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THE RELATIVE FREQUENCY OF CROSSING OVER IN MICRO- SPORE AND IN MEGASPORE DEVELOPMENT IN MAIZE¹

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INTRODUCTION

One of the early developments in the study of linkage in *Drosophila* was the discovery that the phenomenon of crossing over is confined to the female sex (MORGAN 1912). The fact that no crossing over occurs in the male *Drosophila* holds true not only for sex-linked genes but for factors in the autosomes as well and is so well established that it affords a most convenient method of determining to which of the different linkage groups a new factor belongs.

The same phenomenon, but with the sexes reversed, obtains in the silkworm moth. TANAKA (1914, 1915) has found from back-cross tests of both sexes in this organism, that crossing over occurs in the male but not in the female. Similarly GOODALE (1917) has observed crossing over in the sex chromosome of the male fowl but none in the female and more recently COLE and KELLEY (1919) have reported that crossing over occurs in the male pigeon but not in the female. In the latter case back-cross tests were made of both sexes though the number of progeny from back-cross F_1 females to double-recessive males is not large. In the experiments with fowls GOODALE made back-cross tests with the F_1 males

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but not with the F_1 females. No crossing over in the females, however, was noted in any of his original crosses.

In each of the cases referred to above, it will be recalled that crossing over is confined to the sex which is homozygous for the sex-determinants. Taken alone this suggests the possibility of some relation between the mechanism of crossing over and that of sex differentiation in these organisms. This suggestion, however, seems to be vitiated by the observations of NABOURS (1919) of crossing over in both sexes in the grouse locust, *Apotettix*, and by those of CASTLE (1916) and DUNN (1920) of crossing over in both sexes in rats and mice.

The phenomenon of crossing over in the sweet pea was observed by BATESON even before it was noted in insects, although it was not recognized as such. Here evidently crossing over takes place in both megaspore and microspore development and apparently with similar frequency, since the results obtained in F_2 in both "coupling" and "repulsion" crosses are not in accord with the expectancy from crossing over in the production of but one kind of gametes. Not only do the results of BATESON and his co-workers with sweet peas indicate that crossing over occurs in both anthers and ovaries but also that the linkage in each is practically the same. It is, of course, impossible to be certain of the latter point in the absence of adequate back-cross tests, since it is difficult to detect from F_2 data alone any difference in frequency of crossing over in the development of male and of female gametes unless this difference is of considerable magnitude. The results of these experiments have been interpreted by the English school upon the basis of the same gametic series in the pollen and in the eggs. Studies with two other hermaphroditic plants, *Primula* (GREGORY 1911 a, b, ALTENBURG 1916) and maize (LINDSTROM 1917) show that crossing over occurs both in microsporogenesis and megasporogenesis.

RELATIVE FREQUENCY OF CROSSING OVER IN MALES AND FEMALES

Previous investigations

Where crossing over occurs in both sexes in animals as in the grouse locust and in rats and mice, the question naturally arises as to whether there is any difference in the frequency of crossing over in the two sexes. NABOURS'S (1919) results indicated that crossing over in the male grouse locust is much less frequent than in the female but the number of individuals with which he dealt was too small definitely to establish this point. DUNN (1920) in reporting data obtained by CASTLE finds a slight though

statistically significant difference between linkages in male and in female rats. Crossing over in the female rat occurs with greater frequency than in the male.

So far as the writers are aware no comparison of frequency of crossing over in males and females has been made with dioecious plants. In hermaphroditic plants the situation is not quite the same as in dioecious plants or in animals where the sexes are more sharply separated. It is important, however, to determine whether there is any difference in the frequency of crossing over in megasporogenesis and in microsporogenesis in hermaphroditic plants.

ALTENBURG (1916), working with three linked factors in *Primula sinensis*, namely, short style, magenta flower, and green stigma, concluded from back-cross tests that crossing over occurred with about the same frequency in the anthers and the ovaries. GOWEN (1919), however, later reviewed ALTENBURG'S data and concluded that there was a significant difference between the linkage in pollen and in egg formation. The percent of non-crossover eggs was significantly larger than the percent of non-crossover pollen grains, while the percent of crossover eggs was significantly less than that of crossover pollen grains. According to BATESON (1921), GREGORY had noted the same thing in his crosses with *Primula* involving magenta color and short style. BATESON (1921) has recently reported that work on a larger scale with these two factors has confirmed the earlier observations—the linkage value in terms of the gametic series being, for the eggs 10.9:1 and for the pollen 6.4:1. He further states that a similar difference has been found for the linkage between green stigma and “reddish” stem, but curiously enough here the crossover percentage for the pollen is less than that for the eggs (linkage value for eggs, 29.8:1, for pollen, 41.7:1).

Although crossing over in both microsporogenesis and megasporogenesis in maize was recognized by COLLINS (1912) and BREGGER (1918) and specifically mentioned by LINDSTROM (1917) it remained for EYSTER (1921) to compare the frequency of crossing over in the development of the pollen and of the eggs. Plants heterozygous for sugary endosperm and tunicate ears were back-crossed to the double recessive and the sugary-tunicate linkage relation where the F_1 's were used as seed parents compared with that where the F_1 's were used as pollen parents. His data are as follows:

	<i>F</i> ₁ as seed parent	<i>F</i> ₁ as pollen parent
Non-crossovers	621	215
Crossovers	229	115
Total	850	330
Percent crossing over	26.94 ± 1.05	34.85 ± 1.69
Difference = 7.91 ± 1.99	Diff. P.E. = 3.97	P = 0.009

Although the numbers here are small, the difference in frequency of crossing over between pollen and eggs is perhaps significant. A difference of this magnitude would not be expected from chance alone more than once in about 140 such trials.

EYSTER (1921) has made a similar comparison with the $C c$ and $W_x w_x$ factor pairs for aleurone color and waxy endosperm using data from BREGGER. This comparison is as follows:

	<i>F₁ as seed parent</i>	<i>F₁ as pollen parent</i>
Non-crossovers.....	1445	832
Crossovers.....	501	327
Total.....	1946	1159
Percent crossing over.....	25.75 \pm 0.68	28.21 \pm 0.88
Difference = 2.46 \pm 1.11	Diff. P.E. = 2.2	P = 0.14

Here the difference in frequency of crossing over is smaller than with the $S_u s_u$ and $T_u t_u$ factor pairs and is probably not significant. Such a difference might occur by chance about once out of every 7 trials.

In neither EYSTER's nor BREGGER's experiments were the same F_1 plants used both as seed and as pollen parents. It has long been known that the percent of crossing over in *Drosophila* is variable and that it is influenced both by environmental and genetic factors (BRIDGES 1915, PLOUGH 1917, STURTEVANT 1917, GOWEN 1919). Moreover DETLEFSEN (1920) has shown that it is possible by selection to change the percent of crossing over in *Drosophila*. Linkage in maize is likewise variable as will be seen from the data presented later in this paper. It seemed desirable, therefore, to check the results of EYSTER and BREGGER by making experiments on a larger scale and by using each F_1 plant tested both as seed and as pollen parent.

Crossing over between $B b$ and $L_g l_g$ and between $C c$ and $S_h s_h$ in microsporogenesis and megasporogenesis

On account of the labor involved in handling large numbers in a study of this kind with maize, it is desirable to use characters that are readily distinguished in the seeds or at least in the seedlings. Accordingly the $B b$ factor pair for plant color and the $L_g l_g$ pair for liguleless leaves which had previously shown a crossover percentage of about 32 (EMERSON 1921) and the $C c$ factor pair for aleurone color and the $S_h s_h$ pair for shrunken endosperm with a crossover percentage of about 3 (HUTCHISON 1921) were chosen. The latter characters are easily recognized in the seeds and the liguleless condition in the seedlings by the time they are three weeks old.

The $B b$ factor pair, which differentiates purple, $A B P_1$, from dilute purple, $A b P_1$, and sun red, $A B p_1$, from dilute sun red, $A b p_1$, cannot ordinarily be determined in the seedling stage. But the presence of homozygous R^s , which causes the anthers and silks of purple and sun-red plants to be green without affecting the color of other plant parts of these types, insures wholly green plants at all stages in case of dilute sun-red and dilute purple types (EMERSON 1921). Stocks of $A B P_1 R^g L_g$ and $A b P_1 R^g l_g$ were prepared and the F_1 's, $B L_g R^g \cdot b l_g R^g$, back-crossed with the triple recessive, $b l_g R^{g.2}$. In such material, seedlings having B are highly colored red or purple, particularly when grown in infertile soil, while those having $b b$ are green, i.e., wholly devoid of red or purple pigment.

Tests involving $B b$ and $L_g l_g$

The data from back-crosses of 19 F_1 plants involving $B b$ and $L_g l_g$ are recorded in table 1. All these plants were closely related and all were grown in 1919. It will be noted that the percent of crossing over when the F_1 plants were used as seed parents of the back-crosses varied from 29.8 ± 2.6 to 42.9 ± 2.4 , the extreme difference being 13.1 ± 3.5 , a difference that is 3.7 times its probable error. Such a difference would be expected to occur by chance alone not more than once in about 80 trials and might well be regarded as significant. The two F_1 plants that exhibited this difference in percentage of crossing over when used as seed parents in the back-crosses gave 35.1 ± 1.5 and 40.7 ± 4.4 percent of crossing over, respectively, when used as pollen parents, a difference of 5.6 ± 4.6 percent. Such a difference might be expected to occur through the errors of random sampling about twice in five trials and cannot be regarded as significant. If the percentages of crossing over for these two plants when used as seed parents are compared with the average percentage for the entire lot when so used, 36.6 ± 0.5 , the respective deviations are 6.8 ± 2.6 and 6.3 ± 2.4 . Such deviations might be expected to occur by chance about once in thirteen and once in eleven trials, respectively, and can scarcely be regarded as significant.

Similarly, when the 19 F_1 plants were used as pollen parents in the back-crosses, the extreme percentages of crossing over were 30.8 ± 1.7 and 48.5 ± 3.3 , a difference of 17.7 ± 3.7 . Such a difference is 4.8 times its probable error and could not be expected to occur by chance more than once in over 800 trials, apparently a significant difference. When these percentages of crossing over are compared with the average percent for the entire lot of 19 F_1 plants when used as pollen parents of back-crosses, namely, with

² R^g , though dominant with respect to aleurone color, is recessive for plant color.

38.0 ± 0.5 , the deviations are 7.2 ± 1.8 and 10.5 ± 3.3 , respectively. Such deviations are 4 and 3.2 times their probable errors and could be expected to occur through errors of random sampling not more than once in 143 and 32 trials, respectively, and are probably significant. When used as seed parents, however, these two F_1 plants showed percentages of crossing over of 30.6 ± 2.3 and 37.8 ± 2.3 , respectively, a difference of 7.2 ± 3.3 . Such a difference might be expected to occur by chance about once in any seven trials and cannot be regarded as significant. It may be concluded, therefore, that if the extreme differences noted between the 19 F_1 plants were due to genetic diversity with respect to intensity of linkage, the difference did not appear in both megasporogenesis and microsporogenesis. In the absence of selection experiments, it cannot be said definitely that genetic differences existed in this lot of plants.

With respect to individual differences in crossover percentages when the 19 F_1 plants were used as seed and as pollen parents, it will be noted, (table 1) that in eight cases the percentage was greater in megasporogenesis than in microsporogenesis while in eleven cases the reverse was true. In nine cases the difference was less than its probable error, in six cases between one and two times, in two cases between two and three times, and in one case each, three and four times its probable error. In the latter two instances such differences might occur by chance once in about 23 and 143 trials, respectively. In the latter case at least the difference appears significant.

The average percentages of crossing over for the lot as a whole were 36.58 ± 0.50 and 38.01 ± 0.52 when the F_1 plants were used as seed and as pollen parents, respectively. The difference is 1.43 ± 0.72 percent, or 1.99 times its probable error. A difference of this magnitude might occur by chance twice in eleven such trials, P equaling 0.18, and would not ordinarily be regarded as statistically significant.

If the χ^2 method be employed in determining whether there is a significant difference in the percentages of crossing over between megasporogenesis and microsporogenesis, the results are not greatly different from those arrived at by using the probable-error method. In the statement given below, the observed frequencies of the plants of the four classes when the F_1 's were used as seed parents of the back-crosses is compared with the theoretical frequencies calculated from the average percent of crossing over when the F_1 's were used as pollen parents, namely, 38.0. Here there is somewhat better than one chance in five that the observed deviations are due to errors of random sampling, P equaling 0.21. The comparison is as follows:

	BL_g	Bl_g	bL_g	bl_g	Total
Observed.....	1337	762	795	1363	4257
Calculated.....	1320	809	809	1320	4258
Difference.....	+17	-47	-14	+43	-1

When, however, the observed distribution where the F_1 's were used as pollen parents is compared with the theoretical distribution calculated from the average percent of crossing over for F_1 's used as seed parents, namely, 36.6, a much poorer fit is obtained. In this case there is only one chance in about 35 that the observed deviations are due to the errors of random sampling, P equaling slightly less than 0.03. The comparison follows:

	BL_g	Bl_g	bL_g	bl_g	Total
Observed.....	1150	707	762	1246	3865
Calculated.....	1225	707	707	1225	3864
Difference.....	-75	0	+55	+21	+1

That this is a significant difference would probably not be questioned. It does not follow, however, that the difference is due to a differential rate of crossing over between microsporogenesis and megasporogenesis. The χ^2 method takes into account any irregularities of distribution whether due to differences in crossing over or to other causes. That the deviations observed in the above comparison are in considerable part due to irregularities arising from causes other than differences in frequency of crossing over in megaspore and in microspore development is evident from a comparison of the observed frequency distribution where the F_1 plants were used as pollen parents with the theoretical distribution calculated from the average percent of crossing over found from the same observed distribution. Here P equals slightly less than 0.12. The comparison follows:

	BL_g	Bl_g	bL_g	bl_g	Total
Observed.....	1150	707	762	1246	3865
Calculated.....	1198	734	734	1198	3864
Difference.....	-48	-27	+28	+48	+1

On the whole, therefore, it cannot be maintained that significant differences in percentage of crossing over between megasporogenesis and microsporogenesis have been observed in case of plant color and liguleless leaf.

Tests involving Cc and $S_h s_h$

The data from back-crosses of 35 F_1 plants involving Cc and $S_h s_h$ are recorded in tables 2, 3 and 4. Four of these plants, included in table 2, are the result of crossing a plant of the genetic constitution $\frac{C s_h}{C s_h}$ by one of the

constitution $\frac{c S_h}{c S_h}$. They, therefore, represent the "repulsion" series of these factors and have the constitution $\frac{C s_h}{c S_h}$. They were grown in 1919 and back-crossed with $\frac{c s_h}{c s_h}$ plants. From table 2 it will be noted that in two of these plants crossing over between $C c$ and $S_h s_h$ was more frequent in microsporogenesis than in megasporogenesis while in the other two plants the reverse was true. When the data from all of the four plants are summarized the percent of crossing over in megaspore development appears to be slightly greater than in microspore development. By applying the probable error as a measure, however, this difference is not statistically significant.

In table 3 are included data from 20 F_1 plants grown in 1920. These were of the same genetic constitution as regards $C c$ and $S_h s_h$ as the four plants included in table 2. Among these 20 F_1 plants two show a greater frequency of crossing over in microsporogenesis than in megasporogenesis while in the other eighteen, crossing over was more frequent in megaspore than in microspore development. A summary of the data in table 3 gives a percentage of crossing over in megaspore development in these plants of 2.98 ± 0.11 and in microspore development of 1.86 ± 0.15 . The difference is 1.12 ± 0.186 , the ratio of the difference to its probable error being 6.02. This difference is apparently significant. It would be expected by chance alone but once in something more than nineteen thousand trials.

It is unfortunate that more extensive data were not obtained in 1919, especially since the data for the $B b - L_g l_g$ relation considered above also showed no significant difference in the rate of crossing over in microsporogenesis and in megasporogenesis for that season. It is entirely possible that any difference in frequency of crossing over in megaspore and in microspore development in maize might be due to the influence of temperature or other external factors since the time at which microspore development occurs may not be exactly the same as that of megaspore development.

Table 4 represents the "coupling" series of the $C c S_h s_h$ factor pairs. The 11 F_1 plants included in this table resulted from crossing a plant of the genetic constitution $\frac{C S_h}{C S_h}$ by one of the constitution $\frac{c s_h}{c s_h}$. These F_1 plants, $\frac{C S_h}{c s_h}$, were grown in 1920 and back-crossed with the double recessive

$\frac{c S_h}{c S_h}$. It will be noted that in only one of these F_1 plants was the frequency of crossing over in microsporogenesis greater than in megasporogenesis while in all of the other 10 there was more crossing over in megaspore development than in microspore development. When the data from all of these 11 plants are summarized the percent of crossing over in megaspore development is 3.63 ± 0.22 and in microspore development 3.01 ± 0.32 . The difference is only 0.62 ± 0.39 percent or 1.59 times its probable error. A difference as large as this might occur by chance about twice in every seven trials, P equaling 0.28, and would ordinarily not be regarded as statistically significant.

If the data in tables 2, 3 and 4 be summarized the results are as follows

	<i>F₁'s as seed parents</i>	<i>F₁'s as pollen-parents</i>
Non-crossovers.....	14186	7253
Crossovers.....	459	159
Total.....	14645	7412
Percent crossing over.....	3.13 ± 0.092	2.15 ± 0.131

It will be noted that out of a total of 22,057 individuals observed, there were 618 crossovers. Considering both microspore and megaspore development together the average percent of crossing over for the entire lot is 2.8 ± 0.07 . In megaspore development alone the percent of crossing over was 3.13 ± 0.092 while in microspore development it was 2.15 ± 0.131 . The difference here is 0.98 ± 0.16 , apparently a significant one. A difference of this magnitude would not be expected to occur by chance alone more than about once in over twenty thousand such trials.

Objection has been made to using the probable-error method of comparison where there is so great a difference in the values of p and q as in this case. If the χ^2 method be employed the difference in frequency of crossing over between $C c$ and $S_h s_h$ in microspore and megaspore development appears even more strikingly significant. The distribution of the individuals of the various classes where the F_1 plants were used as seed parents in the back-crosses and where they were used as pollen parents, are compared below with the theoretical distribution, in each case calculated on the basis of the average observed percent of crossing over in megasporogenesis, 3.13 for all of the 35 F_1 plants.

F_1 as seed parent:

	$C S_h$	$C s_h$	$c S_h$	$c s_h$	Total
Observed.....	215	7130	7056	244	14645
Calculated.....	229	7093	7093	229	14644
Difference.....	-14	+37	-37	+15	+1

F ₁ as pollen parent:	<i>C S_h</i>	<i>C s_h</i>	<i>c S_h</i>	<i>c s_h</i>	Total
Observed.....	72	3794	3459	87	7412
Calculated.....	116	3590	3590	116	7412
Difference.....	-44	+204	-131	-29	0

There is a little better than an even chance that the differences between the observed and expected distributions where the F₁ plants were used as seed parents of the back-crosses may be due to errors of random sampling, $P = 0.53$. Where the F₁'s were used as pollen parents the observed distribution deviates so markedly from that expected on the basis of the same frequency of crossing over in microspore as in megaspore development, 3.13 percent, that the difference cannot be ascribed to chance,— $\chi^2 = 40.3$. It would seem, therefore, that there is a significant difference in the frequency of crossing over in megaspore and microspore development so far as the *C c* and *S_h s_h* factors are concerned. Such a difference is further indicated by the fact that out of 35 F₁ plants tested 30, or more than 85 percent, showed a greater frequency of crossing over in megasporogenesis than in microsporogenesis, while in only five was the reverse true.

DISCUSSION AND CONCLUSIONS

The only data available for a comparison of the relative frequency of crossing over in microsporogenesis and megasporogenesis in hermaphroditic plants have been obtained from *Primula sinensis* and *Zea mays*. From published accounts it appears that there is a somewhat greater percentage of crossing over in microsporogenesis than in megasporogenesis in *Primula* when short style and magenta flower color are concerned, but that the reverse is true in the case of green stigma and reddish stem. With maize a somewhat greater percentage of crossing over has been reported in microsporogenesis than in megasporogenesis between colored aleurone and waxy endosperm and between tunicate ear and sugary endosperm, but in the former the difference was not significant. The data reported in the present account show a slightly greater percent of crossing over in microspore than in megaspore formation where plant color and liguleless leaf are involved and the reverse relation where the characters concerned are aleurone color and shrunken endosperm. The difference in the former case, however, is probably not a significant one.

In the tests reported here, two possible sources of error have been eliminated. (1) The numbers of individuals observed—a total of 8122 for plant color and liguleless leaf and 22,057 for aleurone color and shrunken endosperm—were sufficient, it is thought, to give reliable indications. (2) Any

genetic difference in linkage intensity that may have existed between the several F_1 plants tested was rendered negligible by the use of each F_1 plant both as pollen and as seed parent in back-crosses with double recessives.

Certain other possible sources of error were not guarded against. (1) It is possible that temperature or other environmental conditions may influence the percent of crossing over in maize as has been shown to be true for *Drosophila*. While this difficulty was avoided in part by the use of each F_1 plant as both seed and pollen parent of back-crosses, no account was taken of the possibility that microsporogenesis and megasporogenesis may occur at somewhat different times in the development of the maize plant and consequently that the relative frequency of crossing over in the two cases may be influenced by changes in temperature or other atmospheric conditions. (2) The relative frequency of double crossing over in microspore and megaspore formation and its possible bearing upon the observed percent of crossing over could not be determined with the material employed. The factor pairs $B b$ and $L_g l_g$ are doubtless sufficiently far apart on the chromosomes,—about 37 units,—to allow of considerable double crossing over between them. The matter cannot be determined until a suitable gene is found between $B b$ and $L_g l_g$. (3) The factor pairs $C c$ and $S_h s_h$ are so close together on the chromosome,—about 3 units apart—that double crossing over could hardly be a disturbing factor. This circumstance, however, makes the probable error, as ordinarily calculated, of questionable value in determining the probable significance of differences in percentages of crossing over when $C c$ and $S_h s_h$ are concerned. When q is relatively very small and p very large, the probable error is commonly considered to be less reliable than when p and q are more nearly equal.

In conclusion it can be said that the results so far reported on crossing over in hermaphroditic plants seem to warrant the following deductions:

1. Crossing over occurs both in microsporogenesis and megasporogenesis.
2. The relative frequency of crossing over is not greatly different in megaspore and microspore development.
3. In some cases the observed differences are apparently significant but they are also somewhat contradictory. They may possibly be due to disturbing conditions, such as temperature effects, rather than to inherent differences in the mechanism of crossing over, although it is conceivable that one pair of chromosomes might give results quite different from those of another pair even in the same individual plant.

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TABLE 1

Crossing over between B and L_0 as shown by the back-crosses,

$$\frac{B L_q}{b l_q} \times \frac{b l_q}{b l_q} \text{ and } \frac{B L_q}{b l_q} \times \frac{B L_q}{b l_q}, 1919.$$

PEDIGREE NUMBERS OF F ₁ PLANTS	F ₁ PLANTS AS SEED PARENT						F ₁ PLANTS AS POLLEN PARENT						DIFFERENCE	Diff. P.E.				
	Number of back-cross seedlings						Number of back-cross seedlings											
	Crossover percentage						Crossover percentage											
	$B L_g$	$b L_g$	$b l_g$	Total	Cross- overs		$B L_g$	$b L_g$	$b l_g$	Total	Cross- overs							
E 9565 — 2	30	19	14	35	98	33	33.7	± 3.3*	15	14	14	27	70	28	40.0	± 3.9	+6.3 ± 5.1	1.2
3	73	28	31	61	193	59	30.6	± 2.3	128	64	50	128	370	114	30.8	± 1.7	+0.2 ± 2.9	0.1
5	73	60	44	74	251	104	41.4	± 2.1	9	3	5	5	22	8	36.4	± 7.0	-5.0 ± 7.3	0.7
10	74	37	50	76	237	87	36.7	± 2.1	20	15	19	26	80	34	42.5	± 3.6	+5.8 ± 4.2	1.4
11	71	38	48	105	262	86	32.8	± 2.0	154	99	105	168	526	204	38.8	± 1.4	+6.0 ± 2.4	2.5
16	110	42	50	88	290	92	31.7	± 1.9	26	21	25	36	108	46	42.6	± 3.1	+10.9 ± 3.6	3.0
17	54	25	53	50	182	78	42.9	± 2.4	17	8	14	15	54	22	40.7	± 4.4	-2.2 ± 5.0	0.4
20	74	51	44	70	239	95	39.7	± 2.1	53	41	44	80	218	85	39.0	± 2.2	-0.7 ± 3.0	0.2
23	83	45	57	101	286	102	35.7	± 1.9	26	19	14	41	100	33	33.0	± 3.3	-2.7 ± 3.8	0.7
24	56	27	31	55	169	58	34.3	± 2.5	46	30	38	57	171	68	39.8	± 2.5	+5.5 ± 3.5	1.6
26	61	43	41	57	202	84	41.6	± 2.3	11	7	11	11	40	18	45.0	± 5.2	+3.4 ± 5.7	0.6
27	62	38	53	60	213	91	42.7	± 2.2	101	63	79	105	348	142	40.8	± 1.7	-1.9 ± 2.8	0.7
28	97	63	40	92	292	103	35.3	± 1.9	49	41	37	69	196	78	39.8	± 2.3	+4.5 ± 3.0	1.5
30	61	37	37	61	196	74	37.8	± 2.3	25	23	24	25	97	47	48.5	± 3.3	+10.7 ± 4.0	2.7
35	78	47	41	78	244	88	36.1	± 2.1	49	26	25	48	148	51	34.5	± 2.7	-1.6 ± 3.4	0.5
36	80	69	53	95	297	122	41.1	± 1.9	84	48	54	70	256	102	39.8	± 2.0	-1.3 ± 2.8	0.5
E 9566 — 1	81	42	58	93	274	100	36.5	± 2.0	100	47	43	92	282	90	31.9	± 1.9	-4.6 ± 2.8	1.6
7	56	24	24	57	161	48	29.8	± 2.6	159	80	85	146	470	165	35.1	± 1.5	+5.3 ± 3.0	1.8
8	63	27	26	55	171	53	31.0	± 2.5	78	58	76	97	309	134	43.4	± 1.9	+12.4 ± 3.1	4.0
Total, 19 tests	1337	762	795	1363	4257	1557	36.58	± 0.50	1150	707	762	1246	3865	1469	38.01	± 0.52	+1.43 ± 0.72	1.99

* Probable errors are determined from the formula $0.6744898 \sqrt{\frac{p}{n}}$, in which n is the number of individuals, p is the average percentage of crossing over, namely, 0.373 for table 1 and 0.028 for tables 2, 3 and 4, and p is 1- q . Values of $\frac{0.6744898}{\sqrt{n}}$ are taken from Gibson's tables (Biometrika 4: 385-393, 1905-1906).

TABLE 3
Crossing over between C and S_h as shown by the back-crosses,

$$\frac{C S_h}{c S_h} \times \frac{c S_h}{c S_h} \text{ and } \frac{c S_h}{c S_h} \times \frac{C S_h}{c S_h}, 1920.$$

PEDIGREE NUMBERS OF F ₁ PLANTS	F ₁ PLANTS AS SEED PARENT							F ₁ PLANTS AS POLLEN PARENT							DIFFERENCE	
	Number of back-cross seeds						Crossover percentage	Number of back-cross seeds						Crossover percentage		
	C S _h	c S _h	C s _h	c s _h	Total	Cross-overs		C S _h	c S _h	C s _h	c s _h	Total	Cross-overs			
H 205 — 1	11	433	465	14	923	25	2.7	2	102	74	1	179	3	1.7	-1.0	
6	2	238	210	3	453	5	1.1	1	138	107	2	248	3	1.2	+0.1	
8	6	324	285	13	628	19	3.0	2	146	143	3	294	5	1.7	-1.3	
15	6	171	168	8	353	14	4.0	2	134	105	3	244	5	2.0	-2.0	
16	24	342	347	11	724	35	4.8	4	171	132	2	309	6	1.9	-2.9	
18	8	400	443	11	862	19	2.2	0	71	74	1	146	1	0.7	-1.5	
20	7	168	219	8	402	15	3.7	2	99	97	1	199	3	1.5	-2.2	
21	4	157	155	4	320	8	2.5	2	148	124	1	275	3	1.1	-1.4	
22	4	212	220	7	443	11	2.5	0	106	100	2	208	2	1.0	-1.5	
23	7	248	223	8	486	15	3.1	2	314	223	8	547	10	1.8	-1.3	
24	7	205	224	9	445	16	3.6	1	80	91	2	174	3	1.7	-1.9	
H 206 — 3	19	423	421	9	872	28	3.2	1	54	54	0	109	1	0.9	-2.3	
	5	230	225	8	468	13	2.8	3	157	151	4	315	7	2.2	-0.6	
	4	146	145	6	301	10	3.3	1	34	29	0	64	1	1.6	-1.7	
	8	221	205	9	443	17	3.8	5	321	276	10	612	15	2.5	-1.3	
	15	10	261	255	8	534	18	3.4	3	116	111	2	232	5	2.2	-1.2
21	1	207	216	10	434	11	2.5	5	316	270	9	600	14	2.3	-0.2	
22	3	376	354	9	742	12	1.6	4	160	145	5	314	9	2.9	+1.3	
24	3	116	103	4	226	7	3.1	4	136	128	0	268	4	1.5	-1.6	
26	7	260	213	9	489	16	3.3	1	156	142	4	303	5	1.7	-1.6	
27																
Total.....	146	5138	5096	168	10548	314	2.98 ± 0.11	45	2959	2576	60	5640	105	1.86 ± 0.15	-1.12 ± 0.186	

