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Variability of recombination frequencies in the Iowa Stiff Stalk Synthetic (*Zea mays* L.)

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Abstract. Variability in recombination frequency has been reported in several plant populations. The objectives of the present research were to establish the range in variability in recombination among genotypes in the important corn population Iowa Stiff Stalk Synthetic and to identify individual genotypes which produced increased or decreased recombination frequencies. Approximately 150 individual S_0 plants were testcrossed to measure male recombination frequency on three chromosomes: 4, *su1-c2*; 5, *a2-bt1-pr1*; and 9, *sh1-bz1-wx1*. Although the variance component for individuals accounted for only 20–33% of the total variation, highly significant variability among individuals was present at all chromosome regions. Thus the environmental effects did not prevent measurement of differences between S_0 individuals. At each chromosome region, individual genotypes with recombination frequencies at least two standard deviations above or below the population mean were isolated. Reports in the literature suggest that the variability reported here for the BSSS population should be representative of that present in other corn breeding populations. Recombination frequencies were positively correlated between adjacent regions of chromosome 9 and also between adjacent regions of chromosome 5. Recombination frequencies were positively correlated between both regions on chromosome 5 with the *su1-c2* region of chromosome 4. Negative correlations were observed between chromosome 9 recombination and recombination in each region of chromosomes 4 and 5. Thus rankings of S_0 individual recombination frequencies were not consistent for all three chromosomes.

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Introduction

The effectiveness of a breeding program is largely dependent upon sound management of the genetic diversity present in breeding populations. The preservation of genetic variability in these populations will guarantee long-term genetic gain through the continuing breakup of negative linkage blocks via genetic recombination. Recombination through hybridization is the principal method used for the production of new genotypes for crop improvement. Repeated intermatings can be used to increase the number of meiotic cycles and thus increase intrachromosomal recombination. This breeding procedure, however, increases the number of years required to complete a selection cycle and, therefore, can decrease the genetic gain per year. Hanson (1961) noted that a 50% increase in genetic recombination would correspond to one generation of intermating of F_2 individuals. Thus, breeders might favor the substitution of repeated intermating by a genetic control of recombination.

A means of control of genetic recombination could be of prime importance to corn (*Zea mays* L.) breeders. For instance, increased genetic recombination would be desirable, particularly in situations of maximum linkage disequilibrium due to intermating of Corn Belt by exotic populations. Enhanced recombination should provide improved germplasm from such crosses. Melchinger et al. (1981) found evidence of increased variability brought about by increased genetic recombination. Alternatively, reduced genetic recombination

could be advantageous in the recycling of elite germplasm or the intermating of narrow base populations, where minimum disturbance of the genome is sought.

An essential condition for genetic improvement of any trait is genetic variability. Variability for, and the polygenic control of, recombination frequency has been demonstrated in several species. Recently, significant variability for recombination frequency has been reported in barley (*Hordeum vulgare* L.; Säll 1990) and in soybeans (*Glycine max* L. Merr.; Pfeiffer and Vogt 1990). In corn, Stadler (1926), Collins and Kempton (1927) and Nel (1973) observed large variability for crossover frequencies. Specific alleles that enhance recombination, often by several fold or greater, have been identified in several species, e.g., *Neurospora crassa* (Catcheside 1977), *Caenorhabditis elegans* (Rose and Baillie 1979), *Drosophila melanogaster* (Brooks and Marks 1986), and petunia (*Petunia hybrida*), where Cornu et al. (1989) showed that meiotic recombination rates were controlled by a major nuclear factor *Rm1* (Recombination modulator 1).

The objectives of the present research were: (1) to establish the range of variability for recombination among genotypes extracted from the corn population Iowa Stiff Stalk Synthetic (BSSS), and (2) to identify individual genotypes that produced increased or decreased recombination frequencies in testcrosses.

Materials and methods

Iowa Stiff Stalk Synthetic is a widely used corn research population and an important source of inbred lines (Hallauer et al. 1983). Population BS 13 (S) C 4 (Hallauer et al. 1983), a recurrent selection-improved subpopulation of BSSS, was the population screened for recombination frequency differences. The inbred genetic marker stocks provided by Dr. E. H. Coe, USDA, ARS University of Missouri (Columbia) were maintained by selfing. The chromosome location, the genetic map for each linkage group, and the phenotypes conditioned by the marker loci are shown in Table 1 (Coe et al. 1988). Screening at the *su1-c2* chromosome region was designed originally to detect decreases in recombination rates. Similarly, screening the *a2-bt1-pr1* and *sh1-bz1-wx1* chromosome regions would enable the detection of increases in recombination frequencies. In general, for each region on the different chromosomes, an F_1 was obtained by crossing two inbred stocks containing the recessive alleles at the marker loci. The resulting recessive marker F_1 then was used instead of the original inbred stocks because of its hybrid vigor.

In the summer of 1988 and 1989, random individual S_0 plants from BSSS were selfed, to maintain the alleles being tested in that individual, and 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 BSSS × marker stock crosses were used as males in testcrosses to F_1 marker stock plants.

Testcross kernels were classified visually into the appropriate phenotypic classes. The waxy starch phenotype [blue (*Wx*) or red (*wx*)] in the *sh1-bz1-wx1* chromosome region required chipping of a small piece of endosperm from each kernel, and staining the endosperm with a dilute iodine/potassium iodide (I_2KI) stock solution (Coe et al. 1988). Phenotypic distributions at each locus, for each of the three testcross ears from each S_0 individual at each linkage group, were evaluated for goodness of fit using a chi-square test (χ^2). Individual ears which departed significantly ($P < 0.05$) from the 1:1 expected segregation ratio at any locus were excluded from the analysis. Standard two- (*su1-c2*) and three-point test cross (*a2-bt1-pr1*, or *sh1-bz1-wx1*) procedures were utilized to obtain recombination frequencies. In the *a2-bt1-pr1* linkage group, the purple aleurone alleles (*Pr1*, *pr1*) can only be screened in the dominant *A2* (colored) background. Therefore, the colored class alone was used to evaluate recombination in the *A2-Pr1* and *Bt1-Pr1* regions (Rhoades 1941).

For each S_0 individual, least square means for two or three testcrosses were used to rank and compare average recombination frequencies. For each linkage group, frequency distribution histograms of the individual S_0 testcross recombination frequency means were constructed (Huntsberger 1967). Each distribution was tested for normality (*D* statistic from the Kolmogorov-Smirnov test) using the SAS Univariate procedure (SAS 1979). The arcsine transformation was used when the assumption of normality was rejected ($P < 0.01$). Analyses of variance (ANOVA) for recombination frequencies were performed using the random statistical model:

$$Y_{ijk} = \mu + \alpha_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{ijk}$$

where μ is the overall mean of the population, α_i is the effect of the ith year, $\beta_{j(i)}$ is the effect of the jth S_0 individual in the ith year, $\gamma_{k(ij)}$ is the effect of the kth testcross ear within the jth S_0 individual in the ith year, and ε_{ijk} is the random error associated

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

Chromosome arm	Alleles	Kernel phenotype of recessive genotype	Genetic map distance
			50
4L	*su1-c2*	Sugary/colorless	*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

with each measurement, and i: 1 to 2; j: 1, ..., n; and k: 1 to 3. The error term used to test the significance of the mean square for S_0 individuals contained the error associated with screening as well as the error associated with testcrosses within S_0 individuals ($\sigma_E^2 = \sigma_\gamma^2 + \sigma_\varepsilon^2$). These error sources were confounded and could not be partitioned. Variance components were calculated and each component was expressed as a percentage of the total variance. Pearson's correlation coefficients on an S_0 individual mean basis were obtained between the recombination frequencies at the five chromosomal regions.

Results

Substantial variability for recombination frequency existed among BSSS individuals. In all chromosome regions, there was a highly significant effect ($P < 0.001$) for S_0 individuals (Table 2). The distributions at the *a2-bt1* and *bt1-pr1* regions of chromosome 5 were not normal. The arcsine transformation restored the normality of distribution to these populations. The analysis of variance indicated a significant year effect for all chromosome regions, except for the *sh1-bz1* region of chromosome 9 (Table 2). This region showed a negative variance component estimate for years, which was treated as zero (Table 3). The variance component attributed to individuals accounted for 20–33% of the total variation, whereas the error variance component accounted for 53–80% of the total variability (Table 3).

On chromosome 4, the mean recombination frequency for the *su1-c2* region was 0.32 (Table 4); 95% of this population had recombination frequencies less than 0.383 and 99% less than 0.414. While the distribution of recombination rates for this population appears skewed to the left (Fig. 1), the distribution tested normal. On chromosome 5, the mean recombination rates for both regions were similar to those reported by Phillips (1969) but much lower than those of Rhodes (1941). The population mean recombination rate for the *a2-bt1* region was 0.048 (Table 4); 95 and 99% of this population had recombination frequencies less than or equal to 0.088 and 0.101, respectively. The adjacent *bt1-pr1* region had a mean recombination of 0.155 (Table 4); 95 and 99% of the population had recombination frequencies inferior to 0.236 and 0.259, respectively. The distribution of recombination frequencies for the *a2-bt1* region clearly showed skewness to the right (Fig. 2). A less pronounced, though still significant, deviation from normality was observed for the adjacent *bt1-pr1* region of chromosome 5 (Fig. 3). For chromosome 9, the population means were 0.024 and 0.19 for the *sh1-bz1* and *bz1-wx1* linkage groups, respectively (Table 4). The mean recombination

Table 2. Significance levels and degrees of freedom from the ANOVAs of S_0 testcross recombination frequency at each of the five chromosome regions

Source	Chromosome region							
	su-c2		*a2-bt*[a]		*bt-pr*[a]	*sh-bz*		*bz-wx*
	df	*P* F > Fcalc	*df*	*P* F > Fcalc	*P* F > Fcalc	*df*	*P* F > Fcalc	*P* F > Fcalc
Year	1	0.0001	1	0.0010	0.0001	1	0.802	0.017
Individual								
S_0 plant	146	0.0001	140	0.0001	0.0001	143	0.0001	0.0001
Error[b]	299		243			269		

[a] Data analysed on arcsine-transformed value
[b] Testcrosses (S_0 ind.)

Table 3. Variance component estimates and the percentage of total variance in recombination frequencies attributable to different variance components

Chromosome region	Variance component					
	Year	%	Individual	%	Error	%
su-c2	3.665×10^{-4}	10	8.737×10^{-4}	25	2.311×10^{-3}	65
a2-bt	7.251×10^{-5}	10	2.240×10^{-4}	33	3.915×10^{-4}	57
bt-pr	7.017×10^{-4}	19	1.038×10^{-3}	28	1.919×10^{-3}	53
sh-bz	0.000	0	1.221×10^{-5}	20	5.046×10^{-5}	80
bz-wx	4.120×10^{-5}	4	3.331×10^{-4}	29	7.548×10^{-4}	67

Table 4. Population distribution statistics for S_0 testcross recombination frequencies at five chromosome regions

Item	Chromosome region				
	su-c2	*a2-bt*	*bt-pr*	*sh-bz*	*bz-wx*
N	148	142	142	145	145
Mean	0.319	0.048	0.155	0.024	0.192
C.V. (%)	13.35	39.88	28.78	22.75	12.86
SD	0.042	0.019	0.044	0.005	0.024
Maximum	0.457	0.119	0.279	0.041	0.275
Minimum	0.213	0.011	0.060	0.008	0.066

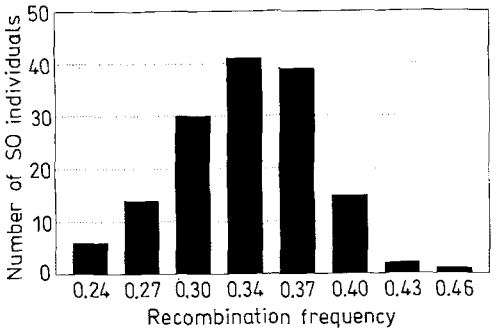

Fig. 1. Distribution of individual S_0 testcross recombination frequencies for the *su1-c2* region on chromosome 4

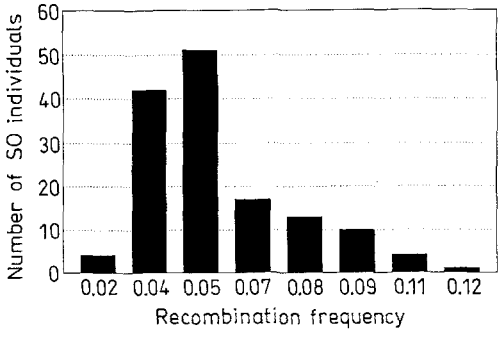

Fig. 2. Distribution of individual S_0 testcross recombination frequencies for the *a2-bt1* region on chromosome 5

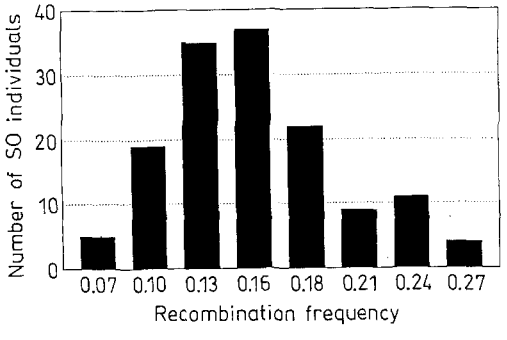

Fig. 3. Distribution of individual S_0 testcross recombination frequencies for the *bt1-pr1* region on chromosome 5

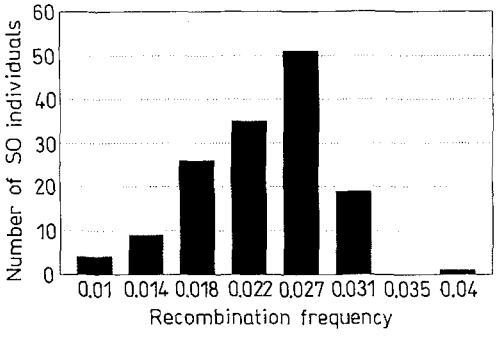

Fig. 4. Distribution of individual S_0 testcross recombination frequencies for the *sh1-bz1* region on chromosome 9

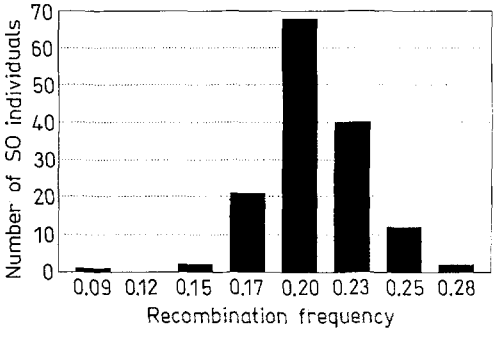

Fig. 5. Distribution of individual testcross recombination frequencies for the *bz1-wx1* region on chromosome 9

frequency for the *sh1-wx1* region was similar to that reported by Stadler (1926). The 95 and 99% fraction of the population had recombination rates below 0.037 and 0.041, for the *sh1-bz1* region and below 0.234 and 0.256 for the adjacent *bz1-wx1* region. The distributions of recombination frequencies for both regions were not significantly different from normality (Figs. 4, 5).

The coefficients of variation at the different linkage groups ranged from 13% (*bz1-wx1*) to 40% (*a2-bt1*) (Table 4). The difference between the maximum and minimum recombination frequencies at a chromosome region ranged from two- (*su1-c2*) to 11-fold (*a2-bt1*)

(Table 4). At each chromosome region, individual S_0 genotypes with recombination frequencies at least two standard deviations above or below the population mean were identified. S_0 individual # 33 in the *a2-bt1* chromosome region had the largest positive deviation from the population mean (+3.74) for any linkage group. The largest negative deviation from a population mean was observed on chromosome 9, where individual # 209 stood at 5.25 standard deviations below the mean for the *bz1-wx1* chromosome region. S_0 individuals # 33, 14, 139, 176, and 208, which were the individuals with the highest recombination frequencies at the *a2-bt1*, *bt1-pr1*, *su1-c2*, *sh1-bz1* and *bz1-wx1* chromosome regions, respectively, were at least 3.2 standard deviations above their respective population means. Genotypes # 76, 92, 93, 10, and 209, which were the genotypes with the lowest recombination frequencies at the *a2-bt1*, *bt1-pr1*, *su1-c2*, *sh1-bz1* and *bz1-wx1* chromosome regions, respectively, were at least 1.95 standard deviations below their respective population means.

Correlation coefficients for recombination frequencies revealed a large positive correlation between the *a2-bt1* and the *bt1-pr1* regions on chromosome 5 (Table 5). Similarly, recombination frequencies for the adjacent regions on chromosome 9 were significantly positively correlated. Recombination frequencies were positively correlated between both regions on chromosome 5 and the *su1-c2* region on chromosome 4. Significant negative correlations were observed between the *sh1-bz1* region of chromosome 9 and each of the regions on chromosomes 4 and 5 (Table 5).

Among those individuals which had extreme recombination frequencies on chromosome 4 (*su1-c2*), the highest and lowest mean recombination frequencies were achieved by individual # 139 (0.457) and individual # 93 (0.213), respectively (Table 6). On chromosome 5, recombination frequencies varied from a 0.011 minimum (individual # 76) to a 0.119 maximum (individual # 33) in the *a2-bt1* region (Table 6). Likewise, the maximum and minimum recombination frequencies achieved in the *bt1-pr1* region were 0.279 (individual # 14) and 0.060 (individual # 92), respect-

Table 5. Correlation coefficients among S_0 testcross mean recombination frequencies at each chromosome region

Chromosome region	Chromosome region			
	bt-pr	*su-c2*	*sh-bz*	*bz-wx*
a2-bt	0.813***	0.225*	−0.346***	−0.161
bt-pr		0.286***	−0.194*	−0.078
su-c2			−0.299***	−0.107
sh-bz				0.232***

*,**,*** Significantly different from zero at $P = 0.05$, $P = 0.01$ and $P = 0.001$, respectively

Table 6. ean recombination frequencies and rankings at the five chromosome regions of selected high and low S_0 individuals and for unique combinations of recombination frequency extremes

S_0[a]	Chromosome region									
	su-c2		*a2-bt*		*bt-pr*		*sh-bz*		*bz-wx*	
	R.F.[b]	Rank[c] (147)	R.F.	Rank (142)	R.F.	Rank (142)	R.F.	Rank (146)	R.F.	Rank (146)
10							0.008	146	0.178	128
14	0.368	17	0.097	3	0.279	1	0.013	140	0.177	135
33	0.310	94	0.119	1	0.239	7	0.013	138	0.180	104
76	0.295	105	0.011	142	0.079	141	0.029	14	0.233	45
92	0.303	110	0.018	139	0.060	142	0.024	78	0.220	63
93	0.213	147	0.036	100	0.101	127	0.025	63	0.217	70
120	0.342	10	0.071	21	0.185	31	0.035	12	0.223	66
139	0.457	1	0.094	4	0.222	16	0.019	117	0.183	136
176			0.050	47	0.148	72	0.041	1	0.204	43
178	0.293	129	0.031	124	0.096	133	0.014	136	0.213	58
188	0.258	142	0.024	137	0.098	131	0.032	6	0.235	35
199	0.273	131	0.025	135	0.125	102	0.021	100	0.184	134
208	0.414	2	0.091	7	0.202	23	0.022	95	0.293	1
209	0.395	6	0.008	95	0.150	73	0.018	121	0.069	146
210	0.323	70	0.016	140	0.091	137	0.028	25	0.253	11
$\bar{x}$	0.319		0.048		0.155		0.024		0.192	

[a] Individual S_0 plant number
[b] Recombination frequency
[c] In each linkage group the S_0 individual with the highest mean has a rank of 1 and the number of individuals ranked is indicated in parentheses

ively (Table 6). For chromosome 9, the highest recombination rates were achieved by individuals # 176 (0.041) and # 208 (0.275) in the *sh1-bz1* and *bz1-wx1* regions of chromosome 9, respectively. The lowest recombination frequencies observed were 0.008 (individual # 10) and 0.066 (individual # 209) for the *sh1-bz1* and *bz1-wx1* regions, respectively (Table 6).

Discussion

After reviewing evidence from experimental laboratory populations, Smith (1978) concluded that genetic variation for recombination frequency will be found whenever it is looked for. The highly significant variation for recombination frequency that we found among individuals in the BSSS population is consistent with other recent reports of genetic variability of recombination rates in plant populations (Cornu et al. 1989; Pfeiffer and Vogt 1990; Säll 1990). Therefore, the variability reported here for the BSSS population agrees with Smith (1978) and suggests that representative genetic variability should also be present in other corn breeding populations.

Although the distributions of recombination rates appear to be slightly skewed in some cases, all were clearly unimodal. It is known that skewness in the distribution of recombination frequencies for tightly-linked genes can be caused by their proximity to the lower limit (Broadhead and Kidwell 1975). This could explain, in part, the departure from normality observed for the *a2-bt1* region on chromosome 5. The *bt1* locus is located near the centromere (Coe et al. 1988). The heterochromatic nature of this region, with the possibility of a lengthened genetic map compared to the physical map, may have contributed to skewing the two chromosome 5 distributions toward lower frequencies. Brooks and Marks (1986) discuss how centromeric heterochromatin may variably influence recombination rates. Overall, the distributions for recombination frequencies were all similar to those expected from most biological characters influenced by environment and/or controlled quantitatively. Confirmation of the heritability of the divergent recombination frequencies is needed.

The highly significant differences between years for all but one chromosome region suggest that enviroments affected recombination rates differently in 1989 than in 1990. Although statistically significant, the yearly environmental influences observed in this study were such that the variance component for years was always the smallest component. The environmental effects did not prevent measurement of differences between individuals.

In our model, the error term represented more than half of the total variance observed in this experiment (Table 3). This large contribution of the experimental error term confirmed the large variability of crossing-over observed previously in corn (Stadler 1926; Collins and Kempton 1927). Experimental error as a large component of total variance is not unique to measurements of recombination. Hallauer et al. (1983) reported that the experimental error component of variance for yield in BSSS was 52.40% of the total variance. That value is of similar magnitude compared to the error variance components from this study (Table 5).

Testcross replication was an important feature of our experimental design and provided a measure of confidence in the differences we are reporting. Testcross variation among S_0 individuals could arise from several sources. First, there could be overall genetic differences controlling the recombination frequency during meiosis in the F_1 of the individual × tester. These are the differences this experiment was designed to determine. Second, the individual S_0 plants could have been heterozygous for those genes controlling recombination frequency. If this was the case each F_1 could receive a different set of recombination-control alleles producing differences in the recombination frequency estimates among the testcrosses of a single individual. Third, with the tester itself being an F_1 hybrid, the tester could donate different recombination-control alleles to the individual × tester F_1's resulting again in differences in recombination frequency estimates among the testcrosses of each BSSS individual. Replication of the testcrosses of each BSSS S_0 individual created an error term which consisted of both the error associated with screening as well as the error associated with testcross ears within individuals. The significance of the S_0 individual term for recombination frequency at all chromosome regions indicates that the variation among individuals, the first factor referred to above, was greater than the variation among testcrosses created by the second and third factors. Butler (1977) stated that using unreplicated recombination frequency estimates to declare treatment differences was a "dangerous practice" and that with replication an analysis of variance could be performed to detect significant treatment differences for recombination frequency.

With only a few exceptions (Rhoades 1941; Nel 1973), the highest recombination rates achieved in our experiment were either comparable to, or largely exceeded, the recombination rates reported in previous studies (Stadler 1926; Kikudome 1959; Hanson 1969; Phillips 1969; Nel 1973, 1975; Ward 1973; Chang and Kikudome 1974; Ghidoni 1975). Most of these previous studies used B chromosomes or other abnormal chromosomes to produce the altered recombination frequencies. B chromosomes, however, are not seen in BSSS, a highly-selected population (Hallauer and

Miranda 1988); and fertility levels were indistinguishable among the S_0 individuals we tested. Thus, although a cytological examination was not conducted, we tend to rule out accessory or abnormal chromosomes as the cause of the variability. In a related way, cytological analysis in *P. hybrida* revealed that *RM1* was effective in the absence of any cytogenetical abnormalities (Mousset 1985).

The correlation coefficient observed for the adjacent *sh1-bz1/bz1-wx1* regions (0.232) is close to the correlation coefficient reported by Stadler (1926) for the comparable *c-sh1/sh1-wx1* regions of chromosome 9 (0.257 ± 0.81). The correlation coefficients for the adjacent regions of chromosome 5 and the adjacent regions of chromosome 9 were notably different, 0.813 at the *a2-bt1/bt1-pr1* regions compared to 0.232 for the *sh1-bz1/bz1-wx1* regions, respectively. All correlations among recombination frequencies for chromosome 9 with either chromosomes 4 or 5 were negative.

The recombination patterns observed among individuals with either high or low recombination frequencies show large differences among chromosomes (Tables 6 and 7). For instance, although individuals # 199 and # 178 exhibit relatively low recombination frequencies on all chromosomes, no individual ranked in the fourth quartile at all five linkage groups (Tables 6 and 7). Furthermore, individual # 209, with the lowest recombination in the *bz1-wx1* region and a recombination frequency in the lowest 15% for the *sh1-bz1* region, ranked 6th out of 148 for chromosome 4 (*su1-c2* region) and had recombination rates close to the population mean for chromosome 5. Individual # 208 ranked high in the first quartile for the *bz1-wx1*, *su1-c2*, *a2-bt1* and *bt1-pr1* regions but fell below the mean recombination frequency for the *sh1-bz1* region (Tables 6 and 7). Similarly, individual # 120 ranked in the top quartile at four linkage groups, but no individual ranked in the top quartile at all five chromosome regions. Individual # 210 ranked among the highest 10% for chromosome 9 (both regions), but among the lowest 5% for chromosome 5. In addition, individuals # 139, # 188, and # 14 illustrate the differential recombination frequency rankings for chromosomes 4 and 5 on one hand and chromosome 9 on the other hand (Tables 6 and 7). Therefore, the disparities across chromosomes indicate that genotypes with high or low recombination frequencies at one linkage group would not necessarily have a comparable high or low recombination frequency across all linkage groups. Individuals ranking high or low on chromosome 4 would be more likely to have high or low recombination rates for the chromosome 5 regions. In contrast, ranking on chromosome 9 would not be a predictor of recombination frequency rank for either chromosome 4 or 5 regions. It remains to be seen whether a selection program can combine the highest or lowest recombination frequencies at all chromosome segments into one genotype.

Table 7. Patterns of recombination frequencies of S_0 individuals exhibiting differing high and low recombination at the various chromosome regions

S_0[a]	Chromosome region				
	su-c2	*a2-bt*	*bt-pr*	*sh-bz*	*bz-wx*
199	4[b]	4	3	3	4
178	4	4	4	4	2
209	1	3	2	4	4
208	1	1	1	3	1
120	1	1	1	1	2
210	2	4	4	1	1
139	1	1	1	4	4
188	4	4	4	1	1
14	1	1	1	4	4

[a] Individual S_0 plant number
[b] Quartile rank, 1: 1–37, 2: 38–78, 3: 76–111, 4: 112–148

Genetic control of recombination has been described as being either coarse or fine (Simchen and Stamberg 1969). Coarse control will affect large regions of the genome while fine control will be region specific. Correlations of recombination frequency across chromosome regions would indicate some coarse control such as the *RM1* gene in petunia (Cornu et al. 1989) or the polygenic system described by Brooks and Marks (1986). Variation, however, also exists for control of recombination frequency to be specific to chromosome regions; even adjacent regions can be affected differently (Chinnici 1971; Tulsieram et al. 1992). Within a population exhibiting recombination frequency differences, individuals may be under different types of control depending on each individual's genotype. Whether the BSSS population has elements of coarse control of recombination remains to be determined.

In conclusion, our study clearly showed large amounts of genetic variability for recombination frequency at five chromosome regions among individual S_0 genotypes isolated from the Iowa Stiff Stalk Synthetic. Differences between the low and the high recombination frequencies for individuals in each chromosome region were two- to ten-fold. At each linkage group, several individuals with a mean recombination frequency of at least two standard deviations above or below the population means were identified. Recombination frequencies displayed continuous variation, were normally distributed, and subject to large fluctuations. Such patterns imply the segregation of multiple loci controlling recombination and, thus, a quantitative genetic control of this trait.

Genetic recombination is essential to maximize the short- and long-term genetic advance in breeding populations. The balance between the conservation of

the genome and its random dispersion is controlled by recombination which is subject to genetic regulation. Genetic control of recombination frequency may now be possible and could enhance genetic gain in plant breeding programs.

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