THE VARIABILITY OF CROSSING OVER IN MAIZE*

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INTRODUCTION

This study is concerned chiefly with the extent and nature of the variability of crossing over in a family (full sibship) of *Zea mays*. It is part of a general study of variation in crossing over in maize, in which it is proposed to parallel the variousstu dies of this problem in Drosophila, as far as the nature of the material will permit, and also to investigate certain phases of the problem for which the plant is well suited and the fly is not.

Although the excellent conditions for the experimental study of linkage in Drosophila cannot be duplicated in maize, with its much longer reproductive cycle and much smaller known linkage groups, the plant offers quite favorable material for work of this kind in one linkage group of three endosperm characters. As far as the inheritance of endosperm characters is concerned, the single grain is the individual, and each well-developed ear comprises a progeny of several hundred. Thus it is possible, when using these characters, to handle the large numbers necessary in a statistical study. EAST (1913) has shown that "double fertilization" regularly occurs in maize, and that endosperm characters, therefore, may safely be used to indicate the genetic constitution of the zygote.

The three linked genes used in this study are C c, which in the presence of certain other genes affects aleurone color; S_h s_h, which affects the degree of shrinkage of the endosperm at maturity; and W_x w_x which affects the

chemical composition of the endosperm. Their linkage relations, which have been studied extensively by KEMPTON (1919), HUTCHISON (1922), and others, are indicated in figure 1.

FIGURE 1.—Linkage relations of the factors C, S_h and W_x. (After HUTCHISON 1922).

The crossover percentages in these two sections of the chromosome are not ideal for the purpose, one being lower and the other somewhat higher than might be desired. The low crossover percentage is undesirable because the probable error computed by the usual formula,

$$E = .6745\sqrt{\frac{pq}{n}}$$

is unreliable when p is very small as compared with q, unless n is very large. The significance of differences in crossing over in this region is, therefore, somewhat doubtful when estimated by the use of this formula. The higher crossover percentage of the S_h-W_x region is undesirable because of the danger that undetected double crossovers may occur within the region. Since no locus between S_h and W_x is known at present, we cannot determine how frequently double crossing over may occur within this region. But double crossovers involving simultaneously the C-S_h and S_h-W_x regions are extremely rare, as HUTCHISON (1922) has shown and as the data of this paper confirm. It therefore seems probable that double crossing over within the S_h-W_x region is negligible as a source of error, although of course it is possible that double crossing over may occur freely in part of the C-W_x region while partly or wholly inhibited in another part.

The chief advantages of the material for the study of linkage problems are:

(1) Crossing over occurs freely in the development of both "male" and "female" gametes, and, since the plant is monoecious, both male and female gametes are produced by the same individual.

(2) A very large progeny may be produced from a single individual. The grains produced by a single heterozygous plant (which, backcrossed, indicate the crossover percentage among the female gametes) number one to two thousand in well-developed plants. The number of grains of multiple-recessive plants which may be pollinated from a single heterozygous plant (and which then indicate the crossover percentage among male gametes) is almost unlimited. By pollinating several ears it is possible to

produce a progeny of 5000 or more in each day's pollination throughout the pollen-shedding period, which, in well-developed plants, often lasts 20 days or more.

(3) Since pollination is easily effected and the sorting of the progenies may be done at one's convenience, it is practicable to determine the variability of crossing over in a large number of individuals of a single family grown simultaneously under uniform conditions.

(4) Tillers may be transplanted in early stages, and these under favorable conditions produce both seed and pollen. Separated parts of the same individual therefore may be exposed to different treatments to determine the effects of the treatments on crossing over.

(5) Samples of the young anthers can be taken at the time of the reduction divisions or even earlier, with no injury to the breeding powers of the plant. The stage in the development of the germ cells and the cytological effects ·of treatments may therefore be determined in the plants which are later to be used in breeding.

The series of studies of which this paper is a partial report was made possible through the generosity of Professor R. A. EMERSON, who furnished me the foundation stock of this favorable material. I am indebted also to Professor EMERSON and to Professor E. M. EAST for criticism of the manuscript.

PREVIOUS STUDIES OF VARIATION IN CROSSING OVER

Crossing over has been found highly variable in Drosophila. GOWEN (1919), in an extensive biometrical study of crossing over in the third chromosome, found coefficients of variability ranging from 18 to 59 for the percentage of single crossovers in various regions, and from 67 to 110 for the percentage of double crossovers. In general the crossover percentages for the shorter regions were more variable than those for the longer regions. GOWEN concluded:

"Crossing over is one of the most variable phenomena known, indicating that the mechanism behind crossing over is not as precise as that found in most physiological studies."

DETLEFSEN also found crossing over in Drosophila "an enormously variable phenomenon" as he remarks in reporting his experiments on selection for high and low crossing over in the sex chromosome (DETLEFSEN and CLEMENTE 1923).

The relation of specific environmental and genetic factors to crossing over in Drosophila has been studied by a number of investigators. A decrease in crossing over with age, limited to certain chromosome regions, was found by BRIDGES (1915). A striking increase in crossing over under

extreme temperatures, either high or low, was found by PLOUGH (1917, 1921), this effect being limited to the "susceptible" regions in which crossing over was affected by age. In PLOUGH's experiments no significant difference in crossing over was found to result from varying amounts of moisture in the food, starvation, increased fermentation of food, or the presence of ferric chloride. MAVOR (1923) and MAVOR and SVENSON (1924) found X rays effective in modifying the crossover percentage in both the second chromosome (susceptible to age and temperature effects) and the first chromosome (not susceptible to age and temperature effects). The same X-ray treatment increased the crossover percentage in the second chromosome and decreased it in the first. PLOUGH (1924), in a preliminary trial of the effect of radium radiations, found a general tendency toward increased crossing over, especially after severe radiation.

Linkage variations due to germinal causes have been investigated especially by STURTEVANT and DETLEFSEN. STURTEVANT (1913, 1915, 1917, 1919) has reported several genes modifying the crossover percentage. The first gene of this kind reported, C_{III}, greatly decreases crossing over in the right-hand end of the third chromosome in flies which are heterozygous for it, though in flies homozygous for it crossing over in the same region is at least as high as normal. Similar results are given by C_{IIr} and C_{IIl}, which affect crossing over in the right-hand end and left-hand end, respectively, of the second chromosome, though the homozygous effect of C_{IIl} has not been determined. Two other crossover modifiers in the third chromosome have also been reported, C_{IIIp} by PAYNE (1918) and C_{IIIM} by BRIDGES and MORGAN (1923). These genes also reduce crossing over when heterozygous. Recently, STURTEVANT (1921) has suggested the possibility that the reduction in crossover percentage ascribed to the action of C_{III} and C_{IIr} may be due rather to an inverted chromosome section, which might prevent synapsis when present in only one chromosome of a pair but not when present in both.

DETLEFSEN (1919), DETLEFSEN and ROBERTS (1920, 1921), and DET-LEFSEN and CLEMENTE (1924) have reported experiments in which the crossover percentage in the sex chromosome was greatly reduced by selection. Selection for increased crossing over was unsuccessful, a result attributed to increased double crossing over. A cross of "normal" stock with one of the low-crossover stocks produced by selection, gave results considered indicative of multiple-factor inheritance.

GOWEN and GOWEN (1922) have reported a third-chromosome gene which apparently inhibits crossing over completely in the female. They suggest that the results of DETLEFSEN's experiments may be accounted for by the action of one or more genes of this type.

NABOURS (1919) reported that crossing over in Apotettix was apparently more frequent in the female than in the male. CASTLE (1919) also found that crossing over was more frequent in the female than in the male in rats. At the time, CASTLE doubted that this difference would be shown under uniform conditions, but in a later and more extensive study, CASTLE and WACHTER (1924) found the higher crossover percentage in females to be consistent and to occur in mice as well as rats. No evidence of any relation of crossing over to age or seasonal conditions was found. Variability in crossing over in different male rats was found to be no greater than could be accounted for as the result of random sampling, with the possible exception of one individual.

Studies of variation in crossing over in plants have thus far been limited to comparisons of the crossover percentages in male and female gametes. GOWEN (1919) pointed out that in the data given by ALTENBURG (1916) for linkage in Primula, the percentage of crossovers in the male gametes tested was significantly higher than that in the female gametes. BATESON (1921) stated that extensive data on linkage of magenta color and short style in Primula show closer linkage in the eggs than in the pollen, but that the linkage of green stigma and reddish stem is closer in the pollen than in the eggs. EYSTER (1921) in a study of the linkage relations of sugary endosperm and tunicate ear in maize, found that the crossover percentage was 7.9 ± 2.0 higher among male than among female gametes. He also compared the C-W_x crossover determinations of BREGGER (1918) in a similar way and found that in these trials the crossover percentage was 2.46 ± 1.11 percent higher in the male gametes.

In all of these trials one group of plants used as male parents was compared with another group used as female parents. EMERSON and HUTCHISON (1921), pointing out that the results of such experiments may be due to environmental or genetic differences other than sex, submit data on crossing over in the production of male and female gametes in the same plants. Using the linkage of plant color and liguleless leaf in maize they found no significant difference in crossing over in the production of male and female gametes. In the linkage of colored aleurone and shrunken endosperm the percentage of crossovers was found to be slightly, but significantly, higher among the female gametes. They point out that this may be due to disturbing conditions such as temperature effects rather than to inherent difference in the mechanism of crossing over. EYSTER (1922) has also supplemented his earlier study with a comparison of the crossover percentage in the S_u-T_u region in male and female gametes of the same plants, in which he found no significant difference between the sexes.

The family of plants used in this study (pedigree number 4003) was grown from seeds of a single ear. This ear was produced by pollinating a plant (1598-14) homozygous for colored aleurone, non-shrunken, starchy endosperm (C C S_h S_h W_x W_x) by a plant (1804-1) homozygous for colorless aleurone, shrunken, waxy endosperm (c c s_h s_h w_x w_x). Both parents were also homozygous for the genes AA, RR, and ii, the factors complementary to C in the production of aleurone color.

The two parental strains have been in genetic cultures for some years past. Family 1804, to which the male parent belonged, was grown from seed obtained from Doctor EMERSON in 1923. Family 1598, which included the female parent, was derived from a stock obtained in 1921 from Doctor E. W. LINDSTROM, who had grown it for several seasons. Through the kindness of Doctor EMERSON and Doctor LINDSTROM I have secured the pedigrees of these strains, which are shown in figure 2.

In order to favor maximum development of individual plants, the crop was planted one grain to a hill, 42 inches apart each way. The soil, which
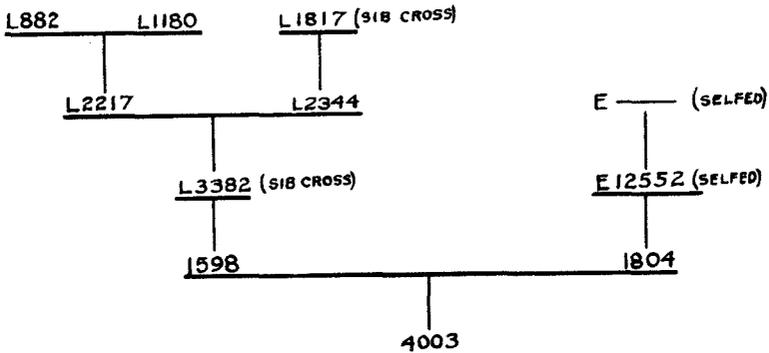
FIGURE 2.—Pedigree of family 4003. Pedigree numbers preceded by E refer to cultures of EMERSON; those preceded by L to those of LINDSTROM.

was naturally fairly fertile, was further improved by the application of a 4-12-3 fertilizer at the rate of 600 pounds per acre shortly before planting. Two rows of 50 hills each were planted to the heterozygous stock. About 75 of the 100 plants reached the flowering stage and all of these were used without selection.

The crossover determinations were made by backcrossing with a multiple-recessive stock. The crossover percentage in male gametes was determined by pollinating at least one ear of the recessive stock from each tassel which shed pollen; in female gametes by pollinating two ears of the main stalk and the first tiller ear of all of the heterozygous plants

which produced these ears. Of the heterozygous plants 58 produced 2 ears on the main stalk, and 31 produced a tiller ear. The multiple-recessive stock used was of low vigor and produced rather small ears. Some of these plants were so injured by chinch-bugs that they produced practically no grain. Consequently, the progenies representing the crossover series in the male gametes are smaller than those representing the female series, and for a few of the plants no determination of crossover frequency in male gametes could be made.

Pollen of the heterozygous plants was used regularly on the third day following the beginning of pollen shedding, to avoid error from any possible tendency towards change in crossing over with age of plant or inflorescence. These pollinations were made daily between 10 a.m. and noon. The ears of heterozygous plants were pollinated when the silks seemed well-enough developed to insure good filling of the ear.

In the sorting of the backcross progenies, each grain was individually tested for composition of endosperm (starchy or waxy) by a modification of the method suggested by WEATHERWAX (1923). Before shelling each ear a spot on each kernel was scraped to expose the endosperm, an operation quickly accomplished by the use of a small emery wheel. Before shelling and sorting the grains of each row, they were tested for endosperm composition by applying a touch of iodine solution to the scraped spot of each grain. The separations for aleurone color and shrinkage of the endosperm were clear and unmistakable except in a few ears of the heterozygous plants in which the shrinkage of the endosperm was very slight. These ears were separated only for C c and W_x w_x, S_h s_h being disregarded.

VARIABILITY OF CROSSOVER PERCENTAGE IN MALE GAMETES

The crossover percentage in male gametes, as shown by backcrossing to the multiple-recessive stock, was determined for 59 plants. The classified progenies of these plants are shown in table 14 (appendix). The extreme range in crossover percentage and the variability of crossing over in the $C\text{-}S_h$, $S_h\text{-}W_x$, and $C\text{-}W_x$[1] sections are shown in table 1 (page 8).

The variability of crossover percentages, as measured by the coefficient of variability, is decidedly higher in the shorter region than in the longer, as was found by GOWEN in Drosophila. In both the $C\text{-}S_h$ and the $S_h\text{-}W_x$ regions the variability is considerably less than that found by GOWEN in

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[1] The crossover percentage for the $C\text{-}W_x$ region is determined by summation from those of the component regions (deducting twice the percentage of double crossovers). It is given to permit direct comparison with the plants in which shrunken endosperm could not be distinguished.

TABLE 1

Variability of crossover percentage in male gametes.

REGION	HIGHEST PERCENTAGE	LOWEST PERCENTAGE	MEAN PERCENTAGE	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
C-S_h	6.3	0.4	3.271 ± 0.101	1.148 ± 0.071	35.10 ± 2.43
S_h-W_x	30.3	13.8	22.115 ± 0.263	2.992 ± 0.186	13.53 ± 0.85
C-W_x	33.1	14.2	25.117 ± 0.265	3.021 ± 0.188	12.03 ± 0.76

Drosophila in regions of similar length. For example, in the three sections of about 20 units length reported for Drosophila, the coefficients of variability were 31.0, 30.3, and 24.3, as compared with 13.5 in the S_h-W_x region of maize, and in the one region of about three units length reported for Drosophila the coefficient was 59.0, as compared with 35.1 for the C-S_h region in maize.

This lower variability of crossover percentages in the maize data does not necessarily mean that crossing over is a less variable process in maize than in the fruit fly, though of course this is a possibility. The two trials were under very different conditions and are not directly comparable. Two conditions in particular tend to make the variability lower in the maize data: (1) the plants compared are of the same parentage and are grown simultaneously under uniform conditions; and (2) the backcross progenies used in determining the crossover percentages are larger, so that the part of the variability which results from fluctuations of sampling is reduced.

The latter point may require some further explanation. Suppose we are dealing with a family of plants in which crossing over is perfectly uniform; that is, each plant *produces* exactly the same percentage of crossover gametes. Now in a study of the variability of crossing over in this family, we determine the crossover percentage in each plant from a backcross progeny of 400. The crossover percentages thus determined will not be uniform; they will fluctuate about the true value, with deviations dependent upon the size of the samples. For example, if the proportion of crossover gametes actually produced by each plant were 20 percent, the crossover percentage determined for each plant, from a backcross progeny of 400, would have a probable error of 1.33 crossover units. If crossover percentages were thus determined for 100 plants, about 50 of them would be below 18.67 or above 21.33 (20.00 ± 1.33) and about 4 of them would be below 16 or above 24 ($20.00 \pm 3 \times 1.33$). Thus, there would be considerable variation in the crossover percentages determined, but it would be variation of sampling, not variation of crossing over. The series of 100

crossover values would have a mean of about 20 crossover units, a standard deviation of about 2 crossover units, and therefore a coefficient of variability of about 10 percent. If backcross progenies of only 100 instead of 400 had been used, the variability due to error of sampling, determined in the same way, would have been about 20 percent instead of 10 percent. If a chromosome region 10 units long, instead of 20, had been used, with backcross progenies of 100, the population of plants, though actually perfectly constant in crossing over, would have given a coefficient of variability of about 30 percent. Thus, when crossover frequency is measured by means of progenies of moderate size, one may find rather high apparent variability, though no lack of precision in the mechanism of crossing over is involved. This is true especially of the shorter chromosome sections, which explains, at least in part, the high variability found in the C-S_h section and in the short sections studied in Drosophila by GOWEN. Probably if large enough progenies were used in the measurement of crossover frequency in the short sections, their crossover percentages would be found no more variable than those of the long sections. But very large progenies would be required. In order to reduce to 10 percent the variability due purely to random sampling, progenies of more than 3000 each would be required for a section 3 units long, while progenies of 400 each would suffice for a section 30 units long.

The foregoing considerations suggest that crossing over may actually have been a very uniform process in the family of maize plants studied, and that such variations as were found may have resulted largely or wholly from error of sampling. Although the coefficients of variability determined are larger than would be expected to result from error of sampling alone, with samples of the size used, it is of interest to determine to what extent the variations may be accounted for by sampling fluctuations.

If all of the plants were actually identical in crossing over, (that is, if the variations found resulted wholly from error of sampling), only about half of the percentages of crossing over determined for individual plants should deviate from the mean percentage by as much as their probable errors, about 18 percent by as much as twice their probable errors, and so on, the expected frequencies being determined from tables of the probability integral. The actual frequency of such deviations, compared with the frequency expected if random sampling were the only cause of variability, is shown in table 2 on page 10.

It is clear that the variation between plants is wider than would be expected to result from error of sampling. In other words, the variability

in crossover percentage found, though due in part to fluctuations of sampling, is due in part also to actual differences in the frequency of crossing over in different plants.

The correlation between crossover percentage in the C-S_h and S_h-W_x regions, in the male gametes of these 59 plants, was $-.247 \pm .082$. There

TABLE 2

Variability of crossover percentage in male gametes compared with variability expected as result of error of sampling.

REGION	DEVIATION FROM MEAN, DIVIDED BY PROBABLE ERROR				
	1 or more	2 or more	3 or more	4 or more	5 or more
Expected	29.50	10.46	2.54	0.41	0.04
Observed:					
C-S_h	37	18	10	3	1
S_h-W_x	36	19	6	3	0
C-W_x	35	19	5	2	1

was thus a slight but possibly significant tendency for a high crossover percentage in one section to be accompanied by a relatively low crossover percentage in the adjoining section.

Variations in crossover percentage were not significantly correlated with height of plant, number of tillers, or number of ears. There was wide variation in vigor of growth among the plants of this family, plant height varying from 5 to $8\frac{1}{2}$ feet, number of tillers from 0 to 4, and number of ears (including all which produced any grain whatever) from 1 to 8. But these differences had no discernable relation to the frequency of crossing over. There was a slight but possibly significant negative correlation of date of first pollen shedding and crossover percentage for the S_h-W_x region. The crossover percentage for C-S_h, which, as stated above, was negatively correlated with that for S_h-W_x, did not show any relation to date of first pollen. The correlation coefficients determined are shown in table 3.

TABLE 3

Correlation of crossover percentage in male gametes with certain plant characters.

PLANT CHARACTER	CORRELATION WITH CROSSOVER PERCENTAGE		
	C-S_h	S_h-W_x	C-W_x
Date of first pollen....	$-.038 \pm .092$	$-.255 \pm .086$	$-.246 \pm .086$
Plant height..........	$.007 \pm .091$	$-.122 \pm .090$	$-.141 \pm .089$
Number of tillers......	$.060 \pm .090$	$.134 \pm .089$	$.178 \pm .087$
Number of ears.......	$.022 \pm .090$	$.013 \pm .090$	$.036 \pm .090$

VARIABILITY OF CROSSOVER PERCENTAGE IN FEMALE GAMETES

A similar study was made of variation in crossover percentage in female gametes in this family. Crossover percentages in the tiller ears were found to differ significantly from those in ears of the main stalk, as will be shown presently. Since many of the plants did not produce tiller ears, it was necessary to disregard all tiller ears in determining the crossover percentages to be used in the study of variability. The crossover percentage in ears of the main stalk was determined in 70 plants. In 7 of these the shrunken character was indistinct, and was disregarded in making separations. There are available for the study of variation in crossover frequency in female gametes, therefore, crossover percentages in all three of the regions studied, in 63 plants, and in the $C \cdot W_x$ region only in 7 additional plants. The classified progenies are shown in table 15 (appendix).

The variability of the crossover percentages thus determined is shown in table 4.

TABLE 4

Variability of crossover percentage in female gametes.

REGION	NUMBER OF PLANTS	HIGHEST PERCENTAGE	LOWEST PERCENTAGE	MEAN PERCENTAGE	STANDARD DEVIATION	COEFFICIENTS OF VARIABILITY
$C\text{-}S_h$	63	5.8	0.4	2.321 ± 0.082	0.966 ± 0.058	41.62 ± 2.91
$S_h\text{-}W_x$	63	28.6	14.8	20.000 ± 0.242	2.851 ± 0.171	14.26 ± 0.87
$C\text{-}W_x$	63	30.7	15.7	22.156 ± 0.264	3.102 ± 0.186	14.00 ± 0.86
$C\text{-}W_x$	70	30.7	15.7	22.374 ± 0.257	3.187 ± 0.182	14.24 ± 0.83

The variability is of the same order as that found in male gametes, though in all cases the coefficients of variability in the female gametes are slightly higher. This slight increase in variability might perhaps be accounted for by increase in sampling fluctuations accompanying the lower mean crossover percentages found in female gametes. On the other hand, sampling fluctuations should be reduced somewhat by the larger progenies used in determining crossover percentages in the female gametes.

The extent to which fluctuations of sampling may account for the variations observed is better shown by direct comparison of the observed deviations from the mean with the deviations expected from sampling errors alone. These are compared in table 5, which is prepared in the same way as table 2 for the male gametes.

TABLE 5

Variability of crossover percentage in female gametes compared with variability expected as result of error of sampling.

REGION	DEVIATION FROM MEAN, DIVIDED BY PROBABLE ERROR							
	1 or more	2 or more	3 or more	4 or more	5 or more	6 or more	7 or more	8 or more
Expected	*31.50*	*11.17*	*2.71*	*0.44*	*0.05*	*0.00+*	*0.00+*	*0.00+*
Observed:								
C-S_h	44	29	16	6	3	0	0	0
S_h-W_x	45	32	16	9	4	1	1	1
C-W_x	43	32	20	12	5	2	1	1

The variability is well beyond that which may be accounted for by fluctuations of sampling. Obviously, the crossover percentage in female gametes, like that in male gametes, varied among individual plants within the population. The extent of variation in crossover percentage beyond that expected from sampling fluctuations is greater in the female gametes than in the male gametes.

The fact that there were individual differences between the plants of this family is further shown by the correlation between crossover percentages in different ears of the same plant. If crossover variations resulted only from error of sampling, different ears of the same plant should be no more similar than ears of different plants, for all ears would be simply random samples from the same population. In other words, if fluctuation of sampling were the only cause of differences between plants, the crossover percentages of different ears of the same plant would be uncorrelated variables. But actually the crossover percentages in different ears of the same plant were highly correlated. The 52 plants which produced two ears of the main stalk gave the following correlations for crossover percentage in the first and second ear:

Region	r
C-S_h	.451 ± .078
S_h-W_x	.614 ± .061
C-W_x	.686 ± .048

These clearly significant correlations show that plants within this family differed significantly in crossing over, though they do not show whether such differences were due to germinal or environmental causes.

In the 63 plants in which crossover percentages for both C-S_h and S_h-W_x were determined, the correlation of crossover percentages in the two regions was .257 ± .081. This is contrary to the condition found in the

male gametes, in which the crossover percentages in these two regions were negatively correlated to about the same extent.

The relation of crossover percentage in female gametes to plant height, number of tillers, number of ears, and date of first pollen shedding is shown in table 6.

TABLE 6

Correlation of crossover percentage in female gametes with certain plant characters.

PLANT CHARACTER	CORRELATION WITH CROSSOVER PERCENTAGE		
	C-S_h	S_h-W_x	C-W_x
Date of first pollen....	.017 ± .088	.130 ± .086	.122 ± .087
Plant height..........	−.153 ± .085	−.348 ± .077	−.340 ± .077
Number of tillers......	−.094 ± .086	−.179 ± .084	−.180 ± .084
Number of ears.......	−.193 ± .083	−.261 ± .080	−.296 ± .079

There is clearly a tendency toward negative correlation of crossover percentage and characters indicating vigor of growth, though all of the correlation coefficients are low. Plant height shows the closest correlation with crossover percentage, but number of ears and number of tillers also show some correlation, at least in the S_h-W_x and C-W_x regions. The correlation coefficients are lower for the C-S_h region, as was found also in the correlations determined above for crossover percentage in different ears of the same plant. The probable reason for this lower correlation in the C-S_h region is that the variations in this short region were more largely the result of sampling fluctuations than the variations in the longer regions. Date of first pollen was not significantly correlated with crossing over.

RELATIVE FREQUENCY OF CROSSOVERS IN MALE AND FEMALE GAMETES

The data already presented show a higher mean crossover percentage in male gametes than in female gametes. The data given for female gametes include several plants in which crossover frequency in male gametes was not determined, and those for male gametes include a few plants in which female gametes were not tested. Crossover percentages in both male and female gametes were determined in 54 plants, including 5 in which separations for S_h s_h could not be made in the ears representing the female gametes. These determinations are shown in table 16.

The low correlation between crossover percentages in the male and female gametes of the same plant is striking. The correlation coefficients are as follows:

Region	Number of plants	Coefficient of correlation
C-S_h	49	.212 ± .092
S_h-W_x	49	.075 ± .096
C-W_x	54	.122 ± .090

This is in agreement with the results of EMERSON and HUTCHISON (1921) on crossing over in the B-l_g and C-S_h regions in maize. These investigators found in plants extreme in crossover frequency in the gametes of one sex no marked tendency toward extreme results in the other sex. Correlation coefficients computed from the data given by them follow:

Region	Number of plants	Coefficient of correlation
B-l_g	19	.358 ± .135
C-S_h	20	.185 ± .146

The crossover percentages in male and female gametes of the same plants, computed from the totalled progenies of table 16, are shown in table 7.

TABLE 7

Crossover percentage in male and female gametes. Family 4003.

REGION	NUMBER OF PLANTS	MALE GAMETES TESTED		FEMALE GAMETES TESTED		DIFFERENCE
		Total progeny	Crossover percentage	Total progeny	Crossover percentage	Crossover percentage
C-S_h	49	23,348	3.42 ± 0.08	38,770	2.34 ± 0.05	1.08 ± 0.09
S_h-W_x	49	23,348	22.08 ± 0.19	38,770	19.99 ± 0.14	2.09 ± 0.24
C-W_x	54	24,982	25.19 ± 0.19	40,847	22.29 ± 0.14	2.90 ± 0.24

There is no question of the statistical significance of these differences, which are 8 to 12 times as large as their probable errors. The probability is inconceivably small that the total progenies representing male and female gametes are random samples from populations of gametes equal in crossover percentage. In both sections of the chromosome studied, the crossover percentage was distinctly higher in male gametes.

But we have seen that there are significant variations in crossing over between individual plants, and table 16 shows that there is great variation between plants, also, in relative frequency of crossovers in male and female gametes. It is possible that the difference in crossover percentage in the totalled data results from error of sampling the varying population of plants. In the method of comparison used above, the variation of plants is not a factor; the results are the same for any given crossover percentage and total number of grains, whether the plants making up the total are perfectly uniform or highly variable in crossing over.

The significance of the difference from this standpoint may be determined by averaging the differences in crossover percentage found in individual plants, and assigning to this average difference a probable error determined by BESSEL's formula,

$$E = .6745 \sqrt{\frac{\Sigma d^2}{n(n-1)}}$$

Computed in this way the differences are as follows:

Region	Number of plants	Mean difference in crossover percentage
C-S_h	49	0.935 ± 0.115
S_h-W_x	49	2.065 ± 0.397
C-W_x	54	2.607 ± 0.375

Although the probable errors are considerably higher than in the preceding comparison, all three differences are distinctly significant. There is a high degree of probability, amounting to practical certainty, that an infinite number of plants of this population, tested under the same conditions, would have given a higher crossover percentage in male gametes than in female gametes, in both sections of the chromosome.

It does not follow, of course, that such a variation in crossing over is consistently associated with sex in maize. In fact, there are three good reasons for favoring the contrary view:

(1) Previously reported studies have given different results. Among the trials in which the same plants were used both as male and female parents, the only case in which a significant difference was found was one reported by EMERSON and HUTCHISON (1921), in which the crossover percentage in the C-S_h region was found significantly higher in *female* gametes. Other trials reported by EMERSON and HUTCHISON and by EYSTER (1922) showed no significant difference.

(2) Crossover variations analogous to those found in male and female gametes are found in different inflorescences of the same sex. For example, of the 21 plants of this family which produced both a main-stalk ear and a tiller ear, the crossover percentage (for C-W_x) was higher in the main-stalk ear in 17 cases. The mean of the differences in crossover percentage in the 21 plants was 2.26 ± 0.40, which is of the same order as the differences reported above for male and female gametes. It is probable that these differences result from the different environmental conditions under which the gametes develop in the main stalk and in the tiller, which is always several days later in flowering.[2] Since distinct differences in

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[2] These data are presented and discussed in the next section of this paper.

crossover percentage are found in female gametes produced at different periods in the development of the plant, it is to be expected that crossover percentages may differ similarly in male and female gametes, for micro-sporogenesis and megasporogenesis also occur at different periods.

(3) The relative frequency of crossing over in the development of male and female gametes was found to differ consistently in different stocks. In addition to the data for family 4003, already reported, fairly extensive data are available in two other families, 4045 and 4070. Family 4045 was unrelated to family 4003, while family 4070 was related to both 4003 and 4045, its female parent being a full sib of that of 4003 and its male parent a full sib of that of 4045.

Two plantings of each of these families were made, the first on May 12 and the second on June 5. The later-planted series began to shed pollen about 10 days later than the earlier series. Thus the plants of the two series were likely to be under quite different weather conditions at any given stage of development. The crossover percentages for C-W_x, deter-mined from the totalled progenies, are shown in table 8.

TABLE 8
Crossover percentage in male and female gametes. Families 4045 and 4070.

FAMILY	PLANT-ING	NUMBER OF PLANTS	MALE GAMETES TESTED		FEMALE GAMETES TESTED		DIFFERENCE CROSSOVER PERCENTAGE
			Total progeny	Crossover percentage	Total progeny	Crossover percentage	
4045	I	9	2745	25.36±0.56	3797	24.73±0.47	0.63±0.73
4045	II	5	1999	29.01±0.68	2045	27.38±0.66	1.63±0.95
4070	I	5	1668	26.26±0.73	2177	21.13±0.60	5.08±0.94
4070	II	10	2992	28.24±0.56	7284	24.71±0.34	3.53±0.65

Both plantings of 4045 gave an insignificant difference in crossover percentage in male and female gametes, while both plantings of 4070 gave a clearly significant difference in favor of the male gametes. Cross-over percentages were higher in the later planting in both families, but increased in both male and female gametes, so that the relative frequency was not much affected.

VARIATION IN CROSSING OVER WITHIN THE INDIVIDUAL

To determine the extent to which crossing over in the development of male gametes might vary within the individual plant, successive pollina-tions were made from four plants at intervals of one or two days through-out the pollen-shedding season. The classified progenies of these plants
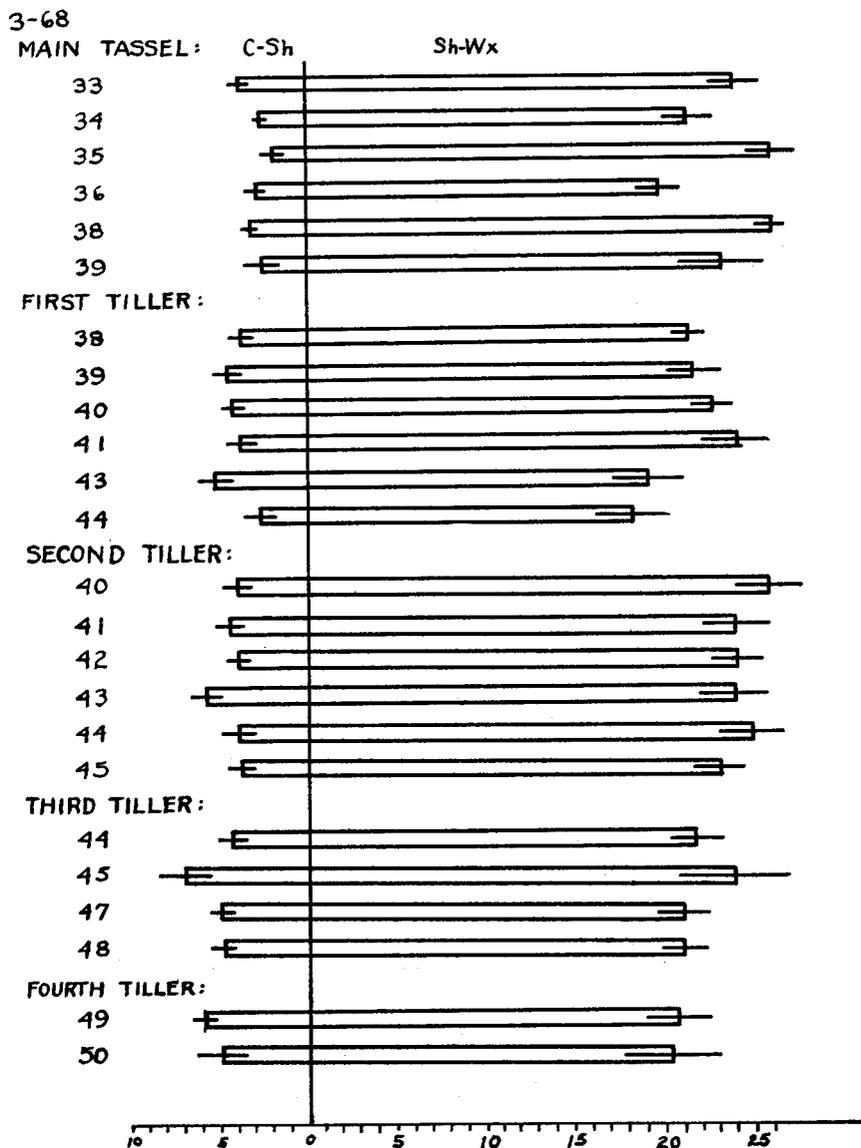
FIGURE 3.—Crossover percentages determined by repeated pollinations from plant 4003-68. Explanation in text.

are shown in tables 17 to 20, inclusive. The most extensive trial was made with plant 4003-68, from which pollinations were made daily, with two exceptions, through a period of 17 days. The plant produced 5 tassels, from each of which repeated pollinations were made. In all, 37 backcross ears were pollinated from this plant. The crossover percentages determined are shown graphically in figure 3. Similar but less extensive trials were made with plants 4013-2, 4017-5, and 4017-21. The results of these 3 trials are shown in figures 4 to 6, inclusive.

SUCCESSIVE POLLINATIONS
FROM PLANT 4013-2
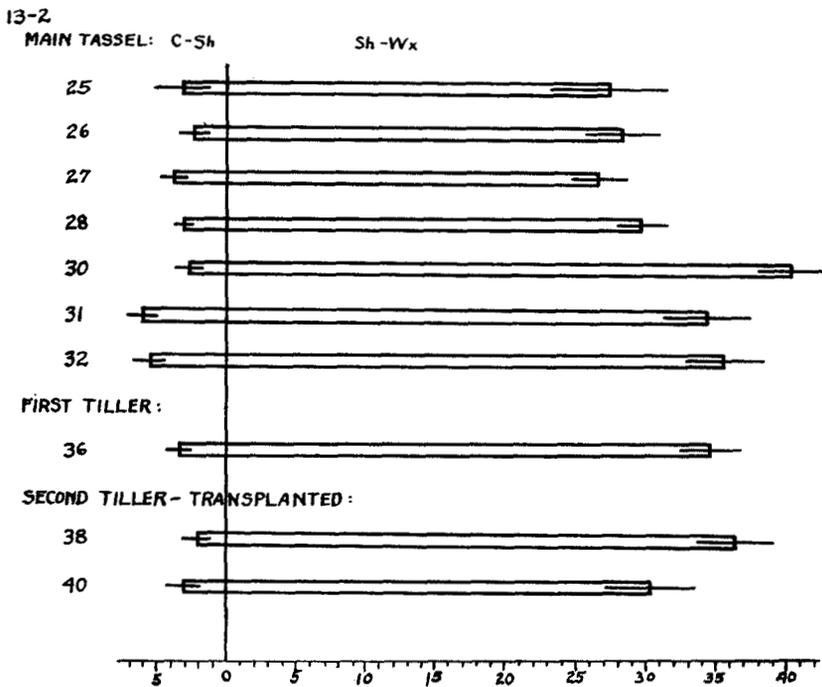
FIGURE 4.—Crossover percentages determined by repeated pollinations from plant 4013-2. Explanation in text.

In these graphs the crossover percentages for the C-S_h and S_h-W_x region are indicated by the length of the bars, while the probable error of each crossover determination is indicated by the length of the single line at the end of the bar. Thus, the first bar of figure 2 indicates crossover percentages of 3.7 ± 0.6 for C-S_h and 23.9 ± 1.4 for S_h-W_x. The dates given are continuous through July and August, July 31 being given as 31, August 1 as 32, etc.

SUCCESSIVE POLLINATIONS
FROM PLANT 4017-5
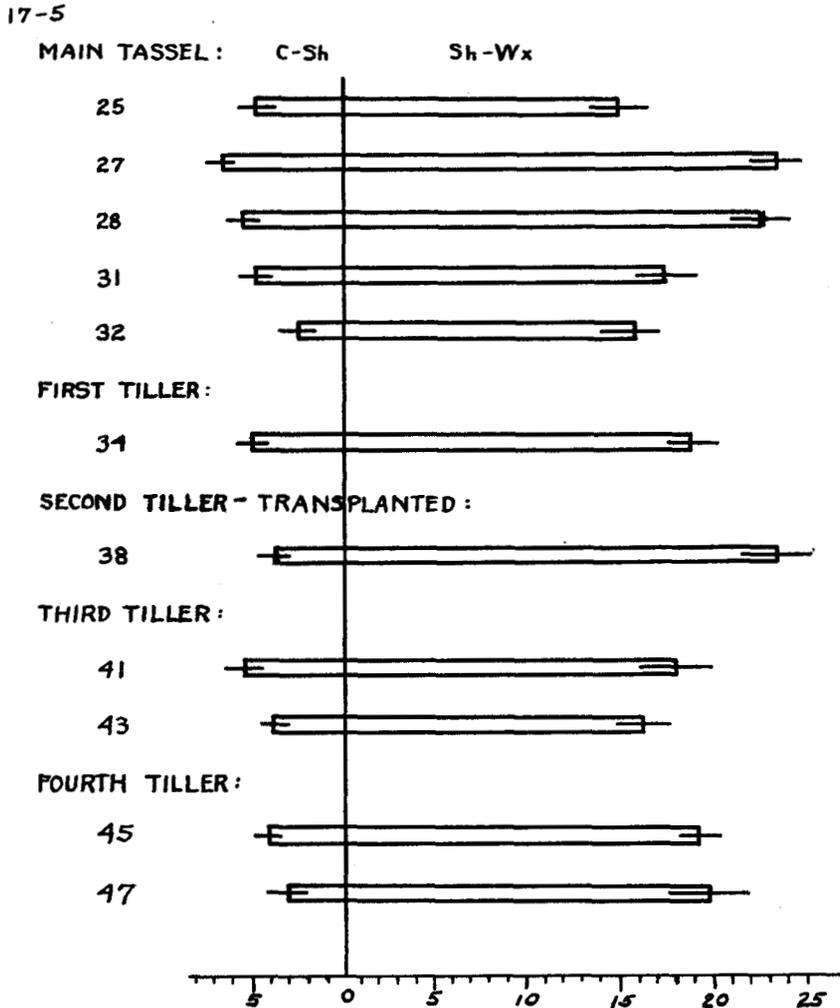
FIGURE 5.—Crossover percentages determined by repeated pollinations from plant 4017-5. Explanation in text.

The crossover percentages determined by successive pollinations from these 4 plants agree in indicating:

(1) There is no consistent increase or decrease in crossing over, with age;

SUCCESSIVE POLLINATIONS
FROM PLANT 4017-21
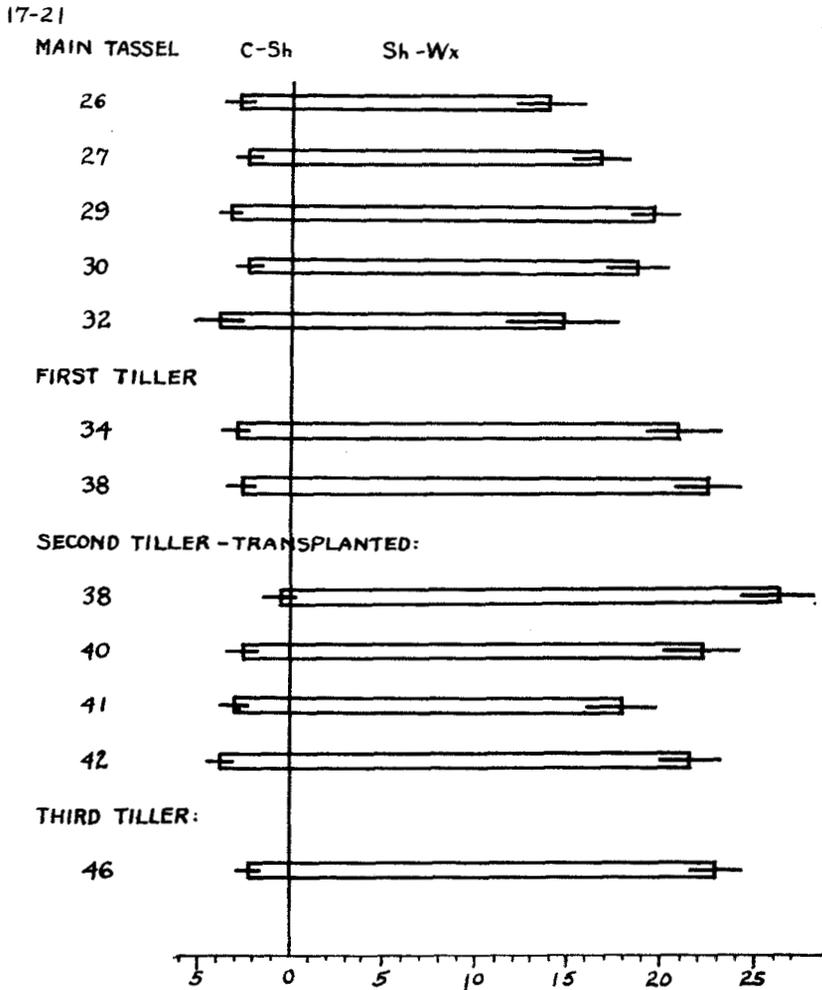
FIGURE 6.—Crossover percentages determined by repeated pollinations from plant 4017-21. Explanation in text.

(2) The fluctuations of the crossover percentage for the C-S_h region are not noticeably correlated, positively or negatively, with the fluctuations of the crossover percentage for the S_h-W_x region;

(3) The crossover percentages determined by pollinations from transplanted tillers were not significantly different from those of other tassels of the same plant; and

(4) The fluctuations in crossover percentage are surprisingly small when their probable errors are considered.

The possibility that these daily fluctuations in crossover percentage are due merely to error of sampling may be examined by the method which was used in studying the variation among different plants. In table 9 are shown the fluctuations from the mean, expected as a result of

TABLE 9

Daily variation in crossing over compared with variation expected as result of error of sampling. Repeated pollinations from 3-68, 13-2, 17-5 and 17-21.

PLANT	NUMBER OF TRIALS	OCCURRENCE	DEVIATIONS FROM MEAN, DIVIDED BY PROBABLE ERROR					
			1.0 or more	1.5 or more	2.0 or more	2.5 or more	3.0 or more	3.5 or more
3–68	24	*Expected*	*12.0*	*7.5*	*4.3*	*2.2*	*1.0*	*0.4*
		Observed:						
		C-S_h	12	10	4	1	0	0
		S_h-W_x	11	6	4	1	1	1
13–2	10	*Expected*	*5.0*	*3.1*	*1.8*	*0.9*	*0.4*	*0.2*
		Observed:						
		C-S_h	4	2	1	0	0	0
		S_h-W_x	8	3	2	2	1	1
17–5	12	*Expected*	*6.0*	*3.7*	*2.1*	*1.1*	*0.5*	*0.2*
		Observed:						
		C-S_h	6	4	3	2	2	1
		S_h-W_x	7	6	5	2	1	0
17–21	12	*Expected*	*6.0*	*3.7*	*2.1*	*1.1*	*0.5*	*0.2*
		Observed:						
		C-S_h	4	3	2	1	0	0
		S_h-W_x	7	5	3	1	1	0
Total....	58	*Expected*	*58.0*	*36.2*	*20.6*	*10.7*	*5.0*	*2.1*
		Observed:	59	39	24	10	6	3

error of sampling, compared with the fluctuations observed. There are, as would be expected, considerable divergences from the expected proportions within individual plants, but in the aggregate, the agreement of expected and observed fluctuations is very close. In other words, crossover percentages determined by repeated pollinations from a single homogeneous supply of pollen would be expected to vary almost as widely

as did the percentages determined by repeated pollinations throughout the pollen-shedding period.

Further evidence on the extent of variability within the individual plant is given by the crossover percentages determined by pollinations from main tassels and tiller tassels. In 19 plants of family 4003 crossover percentages were determined by pollination from both the main tassel and the first tiller tassel. These percentages are shown in table 10.

TABLE 10

Crossover percentage in main tassel and first tiller tassel. Family 4003.

PLANT NUMBER	FIRST TASSEL PERCENT	FIRST TILLER TASSEL PERCENT	DIFFERENCE PERCENT
13	19.4±2.1	30.4±2.2	11.0±3.1
16	26.9±1.7	30.6±1.8	3.7±2.5
18	23.6±1.4	26.0±1.7	2.4±2.2
23	27.0±2.0	26.7±1.5	−0.3±2.5
28	28.1±1.6	24.3±2.1	−3.8±2.6
41	29.5±1.8	26.1±2.2	−3.4±2.8
46	25.8±1.7	23.8±1.6	−2.0±2.3
54	24.8±1.4	25.7±2.2	0.9±2.6
55	27.4±1.7	21.9±1.9	−5.5±2.5
58	24.3±1.8	24.1±1.8	−0.2±2.5
61	25.3±1.9	26.3±1.7	1.0±2.5
65	27.3±2.5	29.7±1.6	2.4±3.0
66	19.8±1.9	22.0±1.5	2.2±2.4
68	27.5±1.4	25.0±1.3	−2.5±1.9
69	29.2±2.1	23.9±2.0	−5.3±2.9
73	25.2±2.4	21.8±2.4	−3.4±3.4
83	27.7±2.2	30.2±1.9	2.5±2.9
85	25.8±2.1	22.0±2.0	−3.8±2.9
99	29.1±1.5	26.1±1.7	−3.0±2.3

The tiller tassels do not differ consistently from the main tassels. In 8 cases the crossover value is higher in the main tassel; in 11 cases in the tiller tassel. Of the 19 differences, 11 are as great as their probable errors, 2 are twice as great, and 1 is three times as great,—again only slightly more variability than would be expected to result from error of sampling. The mean difference in crossover percentage is 0.37 ± 0.60, in favor of the main tassel. The difference is less than its probable error and of course has no significance.

Thus, in this material, crossing over in the production of male gametes has been a relatively constant character of the individual plant. Any environmental variation which has occurred has been too slight to be detected in populations of the size used in this study. Fortunately, the

material used will permit a considerable increase in precision. By using large-eared recessive stocks and pollinating as many ears as possible from each sack of pollen taken from the heterozygous plant, it is possible to reduce the probable error of the crossover percentages representing each day's pollination, at least to 0.2 for the C-S_h region and 0.4 for the C-W_x or S_h-W_x regions. Fluctuations of 1 or 2 crossover units would then be clearly significant.

While crossing over in the production of male gametes varied little within the plant, it varied widely in different plants. The four plants from which daily pollinations were made are favorable material for this comparison, for their large total progenies establish their crossover percentages with a fairly high degree of precision, while the repeated pollinations demonstrate that daily fluctuations were a very minor factor in the differences. These four plants represent three families, of which two were very closely related. Family 4017 was produced by crossing two plants which were full sibs of the parents of family 4003. Family 4013 was not related to the other two families.

The crossover percentages determined from the totalled progenies of the four plants are shown in table 11.

TABLE 11

Individual differences in crossing over.

PLANT	MALE GAMETES			FEMALE GAMETES
	C-S_h	S_h-W_x	C-W_x	C-W_x
3–68	3.9±0.1	22.8±0.3	26.4±0.3	25.8±0.9
13–2	3.3±0.3	30.3±0.7	33.2±0.7	28.7±1.1
17–5	4.3±0.2	19.0±0.5	23.0±0.5	19.6±0.8
17–21	2.9±0.2	20.8±0.5	23.6±0.5	21.0±1.0

There are significant differences in crossing over between any two of the four plants compared. The most striking difference is between 4013-2 and 4017-5, which, as it happened, were planted on the same day, reached pollen-shedding on the same day, and grew under uniform conditions within 5 yards of one another. Plant 17-5, which had a much lower crossover percentage in the S_h-W_x region, had a somewhat higher crossover percentage in the C-S_h region. The latter difference is perhaps insignificant, but there can be no doubt of the significance of the differences in the S_h-W_x region or in the C-W_x region taken as a whole, which are, respectively, 11.3±0.9 and 10.2±0.9. A similar difference in crossover percentage was found in the ears of these two plants, in which the differ-

ence in the crossover percentage for C-W_x was 9.1 ± 1.4. Unfortunately, separations for S_h s_h could not be made in the ears of plant 17-5, so crossover percentages in female gametes could not be determined for the C-S_h and S_h-W_x sections. For the C-W_x region, considered as a whole, crossing over was about 45 percent more frequent in plant 13-2, in the development of both male and female gametes.

In female gametes the crossover percentages in main stalks and tillers showed a relation very different from that found in male gametes. Of the 70 plants for which crossover percentages for C-W_x were determined, 21 produced a backcrossed ear on both the main stalk and the first tiller. The crossover percentages for these ears are shown in table 12.

TABLE 12

Crossover percentage in first ear and first tiller ear. Family 4003.

PLANT	FIRST EAR PERCENT	FIRST TILLER EAR PERCENT	DIFFERENCE PERCENT
7	24.3 ± 1.3	27.0 ± 1.3	2.7 ± 1.8
11	22.6 ± 1.3	26.2 ± 1.4	3.6 ± 1.9
13	20.5 ± 1.5	22.5 ± 1.6	2.0 ± 2.2
16	19.8 ± 1.4	20.9 ± 1.2	1.1 ± 1.8
17	20.5 ± 1.3	24.1 ± 1.3	3.6 ± 1.8
19	20.5 ± 1.6	17.7 ± 2.2	-2.8 ± 2.7
24	17.8 ± 1.3	26.9 ± 1.4	9.1 ± 1.9
31	22.5 ± 1.3	22.7 ± 1.5	0.2 ± 2.0
33	20.3 ± 1.2	18.9 ± 1.2	-1.4 ± 1.7
34	23.1 ± 1.2	25.0 ± 2.1	1.9 ± 2.4
46	25.5 ± 1.3	26.6 ± 1.3	1.1 ± 1.8
52	22.2 ± 1.3	22.0 ± 1.3	-0.2 ± 1.8
53	17.8 ± 1.4	23.6 ± 1.4	5.8 ± 2.0
54	17.5 ± 1.2	17.8 ± 1.3	0.3 ± 1.8
63	25.6 ± 1.2	29.2 ± 1.3	3.6 ± 1.8
67	21.0 ± 1.5	24.2 ± 1.3	3.2 ± 2.0
68	26.4 ± 1.3	25.3 ± 1.2	-1.1 ± 1.8
69	22.9 ± 1.2	25.7 ± 1.4	2.8 ± 1.8
78	27.6 ± 2.3	28.8 ± 1.4	1.2 ± 2.7
85	17.3 ± 1.5	22.4 ± 1.6	5.1 ± 2.2
99	20.0 ± 1.3	25.7 ± 1.3	5.7 ± 1.8

The crossover percentages are consistently higher in the tiller ears. In only 4 of the 21 cases is the main-stalk ear higher in crossover percentage, and only one of these differences is as great as its probable error. The mean of the differences is 2.26 ± 0.40, or 5.65 times its probable error. Similarly, the crossover percentages determined from the totalled progenies are 21.26 ± 0.29 for the main-stalk ear and 23.96 ± 0.31 for the tiller ear, giving a difference in favor of the tiller ear of 2.70 ± 0.42. Thus,

different ears of the same plant have undoubtedly differed significantly in crossover percentage.

Whether this difference is due to age or to different environmental conditions at a critical period cannot be certainly determined from the available evidence. Whatever the cause of the difference between inflorescences of main and tiller stalks, however, it is clear that crossing over was far more affected by it in female than in male gamete development.

The first and second ears of the main stalk were strikingly similar in crossover percentage, in the 52 plants which produced two main-stalk ears. In this family the two ears of the main stalk were usually of about the same size and silked on the same day. Presumably, they developed under practically the same environmental conditions. The differences between their crossover percentages were no greater than those to be expected from fluctuations of sampling, as shown in table 13.

TABLE 13

Differences in crossover percentage in first and second ear compared with differences expected from error of sampling.

	NUMBER OF PLANTS	DIFFERENCE, DIVIDED BY PROBABLE ERROR		
		1.0 or more	1.0 or more	3.0 or more
Expected	47	*23.50*	*8.33*	*2.02*
Observed:				
C-S_h	47	23	8	0
S_h-W_x	47	20	7	0
Expected	52	*26.00*	*9.22*	*2.24*
Observed:				
C-W_x	52	25	6	1

SUMMARY

Among a maize population of full sibs grown under uniform conditions:

(1) Crossing over was found only moderately variable, when due allowance was made for fluctuations of sampling.

(2) Crossover percentages determined for the short C-S_h region were much more variable than those for the long S_h-W_x region. This is probably due to the fact that the former are much more greatly affected by errors of sampling.

(3) Crossover percentages in female gametes were more variable than crossover percentages in male gametes.

(4) Crossover percentages in the first and second ear of the main stalk were highly correlated.

(5) Crossover variations in male gametes were not correlated with plant height, number of ears, or number of tillers, but were possibly correlated, negatively, to a slight extent, with date of first pollen.

Crossover variations in female gametes were correlated negatively with plant height, number of ears, and possibly number of tillers, but were not correlated with date of first pollen.

(6) Crossover percentages in male and female gametes of the same plants were not significantly correlated.

(7) Crossover percentages were significantly higher in male gametes than in female gametes of the same plants.

Within the individual plant:

(8) Crossover percentages in male gametes, determined by repeated pollinations throughout the pollen-shedding season, did not differ significantly.

(9) Pollen of transplanted tillers did not differ significantly in crossover percentage from pollen of other tassels of the same plant.

(10) Crossover percentages in female gametes were significantly higher in tiller ears than in ears of the main stalk. In male gametes no such difference was found. Thus, crossing over in the development of female gametes was apparently affected by age or environmental conditions which had no distinct effect on crossing over in the development of male gametes.

Among plants of different families:

(11) A single random comparison of two plants from unrelated families showed a wide and clearly significant difference in crossing over. The differences were similar in male and female gametes.

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APPENDIX—Tables 14 to 22

TABLE 14

Crossover data, male gametes, family 4003.

PLANT NUMBER	NON-CROSSOVERS		CROSSOVERS IN REGION						TOTAL
			1		2		1, 2		
3	136	115	1	2	33	34	0	0	321
5	59	84	0	4	22	15	1	0	185
7	242	264	13	12	68	64	0	2	665
10	131	109	4	3	33	25	1	0	306
11	245	203	10	8	51	48	2	3	570
12	104	100	5	1	47	26	1	0	284
13	223	211	8	10	63	68	0	0	583
16	186	216	10	7	75	69	0	0	563
18	309	290	16	22	66	87	1	1	792
19	102	95	9	6	37	26	0	0	275
20	81	91	4	1	36	27	0	0	240
23	183	247	13	6	78	63	0	1	591
24	101	105	1	0	13	20	0	0	240
27	101	101	5	2	29	27	0	0	265
28	175	208	5	8	72	55	1	0	524
29	150	148	4	1	43	36	0	1	383
30	178	165	11	5	40	59	0	2	460
33	415	436	14	9	114	114	0	0	1102
34	73	53	3	4	15	18	0	0	166
35	122	114	7	6	32	32	0	1	314
40	92	82	6	3	19	15	0	0	217
41	164	157	9	6	49	62	0	0	447
44	62	74	1	3	26	27	0	0	193
46	209	259	18	14	68	53	1	0	622
47	74	77	2	2	29	25	0	0	209
52	279	296	8	9	91	88	1	1	773
53	121	108	4	4	37	41	0	0	315
54	232	250	10	4	81	66	0	0	643
55	307	291	18	19	76	81	0	1	793
58	209	194	5	11	51	62	0	1	533
60	171	170	16	13	43	44	0	0	457
61	285	301	9	12	83	99	0	1	790
63	78	100	7	2	21	25	0	0	233
65	156	178	8	8	62	58	0	0	470
66	250	228	14	12	54	48	0	0	606
68	669	703	45	32	209	213	1	1	1873
69	268	264	10	12	79	84	0	1	718
70	91	77	3	4	39	37	0	0	251
71	308	278	15	2	78	94	2	0	777
72	143	132	5	7	46	41	0	1	375
73	129	101	2	5	30	34	2	0	303
74	81	131	5	1	26	26	0	0	270
75	196	189	13	6	74	55	1	0	534

TABLE 14 (continued)

PLANT NUMBER	NON-CROSSOVERS		CROSSOVERS IN REGION						TOTAL
			1		2		1, 2		
76	85	111	5	4	28	30	0	0	263
78	97	104	4	5	27	31	0	0	268
80	217	241	10	6	59	67	0	0	600
81	97	80	4	2	18	25	0	0	226
82	135	136	2	4	35	53	0	0	365
83	242	248	11	11	99	64	0	0	675
85	145	161	7	10	39	41	1	4	408
87	96	107	5	2	29	34	0	0	273
88	86	77	7	4	21	21	0	0	216
89	54	45	1	2	13	12	0	0	127
90	219	218	8	9	60	60	0	0	574
92	130	123	10	3	44	32	0	0	342
95	37	43	4	1	12	12	0	0	109
96	73	67	3	3	36	25	0	0	207
98	170	153	8	9	46	49	0	0	435
99	235	261	8	14	81	88	0	1	688
Total	20,178		870		5919		39		27,006

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TABLE 15

Crossover data, female gametes, family 4003.
(Tiller ears excluded).

PLANT	NON-CROSSOVERS		CROSSOVERS IN REGION						TOTAL
			1		2		1, 2		
2	116	96	8	4	24	41	3	2	294
4	187	161	5	4	41	41	1	1	441
5	337	333	10	12	74	72	4	2	844
7	342	324	17	13	99	96	0	0	891
9	307	296	5	6	100	102	1	0	817
10	210	205	6	5	52	33	1	0	512
11	185	178	1	4	40	61	0	0	469
13	292	312	4	6	65	92	0	0	771
15	161	200	6	2	46	61	0	0	476
16	390	360	6	5	65	83	1	1	911
17	206	155	2	4	36	51	0	0	454
18	254	235	6	7	62	77	0	0	641
19	188	221	5	8	55	53	0	0	530
20	331	330	10	9	84	81	1	1	847
24	216	183	3	2	47	38	0	0	489
27	316	328	11	6	109	107	0	0	877
28	464	471	15	15	105	126	0	0	1196
29	448	470	5	8	100	96	0	0	1127
30	262	247	4	3	61	63	0	0	640
31	273	271	7	9	73	79	0	1	713
32	250	258	8	9	50	52	0	0	627
33	221	218	7	6	48	51	0	0	551
34	362	355	11	17	95	73	2	0	915
40	385	377	10	14	89	86	0	0	961
44	406	386	7	11	90	92	0	0	992
46	354	345	14	14	117	112	0	1	957
47	325	335	14	19	102	94	0	0	889
52	358	344	7	15	92	94	0	0	910
53	179	162	4	7	31	34	0	0	417
54	406	459	8	11	93	82	0	0	1059
55	182	160	8	10	50	61	0	0	471
58	70	79	6	1	12	18	0	0	186
59	419	425	17	15	80	92	0	1	1049
61	410	426	3	5	89	91	0	0	1024
63	338	328	12	16	87	86	0	0	867
65	296	277	4	3	60	61	1	0	702
66	393	391	15	15	89	96	0	0	999
67	212	201	5	5	46	56	0	0	525
68	157	168	8	8	50	53	0	0	444
69	206	198	5	5	58	53	0	0	525
70	307	315	18	15	114	104	1	1	875
71	439	424	12	18	87	91	0	0	1071
72	469	419	13	18	106	92	0	0	1117
73	305	277	16	11	96	99	0	0	804

TABLE 15 (continued)

PLANT	NON-CROSSOVERS		CROSSOVERS IN REGION					TOTAL
			1		2		1, 2	
75	268	277	9	9	121	103	1	1	789
76	456	379	22	17	98	104	0	0	1076
77	218	244	9	4	67	75	0	0	617
80	301	274	10	6	60	68	0	0	719
81	338	364	11	6	95	97	0	0	911
83	262	247	4	0	71	67	0	0	651
85	337	331	13	11	45	81	1	0	819
86	262	279	2	4	50	45	0	0	642
87	325	380	9	7	77	102	0	0	900
88	404	403	8	7	130	136	0	0	1088
89	306	297	9	8	93	88	0	0	801
90	207	206	5	6	61	66	1	0	552
93	119	107	1	0	16	31	0	0	274
95	157	155	4	6	44	42	1	0	409
96	348	360	9	8	80	98	0	0	903
98	278	266	4	9	67	67	0	0	691
99	389	375	11	13	97	95	0	0	980
100	50	52	1	3	14	13	0	0	133
Total	35,658		1033		9109		32		45,832

Ears without separation of S_h s_h (crossovers in C-W_x region)

	NON-CROSSOVERS		1		2		1, 2		TOTAL
3	157	148	—	—	44	61	—	—	410
12	95	99	—	—	41	39	—	—	274
14	307	304	—	—	118	99	—	—	828
35	97	108	—	—	30	29	—	—	264
41	384	362	—	—	83	110	—	—	939
42	98	89	—	—	26	20	—	—	233
78	74	65	—	—	33	18	—	—	190
Grand total	38,045		——		10,893		——		48,970

TABLE 16

Crossover percentage in male and female gametes. Family 4003.

PLANT NUMBER	C-S$_h$ REGION			S$_h$-W$_x$ REGION			C-W$_x$ REGION		
	Male gametes	Female gametes	Difference	Male gametes	Female gametes	Difference	Male gametes	Female gametes	Difference
5	2.7±0.9	3.3±0.3	−0.6±0.9	20.5±2.1	18.0±1.0	2.5±2.3	22.2±2.2	19.9±1.0	2.3±2.4
7	4.1±0.5	3.4±0.3	0.7±0.6	20.2±1.1	21.9±0.9	−1.7±1.4	23.6±1.1	25.3±1.0	−1.7±1.5
10	2.6±0.7	2.3±0.4	0.3±0.8	19.3±1.6	16.8±1.2	2.5±2.0	21.2±1.7	18.8±1.3	2.4±2.1
11	4.0±0.5	1.1±0.5	2.9±0.7	18.2±1.2	21.5±1.3	−3.3±1.8	20.5±1.2	22.6±1.3	−2.1±1.8
13	3.1±0.5	1.3±0.4	1.8±0.7	22.5±1.1	20.4±1.0	2.1±1.5	25.6±1.2	21.7±1.0	3.9±1.6
16	3.0±0.5	1.4±0.3	1.6±0.6	25.6±1.2	16.5±0.9	9.1±1.5	28.6±1.2	17.5±1.0	11.1±1.6
18	5.1±0.4	2.0±0.4	3.1±0.6	19.6±1.0	21.7±1.1	−2.1±1.5	24.1±1.0	23.7±1.1	0.4±1.5
19	5.5±0.7	2.5±0.4	3.0±0.8	22.9±1.7	20.4±1.2	2.5±2.1	28.4±1.8	22.8±1.3	5.6±2.2
20	2.1±0.8	2.5±0.3	−0.4±0.9	26.3±1.8	19.7±1.0	6.6±2.1	28.3±1.9	21.7±1.0	6.6±2.1
24	0.4±0.8	1.0±0.5	−0.6±0.9	13.8±1.8	17.4±1.3	−3.6±2.2	14.2±1.9	18.4±1.3	−4.2±2.3
27	2.6±0.7	1.9±0.3	0.7±0.8	21.1±1.7	24.6±0.9	−3.5±1.9	23.8±1.8	26.6±1.0	−2.8±2.1
28	2.7±0.5	2.5±0.3	0.2±0.6	24.4±1.2	19.3±0.8	5.1±1.4	26.7±1.3	21.8±0.8	4.9±1.5
29	1.6±0.6	1.2±0.3	0.4±0.7	20.9±1.4	17.4±0.8	3.5±1.6	21.9±1.5	18.5±0.9	3.4±1.7
30	3.9±0.6	1.1±0.4	2.8±0.7	22.0±1.3	19.4±1.1	2.6±1.7	25.0±1.4	20.5±1.1	4.5±1.8
33	2.1±0.4	2.4±0.4	−0.3±0.6	20.7±0.8	18.0±1.2	2.7±1.4	22.8±0.9	20.3±1.2	2.5±1.5
34	4.2±0.9	3.3±0.3	0.9±0.9	19.9±2.2	18.6±0.9	1.3±2.4	24.1±2.3	21.4±1.0	2.7±2.5
40	4.1±0.8	2.5±0.3	1.6±0.9	15.7±1.9	18.2±0.9	−2.5±2.1	19.8±2.0	20.7±0.9	−0.9±2.2
44	2.1±0.9	1.8±0.3	0.3±0.9	27.5±2.0	18.3±0.9	9.2±2.2	29.5±2.1	20.2±0.9	9.3±2.3
46	5.3±0.5	3.0±0.3	2.3±0.6	19.6±1.1	24.0±0.9	−4.4±1.4	24.6±1.2	26.9±0.9	−2.3±1.5
47	1.9±0.8	3.7±0.3	−1.8±0.9	25.8±2.0	22.0±0.9	3.8±2.2	27.8±2.0	25.8±1.0	2.0±2.2
52	2.5±0.4	2.4±0.3	0.1±0.5	23.4±1.0	20.4±0.9	3.0±1.3	25.4±1.1	22.9±1.0	2.5±1.5
53	2.5±0.7	2.6±0.5	−0.1±0.9	24.8±0.6	15.6±1.4	9.2±1.5	27.3±1.7	18.2±1.4	9.1±2.2
54	2.2±0.5	1.8±0.3	0.⌐ 0.6	22.9±1.1	16.5±0.9	6.4±1.4	25.0±1.2	18.3±0.9	6.7±1.5
55	4.8±0.4	3.8±0.5	1 0.7	19.9±1.0	23.6 1.3	−3.7±1.6	24.5±1.0	27.4±1.3	−2.9±1.6

TABLE 16 (continued)

PLANT NUMBER	C-Sh REGION			Sh-Wx REGION			C-Wx REGION		
	Male gametes	Female gametes	Difference	Male gametes	Female gametes	Difference	Male gametes	Female gametes	Difference
58	3.2±0.5	3.8±0.7	-0.6±0.9	21.4±1.2	16.1±2.1	5.3±2.4	24.2±1.3	19.9±2.1	4.3±2.5
61	2.8±0.4	0.8±0.3	2.0±0.5	23.2±1.0	17.6±0.9	5.6±1.3	25.7±1.1	18.4±0.9	7.3±1.4
63	3.9±0.8	3.2±0.3	0.7±0.9	19.7±1.9	20.0±1.0	-0.3±2.1	23.6±1.9	23.2±1.0	0.4±2.1
65	3.4±0.6	1.1±0.4	2.3±0.7	25.5±1.3	17.4±1.1	8.1±1.7	28.9±1.4	18.2±1.1	10.7±1.8
66	4.3±0.5	3.0±0.3	1.3±0.6	16.8±1.2	18.5±0.9	-1.7±1.5	21.1±1.2	21.5±0.9	-0.4±1.5
68	4.2±0.3	3.6±0.5	0.6±0.6	22.6±0.7	23.2±1.3	-0.6±1.5	26.6±0.7	26.8±1.4	-0.2±1.6
69	3.2±0.4	1.9±0.4	1.3±0.6	22.8±1.1	21.1±1.2	1.7±1.6	25.8±1.1	23.0±1.3	2.8±1.7
70	2.8±0.8	4.0±0.3	-1.2±0.9	30.3±1.8	25.1±0.9	5.2±2.0	33.1±1.9	28.7±1.0	4.4±2.1
71	2.7±0.4	2.8±0.3	-0.1±0.5	24.6±1.0	16.6±0.9	8.0±1.3	26.8±1.1	19.4±0.9	7.4±1.4
72	3.5±0.6	2.8±0.3	0.7±0.7	23.5±1.5	17.7±0.8	5.8±1.7	26.4±1.5	20.5±0.9	5.9±1.7
73	3.0±0.7	3.4±0.4	-0.4±0.8	21.8±1.6	24.3±1.0	-2.5±1.9	23.4±1.7	27.6±1.0	-4.2±2.0
75	3.7±0.5	2.5±0.4	1.2±0.7	24.3±1.2	28.6±1.0	-4.3±1.6	27.7±1.3	30.7±1.0	-3.0±1.6
76	3.4±0.7	3.6±0.3	-0.2±0.8	22.1±1.7	18.8±0.9	3.3±1.9	25.5±1.8	22.4±0.9	3.1±2.0
80	2.7±0.5	2.2±0.4	0.5±0.7	21.0±1.2	17.8±1.0	3.2±1.6	23.7±1.2	20.0±1.1	3.7±1.6
81	2.7±0.3	1.9±0.3	0.8±0.4	19.0±1.9	21.1±1.0	-2.1±2.1	21.7±2.0	22.9±1.0	-1.2±2.2
83	3.3±0.5	0.6±0.4	2.7±0.7	24.1±1.1	21.2±1.1	2.9±1.6	27.4±1.1	21.8±1.1	5.6±1.6
85	5.4±0.6	2.9±0.4	2.5±0.7	20.8±1.4	15.5±1.0	5.3±1.7	23.8±1.5	18.3±1.0	5.5±1.8
87	2.6±0.7	1.8±0.3	0.8±0.8	23.1±1.7	19.9±0.9	3.2±1.9	25.6±1.8	21.7±1.0	3.9±2.1
88	5.1±0.8	1.4±0.3	3.7±0.9	19.4±1.9	24.4±0.8	-5.0±2.1	24.5±2.0	25.8±0.9	-1.3±2.2
89	2.4±1.1	2.1±0.4	0.3±1.2	19.7±2.5	22.6±1.0	-2.9±2.7	22.0±2.6	24.7±1.0	-2.7±2.8
90	3.0±0.5	2.2±0.4	0.8±0.7	20.9±1.2	23.2±1.2	-2.3±1.7	23.9±1.2	25.0±1.2	-1.1±1.7
95	4.6±1.1	2.7±0.5	1.9±1.2	22.0±2.7	21.3±1.4	0.7±3.0	26.6±2.8	23.5±1.4	3.1±3.1
96	2.9±0.8	1.9±0.3	1.0±0.9	29.5±2.0	19.7±0.9	9.8±2.2	32.4±2.1	21.6±1.0	10.8±2.3
98	3.9±0.6	1.9±0.4	2.0±0.7	21.8±1.4	19.4±1.1	2.4±1.8	25.7±1.4	21.3±1.1	4.4±1.8
99	3.3±0.5	2.4±0.3	0.9±0.6	24.7±1.1	19.6±0.9	5.1±1.4	27.8±1.1	22.0±0.9	5.8±1.4

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TABLE 17

Repeated pollinations from plant 4003-68.

TASSEL	DATE AUGUST	NON-CROSSOVER		CROSSOVERS IN REGION						TOTAL
				1		2		1, 2		
Main	2	140	176	8	8	57	47	0	0	436
	4	135	182	4	7	46	42	0	0	416
	4	151	140	4	2	56	47	0	1	401
	5	182	205	10	4	40	58	0	0	499
	7	297	341	19	10	119	115	0	0	901
	8	42	51	0	2	15	14	0	0	124
First tiller	7	184	194	11	7	51	57	0	0	504
	8	111	101	5	8	27	35	0	0	287
	9	268	253	20	10	81	81	0	0	713
	10	77	93	4	5	30	27	0	0	236
	12	70	76	6	4	20	17	0	0	193
	13	74	82	2	2	14	21	0	1	196
Second tiller	9	96	75	6	4	25	38	0	0	244
	10	83	93	6	3	23	33	1	1	243
	11	138	143	6	7	43	48	1	1	387
	12	82	90	6	8	25	33	0	0	244
	13	68	82	5	3	28	24	0	0	210
	14	128	155	7	6	35	53	0	1	385
Third tiller	13	143	141	9	7	48	34	0	1	383
	14	26	32	3	3	8	12	0	0	84
	16	134	138	10	6	26	48	0	2	364
	17	155	171	12	9	51	41	0	0	439
Fourth tiller	18	106	117	11	6	28	37	1	0	306
	19	35	38	4	1	14	6	0	0	98

TABLE 18

Repeated pollinations from plant 4013-2.

TASSEL	DATE	NON-CROSSOVER	CROSSOVERS IN REGION					TOTAL
			1		2		1, 2	
Main	July 25	23 24	0	2	9	8	0 0	66
	July 27	86 96	5	4	30	34	0 0	255
	July 28	153 153	8	4	51	72	0 1	442
	July 29	49 57	2	2	16	23	1 0	150
	July 30	57 58	3	2	30	44	0 0	194
	July 31	41 35	3	4	18	22	0 0	123
	Aug. 1	34 48	3	4	18	27	0 0	134
First tiller	Aug. 5	76 59	4	3	35	34	0 0	211
Second tiller (transplanted)	Aug. 7	49 50	2	0	22	30	0 1	154
	Aug. 9	34 39	1	1	13	16	1 0	105

TABLE 19

Repeated pollinations from plant 4017-5.

TASSEL	DATE	NON-CROSSOVER	CROSSOVERS IN REGION					TOTAL
			1		2		1, 2	
Main	July 25	130 103	7	6	18	24	0 0	288
	July 27	116 121	9	12	39	39	0 1	337
	July 28	115 106	1	16	36	34	0 0	308
	July 31	99 102	9	3	31	14	0 0	258
	Aug. 2	96 107	2	4	24	15	0 0	248
First tiller	Aug. 3	152 145	12	7	35	38	0 0	389
Second tiller (transplanted)	Aug. 7	90 73	5	2	25	26	1 0	222
	Aug. 10	76 64	0	0	14	19	0 1	174
Third tiller	Aug. 10	77 66	4	4	21	10	0 2	184
	Aug. 12	142 151	9	5	32	27	0 0	366
Fourth tiller	Aug. 14	211 176	6	15	55	41	0 0	504
	Aug. 16	67 56	4	1	20	11	0 0	159

TABLE 20

Repeated pollinations from plant 4017-21.

TASSEL	DATE	NON-CROSSOVER	CROSSOVERS IN REGION						TOTAL
			1		2		1, 2		
Main	July 26	82	86	1	5	20	14	0	0	208
	July 27	127	106	2	5	29	21	0	0	290
	July 29	137	146	7	9	32	44	0	0	375
	July 30	94	102	3	3	26	22	0	0	250
	Aug. 2	27	32	2	1	7	4	0	0	73
First tiller	Aug. 3	83	91	4	3	26	24	0	0	231
	Aug. 7	77	87	4	1	25	25	0	1	220
Second tiller	Aug. 7	54	66	0	1	19	26	0	0	166
(transplanted)	Aug. 9	57	57	3	1	18	17	0	0	153
	Aug. 10	75	74	2	4	16	19	0	0	190
	Aug. 11	106	124	9	3	36	33	0	0	311
Third tiller	Aug. 16	106	150	3	4	31	49	0	1	344

TABLE 21

Crossover data, first tassel and first tiller tassel, family 4003.

PLANT	FIRST TASSEL						FIRST TILLER TASSEL					
	Non-crossover		Crossovers in region			Total	Non-crossover		Crossovers in region			Total
			1	2	1, 2				1	2	1, 2	
13	88	70	2 2	16 18	0 0	196	66	62	3 3	22 28	0 0	184
16	112	111	5 4	40 33	0 0	305	74	105	5 3	35 36	0 0	258
18	181	185	12 12	34 51	1 0	476	128	105	4 10	32 36	0 1	316
23	69	85	6 2	27 22	0 0	211	114	162	7 4	51 41	0 1	380
28	110	130	4 5	51 34	1 0	335	65	78	1 3	21 21	0 0	189
41	90	101	5 3	29 43	0 0	271	74	56	4 3	20 19	0 0	176
46	94	121	12 7	27 29	1 0	291	115	138	6 7	41 24	0.0	331
54	165	187	7 2	66 41	0 0	468	67	63	3 2	15 25	0 0	175
55	114	117	10 9	35 33	0 0	318	95	94	5 7	18 23	0 0	242
58	106	99	2 4	25 35	0 1	272	103	95	3 7	26 27	0 0	261
61	80	103	4 2	29 27	0 0	245	107	102	3 4	31 37	0 1	285
65	48	56	1 2	21 15	0 0	143	108	122	7 6	41 43	0 0	327
66	101	89	4 2	23 18	0 0	237	149	139	10 10	31 30	0 0	369
68	140	176	8 8	57 47	0 0	436	184	194	11 7	51 57	0 0	504
69	66	70	3 4	22 27	0 0	192	88	84	2 4	24 24	0 0	226
73	60	49	1 2	17 17	1 0	147	69	52	1 3	13 17	1 0	156
83	67	61	2 2	26 19	0 0	177	85	86	5 6	40 23	0 0	245
85	67	74	3 3	25 18	0 0	190	78	87	4 7	14 23	1 4	218
99	127	144	6 5	50 50	0 0	382	108	117	2 9	31 38	0 1	306
Total	3913		177	1197	5	5292	3818		191	1129	10	5148

TABLE 22

Crossover data, first ear and first tiller ear, family 4003.

PLANT	FIRST EAR					FIRST TILLER EAR				
	Non-crossovers	Crossovers in region			Total	Non-crossovers	Crossovers in region			Total
		1	2	1, 2			1	2	1, 2	
7	195 173	8 5	55 49	0 0	485	181 159	7 7	56 61	0 0	471
11	185 178	1 4	40 61	0 0	469	163 146	5 6	40 53	0 0	413
13	130 157	1 1	34 38	0 0	361	118 127	3 5	34 29	0 0	316
16	162 159	2 1	36 40	0 0	400	219 204	3 1	53 55	0 0	535
17	206 155	2 4	36 51	0 0	454	157 171	3 6	37 55	0 0	429
19	106 123	4 6	25 24	0 0	288	61 69	0 0	12 16	0 0	158
24	216 183	3 2	47 38	0 0	489	165 139	3 3	58 49	0 0	417
31	172 165	3 7	43 45	0 0	435	132 149	4 3	35 43	0 0	366
33	221 218	7 6	48 51	0 0	551	218 227	1 3	44 56	0 0	549
34	198 179	6 9	58 43	2 0	495	59 73	2 2	27 13	0 0	176
46	191 167	7 5	50 61	0 1	482	175 164	5 6	59 53	0 0	462
52	171 173	3 9	41 45	0 0	442	187 165	0 2	40 57	0 0	451
53	179 162	4 7	31 34	0 0	417	158 140	3 1	39 48	0 0	389
54	229 233	4 6	42 46	0 0	560	196 195	7 5	38 37	0 0	478
61	216 234	2 2	47 43	0 0	544	47 66	0 3	12 17	0 0	145
63	182 187	8 8	54 52	0 0	491	160 142	9 12	52 53	0 0	428
67	146 128	4 3	33 33	0 0	347	175 191	3 4	63 48	0 0	484
68	157 168	8 8	50 53	0 0	444	216 214	13 14	67 62	0 1	587
69	206 198	5 5	58 53	0 0	525	144 165	7 7	41 52	0 0	416
80	122 110	5 3	25 26	0 0	291	54 53	1 2	19 17	0 0	146
85	137 135	6 5	16 30	0 0	329	131 111	3 7	30 31	0 0	313
99	198 185	4 6	43 42	0 0	478	158 161	2 9	49 48	1 0	428
Total	7695	209	1870	3	9777	6504	192	1858	2	8557