propagate the strain for the past 50 years. Information was not available to determine how many times BSSS had been increased to maintain viable seed supplies, how many plants were included in each sample, and what method (hand pollination or field isolation) of propagation was used. BSSS was resynthesized from the original 16 lines (Table 1) using the procedures described by SPRAGUE (1946). For a resynthesis of BSSS, all lines except CI617 were recovered; the original BSSS was used in place of CI617 in the resynthesis of BSSS. The resynthesized strain of BSSS was included as one of the check entries in the 1981 diallel. Comparisons between the original and resynthesized strains of BSSS are shown in Table 4 for seven traits. The means were obtained from 16 replications (2 replications at 8 test sites), and, based on the LSD, the differences between the BSSS strain maintained in the Iowa program and the resynthesized BSSS strain were not significant except for stalk lodging. It seems, therefore, that the Iowa State BSSS strain included in the five sets of diallel crosses was representative of the original strain of Stiff Stalk Synthetic.

Based on the data from the five sets of diallel crosses,

Table 4. Comparisons of the original and resynthesized strains of BSSS.

Strain	Days to flower	Yield	Grain moisture	Stand	Lodging Root	Lodging Stalk	Dropped ears
	no.	q/ha	%	M/ha	----------%----------		
BSSS	25	51.5	25.2	47.1	2.8	17.7	1.2
BSSS resyn.	26	48.3	23.6	45.9	2.3	29.6	1.6
LSD (0.05)	--	9.0	1.7	3.9	4.0	10.2	1.6

there do not seem to be any features that would suggest BSSS was strikingly different from other synthetic varieties. For yield, the above average combining ability of BSSS also seemed to be present in the elite lines extracted from it. Above average combining ability and stalk quality of the lines extracted from BSSS, and strains of BSSS improved by recurrent selection, seemed to be consistent with the performance of BSSS per se.

RECURRENT SELECTION

HALF-SIB SELECTION

Recurrent selection based on half-sib performance was initiated in 1939 in BSSS by SPRAGUE (1946). The significance of this selection program is characterized by: 1) being one of the first recurrent selection programs that was initiated to test the suggestion of JENKINS (1940) for the improvement of breeding populations; 2) being under continuous selection to the present time; and 3) being a source of inbred lines (B14, B37, and B73) that have had wide acceptance in the commercial seed corn industry. Half-sib recurrent selection was expected to improve the general combining ability of a population. Seven cycles of half-sib selection have been completed. The common tester used throughout the seven cycles of half-sib selection was Ia13 (L317 x BL349)(BL345 x MC401), a widely grown double-cross hybrid used at the time the study was initiated (SPRAGUE 1946). Details of the experimental procedures used for the seven cycles of half-sib selection were described by EBERHART et al. (1973). This population was designated BS13(HT)Ci for the different cycles of selection.

After the completion of seven cycles of half-sib recurrent selection, selection was based on S_1 and S_2 progenies, and the improved breeding population was redesignated as BS13(S). S_1 progenies were developed and grown in single replications in the first-generation European corn borer (*Ostrinia nubilalis* Hübner) and breeding nurseries. Based on corn borer ratings recorded before flowering, selected plants within S_1 progenies that had acceptable levels of resistance were self-pollinated to produce S_2 generation seed. Final selections were made at harvest for S_2 ears having good seed set on plants that had acceptable stalk quality. S_2 progenies were evaluated per se in replicated trials and recombination of the superior progenies was made the following two seasons (one winter and one summer) to form the next cycle population. Each cycle of selection required three years.

Response to half-sib selection in BS13 has been reported by EBERHART et al. (1973) and SMITH (1979, 1982). Grain yield was the primary trait under selection, and the results presented will emphasize yield although correlated responses for the other traits will be discussed briefly. Response to half-sib recurrent selection was measured for cycle populations per se and in testcrosses with BSSSC0 (the original base population) and Ia13, the double-cross tester. Positive response for yield improvement was realized in all instances (Table 5). Testcrosses with Ia13 showed a response to selection of 1.65 ± 0.38 q/ha per cycle of selection (EBERHART et al. 1973). Response of cycle populations per se was about 50% of the gain realized with the Ia13 testcrosses (0.74 ± 0.27 q/ha). SMITH (1982) reevaluated the BS13 cycle populations per se and calculated separately the response to selection for the C0 to C4 (hand harvesting was used) and C4 to C7 (machine harvesting was used) cycles; responses to selection were 0.80 ± 0.24 q/ha for cycles C0 to C4 and 2.48 ± 0.37 q/ha for cycles 4 to 7, which were very similar to the estimates for the data reported by EBERHART et al. (1973) (Table 5).

Methods usually used to evaluate the response to recurrent selection have included regressing the means of the selected populations and population crosses on the cycles of selection. SMITH (1979) suggested a model that related changes in the means of selected populations due to changes in allelic frequency and inbreeding. The model also permitted estimates of direct (based on method of progeny evaluation) and indirect responses to selection. Direct response (1.65 ± 0.38) was the same as reported by EBERHART et al. (1973) (Table 5). Indirect response to half-sib selection, as measured by BS13 per se, was similar (0.69 ± .27 vs. 0.74 ± .27) to that reported by EBERHART et al. (1973), but a significant inbreeding effect was detected (-1.13 ± 0.47) in the BS13 population per se (SMITH 1979). SMITH (1982) conducted a detailed study on the response of BS13 after seven cycles of half-sib recurrent selection; indirect response for yield was similar to that reported by EBERHART et al. (1973), and the effect of drift was relatively small. Correlated changes for other agronomic traits were generally in the desired direction except for grain moisture at harvest.

RECIPROCAL RECURRENT SELECTION

Reciprocal recurrent selection was initiated in 1949 following the suggestion of COMSTOCK et al. (1949). Selection also was based on half-sib progeny selection, but parallel selection programs were conducted for two populations, each acting as the tester for the other. The objective of reciprocal recurrent selection is the maximum improvement of the population cross, which can be achieved only if two populations are improved simultaneously; the improvement in each population

Table 5. Summary of response to half-sib recurrent selection for grain yield in BS13(HT) using Ia13 as the tester.

Entry	Populations per se	Testers	
		BSSSC0	Ia13
	----------q/ha----------		
BSSSC0†	54.8	54.8	63.1
BS13(HT)C2	54.5	56.2	67.4
BS13(HT)C3	55.7	51.4	67.7
BS13(HT)C4	51.7	55.0	68.0
BS13(HT)C5	54.9	56.1	71.6
BS13(HT)C6	58.3	59.7	73.4
BS13(HT)C7	59.6	61.3	74.8
b(C0 to C7)	0.74 ± 0.27**	0.93 ± 0.27**	1.65 ± 0.38**
b‡	0.69 ± 0.27**	0.91 ± 0.27**	1.65 ± 0.38**
R††	-1.13 ± 0.47**	----¶	----
b(C0 to C4)#	0.53	----	----
b(C4 to C7)#	2.01	----	----
BSSSC0	59.7	59.7	----
BS13(HT)C4	59.0	66.3	----
BS13(HT)C7	67.4	66.2	----
b(C0 to C4)§	0.80 ± 0.24**	----	----
b(C4 to C7)§	2.48 ± 0.37**	----	----

**Significant at the 1% probability level.

†, ‡, and § are data reported by EBERHART et al. (1973), SMITH (1979), and SMITH (1982), respectively.

¶Data were not available.

#Based on data reported by EBERHART et al. (1973).

††R is a measure of the effects of inbreeding.

is complementary with the improvement in the other population with respect to the population cross.

The two populations included in reciprocal recurrent selection conducted in Iowa were BSSS and Iowa Corn Borer Synthetic #1 (BSCB1). BSSS was the same base population that was used for half-sib selection to form BS13. BSCB1 also is a synthetic variety that was formed from 12 inbred lines, which, at the time of synthesis, were considered to have acceptable levels of leaf feeding resistance to the first-generation European corn borer. Details of the methods used for conducting reciprocal recurrent selection in BSSS(R) and BSCB1(R) were given by PENNY & EBERHART (1971). Ten cycles of selection have been completed, but data to evaluate progress are available for only the first eight cycles.

Response to reciprocal recurrent selection was positive

Table 6. Summary of response to reciprocal recurrent selection for grain yield for BSSS(R) and BSCB1(R).

BSSS			BSCB1	
Entry	Populations per se	Populations crosses	Populations per se	Entry
	----------q/ha----------			
BSSSC0†	55.2	66.8	57.9	BSCB1C0
BSSS(R)C1	56.6	68.0	57.3	BSCB1(R)C1
BSSS(R)C2	58.0	69.2	56.7	BSCB1(R)C2
BSSS(R)C3	59.4	70.4	56.0	BSCB1(R)C3
BSSS(R)C4	----	71.5	----	BSCB1(R)C4
b	1.38 ± 0.62**	1.18 ± 0.24**	-0.64 ± 0.62	
Gain (%)	7.6	7.0	-3.3	
BSSSC0‡	54.8	61.1	52.0	BSCB1C0
BSSS(R)C1	52.5	65.9	50.5	BSCB1(R)C1
BSSS(R)C2	54.5	65.5	51.1	BSCB1(R)C2
BSSS(R)C3	52.7	68.3	53.9	BSCB1(R)C3
BSSS(R)C4	52.4	73.8	52.0	BSCB1(R)C4
BSSS(R)C5	54.6	73.8	54.7	BSCB1(R)C5
b‡	0.24 ± 0.40	2.73 ± 0.25**	0.47 ± 0.44	
b¶	1.35 ± 0.40**	2.70 ± 0.25**	1.48 ± 0.47**	
R††	-2.52 ± 0.73**	----	-2.40 ± 0.76**	
Gain (%)	0.0	20.8	5.2	
BSSSC0§	50.0	58.5	51.8	BSCB1C0
BSSS(R)C1	49.1	----	51.3	BSCB1(R)C1
BSSS(R)C3	51.5	67.4	53.4	BSCB1(R)C3
BSSS(R)C5	55.0	----	50.4	BSCB1(R)C5
BSSS(R)C7	52.4	70.7	47.4	BSCB1(R)C7
b	0.61 ± 0.33	1.75 ± 0.37**	0.57 ± 0.33	
Gain (%)	4.8	20.8	-8.5	
BSSSC0¶	59.7	73.1	53.4	BSCB1C0
BSSS(R)C4	62.4	79.0	55.2	BSCB1(R)C4
BSSS(R)C7	68.9	91.3	56.1	BSCB1(R)C7
b(C0 to C4)	1.38**	2.47 ± 0.33**	----	
b(C4 to C8)	3.38**	3.61 ± 0.45**	----	
Gain (%)	15.4	24.9	5.1	
BSSSC0#	50.3	55.8	63.7	BSCB1C0
BSSS(R)C7	64.3	84.1	41.0	BSCB1(R)C7
Gain (%)	27.4	50.7	-35.6	
BSSSC0#	70.5	79.1	86.3	BSCB1C0
BSSS(R)C7	81.1	108.3	73.6	BSCB1(R)C7
Gain (%)	15.0	36.9	-14.7	

**Significant at the 1% probability level.

†, ‡, §, ¶, and # are data reported by PENNY & EBERHART (1971), EBERHART et al. (1973), MARTIN & HALLAUER (1980), SMITH (1982), and STANGLAND et al. (1983a), respectively.

††R is a measure of the effects of inbreeding.

in the population crosses (Table 6). The trend of the yield response seemed to be increasing as additional cycles of selection were completed. Total gain for direct response in the population crosses ranged from 7.0% (PENNY & EBERHART 1971) to 36.9% (STANGLAND et al. 1983a). Gain per cycle of selection ranged from 1.0 to 6.3% for the individual studies or an average gain per cycle of 3.6%. Indirect response in BSSS and BSCB1 was erratic, but the response in BSSS was usually positive (11.7% or 1.8% per cycle), whereas BSCB1 tended to have a negative response (-8.6% or -1.2% per cycle) (Table 6). SMITH (1982) partitioned the response to selection for cycles C0 to C4 and cycles C4 to C8; average response increased 46.2% from 2.47 $\pm$ 0.33 (cycles C0 to C4) to 3.61 $\pm$ 0.45 (cycles C4 to C8). As emphasized by SMITH (1982), the increased direct response probably was caused by changes made in field techniques after the C4 cycle: 1) S_1 plants were crossed to their respective testers and 2) evaluation trials were machine-harvested rather than hand-harvested. These two changes increased the variability among the half-sib progenies tested. Harvest method also was reflected in the regression estimates reported for evaluating response to selection: response was less for the hand harvested trials (PENNY & EBERHART 1971; MARTIN & HALLAUER 1980) than for the machine-harvested trials (EBERHART et al. 1973; and SMITH 1982) (see Table 6). SMITH (1979) reanalyzed the data reported by EBERHART et al. (1973) by use of the same genetic model used for the BS13 population. Response to selection was estimated as 2.70 $\pm$ 0.25, which was similar to EBERHART et al. (1973).

Indirect responses in BSSS(R) per se were generally less than in the population crosses. Population performance per se, however, was confounded with the effects of inbreeding and genetic drift due to the small effective population sizes because only 10 parents were used in recombination. Estimates reported by EBERHART et al. (1973) and MARTIN & HALLAUER (1980) show no significant indirect response in either BSSS(R) or BSCB1(R) (Table 6). Separation of the effects due to changes in allelic frequencies and inbreeding by SMITH (1979) shows that the indirect responses of BSSS(R) and BSCB1(R) were similar to the direct response of the population cross (Table 6). Regression estimates of yield on cycles of selection, however, show that all but one of the estimates of indirect responses [BSSS(R) by PENNY & EBERHART (1971)] were less than the direct response of the population crosses. However, these latter estimates confound the effects of inbreeding with the estimates of indirect effects.

SPRAGUE & EBERHART (1977) and HALLAUER & MIRANDA (1981) presented summaries of response to selection based on half-sib progenies in several different corn populations. Rates of gain expressed on a per-cycle basis for intrapopulation half-sib selection were similar for the different populations; BSSS, therefore, was not a unique population as measured by rates of response to half-sib recurrent selection.

Direct response in the population cross and indirect response of the populations per se for five different reciprocal recurrent selection programs were summarized by MARTIN & HALLAUER (1980). Direct response for the population crosses that did not include BSSS(R) averaged 5.0% per cycle, whereas the two studies that included BSSS(R) and BSCB1(R) averaged 3.25%. Indirect response of the populations per se in the reciprocal recurrent selection programs was generally less than the direct response. Average gain per cycle for all populations was 2.06%, but the average gain per cycle for BSSS(R) was only 0.55%. Comparisons of the response to selection in BSSS show that the rate of response tended to be less per se and in crosses than for other populations. Indirect response in BSSS(R) per se was, however, confounded with the effects of inbreeding due to small effective population size (SMITH 1982). In comparison with other populations included in the reciprocal recurrent selection programs, the direct effects of selection in the population crosses of BSSS(R) and BSCB1(R) were not outstandingly different from other varieties included in reciprocal recurrent selection programs.

SPIN-OFFS OF RECURRENT SELECTION

Response of BSSS to two methods of recurrent selection was the direct result of selection. The ultimate usefulness of recurrent selection methods, however, is whether they contribute to developing superior lines and hybrids; i.e., do the recurrent selection methods contribute breeding materials to applied breeding programs? Evidence in Table 7 suggests recurrent selection methods can have a direct impact for contributing to the genetic improvement of hybrids.

Table 7. Agronomic data for four single crosses compared in trials conducted at four locations for five years (1976-1982).

	Trait				
		Grain	Lodging		Dropped
Single cross†	Yield	moisture	Root	Stalk	ears
	q/ha	%			
B14 x Mo17	72.5	20.2	10.5	6.4	1.2
B37 x Mo17	77.0	22.1	18.2	13.3	1.3
B73 x Mo17	84.4	21.7	14.1	8.2	1.8
B84 x Mo17	94.8	22.3	10.6	8.3	1.0
Average	82.2	21.6	13.4	9.0	1.3
LSD (0.05)‡	3.2	0.5	4.0	2.2	0.3

†Years of release were 1953, 1958, 1972, and 1978 for B14, B37, B73, and B84, respectively.

‡LSD calculated on the basis of 78 replications of data for yield, grain moisture, and stalk lodging, 45 for root lodging, and 12 for dropped ears.

Data were collected for four single-cross hybrids tested at four Iowa locations for five years (1976 to 1980). Four lines (B14, B37, B73, and B84) were crossed to a common inbred tester, Mo17. Each of the lines was developed from the half-sib recurrent selection program of BS13. B14 and B37 were derived from the original sampling of BSSSC0, B73 was derived from BS13(HT)C5, and B84 was derived from BS13(HT)C7. B14, B37, and B73 have been used in commercial hybrids, but the extent to which B84 will be used is unknown at the present because of its recent release. Each successive release had a significant yield increase over the previously released line: B37 x Mo17 yielded 6.2% greater than B14 x Mo17; B73 x Mo17 yielded 9.6% greater than B37 x Mo17; and B84 x Mo17 yielded 12.3% greater than B73 x Mo17 (Table 7). The successive yield increases were not at the expense of other important agronomic traits. B37, B73, and B84 crosses had significantly greater grain moisture than B14 x Mo17, but there was no increase in grain moisture among the B37, B73, and B84 crosses. There were no trends among hybrids for root and stalk lodging and dropped ears. Hence, a 30.8% increase for grain yield from B14 x Mo17 to B84 x Mo17 was not at the expense of later maturity and greater susceptibility to lodging and ear droppage. These comparisons are informative because they support the objectives of recurrent selection methods. New genotypes were identified that contributed to applied breeding in the context of 1) making new genetically superior hybrids available to the farmers and 2) providing new genotypes to use in pedigree selection programs for line recycling.

SUWANTARADON & EBERHART (1974), RUSSELL & EBERHART (1975), and STANGLAND et al. (1983b) have evaluated lines in crosses derived from the recurrent selection programs. Lines included were a portion of those selected from the different cycles of selection for use in recombination to form the next cycle populations. Lines from BS13 (half-sib recurrent selection) and BSSS(R) and BSCB1(R) (reciprocal recurrent selection) were crossed in all possible combinations among the three populations by RUSSELL & EBERHART (1975) and STANGLAND et al. (1983b), whereas SUWANTARADON & EBERHART (1974) crossed selected lines from BSSS(R)C5 with lines from BSK(S)C5. Single-cross hybrids of elite lines were included as checks in each study (Table 8).

Average yield of the single crosses among the selected lines was statistically greater than the variety-cross means for all except the BS13(S2)C1 x BSCB1(R)C7 tested by STANGLAND et al. (1983b). From the group of hybrids tested in each study, an elite group of hybrids was selected for comparison with the mean of all hybrids and the check hybrids. Selection of the elite hybrids also was based on traits other than yield. Mean yield of the elite hybrids was greater than the mean of the check hybrids for all but the BS13(S2)C1 x BSCB1(R)C7 crosses reported by STANGLAND et al. (1983b). The best hybrids also were similar to the best check hybrids for grain moisture and lodging resistance. These results are very encouraging for the potential of recurrent selection for developing materials that can contribute to the genetic improvement of hybrids. In each instance, the authors speculated that con-

Table 8. Summary of comparisons among hybrids of lines derived from populations improved by recurrent selection, variety-cross means, and means of check hybrids produced from elite lines.

Entries	Yield	Grain moisture	Lodging Root	Lodging Stalk
	q/ha	%		
BSSS(R)C5 x BSK(S)C5†				
Mean of elite hybrids (9)¶	78.7	21.7	--	23.9
Mean of all hybrids (49)	73.1	21.7	--	24.0
Variety-cross mean	68.8	19.9	--	25.8
Mean of check hybrids (3)	74.5	18.8	--	12.3
LSD (0.05)	10.2	1.5	--	15.6
BSSS(R)C5 x BSCB1(R)C5‡				
Mean of elite hybrids (3)	87.0	23.5	1.2	11.2
Mean of all hybrids (25)	78.7	24.0	3.8	12.6
Variety-cross mean	65.5	23.6	3.6	16.4
BSSS(R) x BS13(HT)C6‡	82.8	27.6	23.1	6.4
Mean of all hybrids (25)	71.0	26.8	29.9	12.5
Variety-cross mean	66.9	25.2	16.3	8.8
BS13(HT)C6 x BSCB1(R)C5‡	86.7	27.1	16.1	19.3
Mean of all hybrids (25)	71.8	23.7	14.6	19.0
Variety-cross mean	66.5	22.5	4.0	11.5
Mean of check hybrids (3)	74.3	23.3	6.1	8.4
LSD (0.05)	9.9	1.3	10.9	10.6
BSSS(R)C7 x BSCB1(R)C7§				
Mean of elite hybrids (4)	92.8	20.4	2.4	6.3
Mean of all hybrids (32)	84.5	20.8	2.1	5.3
Variety-cross mean	84.1	21.3	2.5	10.5
BS13(S2)C1 x BSCB1(R)C7§				
Mean of elite hybrids (4)	89.7	20.0	4.2	5.3
Mean of all hybrids (32)	83.7	19.8	4.4	12.3
Variety-cross mean	85.1	20.2	6.8	14.3
Mean of check hybrids	95.5	21.9	6.2	8.4
LSD (0.05)	9.4	1.2	6.7	8.3

†, ‡, and § are data reported by SUWANTARADON & EBERHART (1974), RUSSELL & EBERHART (1975), and STANGLAND et al. (1983b), respectively.

¶Numbers in parenthesis indicate the number of crosses included in the means.

tinued inbreeding, selection, and testing would identify hybrids that should be superior to the check hybrids for the important agronomic traits. The greatest weakness of most hybrids in comparison with the check hybrids was for root and stalk lodging. Recent modifications of recurrent selection that emphasize greater selection for resistance to lodging should contribute to developing materials having better roots and stalks. These changes can be made without sacrificing gains made for yield.

GENETIC VARIABILITY

COMPONENTS OF VARIANCE

Genetic variability is essential for effective selection; it is the raw material manipulated by breeders to develop new, improved genotypes. The relative amount of genetic variability within and among populations is important to determine the relative progress that can be expected from selection. If there is limited genetic variability, progress from selection also would be expected to be limited. Considering all items to be comparable including the mean level, breeders would choose those populations that have the greatest genetic variability.

Estimates of genetic variability have been determined for several corn populations because of the questions raised by HULL (1945) for the predominant type of gene action expressed in heterosis of corn. HULL (1945) theorized that genetic progress in corn breeding would be limited because of the paucity of additive genetic variance in corn populations. He suggested that breeding procedures that took advantage of overdominant genetic effects should be developed. This suggestion stimulated studies to estimate and determine the relative importance of different types of genetic variance in different corn populations. A summary of the estimates for several corn populations was given by HALLAUER & MIRANDA (1981).

Estimates of genetic variability have been obtained for BSSS from use of mating designs that included half-sib and full-sib families, unselected lines developed by single-seed descent, and half-sib progenies included in recurrent selection programs. Six estimates of the additive genetic variability (σ_A^2) were available (Table 9). The estimates of σ_A^2 ranged from 147 (determined from the variation among 247 unselected S_7 lines derived from BSSS) to 386 (the variation among half-sib progenies of the reciprocal recurrent selection program). The average of the six estimates of σ_A^2 was 226. Two studies permitted the partition of the total genetic variance into variance due to additive effects (σ_A^2) and deviations due to dominance (σ_D^2). Both studies included half-sib and full-sib families produced from use of the North Carolina Designs I and II (COMSTOCK & ROBINSON 1948). Estimates of σ_A^2 and σ_D^2 were very similar for the two studies (estimates 1 and 3, Table 9), and the interaction of the additive and dominance variances with environments and experimental errors also were very similar.

Estimates of genetic components of variance for grain yield of corn for 99 studies were summarized by HALLAUER & MIRANDA (1981); the average estimates of σ_A^2 and σ_D^2 were 469 and 287, respectively (Table 9). The magnitude of the average estimate of σ_A^2 for BSSS was only 46% of the average estimate of σ_A^2 for the other corn populations. BSSS is a synthetic

Table 9. Summary of estimates of additive genetic and dominance components of variance and their interactions with environments for yield (g/plant) for BSSSCO.

Sources of estimates†	Components of variance‡					
	σ^2_A	σ^2_{AE}	σ^2_D	σ^2_{DE}	σ^2	h^2 §
1	156	83	174	74	387	35
2	147	44	---	---	129	80
3	166	91	184	72	364	59
4	283	22	---	---	157	89
5	217	183	---	---	1203	40
6	386	210	---	---	1417	50
$\bar{X}_{BSSS}$	226	106	179	73	610	59
$\bar{X}_{Corn}$	469	---	287	---	----	--

†Estimates 1 to 4, 5 and 6, and $\bar{X}_{Corn}$ are from Tables 5.4, 5.12, and 5.1, respectively of HALLAUER & MIRANDA (1981).

‡σ^2_A, σ^2_{AE}, σ^2_D, σ^2_{DE}, and σ^2 are additive genetic, interaction of additive effects with environments, dominance, interaction of dominance effects with environments, and experimental error components of variance, respectively.

§Progeny mean heritabilities based on three environments and two replications in each environment.

variety and, as pointed out by HALLAUER & MIRANDA (1981), the estimates of σ^2_A for synthetic varieties tended to be less than the estimates of σ^2_A for other types of corn populations. The two estimates of σ^2_D for BSSS also were less (63%) than the average of the estimates of σ^2_D for other populations (Table 9). Comparisons of the estimates for BSSS with those for other corn populations suggest that the genetic variability within BSSS tends to be less than for other corn populations. But the genetic variability available in BSSS has been sufficient to permit effective selection.

Additive effects can be fixed by the breeder and are of primary concern in planning appropriate breeding methods. Although the estimates of σ^2_A were smaller for BSSS than for other populations, the average estimates of σ^2_A suggest additive effects were generally more important than the dominance effects. But the two studies of BSSS that permitted the estimation of σ^2_A and σ^2_D show that the estimates of σ^2_D were slightly greater than the estimates of σ^2_A. It seems that the dominance effects were of greater importance than the additive effects in BSSS than in other corn populations. In comparing the estimates of σ^2_A and σ^2_D for BSSS and other corn populations, two conclusions can be made: 1) BSSS had less genetic variability than other populations; and 2) dominance variance was of greater importance in BSSS than for other populations of corn.

INBREEDING DEPRESSION

Extensive inbreeding studies have been conducted in BSSS to obtain estimates of the rate of inbreeding depression for several traits. Different levels of inbreeding were established by self-fertilization, full sibbing, and a combination of full-sibbing and selfing. Because the estimates of inbreeding depression were similar for the different methods of inbreeding, only the estimates determined from the progenies developed by self-fertilization will be discussed. Two independent estimates of inbreeding depression for yield in BSSS were obtained for seven generations of inbreeding (Table 10). Both estimates of inbreeding depression, expressed as change in yield per one percent increase in homozygosity, were very similar (-0.449 and -0.465). Yield decreased about 0.45 q/ha per one percent increase in homozygosity or about 45 q/ha from the S_0 to S_8 generations of BSSS.

Table 10. Estimates of inbreeding depression for yield by self-fertilization in BSSSCO.

Generation	Level (%) of homozygosity	Mean yield (q/ha)†	Mean yield (q/ha)†
S_0	0.00	64.9	68.0
S_1	50.00	44.6	45.2
S_2	75.00	30.8	35.1
S_3	87.50	26.1	30.3
S_4	93.75	23.9	26.2
S_5	96.88	22.4	--
S_6	98.44	21.9	24.7
S_7	99.22	19.3	--
S_8	99.61	--	22.0
Change (%)		70.3	67.6
b		-0.449	-0.465
b‡		-0.510	-0.510

†Estimates of inbreeding depression reported by HALLAUER & SEARS (1973) and by GOOD & HALLAUER (1977).

‡Average estimate of inbreeding depression for yield of corn reported by HALLAUER & MIRANDA (1981).

Estimates of inbreeding depression for yield in other corn populations were summarized by HALLAUER & MIRANDA (1981). The average estimate of inbreeding depression in corn was 0.51 q/ha per one percent increase in homozygosity. On the average, therefore, the inbred generation at 100% homozygosity would be expected to yield 51 q/ha less than the noninbred generation. Effects of inbreeding tended to be less in BSSS, on the average, than for other corn populations, although probably not significantly less.

OTHER TRAITS

Estimates of genetic variability, level of dominance, and inbreeding depression were obtained for other plant and ear traits, physiological traits, and pest resistance in BSSS. Most estimates of genetic variability were obtained either from use of unselected S_7 lines or use of unselected S_1 or S_2 lines developed from the original population of BSSS. Estimates of inbreeding depression were obtained from the use of a set of unselected lines that included The S_1 through S_7 generations of BSSSC0. Precision of the estimates varied from trials conducted in 1 to 10 environments with 2 to 5 replications per environment.

Estimates of genetic components of variance and inbreeding depression for BSSS plant and ear traits were summarized by HALLAUER & MIRANDA (1981). In all instances, the estimates of additive genetic variance were significantly greater than zero and greater than the estimates of the dominance variance for each trait. Heritability estimates on a plot mean basis ranged from about 50% for ear diameter and kernel depth to over 80% for plant and ear height. Except for days from planting to flowering, all estimates from BSSS tended to be smaller than those for other corn populations. Heritability estimates for BSSS, however, tended to be greater than for the other populations, primarily because the genotype by environment interactions and experimental errors were smaller for the BSSS studies. Estimates of inbreeding depression of BSSS tended to be smaller than for other corn populations for yield. Except for days from planting to flowering and percentage of barrenness, inbreeding had a negative effect on the traits; i.e., there was a reduction in size and vigor with increased inbreeding.

CROSBIE et al. (1977) studied the variability of traits related to photosynthetic efficiency: CO_2-exchange rate during vegetative growth (CER 1) and during grain filling (CER 2), specific leaf weight, and leaf thickness. Estimates of additive genetic variance for CER 1 (23.8 ± 7.8) and CER 2 (34.3 ± 7.7) were 1.7 and 4.9 times greater than their respective genotype by environment interaction variances. A significantly positive genetic correlation ($r = 0.90$) was observed between CER 1 and CER 2, but the correlations between specific leaf weight and leaf thickness and CER were too low to permit their use as selection index traits for CER in BSSS. They concluded selection would be effective for improved CER in BSSS and that selection must be based on CER per se.

Genetic resistance to pests is the most effective method for their control. Selection pressure for the pests common to corn production in Iowa was imposed either directly or indirectly during the course of the recurrent selection programs of BSSS. Additionally, lines from BSSS have been evaluated to determine the genetic variability for the common pests. A summary of the estimates of variability for traits that contribute to resistance to pests is included in Table 11. The traits included were evaluated to determine the variability

Table 11. A summary of the estimates of ten traits that have been studied in BSSS relative to pest resistance.

Estimates[†]	First-generation European corn borer			Stalks: Rind puncture[‡]	Stalks: Diplodia zeae[‡]	H. turcicum		Root damage	
	1[‡]	2[§]	3[§]			1[§]	2[§]	1[¶]	2[#]
σ^2_G	1.04	1.93	0.52	4.17	0.53	0.33	0.26	0.34	0.01
σ^2_{GE}	--	--	--	--	--	--	--	--	0.01
σ^2	2.55	1.50	1.50	2.10	0.59	0.36	0.36	5.18	0.28
h^2 (%)	54.9	72.0	40.9	85.6	72.9	64.7	59.1	20.6	20.0

Estimates[†]	Roots: Size		Roots: Secondaries		Roots: Root angle[¶]	Roots: Lodging, %		Stalk lodging, %		Root pull (kg)	
	1[¶]	2[#]	1[¶]	2[#]		1[¶]	2[#]	3[††]	4[††]	1[††]	2[††]
σ^2_G	3.46	0.06	4.22	0.07	1.37		6.11	80.8	131.0	114.8	48.9
σ^2_{GE}	--	0.07	--	0.05	--	--	7.44	-35.2	29.4	32.6	14.3
σ^2	5.84	0.26	3.97	0.28	1.63		44.30	263.6	263.6	327.7	327.9
h^2 (%)	70.3	47.1	80.9	53.8	77.2	63.1	29.2	75.2	72.8	72.5	58.7

†σ^2_G, σ^2_{GE}, σ^2, and h^2 are the estimates of genetic variability, genotype by environment interaction, experimental error, and heritability on an entry mean basis, respectively.

‡Unselected S_7 lines from BSSSC0 reported by Hallauer and Miranda (1981); 221 lines were included.

§Unselected S_1 lines from BSSSC0 (1) and BSSS(R)C8 (2) evaluated by Grady (1980); 100 lines were included for each population.

¶Unselected S_7 lines from BSSSC0 evaluated by Owens et al. (1974); 221 lines were included.

#Unselected S_1 lines from BSSSC0 evaluated by Rogers et al. (1977); 136 lines were included.

††Unselected S_1 lines from BSSSC0 (3) and BSSS(R)C8 (4) evaluated by Kevern (1981); 98 lines were included for each population.

for first-generation European corn borer [*Ostrinia nubilalis* (Hübner)], traits related to root and stalk quality, and northern corn leaf blight (*Helminthosporium turcicum* Pass.). The estimates of heritabilities suggest that adequate genetic variability was available in BSSS to expect effective response to selection for most traits. The two estimates of heritability for root damage were low (about 20%) and one estimate of stalk lodging was 29.2%. All other estimates of heritability exceeded 40%.

Although yield was the primary trait considered in the recurrent selection programs of BSSS, it seems adequate genetic variability exists for most traits to expect effective selection for the trait of interest, which suggests that BSSS was not different from other corn populations for pest resistance. Variability for root lodging was less in BSSS than for other populations studied by ROGERS et al. (1977). But BSSS was developed from lines judged to be above average for standability, and the frequency of desirable alleles contributing to standability may be above average. Generally, it seems factors for pest resistance are available in BSSS and one only needs to impose selection to increase the frequency of favorable alleles.

CORRELATED RESPONSES

Grain yield was emphasized in the recurrent selection programs that included BSSS. Because the primary objective of recurrent selection is the development of source populations for the extraction of lines for use in hybrids, the correlated responses of other traits were of interest, particularly for maturity and standability. Data have been collected for other traits of BSSS, either in the same trials evaluating response to selection for yield or in experiments designed to measure correlated changes in other traits.

Correlated responses for plant and ear traits with cycles of selection were reported by EBERHART et al. (1973), MARTIN & HALLAUER (1980), and CROSBIE & MOCK (1980). Ears per plant increased in all instances, and days to flower decreased in the studies reported by EBERHART et al. (1973) and MARTIN & HALLAUER (1980) with no change in the one reported by CROSBIE & MOCK (1980). EBERHART et al. (1973) also reported that grain moisture and stalk lodging decreased with selection in both populations. Data reported by MARTIN & HALLAUER (1980) showed that plant height, ear length, and kernel size had increased in BSSS(R) after seven cycles of reciprocal recurrent selection. CROSBIE & MOCK (1980) reported an increase for ear height and ear length in BSSS(R), but no change in kernel size. Except for the increase in plant height, the correlated changes were favorable for developing germplasm for applied breeding programs.

CROSBIE & MOCK (1979, 1980, 1981) studied the changes that had occurred for ear components and physiological traits related to yield in BSSS(R) after seven cycles of reciprocal recurrent selection. Most changes with selection were in the desired direction: significant increases were reported for grain per leaf area, harvest index, duration of grain filling, and rate of grain filling. Stay-green (a measure of plant health) increased 2.1 days, but the change was not significant. Grain per ear also increased, and there was a significant decrease in number of tassel branches. Seven cycles of reciprocal recurrent selection also improved plant density tolerance of BSSS(R) testcrosses. They concluded that the grain yield improvements in BSSS(R) were primarily associated with increases in ear-sink size.

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