Theor Appl Genet (1996) 93: 990–996

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Repeatability and heritability of divergent recombination frequencies in the Iowa Stiff Stalk Synthetic (*Zea mays* L.)

Received: 30 October 1995 / Accepted: 24 May 1996

Abstract Variability in recombination frequency was reported in the Iowa Stiff Stalk Synthetic. The objectives of the present research were to verify the differences in recombination frequency among individuals in the Iowa Stiff Stalk Synthetic maize population and to determine if the recombination frequency differences persisted among the S_1 progeny. Testcrosses to measure male recombination frequency on three chromosomes (4, *su1-c2*; 5, *a2-bt1-pr1*; 9, *sh1-bz1-wx1*) were repeated for eight S_0 individuals. Recombination frequencies were repeatably divergent among those individuals which were selected based on high or low recombination frequencies on specific chromosomes. Individuals which had been selected for long and short total map distances across the three chromosome regions produced repeatably divergent recombination frequencies only at the *su1-c2* region. The recombination frequencies of the S_1 lines, derived from the S_0 individuals which had the most divergent recombination frequencies on a single chromosome, were significantly different. The broad-sense heritability estimates derived from the regression of six S_1 lines on six S_0 individuals ranged from 0.69 to 0.20 for the five chromosome regions. We conclude that genetic differences for recombination frequency exist in this population and that modification by selection should be possible.

Key words Crossing-over · Testcross · Corn

Introduction

Variation in the frequency of genetic recombination has been measured in numerous organisms, and Smith (1978) speculated that variability in recombination frequency could be found in most populations. In plant species chiasma frequency has been found to vary significantly between individuals in barley (*Hordeum vulgare*; Gale and Rees 1970), radish (*Raphanus sativus* L.; Dayal 1977), rye (*Secale cereale* L.; Jones, 1974), and wheat (*Triticum aestivum* L.; Rao and Murty 1972). Similarly, recombination frequency showed significant variability in maize (*Zea mays* L.; Stadler 1926; Tulsieram et al. 1992; Fatmi et al. 1993), barley (Säll 1990), tomato (*Lycopersicon esculentum*; Griffing and Langridge 1973), and soybean (*Glycine max* L., Pfeiffer and Vogt 1990).

Selection for increased or decreased recombination frequency has been used to document the genetic control of recombination. Numerous selection programs have been carried out using insects, including *Drosophila melanogaster* (Chinnici 1971; Kidwell 1972; Valentin 1973; Charlesworth and Charlesworth 1985), *Bombyx mori* (Turner, 1979) and *Tribolium castaneum* (Dewees 1975). In general, control was polygenic, and additive genetic variance predominated. In plants, Gale and Rees (1970, barley) and Rees and Thompson (1956, rye) indicated predominately additive genetic variance accounted for the genetic variability in chiasma frequency. Allard (1963), obtained differences of 7.5, 10.0 and 20.0 map units between high and low lines following four generations of selection for high and low recombination at three pairs of linked loci in *Phaseolus lunatus*. These results indicate that polygenic quantitative control of recombination frequency can be expected in plant populations.

Single gene control of recombination frequency, however, does exist in plants. The incompletely dominant *Rm1* allele in *Petunia hybrida* (Cornu et al. 1989; Robert et al. 1991) increased the recombination frequency approximately three-fold in female gametes for pairs of closely linked genes on five chromosomes. While Tulsieram et al. (1992) indicated polygenic control of recombination frequency at two chromosome regions, they also demonstrated single gene control at the *Pgm1–Adh1* region on chromosome 1 in maize. Recently, variability in recombination frequency has been catalogued in several plant breeding populations (Pfeiffer and Vogt 1990; Tulsieram et al. 1992; Fatmi et al. 1993). Plant geneticists are inter-

Communicated by G. E. Hart

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ested in finding and isolating genetic control of recombination so that this control may be used in plant improvement efforts. But, substantial variability in recombination frequency has been attributed to environmental conditions (Allard 1963; Pfeiffer and Vogt 1989) and sampling factors (Broadhead and Kidwell 1975; Butler 1977) as well as to genetic causes. In order to utilize the variation in recombination frequency, that variation must be heritable.

Fatmi et al. (1993) reported a range in recombination frequencies among genotypes at five chromosome regions in the Iowa Stiff Stalk Synthetic (BSSS) maize population. The distributions of recombination frequencies at regions on chromosomes 4 and 9 were normal. Although the distributions of recombination frequencies at regions on chromosome 5 were skewed towards lower frequencies, they were unimodal. Highly significant variability was present among individuals, but this individual variation was only one-quarter of the total variation. Approximately one-tenth of the variability was partitioned to the yearly environment and two-thirds to the error variance. The objectives of the present study were to verify the differences in recombination frequency among individuals in BSSS and to determine if these recombination frequency differences were heritable in the S_1 progeny of selected individuals.

Materials and methods

Iowa Stiff Stalk Synthetic is a widely used maize research population and an important source of inbred lines (Hallauer et al. 1983). Population BS13(S)C4 (Hallauer et al. 1983), a recurrent selection-improved subpopulation of BSSS, was the original population screened for recombination frequency differences (Fatmi et al. 1993). The chromosome location, the genetic map for each linkage group, and the phenotypes conditioned by the recessive morphological marker loci (Coe et al. 1988) are shown in Table 1. The inbred genetic marker stocks were provided by Dr. E. H. Coe, USDA, ARS University of Missouri (Columbia). Two converted inbred lines [the alleles of interest were backcrossed into an inbred line, either W23, K55 or N (Neuffer background)] were available for each recessively marked chromosome. For each chromosome region evaluated, an F_1 was obtained by crossing the two inbred stocks containing the marker loci. The resulting recessive marker F_1 then was used in testcrosses instead of the original inbred stocks because its hybrid vigor provided much larger seed populations for each testcross pollination, e.g., [K55 (*sh1-bz1-wx1*) × W23 (sh*1-bz1*-wx*1*)] × [W23 (sh*1-bz1-wx1*) × BSSS – S1 – 14]. In all cases, recombination frequencies were measured by testcrosses of plants heterozyous for the marker genes crossed as males onto appropriate F_1 marker stock plants. The classification of kernel phenotypes and the estimation of recombination frequencies were as described previously (Fatmi et al. 1993).

The repeatability of differences in recombination frequencies was evaluated. In the original experiment (Fatmi et al. 1993), random individual S_0 plants from BSSS were crossed to each of the three F_1 marker stocks (*su1-c2, a2-bt1-pr1* and *sh1-bz1-wx1*) to obtain the heterozygous genotypes for testcrossing. In the summers of 1989 and 1990 the marker stock × BSSS-S_0 crosses were used as males in testcrosses to F_1 marker stock plants. To repeat these measurements, remnant seeds of the marker stocks × BSSS-S_0 crosses were planted, and these plants were used in testcrosses during the summer 1992. The repeated individuals and their original recombination frequencies are shown in Table 2.

Twelve testcrosses were analyzed for each S_0 individual. Each distribution was tested for normality. All testcross populations fit a normal distribution, so no data transformations were necessary in order to utilize the analysis of variance. For each linkage group, an analysis of variance of recombination frequencies was performed using the statistical model: $Y_{ij} = \mu + \alpha_i + \beta_{j(i)} + \varepsilon_{ij}$ where μ is the overall mean of the population, α_i is the effect of the ith individual, $\beta_{j(i)}$ is the effect of the the jth testcross ear within the ith individual and ε_{ij} is the random error associated with each measurement, where i=1 to 8 and j=1 to 12. The error term used to test the significance of the mean square for S_0 contained the error associated with screening as well as the error associated with testcrosses within individuals ($\sigma^2_E = \sigma^2_\beta + \sigma^2_\varepsilon$). These error sources were confounded and could not be partitioned, making the analysis of the individual effect more conservative than it would be if the error effects were separable.

In terms of the repeatability of recombination frequencies among these individuals, we were interested in two comparisons: (1) individuals having overall high recombination (120 and 208) vs individuals having overall low recombination frequencies (185 and 199); and (2) between pairs of individuals with recombination frequencies which were high on some subset of chromosomes and low on another subset of chromosomes (14 and 139 vs. 76 and 188). For each linkage group two single degree-of-freedom contrasts were used to test the significance of these comparisons. Differences were declared significant at ($P<0.05$).

Because of the large amount of variability attributed to the error variance in the previous screening (Fatmi et al. 1993), a subsampling experiment similar to that of Butler (1977) was conducted. The inbred line B84 (derived from BSSS) was crossed to the three different marker stocks in the W23 inbred line background, and these F_1s were subsequently testcrossed to the appropriate F_1 hybrid marker stocks. Twenty-four testcrosses from each marker background were analyzed and used as an indicator of the amount of variation inherent in the technique, as genetic variation among plants was minimal

Table 1 Characteristics[a] of the linkage groups used to evaluate recombination frequency

Chromosome arm	Alleles	Kernel phenotype of recessive genotype	Genetic map distance		
4L	*su1-c2*	Sugary/colorless	50		
			su1	*c2*	
5S	*a2-bt1*	Colorless/brittle	7	25	
5L	*bt1-pr1*	Brittle/red			
			a2	*bt1*	*pr1*
9S	*sh1-bz1*	Shrunken/bronze	2	25	
9S	*bz1-wx1*	Bronze/waxy			
			sh1	*bz1*	*wx1*

[a] Characteristics summarized by Coe et al. 1988

Table 2 Mean recombination frequencies (Fatmi et al. 1993) of S_0 individuals used in our repeatability and heritability experiments. The S_0 individuals were selected for having the highest or lowest recombination frequency on a chromosome, or for having differing patterns of recombination frequencies

S_0 individual	Exp.[a]	Selection criterion[b]	Recombination frequency for linkage group				
			Sul-C2	*A2-Bt1*	*Bt1-Pr1*	*Sh1-Bz1*	*Bz1-Wx1*
14	Rep.	H-C4, C5; L-C9	0.37	0.10	0.28	0.01	0.18
	Her.	Highest-C5					
76	Rep.	L-C4, C5; H-C9	0.30	0.01	0.08	0.03	0.23
92	Her.	Lowest-C5	0.30	0.02	0.06	0.02	0 22
120	Rep.	H-C4, C5, C9	0.34	0.07	0.18	0.04	0.22
139	Rep.	H-C4, C5, L-C9	0.46	0.09	0.22	0.02	0.18
	Her.	Highest-C4					
142	Her.	Lowest-C4	0.23	0.05	0.16	0.02	0.18
185	Rep.	L-C4, C5, C9	0.27	0.03	0.13	0.02	0.20
188	Rep	L-C4, C5; H-C9	0.26	0.02	0.10	0.03	0.24
199	Rep.	L-C4, C5, C9	0.27	0.02	0.12	0.02	0.18
208	Rep.	H-C4, C5, C9	0.41	0.09	0.20	0 02	0.29
	Her.	Highest-C9					
209	Her.	Lowest-C9	0.40	0.01	0.15	0.02	0 07

[a] Experiment reported in this article in which these individuals were used, Rep. – repeatability, Her – heritability

[b] H – high recombination frequency, L – low recombination frequency, C4 – chromosome 4 (*sul-c2*), C5 – chromosome 5 (*a2-bt1-pr1*), C9 – chromosome 9 (*sh1-bz1-wx1*)

when two inbred lines were used to produce the heterozygous F_1.

The heritability of the recombination frequency was estimated for each linkage group. The S_0 (six total) with the highest or lowest recombination frequency on one of the three chromosomes were selected. Their original recombination frequencies (Fatmi et al. 1993) are shown in Table 2. In the summer of 1993 the S_1 lines from these six individuals were crossed onto the inbred W23 marker stock for each chromosome. Twelve S_1 plants per line were used in hybridizations. Eight seeds per W23 marker × S_1 plant were composited for each marker line combination. These marker heterozygous individuals were grown in the summer 1994 and a subset used once as males in testcrosses onto F_1 marker stock plants. Twelve testcross ears per marker × S_1 line combination were analyzed.

For each linkage group the recombination frequency of the S_1 line derived from the S_0 parent which had expressed the highest recombination frequency was compared to the recombination frequency of the S_1 line from the S_0 which had expressed the lowest recombination frequency. An analysis of variance similar to that described above (except replace S_0 with S_1 line in the model) tested this comparison. For each linkage group a parent-offspring regression was calculated using mean recombination frequencies of the six S_0 parents from the original 1990 testcrosses and the mean recombination frequencies of the six S_1 lines measured on the 1994 testcrosses. The regression coefficient was calculated using the equation $Y_i = a + bX_i + e_i$ (Fehr 1991). Because the offspring are selfed progeny, an estimate of broad-sense heritability is obtained from the linear regression coefficient with $H^2 = b$ (Fehr 1991).

Results and discussion

Estimates of recombination frequencies are inherently variable. Butler (1977) showed that repeated subsamples exhibited more significant differences than one would expect by chance. He cited reports from the literature in which initial declarations of significance between treatment and control recombination frequencies were not verified in repeated experiments. In order to eliminate this possibility in our material we conducted the repeatability study to verify the S_0 plant differences for recombination frequency reported by Fatmi et al. (1993).

In the original study (Fatmi et al. 1993) positive correlations were observed within the BSSS population between recombination frequencies on chromosomes 4 and 5 while negative correlations existed between recombination frequencies on chromosome 9 with those on both chromosomes 4 and 5. Several genotypes, however, exhibited high or low mean recombination frequencies across the three chromosomes. The S_0 individuals chosen for the repeatability experiment were placed into two categories: (1) individuals that had produced high (individuals 120 and 208, summed genetic map distances of 85 and 101 cM) or low (individuals 185 and 199, summed genetic map distances of 65 and 61 cM) recombination frequencies across the five chromosome regions, and (2) individuals that had produced recombination frequencies following the correlation patterns of the population as a whole (individuals 14 and 139, high recombination frequencies for chromosomes 4 and 5 but low for chromosome 9; individuals 76 and 188, high recombination frequencies for chromosome 9 but low for chromosomes 4 and 5).

The comparisons between the pairs of individuals are presented in Table 3. Four of the five repeated comparisons were significantly different when individuals with varying recombination frequency rankings on the three chromosomes were compared (14–139 vs 76–188). On the other hand, only the recombination frequencies at the *sul-c2* linkage group remained significantly different when individuals selected for overall high recombination or overall low recombination (120–208 vs 185–199) were compared. In these four individuals the *sul-c2* linkage group constitutes 40–44% of the total map distance of the five chromosome regions. Selection for recombination frequency summed over all these regions would have placed

Table 3 Mean recombination frequencies [original frequency from 1990 testcrosses (Fatmi et al., 1993) and repeated frequency from 1992 testcrosses] of pairs of lines which had originally shown differing patterns for divergence of recombination frequencies (pair 199, 185 – low on all three chromosomes; pair 120, 208 – high on all three chromosome; pair 14, 139 – high on chromosome 4 and chromosome 5 but low on chromosome 9; pair 76, 188 – low on chromosome 4 and chromosome 5 but high on chromosome 9). The pair 199–185 is compared to pair 120–208, and the pair 14–139 is compared to pair 76–188

Pair	Linkage group														
	Su1-C2			*A2-Bt1*			*Bt1-Pr1*			*Sh1-Bz1*			*Bz1-Wx1*		
	Org.[a]	Rep.[b]	Sig.[c]	Org.	Rep.	Sig.	Org.	Rep.	Sig.	Org.	Rep.	Sig	Org.	Rep.	Sig.
14–139	0.42	0.40		0.10	0.09		0.25	0.23		0.02	0.04		0.18	0.20	
76–188	0.28	0.31	*	0.02	0.07	NS	0.09	0.17	*	0.03	0.05	*	0.24	0.22	*
185–199	0.27	0.27		0.02	0.05		0.12	0.14		0.02	0.05		0.19	0.22	
120–208	0.38	0.33	*	0.08	0.07	NS	0.19	0.18	NS	0.03	0.04	NS	0.26	0.23	NS

[a] Org.=orginal recombination frequency, mean of three testcrosses
[b] Rep.=repeated recombination frequency, mean of 12 testcrosses
[c] * The pair with the higher original recombination frequency has a significantly greater repeated recombination frequency ($P<=0.05$). NS, the repeated recombination frequency measurement for the pair with the higher original recombination frequency is not significantly greater than that of the alternate pair

higher selection pressure on the *su1-c2* region than the others, increasing the likelihood that differences in this region would be repeatable. But, although a statistical comparison was not possible, because there was no relationship between testcrosses of the different chromosome regions (i.e., testcross 1 of *su1-c2* is no more related to testcross 1 of *a2-bt1-pr1* than to testcross 2) and thus replicated recombination frequencies summed across all three chromosomes were not available, the mean total map distance summed for the five chromosome regions was 86 cM for the overall high recombination pair (120–208) and 75 cM for the overall low recombination pair (185–199).

The ranges in recombination frequencies among heterogenous testcrosses from the selected individuals in the repeatability experiment were wider for all chromosome regions than in the subsampling experiment in which recombination frequencies were estimated for 24 homogeneous testcrosses: *su1-c2*, 0.13–0.43 vs 0.15–0.36; *a2-bt1*, 0.01–0.23 vs 0.04–0.09; *bt1-pr1*, 0.04–0.41 vs 0.09–0.26; *sh1-bz1*, 0.02–0.18 vs 0.02–0.10; *bz1-wx1*, 0.11–0.39 vs 0.11–0.22 (repeatability experiment range–subsampling experiment range, respectively). This indicates greater variability in recombination frequencies when presumed genetic differences were present than when genetic differences were absent. This supports true recombination frequency differences among these selected individuals. At all five chromosome regions the difference between the highest recombination frequency estimate produced by the selected individuals and the highest recombination frequency of the control testcross was greater than the difference between the lowest recombination frequency estimates of the selected individuals and the lowest recombination frequency of the control testcross.

Two generalizations may be stated. (1) Selection for individuals which showed differences in recombination frequencies at specific regions (the comparison of individuals 14 and 139 vs 76 and 188) provided more repeatable differences than selection for individuals based on the total map distance of five chromosome regions (the comparison of individuals 185 and 199 vs 120 and 208). (2) Selection for high recombination frequencies were more repeatable than selection for low recombination frequencies. The high recombination frequencies estimated from specific testcrosses from selected individuals were more distant from the highest recombination frequency of control testcrosses than the similar comparisons at low recombination frequencies. Both generalizations may be explained in part by comparing the selection differentials, the magnitude by which the selected individuals differed from the original population mean. For those individuals selected for recombination frequency differences at specific regions, the five-region mean standardized selection differentials (Falconer 1960) were 2.03 for high recombination frequency and –1.29 for low recombination. For those individuals selected for overall differences in recombination frequency, the mean standardized selection differentials were 1.53 for high recombination frequency and –0.79 for low recombination frequency. One can see that the difference between the standardized selection differentials for high and low recombination frequency was greater for selection at specific regions than for selection at all regions simultaneously. Also, for both specific and overall selection, the standardized selection differentials were 30–50% larger for high recombination frequency than for low recombination frequency.

The different environments in which the testcrosses were produced had little affect on the mean recombination frequencies for the eight repeated S_0 individuals . While the mean recombination frequency of the *sh1-bz1* chromosome region more than doubled in 1992 (0.05) compared to the earlier years (0.02), at the other four chromosome regions the differences in mean recombination frequency between the different years were all less than 0.02. Specific individuals, however, did exhibit changes in recombination frequencies between the years. Because the magnitude and direction of these changes differed for the indi-

Table 4 Mean recombination frequencies of the S_0 individuals and their S_1 lines [original S_0 recombination frequency from 1990 testcrosses (Fatmi et al. 1993) and S_1 recombination frequency from 1994 testcrosses] for those individuals selected as having the highest or lowest recombination frequency for each chromosome

Line	Linkage group			Line	Linkage group						Line	Linkage group					
	Su1-C2				*A2-Bt1*			*Bt1-Pr1*				*Sh1-Bz1*			*Bz1-Wx1*		
	S_0	S_1	Sig.		S_0	S_1	Sig.	S_0	S_1	Sig.		S_0	S_1	Sig.	S_0	S_1	Sig.
142	0.23	0.20		92	0.02	0.04		0.06	0.11		209	0.02	0.02		0.07	0.18	
139	0.46	0.34	**	14	0.10	0.08	**	0.28	0.20	**	208	0.02	0.06	**	0.29	0.23	**

** The recombination frequencies of the S_1 lines within each pair are highly significantly different ($P<=0.01$)

viduals, some genotype × year interaction effects are indicated. Among the four individuals selected for high recombination frequencies on chromosomes four and five, individuals 14 and 120 had higher or equivalent recombination frequencies on these chromosomes in 1992 than in the earlier years, while individuals 139 and 208 had lower recombination frequencies on those chromosomes in 1992 compared to 1990. For chromosome five, all four individuals originally selected for low recombination frequencies had higher recombination frequencies in 1992 than in earlier years (1992 map distance of 31 cM vs 21 cM for 1990 map distance). Individual 185, selected for its overall low recombination frequencies in 1990; had an increased recombination frequency at each chromosome region in 1992.

The recombination frequencies of the S_1 line pairs derived from the S_0 individuals which had the extreme high or low recombination frequencies on a single chromosome (regions *su1-c2, a2-pr1, sh1-wx1*) were significantly different for all five chromosome regions (Table 4). For the *sh1-bz1* chromosome region, the difference in recombination frequency between the two S_1 lines was greater than the difference between the two S_0 individuals. For the other four chromosome regions, the difference in recombination frequency between the two S_1 lines was less than the difference between the two S_0 individuals, ranging from 60% to 20% of the difference seen between the S_0 individuals. In other plant species true genetic differences controlling recombination frequencies exist. Cornu et al. (1989) and Robert et al. (1991) have demonstrated this in petunia through inheritance studies, and Allard (1963) demonstrated it in lima bean through selection experiments. In this experiment the maintenance of differences from the S_0 to the S_1 generation between the high and low individuals at each chromosome region demonstrates that genetic variation for recombination frequency does exist in BSSS.

The broad-sense heritability estimates derived from the regression of six S_1 lines on six S_0 individuals ranged from 0.69 to 0.20 for the five chromosome regions (Table 5). All regression coefficients were significantly different from 0. Selection experiments in non-plant species have produced estimates of realized heritability for recombination or chiasma frequency: Kidwell (1972) $h^2 = 0.12$; Shaw (1972) $h^2 = 0.27$ and 0.49; Dewees (1975) $h^2 = 0.16$. Valentin (1973) used parent-offspring regression and full-sib families to estimate heritability as "closer to 0 than to 1". In the present maize experiment the heritability estimates were fairly high compared to reported estimates from other organisms. But, it must be noted that these estimates are called heritability only in the loosest definition of the term. Any estimate of heritability is unique; it is dependent on the specific population and the conditions under which that population is analyzed. For these estimates the selection of S_0 individuals was not random. Two of the individuals used to obtain each estimate were the most extreme individuals from the population. For each estimate the other four individuals appeared to be random but certainly exhibited some large differences in recombination frequencies at other regions of the genome. Therefore, unbiased estimates of heritability were not obtained. These "heritability" estimates also relate to selection of the parental unit with no intermating between the parental and progeny generations, so they are not predictive of progress from selection following intermating (e.g., in a recurrent selection program). On the other hand, these estimates were derived when measurements for selection were made in one environment. So, the estimates do indicate that measuring recombination frequencies in one environment on a reasonable scale (three testcrosses) is adequate to select individuals whose S_1 lines (serving as the reservoir of alleles from the measured individual) mimic, to a reasonable degree, the recombination frequencies of their S_0 parents.

Table 5 Broad-sense heritability estimates obtained from the regression of S_1 line recombination frequency (1994 testcrosses) on S_0 individual recombination frequency (1990 testcrosses). The six S_0 individuals were each selected as having the highest or lowest recombination frequency for the measured chromosome regions on a single chromosome

Linkage group	H^2
Su1-C2	0.69
A2-Bt1	0.36
Bt1-Pr1	0.37
Sh1-Bz1	0.21
Bz1-Wx1	0.20

Differences existed among chromosome regions in the degree to which divergent recombination frequencies are repeatable or heritable. Selection for divergent recombina-

tion frequencies at the *su1-c2* region on chromosome four was obviously the most successful; all comparisons were significant and the heritability estimate was the highest of the five regions. Because of the small number of regions examined, we cannot say whether these chromosome region differences are due to the specific chromosome, the location of the chromosome region in relation to the centromere, or the size of the chromosome region. Chromosome regional differences are expected. Brooks and Marks (1986) noted that regional systems exist; thus, from region to region both the amount and distribution of recombination can respond independently to selection pressures. When Nel (1975) summarized studies of several recombination-modification mechanisms which had produced dissimilar effects, he hypothesized that all ten maize chromosomes may have unique recombination systems.

The experiments presented herein were designed to determine whether differences in recombination frequencies among individuals in BSSS were due to genetic differences. The recombination frequencies of individuals selected for differences over all five chromosome regions were not repeatable. A gene controlling recombination frequency genome-wide, similar to the *Rm1* gene in petunia (Cornu et al. 1989), was not found. When individuals were selected for divergent recombination frequencies at specific chromosome regions the direction, although not the magnitude, of the differences was repeatable. S_1 lines from divergent S_0 individuals had recombination frequencies which remained significantly different, and S_1 heritability estimates of recombination frequency were significant for all five chromosomes regions. This information leads us to conclude that genetic control of recombination frequency at specific chromosome regions truly exists.

In these experiments, as well as those reported previously (Fatmi et al. 1993), all distributions of recombination frequency have been unimodal, and most have been normal. Our hypothesis is that the genetic control is polygenic. Tulsieram et al. (1992) concluded that in three maize populations genetic control of recombination frequency at two chromosome regions was polygenic. They, however, also reported a bimodal distribution at one chromsome region and concluded that a single gene controlled the frequency of recombination. In the present study results with the *su1-c2* linkage group differed from the other chromosome regions. The heritability estimate was much higher than those for the other chromosome regions and recombination frequency differences were repeatable at the *su1-c2* region even when selection was based on overall recombination frequency. While these results might indicate a simpler genetic control at the *su1-c2* region, data are not available for us to reject our hypothesis of quantitative inheritance.

A means of controlling recombination could be of prime importance to maize breeders. Felsenstein (1965) demonstrated that artificial selection for an additive trait would create negative linkage disequilibrium so that tight linkage would reduce the response to selection. Melchinger et al. (1981) found evidence of increased variability brought about by increased genetic recombination. In instances such as these, breeding material exhibiting increased recombination could prove useful for increasing the selection response. On the other hand, reduced genetic recombination might be advantageous in the recycling of elite germplasm where minimum disturbance of the genome is sought, and could make marker-assisted backcross selection quicker and more economical by increasing the size of parental chromosome blocks. Our long-term goal is to produce maize populations with overall divergent recombination rates in order to test these possibilities.

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