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Radon in Iowa Homes: Results of Screening Measurements

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Homeowner-initiated short-term radon screening measurements in Iowa homes show that only about 30% of the homes have low enough radon levels — below 148 Bq/m³ (4.0 pCi/L) — that no follow-up measurements are necessary. Over 6 percent of the homes have screening measurements in excess of 740 Bq/m³ (20 pCi/L), a level at which prompt follow-up measurements are recommended. In all parts of the state, the range of radon results extends from low levels (below 37 Bq/m³ = 1 pCi/L) to high levels (above 740 Bq/m³). The average radon results tend to be higher than the state average in western Iowa and lower than the state average in eastern Iowa, with the highest average in northwest Iowa and the lowest in southeast Iowa; the reason for this geographical distribution is not known. These data indicate that a greater fraction of radon screening tests in Iowa exceed 148 Bq/m³ than in any other state for which the U.S. Environmental Protection Agency has carried out random radon screening surveys.

INDEX DESCRIPTORS: Radon, Iowa, single-family houses

It is now believed that exposure to radon and radon progeny (decay products) constitutes the major radiation exposure to Americans and poses a significant risk of lung cancer. The National Council on Radiation Protection and Measurements (1987) estimated that about 55% of the average radiation exposure to Americans is due to radon — approximately 200 millirem compared to 96 millirem for other natural radiation sources (cosmic rays, terrestrial radiation, and radiation inside the human body) and 65 millirem for non-natural radiation sources (such as medical x rays, nuclear medicine, and consumer products). Lubin and Boice (1989) of the National Cancer Institute have estimated 13,300 annual radon-related lung cancer deaths in the U.S., the majority occurring among tobacco smokers.

In 1986 the EPA set an "action guideline" for radon in air of 4 pCi/L, or 148 Bq/m³; one becquerel (Bq) is one radioactive disintegration per second, while one picocurie (pCi) is 0.037 disintegrations per second. EPA recommends that homeowners take action to reduce the radon levels in their homes if the annual average radon level exceeds 4.0 pCi/L in the parts of the home in which the occupants spend the majority of their time; this recommendation is based on the predicted health effects from spending 75 percent of a person's life in the home for a period of 70 years. More recently, in the Radon Program Development Act of 1988, the federal government stated that "The national long-term goal of the United States with respect to radon levels in buildings is that the air within buildings in the United States should be as free of radon as the ambient air outside of buildings." This corresponds to only about 0.2 pCi/L (7 Bq/m³) of radon, substantially lower than the EPA action guideline.

In 1986 the EPA produced a map which showed the parts of the U.S. likely to have significant radon problems because of the presence of radioactive geological features; no part of Iowa was included. Nevertheless, the Iowa State University Energy Extension Service was interested in measuring radon in Iowa homes because of speculation that radon levels might be higher in homes "tightened" to reduce air infiltration and exfiltration for the purpose of reducing energy consumption. If radon turned out to be a significant health problem in energy-efficient homes the recommendations for energy conservation measures might have to be re-examined.

Lacking a source of funds for measuring radon in a random survey of homes in Iowa, ISU extension decided to encourage radon testing by homeowners. For this purpose the Iowa Radon Project was initiated with the purpose of creating a radon database in Iowa by

selling at cost a good radon detector and obtaining the test results and other information about the homes from homeowners and the radon analysis laboratory. During most of 1987 and 1988, until radon detectors became widely available at retail outlets in the state, the Iowa Radon Project sold diffusion-barrier charcoal canisters from the Radon Project at the University of Pittsburgh (Pennsylvania) and later from American Radon Services, Inc. (Ames, Iowa). Both laboratories have cooperated in providing results from the lab analyses and questionnaires.

THE RADON SCREENING MEASUREMENT

The EPA has recommended that homeowners begin testing for radon in their homes with a screening measurement, defined as a short-term test (typically 2 to 7 days in length) carried out on the lowest livable level of the home under closed-house conditions. This protocol is intended to avoid false negatives, but maximizes false positives; consequently the screening measurement only indicates whether or not follow-up measurements are necessary. If the test result is low (below 148 Bq/m³ = 4 pCi/L) no further action is necessary, while if it is above 148 Bq/m³ = 4 pCi/L follow-up measurements are recommended to verify the screening measurement and determine the extent of the radon problem. If the screening test result is medium (148 to 740 Bq/m³ or 4 to 20 pCi/L) the EPA recommends a one-year test using one or more long-term (such as alpha-track) detectors in the regularly-occupied portions of the home. If the screening result is high (above 740 Bq/m³ = 20 pCi/L) quicker follow-up measurements are recommended.

The most commonly-used short term detector, the type used in this study, consists of a metal can 7 cm across containing several grams of activated charcoal. The lid has a small hole (uncovered during the testing period) directly under which is a rubber membrane which acts as a diffusion barrier. The diffusion barrier allows only gases to diffuse into the container; the activated charcoal absorbs the radon gas. The canisters are exposed to the air for a period of four to seven days and then promptly mailed to the laboratory for analysis. The major radon isotope collected is radon-222, which has a half-life of 3.8 days and whose immediate decay products are all short-lived. In the laboratory the gamma radiation from selected radon decay products (normally bismuth-214 and lead-214) is measured with NaI detectors. From the knowledge of when the container was uncovered the laboratory determines and reports the constant radon concentration over the period of the test that would have produced the same number of gamma-ray counts.

The purpose of the screening measurement is to find houses with high radon levels. By testing on the lowest livable level under closed-

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house conditions the test has been biased towards a high reading that is unlikely to correspond to the average annual radon level to which the occupants are exposed. A long-term measurement, particularly a 12-month measurement taken in an area of the home most frequently occupied, gives a better indication of the average annual radon level, and therefore of the health risks of living in the house. For purposes of determining average annual radon levels in Iowa homes, or estimating the health risks of radon to Iowans, 12-month measurements are desirable, but neither we nor anyone else has a large enough sample of such measurements in Iowa homes. However, we do have a large sample of short-term tests carried out in the state, a sample large enough to make comparisons with other states and to compare different geographical regions within Iowa.

RADON MEASUREMENTS IN IOWA

The Iowa Radon Project currently has data on over 15,000 short-term radon tests carried out in the period 1986-1989. These tests were initiated, paid for, and carried out by homeowners and do not constitute a random sample of homes in the state. However, an attempt has been made to remove possible sources of bias so that the results approximate those of a random survey. One is that homes with elevated radon levels may be overrepresented due to extra tests carried out in such homes, as when a homeowner receives a high result and then carries out verification or follow-up tests. We have tried to remove this source of bias by including only first-time tests. Cohen and Gromicko (1990) report that using first-time tests is a good bias remover. Another possible source of bias is the higher probability of testing in homes that have characteristics or a location suggesting the possibility of elevated radon levels. This appears to be unlikely as correlations with house characteristics, construction features, and geographical location were not generally known to the general public during the bulk of the period under consideration. Another possible source of bias is that the average tester is probably better educated and has a higher socioeconomic status than the average Iowan. Cohen and Pondy (1988) compared the information that they received from purchased measurements and from randomly-selected no-charge measurements in the same communities and found no clear statistically significant differences in the results obtained from these two different groups. Despite the attempts to remove possible sources of bias, it should be recognized that most of the measurements reported in this paper were in homeowner-occupied single-family detached homes, and that mobile homes, apartments, and townhouses are underrepresented.

For the purpose of this study 7,100 radon screening tests have been selected for analysis. These are all first time tests carried out on the lowest livable level of the home — either the basement (6,926 of the tests) or on the first level of a home without a basement (the other 174

Table 1. Results from the 7,100 short-term first-time radon screening tests reported in this study.

Below-ground (basement) tests	6,926
Above-ground tests	174
Total	7,100
Geometric mean	216 Bq/m ³ (5.8 pCi/L)
Standard error of the mean	2 Bq/m ³
Arithmetic average	308 Bq/m ³ (8.3 pCi/L)
Standard error of the average	4 Bq/m ³
Tests 0-140 Bq/m ³	2,138 (30.1%)
Tests 140-170 Bq/m ³	4,529 (63.8%)
Tests above 740 Bq/m ³	433 (6.1%)

Table 2. Fraction of homes in selected states with screening tests above 140 Bq/m³ (4.0 pCi/L) in this study and in EPA random surveys (Iowa Dept. of Public Health, 1989).

State	Number of tests	Fraction above 140 Bq/m ³
Iowa	1,200	71%
Iowa (this study)	7,100	70%
North Dakota	1,596	63%
Minnesota	919	46%
Colorado	900	39%
Pennsylvania	429	37%
Wisconsin	1,200	27%
Wyoming	800	26%
Indiana	1,217	26%
Massachusetts	1,659	24%
Kansas	1,000	21%
Connecticut	1,500	19%
Kentucky	900	17%
Missouri	1,859	17%
Tennessee	1,800	16%
Arizona	1,507	7%
Alabama	1,200	6%

tests). Table 1 lists some of the major results from an analysis of these 7,100 screening tests.

The 7,100 screening tests were found to have an arithmetic mean of 308 Bq/m³ = 8.3 pCi/L and a geometric mean of 216 Bq/m³ = 5.8 pCi/L. The geometric mean is statistically the more meaningful, because radon measurements are log-normally distributed rather than normally distributed, i.e., the logarithms of the radon results, rather than the radon results themselves, are normally distributed; the distribution of our results appears to be log-normal.

Of the 7,100 screening measurements, 2,138 (30.1%) fell into the low category (up to 148 Bq/m³ = 4.0 pCi/L), 4,529 (63.8%) fell into the medium category 148-740 Bq/m³ or 4-20 pCi/L, and 433 (6.1%) fell into the high category (over 740 Bq/m³ = 20 pCi/L). Thus approximately 30% of the homes do not need to carry out a follow-up measurement, approximately 64% are advised to carry out 12-month follow-up measurements to determine the annual average radon level in the home, and approximately 6% are advised to carry out prompt follow-up measurements.

In the winters of 1986-1987 through 1988-1989 the U.S. Environmental Protection Agency carried out random surveys, typically of up to about 2,000 homes per state, in 25 of the states. Iowa was included in the 1988-1989 testing; the EPA reported (Iowa Department of Public Health, 1989) that in Iowa the fraction of homes whose radon screening measurement was over 148 Bq/m³ (4.0 pCi/L) was 71%, in excellent agreement with the 70% fraction found in our 7,100 homes. No other state surveyed by EPA has this large a fraction, the next highest being North Dakota (with 63%) and Minnesota (with 46%); these fractions are shown for selected states (including the five highest) in Table 2.

Radon screening measurements are supposed to be carried out under closed-house conditions. In theory, the house can be closed up for a short-term test any month of the year, but in practice, this is easiest to accomplish during the winter months. We have information on the month in which all but 11 of the screening measurements were carried out. Table 3 shows the number of tests in each season and the fraction of the screening measurements exceeding 140 Bq/m³ (4.0 pCi/L). This fraction is highest in the autumn and appears to be lowest in summer (for which the number of tests is very small). We have no explanation for the fact that autumn averages are slightly higher than winter averages. The lower readings in spring and summer are probably partly due to the greater difficulty of maintain-

Table 3. Fraction of radon screening measurements in each season that exceed 140 Bq/m³ (4.0 pCi/L).

Season	Tests	Fraction
Winter (December-February)	2,696	70%
Spring (March-May)	2,072	64%
Summer (June-August)	120	53%
Autumn (September-November)	2,201	76%

ing closed-house conditions during those seasons and partly due to several factors which cause depressurization of the lower levels of a building during the heating system; these factors include convection of warm indoor air and its exfiltration through ceilings and roofs, the stack effect from winter winds blowing over the roof of closed houses, and the exhaust up a flue of combustion gases from furnaces.

GEOGRAPHICAL DISTRIBUTION OF RADON

Information about the geographical distribution of radon in Iowa has been gathered by county and by area of the state. Results are available in every one of Iowa's 99 counties, but few statistically meaningful statements can be made about individual counties. However, the county-by-county results of screening measurements indicate that in all parts of the state some homes have very low radon readings while others have high readings.

In order to obtain more significant geographical information the state has been divided into nine groups consisting of the following counties:

1. Northwest: Lyon, Osceola, Dickinson, Emmet, Sioux, O'Brien, Clay, Palo Alto, Plymouth, Cherokee, Buena Vista, and Pocahontas counties.
2. North Central: Kossuth, Winnebago, Worth, Mitchell, Hancock, Cerro Gordo, Floyd, Humboldt, Wright, Franklin, and Butler counties.
3. Northeast: Howard, Winneshiek, Allamakee, Chickasaw, Bremer, Fayette, Clayton, Black Hawk, Buchanan, Delaware, and Dubuque counties.
4. West Central: Woodbury, Ida, Sac, Calhoun, Monona, Crawford, Carroll, Harrison, Shelby, Audubon, and Guthrie counties.
5. Central: Webster, Hamilton, Hardin, Grundy, Greene, Boone, Story, Marshall, Dallas, Polk, and Jasper counties.
6. East Central: Tama, Benton, Linn, Jones, Jackson, Poweshiek, Iowa, Johnson, Cedar, Clinton, and Scott counties.
7. Southwest: Pottawattamie, Cass, Adair, Mills, Montgomery, Adams, Union, Fremont, Page, Taylor, and Ringgold counties.
8. South Central: Madison, Warren, Marion, Mahaska, Clarke, Lucas, Monroe, Decatur, Wayne, and Appanoose counties.
9. Southeast: Keokuk, Washington, Muscatine, Louisa, Wapello, Jefferson, Henry, Des Moines, Davis, Van Buren, and Lee counties.

In each of these nine parts of Iowa some radon screening tests are very low (below 37 Bq/m³ = 1 pCi/L) and some are high (above 740 Bq/m³ = 20 pCi/L).

Table 4 shows for each of these regions the number of screening tests and their geometric means, together with the one-standard-error confidence intervals for the geometric means.

The geographical means exhibit a general pattern of increasing from eastern Iowa to western Iowa. There is also a pattern of increasing from southern Iowa to northern Iowa with the sole exception that Central Iowa has a higher geometric mean than North Central Iowa. Consistent with these trends, the highest average screening result is 285 Bq/m³ (7.7 pCi/L) in Northwest Iowa and the lowest — barely half as great — is 151 Bq/m³ (4.1 pCi/L) in Southeast Iowa. These trends are consistent with unpublished information from nearby states, which indicate that Missouri has lower

Table 4. Geometric mean (and one-standard-error confidence interval) of radon screening measurements by region.

Region	Tests	Geometric Mean (Interval)
Northwest	397	285 Bq/m ³ (274-295)
North Central	549	201 Bq/m ³ (194-208)
Northeast	532	186 Bq/m ³ (178-194)
West Central	260	248 Bq/m ³ (236-262)
Central	3,189	244 Bq/m ³ (241-248)
East Central	1,247	178 Bq/m ³ (173-183)
Southwest	161	215 Bq/m ³ (201-230)
South Central	357	191 Bq/m ³ (181-202)
Southeast	408	151 Bq/m ³ (144-159)
All regions	7,100	216 Bq/m ³ (213-218)

levels than Iowa or Minnesota and that Illinois has lower radon levels than Iowa. We are not aware of any information about radon levels in Nebraska or South Dakota, to the west of Iowa, but the trends suggest that at least in the eastern parts of those states there might be a substantial fraction of homes with screening measurements in excess of 148 Bq/m³ (4 pCi/L).

At the 99% confidence level, the screening measurement geometric means for Northwest, West Central, and Central Iowa are significantly greater than the state geometric mean while those for Northeast, East Central, and Southeast Iowa are significantly lower. At the 95% confidence level the geometric means for North Central and South Central Iowa are also significantly lower than the state mean. It should be noted that the distribution of screening measurements does not exactly match the population of the state, with central Iowa overrepresented in the data. However, the population-weighted geometric mean has been computed to be 209 Bq/m³, which is only about 3% less than the 216 Bq/m³ geometric mean of the 7,100 screening measurements reported here.

At present, we have no information on the reason for the geographical differences in the screening measurements. It is likely that geological factors play a role, but there is no information yet on the distribution of radon concentrations in soil in different parts of Iowa. It is also likely that house construction practices play a role in radon levels, but it remains to be studied how construction affects radon concentrations in homes and whether there are significant differences in construction practices in different parts of the state.

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Response to S_2 Recurrent Selection in Exotic and Semiexotic Populations of Maize (*Zea mays* L.)¹

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The main objectives of recurrent selection are to increase the frequency of favorable alleles for a trait, which will be reflected in a desired change in the mean of the trait, and to maintain genetic variability for future genetic improvements. S_2 recurrent selection is expected to result in a greater response per cycle and in an indirect improvement in general combining ability (GCA) because such selection emphasizes additive genetic effects. The objectives of this study were to evaluate the response to S_2 recurrent selection in maize populations involving exotic germplasm, to relate changes in the population means to changes in additive and dominance gene effects and inbreeding, to determine the heterotic pattern among those populations, and to study the changes in GCA occurring with subsequent cycles of selection.

Three populations with different proportions of exotic germplasm [BS16 (100%), BS2 (50%), and BSTL (25%)] were included. Original populations and intermediate and advanced cycles of selection were evaluated in diallel crosses and testcrossed to four elite inbred testers (B73, B84, Mo17, and Oh43).

The response to selection in grain yield was significant in the intermediate cycles, but no further response was obtained in later cycles. Changes in the frequency of alleles with additive effects were significant for the intermediate cycle. A significant coefficient due to inbreeding depression was detected for BS16. The observed response was significant for most of the other agronomic traits in the population representing 100% exotic germplasm. The expected trend, that inbreeding depression would decrease with subsequent cycles of selection, was not observed. Changes in GCA were associated with the observed direct response to selection. An increase in the frequency of alleles with additive effects contributed to the response of selection. Thus, S_2 recurrent selection can improve the performance of lines derived from improved populations with two to three cycles of selection.

INDEX DESCRIPTORS: Corn, germplasm, genetic vulnerability, adaptation, genetic improvement.

Maize (*Zea mays* L.) breeders have been reluctant to use exotic germplasm as breeding populations because the frequency of desirable lines from exotic germplasm has been lower than from pedigree selection within elite line crosses (Hallauer, 1981). Inbred (S_1 and S_2) recurrent selection for grain yield in BS16, BS2, and BSTL maize populations was initiated in 1971 at Iowa State University (Hallauer, 1978). The relative proportions of exotic germplasm were 100, 50, and 25% for BS16, BS2, and BSTL populations, respectively. Differences in expected response among populations were not predicted from the initial estimates of variance components, but recent reports have indicated that BS2 and BSTL responded to selection (Iglesias and Hallauer, 1989). When additive genetic variance is the greatest fraction of the total genetic variance, S_1 and S_2 recurrent selection are expected to improve the performance of the population, derived lines, and general combining ability (GCA).

Changes in gene frequency imposed by recurrent selection methods will alter the heterotic response of the original population. Inbred family selection (S_1 or S_2) is expected to result in the development of superior inbred lines, but changes in GCA brought about by cycles of selection deserve further consideration. Studies comparing the changes in GCA produced by inbred family selection and testcross methods have been reported. Inbred family selection was found to be significantly less efficient than (Horner et al., 1969; Jensen et al., 1983), not different from (Horner et al., 1973; Horner, 1985), or significantly more efficient than testcross selection (Genter, 1973). General combining ability effects reflect additive gene effects with partial to complete dominance (Jenkins, 1940), and inbred family selection is particularly effective in increasing the frequency of those alleles (Hallauer and Miranda, 1988). It is expected, therefore, that improvements in the population will be reflected in an improvement

in GCA. A correlated response in GCA, however, will depend upon the tester used to evaluate that trait. The ultimate use of derived inbred lines in crosses must be determined from yield evaluations of specific hybrid combinations (Hallauer, 1986).

The objectives of this study were to evaluate and compare the changes associated with cycles of S_2 recurrent selection in populations with different proportions of exotic germplasm, to relate changes in the mean of selected populations to changes in additive and dominant gene effects and inbreeding, to determine the heterotic pattern among populations involving exotic germplasm and adapted materials, and to study changes in GCA over cycles of selection.

MATERIALS AND METHODS

The populations studied were BS16, which had been derived from 'ETO Composite' (obtained from Colombia, South America) after six cycles of mass selection for earlier flowering (Hallauer and Smith, 1979); BS2, which had been derived from crosses of 40 ETO Composite plants to each of six early lines (A251, A554, A575, A619, Mt42, and ND203) followed by five generations of intercrossing and random mating (Hallauer, 1978); and BSTL, which had been derived by crossing Tuxpeno (a race from Mexico) by 'Lancaster Sure Crop' and backcrossing to Lancaster Sure Crop (Hallauer, 1972). The sequence of breeding and selection operations for each cycle of S_2 recurrent selection was conducted in the following manner: self-pollination of S_0 plants in the winter nursery; selection [ear size, maturity, and resistance to stalk root rot (*Diplodia zeae* Pass.) and first-generation European corn borer (*Ostrinia nubilalis* Hübner)] among and within S_1 progenies (approximately 400) and self-pollination of selected S_1 plants (S_2 seed harvested) in Iowa; replicated yield trials of S_2 progenies conducted in Iowa; recombination based on S_2 progeny data of remnant S_1 progeny seed in the winter nursery; and an intercrossing generation in the summer nursery in Iowa. Five seasons in 3 years were used to complete each cycle of selection. Effective population sizes were 20 progenies for BSTL and 25 progenies for BS2 and BS16.

The original populations (CO) and the synthetics resulting from

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cycles 2 and 4 for BS16 and from cycles 3 and 5 for BS2 and BSTL were evaluated. Experiments included the three original populations (BS16, BS2, BSTL), six synthetic populations (C2 and C4 of BS16 and C3 and C5 of BS2 and BSTL), nine selfed populations, a diallel among the nine populations, testcrosses of the nine populations to B73, B84, Mo17, and Oh43 inbred lines, population crosses (CO × Cn) selfed, and the following checks: populations BS10 and BS11 (0, 4, and 8 cycles of reciprocal full-sib recurrent selection) crossed to Mo17 and B73, respectively; crosses between cycles 0 and 8 of BS10 and BS11; and six single-crosses among B73, B84, Mo17, and Oh43.

The study was conducted during 1987 and 1988 at four Iowa locations: the Ames Agronomy Research Center, the Ames Atomic Energy Farm, Ankeny, and Martinsburg. Each experiment was planted as a 10 × 11 triple rectangular lattice design. The experimental unit was a two-row plot 5.5 m long with 76.2 cm between rows. All experiments were machine planted the last week of April. Plots were overplanted and thinned to 52 plants plot⁻¹ (62, 150 plants ha⁻¹). Recommended rates of fertilization and weed control practices were followed at all locations. Particularly dry conditions were present throughout most of the vegetative period during 1988. All experiments were machine harvested.

Data were collected in all experiments for stand (plants ha⁻¹), root lodging (% plants leaning more than 30° from vertical), stalk lodging (% plants broken at ear node or below), dropped ears (% of ears detached from plant), grain yield (q ha⁻¹ at 15.5% grain moisture), and grain moisture (%). For experiments located at the Ames Agronomy Research Center and at the Ames Atomic Energy Farm, flowering date (days from planting to 50% of plants shedding pollen) and ear height (in cm, as measured in 10 competitive plants from ground level to upper ear node) were recorded.

Analyses of variance (not reported) were conducted for experiments at each location and combined over years (years and locations were equal among the eight environments). Years and locations were considered random samples of environments and entries were considered fixed effects. The model used to estimate genetic parameters through generation mean analysis was described by Smith (1983). For each population, the following components were estimated:

AOI = the mean of a base genotype plus the intercept of homozygote contributions regressed on cycles of selection, $\{(2p - 1)[a/\sigma_{ph}] + \mu/\sigma_{ph}\}$;

DOI = one-half of the intercept of heterozygote contributions regressed on cycles of selection, $\{p(1 - p)[d/\sigma_{ph}]\}$;

ALI = the partial linear regression coefficient of homozygous contributions regressed on cycles of selection, $\{\Delta p[a/\sigma_{ph}]\}$;

DLI = the partial linear regression coefficient of heterozygous contributions regressed on cycles of selection, $\Delta p(1 - 2p)[d/\sigma_{ph}]\}$;

DQI = the partial quadratic regression coefficient of heterozygous contributions regressed on cycles of selection, $\{(\Delta p)^2[d/\sigma_{ph}]\}$;

DLI' = a linear function of the changes in dominance effects and in allelic frequencies in the Ith and the Ith-prime populations $\{\Delta p[(p - p')d/\sigma_{ph}]\}$;

HII' = heterosis in the cross of the Ith and the Ith-prime populations if I ≠ I', $\{(p - p')^2[d/\sigma_{ph}]\}$;

HQII' = a quadratic function for the change in allelic frequencies and heterozygous effects in the cross of the Ith and Ith-prime populations if I ≠ I', $\Delta p \Delta p' [d/\sigma_{ph}]$,

where μ = the mean of the base genotype;

σ_{ph} = the phenotypic standard deviation; and

p = the initial frequency of a particular allele (G_i) at the ith locus in population I;

p' = the initial frequency of the G_i allele at the ith locus in population I';

Δp = the change in frequency for the G_i allele after one cycle of selection in population I;

$\Delta p'$ = the change in frequency for the G_i allele after one cycle of selection in population I';

a = one half of the difference in genotypic value for homozygous genotypes G_iG_i and g_ig_i; and

d = genotypic value of the G_ig_i genotype as a deviation from the mean of the homozygous genotypes.

Genetic parameters (β) were estimated using least-squares analysis, where $\beta = (X'X)^{-1}X'Y$; and entry means over all environments were used as the Y matrix. The elements of the X matrix were calculated in terms of the functions of cycle number and genetic parameter coefficients. The variances of the estimated parameters were calculated as $V(\beta) = (X'X)^{-1}\sigma^2/re$; where σ^2 is the genotype by environment mean square, and where re is the number of observations (r is the number of replications, and e is the number of environments) included in the entry mean.

The analysis for genetic diversity was adapted from Moll and Hanson (1984) and was based on data from the diallel among populations and advanced cycles (n = 9). Dominance-associated distance (Dd) was estimated from specific combining ability effects (S_{ij}), as follows: $Dd = [\sum_s(S_{ij} - S_{ij})^2 - 2(n^2 - n + 1)S_x^2/n]^{1/2}$, where S_x² is the variance of either a population or a population-cross-mean based on either the genotype-by-environment or the pooled-error mean squares. Additive-associated distance was estimated from GCA effects (A_i), as follows:

$$\hat{D}a = [n(A_i - A_i)^2 - 2(n - 1)S_x^2/n^2]^{1/2}.$$

Tests of significance for both distances, standardized by the respective standard deviations, are available from the F statistics table for n - 1 and for genotype x environment degrees of freedom.

Lattice-design analyses were used to determine entry mean differences among the 110 entries. Analyses II and III proposed by Gardner and Eberhart (1966) were used to derive genetic information from the diallel and testcrosses. Analysis II was based on fitting the variety (population) and variety-cross (population cross) means to the linear model

$$Y_{ij} = \mu_v + 1/2(v_i + v_j) + \gamma\bar{h} + \gamma(h_i + h_j) + \gamma S_{ij},$$

where

μ_v = the mean of all parental varieties included;

v_i, v_j = the variety effect when parent varieties (v_i and v_j) are included in the analysis;

\bar{h} = the average heterosis contributed by the particular set of varieties;

h_i, h_j = the average heterosis contributed by varieties i and j; and

S_{ij} = the specific heterosis occurring when variety i is mated to variety j; $\gamma = 0$ when i = j, and, $\gamma = 1$ when i ≠ j.

Analysis III was based on fitting the variety and variety crosses to the following respective linear models:

$$Y_{ii} = \mu_v + v_i$$

and

$$Y_{ij} = \mu_c + g_i + g_j + S_{ij},$$

where

μ_v = the mean of all varieties;

v_i = the variety effect when parent varieties are included in the analysis;

μ_c = the mean of all crosses;

g_i, g_j = GCA effects; and

S_{ij} = specific combining ability (SCA) effects.

Years and locations were considered a random sample of environments, and genotypes-by-environment mean squares were used to test significance. The variance of the estimated parameters was calculated as $V(\beta) = (X'X)^{-1}\sigma^2/re$, where σ^2 is the genotype by environment mean square, and re (r is the number of replications and e is the number of environments) is the number of observations in the

entry mean. Means squares for testcrosses were partitioned to allow comparisons among testers and among and within populations.

RESULTS AND DISCUSSION

Significant ($P \leq 0.05$) increases in grain yield were observed when the intermediate cycles were compared with original populations (Table 1). The average rates of gain cycle⁻¹ were 3.4 (7.2%), 3.8 (9.5%), and 4.2 q ha⁻¹ (10.6%) for BS16, BS2, and BSTL, respectively. Between the intermediate and advanced cycles of selection for BS16, there was a significant reduction in yield (4.5 q ha⁻¹ cycle⁻¹). BS2 and BSTL populations did not change significantly after the intermediate cycles.

Evaluation of the response to S₂ recurrent selection of synthetic populations by the different cycles of selection is an indirect method: the direct method evaluates the populations after two generations of selfing. No significant effects due to selection were detected in the means of selfed populations, except for the increase in BSTL C3. There was, however, a trend for an increase of yield in each population. S₂ recurrent selection is based on the exposure and elimination of recessive deleterious alleles and on the selection for favorable alleles, which, in the advanced cycles of selection, can result in less inbreeding depression by selfing. But there may be more

inbreeding in Cn cycles relative to CO due to fixation of alleles either by selfing or by genetic drift. No clear tendency in terms of inbreeding depression for grain yield was evident from the results presented in Table 1.

Data for grain yield are similar to those reported by Iglesias and Hallauer (1989). They found a significant reduction in the first cycle of selection as a consequence of abnormal environmental conditions during the progeny evaluation and no trend for recovery was evident for BS16. BSTL revealed a lack of response in the first four cycles of selection and an increase in response in the last cycle ($P < 0.10$). Results from this study confirmed the inability of S₂ recurrent selection to change population means or to maintain response in later cycles of selection (Iglesias and Hallauer, 1989). BS16CO, which represented the population with 100% exotic germplasm, was superior to the other CO populations. BS16CO was comparable in performance to that of the adapted populations.

The response to selection observed for the other agronomic traits was population dependent (Table 1). Tallness and lateness are among the main problems encountered during introgression of exotic germplasm into adapted Corn Belt populations (Brown, 1983). A close relation between flowering date and ear height was observed. Flowering date is one of the principal determinants of plant and ear height, and earlier plants tend to be shorter. Adaptative selection was

Table 1. Population means (*per se* and selfed) and inbreeding depressions (I.D., %) for seven traits measured in three maize populations under S₂ progeny recurrent selection.

Population	Grain yield	Grain moisture	Lodging		Dropped ears	Date of flower	Ear height
	q ha ⁻¹	-----	Root	Stalk	-----	no.	cm
BS16CO <i>per se</i>	47.1	19.8	9.8	21.0	0.7	74.1	132.6
selfed	27.5	19.7	7.4	15.2	0.5	75.3	108.1
I.D.	-41.6	-0.5	-21.3	-27.6	-28.6	+1.6	-18.5
BS16C2 <i>per se</i>	53.9	17.4	8.7	12.9	0.8	69.3	102.8
selfed	26.1	17.0	4.2	14.0	0.5	71.6	95.1
I.D.	-51.6	-2.3	-51.7	+8.5	-37.5	+3.3	-7.5
BS16C4 <i>per se</i>	44.9	16.3	2.8	16.2	0.7	69.1	100.8
selfed	30.0	16.9	1.5	15.3	0.9	69.8	86.1
I.D.	-33.2	+3.7	-46.4	-5.6	+28.0	+1.0	-14.6
BS2C0 <i>per se</i>	40.1	17.5	17.7	21.5	0.3	70.7	121.2
selfed	24.2	17.2	11.5	16.8	0.8	73.7	106.0
I.D.	-39.6	-1.7	-35.0	-21.9	+167.0	+4.2	-12.5
BS2C3 <i>per se</i>	51.5	18.0	4.8	22.3	0.8	71.9	118.6
selfed	29.5	17.7	5.6	18.6	0.3	72.7	103.8
I.D.	-42.7	-1.7	+16.7	-16.6	-62.5	+1.1	-12.5
BS2C5 <i>per se</i>	49.1	17.8	3.3	21.0	0.5	70.5	104.0
selfed	30.2	17.7	4.5	18.8	0.7	71.1	98.3
I.D.	-38.5	-0.6	-36.4	-10.5	+40.0	+0.8	-5.5
BSTLC0 <i>per se</i>	39.6	19.3	6.8	14.9	1.5	73.2	116.5
selfed	23.4	18.3	5.1	12.4	0.5	74.9	100.9
I.D.	-40.9	-5.2	-25.0	-16.8	-66.7	+2.3	-13.4
BSTLC3 <i>per se</i>	52.2	18.6	3.6	17.4	1.0	71.7	113.3
selfed	31.2	18.3	3.8	14.6	0.5	74.1	104.4
I.D.	-40.2	-1.6	+5.6	-16.1	-50.0	+4.7	-8.0
BSTLC5 <i>per se</i>	49.8	17.8	1.6	13.4	0.4	71.7	109.8
selfed	30.7	18.0	1.8	9.5	0.6	72.8	95.8
I.D.	-38.4	+1.1	+12.5	-29.1	+50.0	+1.5	-12.8
LSD (0.05)	6.9	0.8	4.4	5.3	0.8	2.0	6.5

conducted in exotic and semiexotic populations by selecting plants that flowered before a specified date. ETO Composite, when introduced, had a plant height of 4.5 m and a flowering date in late August, which are undesirable standards for the U.S. Corn Belt (Hallauer, 1978). After six cycles of adaptive selection, ETO Composite (renamed BS16) flowered in the first week of August.

Earliness was not one of the traits considered when selecting S_2 progenies, but abnormal conditions during the first cycle of selection in BS16 resulted in the selection of earlier and shorter families that had escaped the drought. No significant changes in flowering date were observed in the other two populations. The advanced cycle of selection for the BS2 population presented a significant reduction in ear height relative to the intermediate cycle, indicating that the association between earliness and ear height was not as strong as in BS16.

Grain moisture is an indicator of maturity; assuming similar rates of grain-moisture loss, those entries with the lowest grain moisture at harvest were the ones that matured earliest. In general, grain moisture was associated positively with flowering date. It can be concluded that selection did not affect the length of the grain filling period, except for the significant reduction in grain moisture between intermediate and advanced cycles of selection in BS16. If the change in BS16 resulted in a reduced grain filling period, it could be one cause of the significant reduction in grain yield for the same stages of selection in BS16.

Improvement in grain yield during the initial cycles of selection in BS2 was accompanied by a significant reduction in root lodging, which was observed in advanced cycles of selection in BS16 (Table 1). Standability was one of the component characteristics of the heritability index used in selection (Smith et al., 1981). The tendency to reduce root lodging with cycles of selection in BSTL was significant, but it was proportionally smaller than in BS16 and BS2. BS16 was the only population exhibiting a significant reduction in stalk lodging. The reduced plant size with cycles of selection probably was the trait most responsible for the improvement in standability of BS16. Selection did not change the average stalk lodging of BS2 and BSTL. Although BS16 exhibited reduced stalk lodging in advanced cycles, the means for stalk lodging were greater than desirable. Because further reduction in plant size can affect grain yield by reducing the photosynthetic area, a restricted selection index, holding ear height and flowering date constant, can be applied to improve stalk lodging and grain yield (Smith et al., 1981).

Except for BSTL, no change with cycles of selection occurred in the percentage of dropped ears. The overall mean for the trait was approximately 1% in the original populations. This could be the consequence of populations having intrinsically low values for the trait, of the method of selection, and/or of the environments, not favoring expression of the trait.

Inbreeding depression is dependent upon the initial gene frequencies of populations. Results reported previously for BS16, BS2, and BSTL showed a reduction in inbreeding depression with selection, but the reductions were population- and trait-dependent (Rodriguez and Hallauer, 1988). If one ignores genetic drift, inbreeding depression either increases, if gene frequency is less than 0.5, or decreases if gene frequency is 0.5; and S_2 recurrent selection increases the frequency of favorable alleles. When original cycles of selection were compared with advanced cycles in terms of inbreeding depression (Table 1), significant reductions were obtained for grain yield and stalk lodging in BS16, for flowering date and stalk lodging in BS2, and for grain moisture and root lodging in BSTL. Differences in levels of inbreeding depression among populations may be explained because of differences in initial gene frequency, level of dominance, genetic drift, and sampling (Hallauer and Sears, 1973).

Comparisons of the changes produced by selection to the proportions of exotic germplasm showed significant changes in 6, 3, and 4

of the seven evaluated traits were observed in BS16, BS2, and BSTL, respectively. The check population crosses exhibited a significant improvement in grain yield and in root and stalk lodging for crosses involving BS10CO and BS11CO after the eight cycles of reciprocal full-sib recurrent selection.

The model proposed by Smith (1983) was used to estimate genetic parameters based on the overall means for populations and population crosses. The results are presented in Table 2. The heterozygote contributions (DOI) for grain yield showed a greater effect due to dominance gene action than those effects due to additive gene action in the CO populations. Changes in frequency of alleles with either additive or dominance effects with cycles of selection were not significant, indicating that, with respect to grain yield, the average response to selection was not significantly different from zero in any of the populations.

The effect of genetic drift (DQI) over cycles of selection was important for BS16. Previous studies considered this effect to be a consequence of selecting a set of earlier and shorter progenies in the initial cycle of selection (Iglesias, 1987; Iglesias and Hallauer, 1989). A shift in the genetic composition of the population in the initial cycle resulted in a population not suited to normal conditions for this area. The significance of the DQI term supports the observed decrease in grain yield for the advanced cycles of selection in BS16.

The estimated parameter HQII', representing heterosis in the population crosses, was significantly different from zero for the cross BS16 \times BSTL. According to Smith's model, these two populations should express greater diversity with cycles of selection.

For the other agronomic traits evaluated, except for root lodging and dropped ears in BSTL and dropped ears in BS16, the estimated AOI showed a significant effect due to additive gene action in the base populations. The mean of random lines derived from the original populations for those traits will be significantly different from zero. No significant contribution from dominance effects for grain moisture was observed in any of the populations. DOI estimates for grain yield were significant for all populations. For the remaining agronomic traits, significant dominance gene effects were observed in 1 or 2 of the original populations (Table 2).

The direct effect of selection, measured as $2ALI + 2DLI$, was significant for grain moisture, flowering date, and ear height in BS16. A significant change in flowering date, ear height, and root lodging with cycles of selection was detected for BS2. Ear height and root lodging were both reduced as a consequence of the increased frequency of loci in the heterozygous condition. Genetic drift, as measured by the DQI term, was important in determining reductions in grain moisture and ear height in BS16.

The linear and quadratic coefficients (DLII' and HQII') for the changes in allelic frequency and heterotic effects in the population cross BS2 \times BSTL accounted for the changes observed in ear height when different cycles of selection were crossed. The HQII' term also explained the increase in stalk lodging when advanced cycles of BS2 \times BSTL population were crossed, as well as the increase in grain moisture for the cross BS16 \times BSTL.

The coefficient accounting for heterotic effects when two CO populations (HII') were crossed represented a significant reduction in root lodging for BS2 \times BSTL, flowering date for BS16 \times BSTL, and stalk lodging for BS2 \times BS16. The precision of estimates of the set of parameters involving population crosses was limited because few cycles of recurrent selection for the terms were included in the equations and because of the correlation with other population parameters.

Estimates of the additive- and dominance-associated distances (D_a and D_d) were obtained by applying of the model proposed by Hanson (1983). For D_a to be nonzero, there must be differences in allele frequencies for loci having additive effects. For D_d to be nonzero, there must be dominance at the locus level and differences in allele

frequencies (Hanson and Casas, 1968). Changes in allele frequency for loci having dominance effects (Dd) were only important for ear height and grain moisture in BS2 and for ear height in BS16 (Table 3). Additive-associated distances (Da) accounted for most of the differences among the cycles of selection. If selection was effective, the distance between the original CO population and the successive cycles of selection was expected to increase. For grain yield, the estimates of Da supported the observed changes in the populations themselves.

For other agronomic traits, the estimates of Da effects supported the previously observed responses to selection. Significant changes in flowering date and stalk lodging for BSTL and grain moisture and stalk lodging for BS2, however, had not been observed previously. Changes generally not significant when the sums of squares were partitioned in orthogonal contrasts were detected as significant when Hanson's model was used to estimate Da.

The population effect (v_i) for grain yield tended to be lowest for the

Table 2. Genetic parameters (Smith, 1979, 1983) for all traits evaluated in populations and population crosses for BS16, BS2, and BSTL undergoing S_2 progeny recurrent selection.

Trait	Population	Parameter ^a							
		AOI	DOI	ALI	DLI	DQI	DLII'	HQII'	HII'
Grain yield (q ha ⁻¹)	BS16	2.33	23.90**	1.15	-0.96	0.21*			
	BS2	5.04	19.08**	0.52	0.76	0.12			
	BSTL	6.91	17.55**	0.56	0.57	0.05			
	BS16 × BS2						-0.01	0.03	0.42
	BS16 × BSTL						-0.27	-0.04	3.55**
	BS2 × BSTL						-0.02	0.02	2.19
Grain moisture (%)	BS16	19.02**	0.30	-0.36**	-0.08	-0.03*			
	BS2	16.64**	0.42	0.09	-0.14	0.01			
	BSTL	17.95**	0.60	0.06	-0.19	0.00			
	BS16 × BS2						0.07	-0.02	-0.18
	BS16 × BSTL						-0.06	0.04*	0.08
	BS2 × BSTL						0.03	-0.01	-0.04
Date of flowering (no.)	BS16	76.34**	-1.20	-0.81**	0.06	-0.05			
	BS2	76.47**	-2.80**	-0.45*	0.43	0.00			
	BSTL	77.29**	-2.01*	-0.23	-0.04	-0.02			
	BS16 × BS2						-0.03	0.00	-0.04
	BS16 × BSTL						0.11	-0.02	-0.73*
	BS2 × BSTL						0.10	-0.03	-0.34
Ear height (cm)	BS16	86.30**	23.09**	-2.46**	-2.18*	-0.30**			
	BS2	89.75**	17.81**	0.22	-1.98*	0.04			
	BSTL	91.92**	13.55**	-0.21	-0.71	0.02			
	BS16 × BS2						0.33	-0.01	-1.36
	BS16 × BSTL						0.35	-0.01	-1.86
	BS2 × BSTL						1.53**	-1.63**	-1.21
Root lodging (%)	BS16	6.96**	1.75	-0.81	0.05	0.04			
	BS2	5.37*	5.10*	0.04	-1.49**	-0.03			
	BSTL	3.91	1.80	-0.10	-0.60	-0.02			
	BS16 × BS2						-0.25	0.13	0.60
	BS16 × BSTL						0.06	0.03	-0.61
	BS2 × BSTL						0.16	0.03	-1.62*
Stalk lodging (%)	BS16	9.80**	4.39*	0.16	-0.62	-0.08			
	BS2	15.28**	3.65	0.43	-0.70	-0.01			
	BSTL	11.35**	1.83	-0.42	0.32	-0.01			
	BS16 × BS2						0.35	-0.05	-1.93*
	BS16 × BSTL						0.24	-0.08	-1.12
	BS2 × BSTL						-0.35	0.18*	0.63
Dropped ears (%)	BS16	0.07	0.28	0.08	-0.11	-0.01			
	BS2	1.37*	-0.44	-0.06	0.08	0.00			
	BSTL	-0.27	0.84*	0.10	-0.11	0.02			
	BS16 × BS2						-0.03	0.00	0.32*
	BS16 × BSTL						-0.04	0.02	0.08
	BS2 × BSTL						0.02	-0.01	-0.10

^aSee text for explanation of genetic parameters.

^bNumber of days from planting to 50% of plants shedding pollen.

*, **Significantly different from 0 at the 0.05 and 0.01 levels of probability, respectively.

Table 3. Estimated standardized distances between BS16, BS2, and BSTL maize populations, based on additive-associated (Da) and dominance (Dd) effects for different cycles of S₂ progeny recurrent selection.

Trait		BS16			BS2			BSTL		
		C0-C2	C0-C4	C2-C4	C0-C3	C0-C5	C3-C5	C0-C3	C0-C5	C3-C5
Grain yield	Da	4.53*	2.76	7.51**	6.99**	16.21**	0.00	10.07**	10.96**	0.00
	Dd	0.55	0.64	0.00	0.00	0.80	0.00	0.00	0.53	0.00
Grain moisture	Da	25.93**	32.36	6.35	1.89	10.19**	12.34**	8.27**	12.34**	3.92
	Dd	1.00	1.32	0.50	0.43	0.60	1.22	0.68	0.71	0.00
Date of flower	Da	19.83**	22.83**	2.83	0.00	0.36	0.36	6.09**	10.00**	3.75
	Dd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ear height	Da	37.00**	40.90**	3.79	9.32**	25.77**	16.67**	4.15*	9.18**	4.86*
	Dd	0.00	0.79	1.02*	1.49*	1.41	0.00	0.00	0.00	0.00
Root lodging	Da	0.00	4.90*	2.36	10.67**	10.94**	0.00	1.79	4.39*	2.12
	Dd	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00
Stalk lodging	Da	7.41**	1.38	5.69*	3.30	1.08	4.82*	4.90*	0.00	4.56*
	Dd	0.31	0.59	0.00	0.00	0.00	0.00	0.65	0.00	0.00
Dropped ears	Da	1.26	2.84	0.98	0.00	0.00	1.28	0.00	3.81*	2.85
	Dd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

*, ** Significantly different from 0 at P≤0.05 and 0.01 levels of probability, respectively.

Table 4. General combining ability (GCA) and population effects (v_i) estimated from a diallel involving three maize populations (BS16, BS2, and BSTL) undergoing S₂ progeny recurrent selection.

Trait	Parameter	BS16			BS2			BSTL		
		C0	C2	C4	C0	C3	C5	C0	C3	C5
Grain yield	GCA	0.36	1.49	-0.80	-2.94**	-1.24	3.43**	-2.34**	0.63	1.39
	v _i	-0.48	6.32**	-2.68	-7.48**	3.92	1.52	-7.98**	4.62*	2.22
Grain moisture	GCA	0.68**	-0.53**	-0.76**	-0.15	-0.35	0.42**	0.54**	0.14	0.01
	v _i	1.74**	-0.66*	-1.76**	-0.56*	-0.06	-0.26	1.24**	0.54	-0.26
Date of flower	GCA	1.28**	-0.99**	-1.39**	0.08	-0.12	-0.06	0.98**	0.32	-0.12
	v _i	2.74**	-2.06**	-2.26**	-0.66	0.54	-0.86	1.84**	0.34	0.34
Ear height	GCA	7.06**	-5.23**	-8.12**	4.60**	2.23**	-3.00**	2.36*	0.91	-0.80
	v _i	19.31**	-10.49**	-12.49**	7.91**	5.31**	-9.29**	3.21	0.01	-3.49
Root lodging	GCA	1.67**	1.42*	-0.77	4.30**	-1.11*	-1.08	-0.42	-1.35*	-2.65**
	v _i	2.88	2.18	-3.72*	11.18**	-1.72	-3.22*	0.28	-2.92	4.92*
Stalk lodging	GCA	-0.30	-1.90**	-0.25	1.82**	2.98**	1.35*	-1.84**	-0.36	-1.50*
	v _i	3.16	-4.94**	-1.64	3.66*	4.46*	3.16	-2.94	-0.44	-4.44*
Dropped ears	GCA	0.01	-0.10	-0.17	0.00	-0.03	-0.09	0.15	0.17	0.07
	v _i	-0.44	0.06	-0.24	-0.44	0.06	-0.24	0.76*	0.26	-0.34

*, ** Significantly different from 0 at P≤ 0.05 and 0.01 levels of probability, respectively.

original CO populations and to significantly increase during the intermediate cycles and decrease during the latest cycles of selection (Table 4). Changes in population effects due to selection were the same as changes in population-means. The estimated changes in GCA effects were related to changes in population effects; the greatest GCA effects corresponded with the best-performing populations and cycles. These results support the previous conclusion based on genetic distances: the restricted changes produced by selection are based on Da effects.

Means of the population crosses ranged from 47.1 to 60.9 q ha⁻¹ (Table 5). The average midparent heterosis in crosses among populations was lower (8.0%) for BS2 and BS16, both of which shared the common ETO Composite germplasm. BSTL had a different source of exotic germplasm, and even though the adapted germplasm was chosen within the same heterotic group as for BS2, the genetic materials were different. The genetic divergence of BSTL, with

respect to BS16 and BS2, was reflected in higher average midparent heterosis values when crossed to BS16 (12.3%) and BS2 (14.5%). The estimates of heterosis were not confirmed when Gardner and Eberhart's models were applied. No significant differences in SCA and heterosis effects, as contributed by population, were detected. Parameter (h_{ij}), which represents the heterosis expressed in the crosses of populations i and j, is a function of the difference in gene frequencies between populations and dominance. According to Gardner and Eberhart (1966), the h_{ij} parameter can be estimated as the summation of the average heterosis in the diallel, or the average heterosis contributed by each population and by the SCA for the specific cross. The estimated heterosis among populations was different from zero due to a significant average heterosis effect in the diallel, but no differences due to specific population contributions were detected. Populations were not sufficiently divergent genetically to be classified according to different heterotic gene pools.

Populations expressed a low-yield performance in testcrosses with elite inbred lines from the 'Lancaster Sure Crop' (Mo17 and Oh43) heterotic group (Table 6). This poor performance supports previous conclusions about the three populations belonging to the same heterotic group as Lancaster Sure Crop Composite (Iglesias, 1987). There was a significant difference between the two BSSS testers: testcrosses with B73 had a yield performance superior to that of testcrosses with B84.

The BSTL population showed a significantly higher average performance in testcrosses (66.5 q ha^{-1}) when compared with BS16 (63.1 q ha^{-1}) and BS2 (63.3 q ha^{-1}). Testcross performance confirmed the observed tendency for a higher average heterosis expressed in crosses involving BSTL. BSTL seemed to have a higher frequency of alleles complementary to the testers and populations included.

Changes in testcross performance with cycles of S_2 recurrent selection were significant for BS2 and BSTL, which represent the populations exhibiting a significant response to selection, up to the intermediate cycles. Testcrosses with BS16 did not reflect the trends observed in the direct response to selection. No significant tester \times population interaction was observed, but the differences among cycles of selection within a population were detected with different testers: B84 and Oh43 for BS2; and B84 and Mo17 for BSTL (Table 6). No improvement was observed in testcrosses with B73.

The populations used as checks (BS10 and BS11) were classified into different heterotic groups. The response to reciprocal full-sib recurrent selection in BS11, reflected in the testcross performance with B73, seemed to plateau between the C4 and C8 cycles of selection. Testcrosses of BS10 with Mo17, however, exhibited significant indirect responses, which were maintained in the advanced cycles of selection (Table 6). BS11 had a better testcross performance than BS10 did, and BS10 required another six to eight cycles of selection, at the same rate of response, to attain the performance level of BS11 advanced-cycle testcrosses.

In regard to other agronomic traits, negative GCA effects for flowering date and ear height represented earlier maturing and shorter progenies, both of which resulted from crosses of BS2, BS16, and BSTL populations. Positive estimates of GCA for BS16CO for date of flower and ear height, when compared with the negative estimates of GCA for BS16C2 and BS16C4, agree with the significant direct change observed in BS16 with cycles of selection (Table 4). The same relation can be observed with respect to ear height in the BS2 population. Significant GCA effects for date of flower and ear height in BSTL differed from the lack of response to selection observed in BSTLC5 for date of flower and ear height.

The changes in GCA effects corresponded with the average changes in population testcross performances. Important differences among testers were detected (Table 6). Testers of the Lancaster Sure Crop heterotic group produced the earliest and shortest testcross progenies, particularly Oh43. Testers with the latest date of flower and the tallest progenies (B73 and B84) were those allowing the best discrimination among testcrosses involving different cycles of selection. No significant tester \times population interactions were detected for date of flower and ear height, and most of the differences among populations could be attributed to the lateness of BS16CO and of BSTLCO, and to the tallness of BS16CO, compared with the tallness of testcrosses involving advanced cycles. For testcrosses involving BS10 and BS11, no changes were observed in date of flower with cycles of reciprocal full-sib recurrent selection. There were no consistent trends for ear height in the BS10 and BS11 testcrosses.

Grain moisture was the only trait for which population heterosis and SCA effects were significant. Differences among population crosses were expected to be significant because of variations in heterosis and SCA effects. General combining ability effects for grain moisture were related closely to GCA effects for flowering date (Table 4), suggesting that the lower grain moisture in advanced cycles of selection for BS16 and BSTL was a consequence of the earlier flowering date, with no changes in length of the grain-filling period.

The indirect effects of selection upon testcross grain moisture were significant for all populations. BS16 and BSTL transmitted lower grain moisture to their testcross progenies in advanced cycles. Testcrosses involving BS2 tended to have higher grain moisture in the advanced cycles of selection. Population testcrosses compared favorably with hybrid checks for grain moisture. Testcrosses of BS10 and BS11 showed significant differences among populations but not within cycles of selection. On the average, testcrosses of BS11 had the greatest amount of grain moisture.

Root and stalk lodging and dropped ears were component traits of the selection index applied for S_2 progeny selection. All populations showed significant improvement in resistance to root lodging (Table 1). Associated with the population means, there were changes in GCA effects. The greatest improvement was observed in the initial cycles for BS2. In BSTL, changes in GCA for root lodging corresponded with changes in GCA for ear height, and a decrease in root lodging occurred either because of a lowering of the center of gravity or because of an effective selection for improved root characteristics. In BS16 and BS2, changes in root and stalk lodging were not highly associated; decreased root lodging could have been the result of improved root characteristics and/or stalk strength rather than of a

Table 5. Average grain yield (q ha^{-1}) for the populations (diagonal) and their crosses (above diagonal) and midparental heterosis (%) for population crosses (below diagonal).

Populations	BS16C0	BS16C2	BS16C4	BS2C0	BS2C3	BS2C5	BSTLC0	BSTLC3	BSTLC5
BS16C0	47.1	57.2	51.8	47.1	50.5	54.0	52.3	54.9	53.0
BS16C2	13.27	53.9	49.0	49.5	53.0	57.2	51.5	57.6	53.7
BS16C4	12.60	-0.01	44.9	47.3	48.7	56.5	54.2	53.4	51.8
BS2C0	8.03	5.32	11.29	40.1	47.7	52.5	47.3	50.6	55.7
BS2C3	2.85	0.06	1.04	4.15	51.5	51.4	51.5	50.9	56.3
BS2C5	12.27	11.07	20.21	17.94	2.19	49.1	51.1	58.7	60.9
BSTLC0	20.64	10.16	28.28	18.69	13.06	15.22	39.6	47.2	47.2
BSTLC3	10.57	8.58	9.99	9.64	-0.02	15.89	2.83	52.2	49.4
BSTLC5	9.39	3.57	9.40	23.92	11.15	23.15	5.59	-3.14	49.8

LSD (0.05): 6.99 q/ha

*CO indicates original unselected population and Cn indicates the number of cycles of selection.

Table 6. Average performance for seven traits in testcrosses of populations and four check hybrids evaluated in eight environments.

Testcross or hybrid	Grain yield			Grain moisture			Date of Flower			Ear height			Root lodging			Stalk lodging			Dropped ears		
	Cycle ^a																				
	O	I	A	O	I	A	O	I	A	O	I	A	O	I	A	O	I	A	O	I	A
	q ha ⁻¹			%			no.			cm			-----			%			-----		
BS16 x B73	67.9	72.7	68.0	18.8	17.6	17.9	75.2	70.9	72.3	130.4	121.7	114.7	9.0	8.7	4.2	11.5	8.9	13.7	0.3	0.7	0.4
BS2 x B73	69.9	68.7	73.8	17.5	18.3	18.1	71.9	72.7	72.3	125.6	122.1	115.6	8.0	3.6	5.0	12.9	11.3	10.7	0.3	0.4	0.9
BSTL x B73	75.0	73.8	72.6	19.9	18.2	19.1	73.8	72.4	72.7	125.2	124.6	116.9	5.2	3.4	2.1	11.2	11.9	10.4	1.0	0.8	0.7
Tester average	71.4			18.4			72.7			121.9			5.5			11.4			0.6		
BS11 x B73	66.8	79.3	80.6	19.7	19.2	19.9	74.9	74.0	74.2	126.4	124.9	130.4	6.2	6.2	6.4	15.1	8.6	7.9	1.0	1.1	0.3
BS16 x B84	64.8	65.7	64.6	19.7	18.0	17.8	74.8	72.1	72.1	129.7	122.7	119.5	15.8	16.9	8.6	10.3	11.2	13.1	0.8	1.2	0.8
BS2 x B84	59.2	69.2	72.7	18.2	17.9	18.9	73.0	72.8	72.4	130.6	126.1	121.1	21.0	10.7	7.6	9.5	10.8	12.2	1.6	0.6	0.7
BSTL x B84	66.9	67.4	74.2	19.1	18.6	18.8	74.2	72.4	72.4	130.3	125.5	123.4	12.2	6.8	5.4	11.7	12.1	11.9	1.9	0.7	1.0
Tester average	67.2			18.6			72.9			125.4			11.7			11.4			1.0		
BS16 x Mo17	62.6	58.1	62.0	18.5	17.6	16.5	74.5	70.5	70.7	117.8	107.8	107.3	3.3	3.7	1.6	9.7	7.1	10.2	1.3	0.9	1.1
BS2 x Mo17	59.3	60.2	62.4	17.3	17.9	18.0	71.8	72.6	72.0	118.9	118.7	112.7	5.9	2.7	1.2	10.3	14.1	12.1	1.1	0.9	0.8
BSTL x Mo17	57.2	63.5	66.4	18.7	18.1	18.5	73.7	72.9	72.7	115.7	118.6	113.6	3.2	1.7	0.4	8.7	10.0	10.0	1.3	1.4	1.0
Tester average	61.3			17.9			72.4			114.6			2.6			10.2			1.1		
BS10 x Mo17	57.0	65.0	71.0	17.2	17.7	16.8	73.3	73.8	73.3	114.7	120.8	112.6	1.2	0.9	1.1	12.4	13.5	9.9	0.5	0.8	0.5
BS16 x Oh43	57.7	57.9	55.6	19.6	17.9	18.1	71.1	69.2	67.4	102.0	90.7	87.3	4.3	4.9	1.2	12.6	13.1	12.7	0.9	0.2	0.3
BS2 x Oh43	55.6	60.6	62.0	17.4	18.0	18.8	67.4	68.0	68.9	100.5	96.6	92.6	3.9	3.7	3.9	16.2	16.0	12.1	0.8	1.0	0.7
BSTL x Oh43	58.1	60.1	63.3	18.6	18.7	18.2	69.8	69.1	68.2	97.5	98.4	95.8	3.2	3.3	3.1	15.7	16.6	11.1	1.0	0.4	0.7
Tester average	60.0			18.4			68.8			95.7			3.5			14.0			0.7		
B73 x Mo17	84.6			18.5			74.4			118.6			2.6			2.4			0.4		
B73 x Oh43	80.5			19.6			71.1			105.4			1.4			6.6			0.5		
B84 x Mo17	83.4			18.6			74.3			120.9			3.5			4.8			0.9		
B84 x Oh43	77.7			19.9			72.0			112.5			7.1			8.4			0.6		
S.E. testcross \bar{x}	2.48			0.30			0.71			2.35			1.58			1.91			0.30		
S.E. tester \bar{x}	0.83			0.10			0.24			0.78			0.53			0.64			0.10		

^aO, I, and A indicate the original population, intermediate cycle of selection, and most advanced cycle of selection, respectively.

lower center of gravity. Population testcross performance was related to changes in GCA effects for root lodging. The best tester for root lodging was B84 because this line allowed the best discrimination among the cycles within populations. This supports the hypothesis that the tester having the lower frequency of favorable alleles for a trait is the one allowing the best discrimination among testcross progenies (Rawlings and Thompson, 1962). Lower root lodging was observed in BS10 and BS11 testcrosses with no particular trend related to cycles of selection. Except for the testcrosses with B84, root lodging scores of the other advanced cycle population testcrosses compared well with those obtained for the elite check hybrids (Table 6).

Significant improvement in the population ALI + DLI for stalk lodging associated with cycles of selection in BS16 was not reflected in a trend to decrease GCA effects. The principal differences with respect to stalk lodging were expressed among populations, with BS2 exhibiting the highest incidence of stalk lodging and GCA effects. Although significant differences among testcrosses were not detected, the greater precision with which tester effects were evaluated resulted in significant tester effects. Testcrosses with Oh43 had, on the average, 3% more lodged plants than other testcrosses had. Stalk lodging was one of the agronomic traits for which populations involving exotic germplasm did not compare favorably with the elite check hybrids. Lack of response in this trait might be a consequence of limited genetic variability in populations.

The percentage of plants with dropped ears was small (<2%), and significant differences among populations were not detected. No differences were detected among population crosses in the diallel, but there were significant differences at the 5% level among testcrosses. The average proportion of dropped ears for testcrosses involving B84 and Oh43 was greater than the average values for the B73 and Mo17 testers. When testcrosses involving the CO population were compared in terms of advanced cycles of selection, BSTL usually showed a significant reduction in dropped ears, which reflects the observed response to selection. The best discrimination for percentage of dropped ears was provided by one of the otherwise lower-performing tester (B84).

CONCLUSIONS

S₂ recurrent selection for improved grain yield was conducted in three populations with different proportions of exotic germplasm. Significant increases in grain yield were observed up to the intermediate cycle, at average rates of 3.4, 3.8, and 4.2 q ha⁻¹ cycle⁻¹, for BS16, BS2, and BSTL, respectively. BS16 significantly decreased after the intermediate cycle at a rate of 4.5 q ha⁻¹ cycle⁻¹, whereas BS2 and BSTL did not respond to further selection. In selfed populations, no significant improvement was observed reflecting the response to S₂ recurrent selection, although there was a trend for greater yields with selection. Estimated genetic parameters failed to detect with cycles of selection a significant change in the frequency of favorable alleles. A significant effect due to genetic drift was observed in BS16. An estimate of heterosis in population crosses indicated a significant change for the cross BS16 × BSTL, suggesting a tendency for greater divergence between those populations in advanced cycles of selection. Additive associated distances estimated from the model proposed by Moll and Hanson (1984) corresponded with the observed response to selection, indicating that response had been based on changes in the frequency of alleles with additive effects.

The estimated changes in GCA effects for grain yield over cycles within a population were highly related to the observed changes in population effects; the largest GCA estimates corresponded to the best-performing population cycles. Specific combining ability and population heterosis effects were not important in the determination of differences among population crosses. Average midparent heterosis in crosses among BS16, BS2, and BSTL tended to be associated with

their genetic divergence. Differences in heterosis were not large enough to allow the classification of populations into different heterotic groups. With respect to heterotic response, the high yield performance of testcrosses with elite inbred lines from the BSSS group suggests that BS16, BSTL, and BS2 can be grouped with Lancaster Sure Crop. Except for BS16, the changes in testcross yield performances with cycles of S₂ recurrent selection were related to the observed direct responses to selection. Testcrosses involving advanced cycles of selection for BS2 did not differ significantly from the check hybrids B73 × Oh43 and B84 × Oh43, indicating that a line as good as Oh43 can be selected from BS2.

The reasons for the lack of response to S₂ recurrent selection in BS2, BS16, and BSTL are not clear. Evidence suggests additive effects with partial to complete dominance are the major contributors to the genetic variability within maize populations (Hallauer and Miranda, 1988). If additive effects are of major importance to the inheritance of maize traits, it seems inbred progeny selection should be as effective, or more effective than half-sib or full-sib progeny selection. Limited response may have occurred because of rapid fixation of important alleles because of either effective selection or because of genetic drift due to small effective population sizes. In all instances, there were trends for response to S₂ progeny selection in each population at the inbred level, which was not expressed in the noninbred populations and their testcrosses. If overdominant effects were expressed at important loci, fixation of alleles by S₂ progeny selection would negate their effects in advanced cycles of selection. Additional cycles of S₂ progeny selection are necessary to determine the relative importance of genetic effects and their response to selection. The inclusion of exotic germplasm for S₂ progeny selection within temperate areas may not be appropriate in the earlier cycles of selection.

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