CHROMOSOMAL INTERCHANGES IN MAIZE

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Received February 19, 1934

INTRODUCTION

Chromosomal interchanges, or reciprocal translocations, in maize are of primary interest because of the opportunities they offer for the study of chromosome behavior and crossing over. The great volume of work which has been done on crossing over and on translocations in *Drosophila* has yielded an abundance of statistical data on crossing over and chromosome distribution. For this type of work *Drosophila* is admirably adapted, and great advances in the statistical analysis of crossing over not only have been made but continue still to be made. But for the cytological study of the chromosomal basis of crossing over, *Drosophila* is less well adapted. Maize, on the other hand, while not so well fitted for crossing over statistics, has the exceptional merit of being excellent material for the cytological study of the earlier stages of meiosis. This presents the opportunity of making studies on the chromosome mechanism in which crossing over statistics and cytological observations are intimately correlated. A beginning has already been made as for example in the studies on the behavior of ring fragments (McCLINTOCK 1932b) and on crossing over in the ninth chromosome (CREIGHTON and McCLINTOCK 1931), in interchange T8-9 (BURNHAM 1934c), in maize-teosinte hybrids (BEADLE 1932a) and in trisomics (RHOADES 1933a). But in order to take full advantage of the opportunities presented, it is first necessary to build up a fair knowledge of such items as the location of given genes on the observed chromosome thread, and the linkage relationships of conspicuous markers on the chromosomes; also to make available means of marking or of controlling desired portions of chromosomes.

For building up the required groundwork chromosomal interchanges are of especial value. The synaptic pairing of the interchanged chromosomes with their normal homologs may be observed at mid-prophase when the chromosomes are spun out as long thin threads with their finer structures most clearly visible and with the homologous threads closely conjugated. This makes it possible to determine rather accurately the correspondence of loci on the linkage maps with visible points on the chromosomes themselves, and prepares the way for direct observation of the stages immediately following crossing over. Interchanges are also of great value as means of marking or controlling chromosomes or parts of chromosomes which are being studied.

The need of a combined genetical and cytological study of an extensive series of interchanges in maize led the writer to assemble a large number of cultures from partially sterile plants, mostly from X-ray treatment. Those which gave consistent rings or chains of chromosomes at diakinesis have been subjected to tests for the chromosomes involved in the interchange. The purpose of this paper is to summarize these tests and to establish the chromosome constitution of each of the interchanges. Studies are in progress on the prophase cytology and linkage relationships. Reports on these studies will follow as the studies are completed.

The writer wishes to acknowledge his indebtedness to Dr. C. R. BURNHAM for the use of his unpublished interchanges as testers, and to Miss GERTRUDE GEERTSEN, laboratory technician, whose skill and industry have made possible the large number of microscopic preparations required.

GENERAL CHARACTERISTICS OF INTERCHANGES IN MAIZE

The behavior of interchanges may be illustrated by a brief review of some of the earlier reported cases. Semisterile-1 (T1-2a), reported by BRINK (1927) and later studied by BRINK and BURNHAM (1929), BRINK and COOPER (1931, 1932a) and COOPER and BRINK (1931) is a typical example. The chromosomes involved are No. 1 and No. 2. The semisterile plants are heterozygous for the interchange. When selfed they give fifty percent of semisterile plants, and fifty percent of normals. But the normals are of two types, (1) ordinary or standard normals having only normal chromosomes and giving fully fertile plants in outcrosses to standard stocks, and (2) homozygous interchanges (X-normals) having both interchanged chromosomes homozygous and giving only semisterile plants in outcrosses to standard stocks. These homozygous interchange plants are normal, fully fertile plants not visibly different from the ordinary standard normals.

In the heterozygous interchange (semisterile) plants, the distribution of the interchange chromosomes and the corresponding normal chromosomes is such that one-half of the spores receive a normal and an interchange chromosome, one-fourth receive both normal, and one-fourth both interchange chromosomes. The two classes have all parts of both chromosomes represented and are viable. The spores receiving a normal and an interchange chromosome are deficient for a portion of one chromosome whereas a portion of the other is duplicated. These fail to form normal pollen grains and appear as empty or starch-free abortive grains. The elimination of these types of spores makes the interchange appear to be transmitted as a single unit. Crossing over may occur between an interchange chromosome and its normal homolog at any point. The interchange may thus be followed in linkage tests by means of the semisterility, which be-

haves in outcrosses like a dominant gene at the locus of the interchange in both linkage maps.

Cytological examination shows a cross-shaped figure at mid-prophase with a change of partners at the cross or point of interchange. At all points homologs are paired as in normal chromosomes. The chromosomes begin separating at late pachytene or diplotene, continuing separation until at diakinesis only the ends remain joined. By this stage the chromosomes have also shortened and thickened, giving the typical ring configurations characteristic of interchanges. At anaphase these rings separate or are pulled apart, two chromosomes going normally to each pole.

Semisterile-2 (T8-9a) has been studied in more detail by BURNHAM (1930, 1934c), McCLINTOCK (1930, 1931a) and CREIGHTON and McCLINTOCK (1931). It differs from semisterile-1 in showing somewhat more pollen sterility (59 percent). The chromosome distribution is a little more irregular, figures often showing three of the chromosomes from the ring going to one pole and one to the other. The ring occasionally opens into a chain of four chromosomes at diakinesis.

A low sterile described by BURNHAM (1932a) differs in that it forms chains consistently but never rings. The interchange has taken place in the satellite of chromosome 6. The point of interchange was within one or two chromomeres of the end of the chromosome. The interchanged end of the satellite did not show pairing with the normal satellite. This gave a T-shaped pachytene figure, opening out to form a chain of diakinesis. One of the duplicate-deficient classes of spores lacked only a few chromomeres of having all parts of the chromosomes represented and did not form visibly bad pollen. A low sterile not involving chromosome 6 has been described by BRINK and COOPER (1932c).

A more extreme case has been described by CLARKE and ANDERSON (1934) in which chains are found in only a portion of the diakinesis figures, the majority showing two slightly unequal "pairs." Here the interchange is also in the satellite of chromosome 6 and likewise near the end of chromosome 3. The visible sterility is again about 25 percent.

Two interchanges reported by BURNHAM (1932b, 1934a) show a great amount of non-homologous pairing (see also McCLINTOCK 1932a, 1933). Such non-homologous pairing is rather frequent in many of the interchanges and is generally associated with a reduction of crossing over.

In crosses with teosinte (*Euchlaena mexicana*) where no crossing over takes place in the short arm of chromosome 9, semisterile-2 (T8-9a) seldom shows ring configuration. Most of the diakinesis and metaphase figures show either a chain of four or two unequal "pairs" (BEADLE 1932a).

The above types show the range of variation among the interchanges

studied. A complete list with citations to literature is included in the catalog of interchanges on page 77.

TERMINOLOGY

The large number of interchanges now being investigated in maize makes it convenient to apply a uniform set of names or symbols for them. The capital letter T will be used as a general designation of interchanges. It will be used in the same way that we ordinarily use the gene symbol for a dominant gene. The specific interchange will be designated by numbers which indicate the chromosomes involved. These may be followed by the letters a, b, c, etc. when dealing with more than one interchange between the same chromosomes.

The ten chromosomes of maize are numbered from the longest to the shortest. The following list gives the linkage group associated with each chromosome.

1. <i>P br f bm₂</i>	5. <i>bm₁ pr v₂</i>	8. <i>j</i>
2. <i>lg B sk v₄</i>	6. <i>Y Pl sm</i>	9. <i>yg₂ c sh wx</i>
3. <i>a na ts₄</i>	7. <i>gl₁ ra</i>	10. <i>R g nl</i>
4. <i>su Tu gl₃</i>		

SOURCES OF MATERIAL

Most of the interchanges reported in this paper came from four lots of mature seed submitted to X-rays. Details of treatment dosage and sources of interchanges are given in the appendix. The seed was grown and the plants selfed. Ears which did not look well-filled were selected for further study. The plants from these ears were examined for pollen sterility. Each culture giving partially sterile plants was given an index number under which it appears in table 1 and in the appendix.

A few additional interchanges were obtained from other sources. Of those listed in table 1, No. 52 was obtained by Dr. L. J. STADLER, also from X-ray treatment; Nos. 33, 122, and 133 were picked up from untreated stocks; and No. 129 was obtained by Dr. G. W. BEADLE from his "sticky chromosome" line (BEADLE 1932b). The writer is indebted to Dr. STADLER and Dr. BEADLE for the two semisterile lines obtained from them.

METHOD OF IDENTIFICATION OF CHROMOSOMES

The new interchanges were crossed with a series of tester stocks each homozygous for a known interchange. The F₁ plants were examined for chromosome configuration at diakinesis. When two interchanges are combined in heterozygous form, there will be obtained a ring or group of six chromosomes at diakinesis if one chromosome is in common. If the two interchanges involve no common chromosome, two separate rings of four

will be obtained. Eight interchanges were chosen from among the limited number available at the time for use as testers. They were available in homozygous form or could be gotten in homozygous condition very quickly.

T1-2 Semisterile-1	BRINK 1927
T8-9 Semisterile-2	BURNHAM 1930
T1-7 Semisterile-3	BURNHAM 1930
T4-8 Culture 6467	ANDERSON and CLOKEY 1934
T3-9 Culture 6465	ANDERSON and CLOKEY 1934
T5-7 Semisterile-6	BURNHAM unpublished
T4-5 Culture 6472	ANDERSON and CLOKEY 1934
T2-3 Semisterile-7	BURNHAM unpublished

The above tests furnish ready means of identifying all chromosomes except 6 and 10. Chromosome 6, the satellited chromosome, is attached to the nucleolus. The attachment of the ring to the nucleolus served to identify chromosome 6 as one member of the interchange. Chromosome 10 was determined by elimination and also by examination of the free pairs at diakinesis. This was usually done in the intercrossoes with T8-9 where the two next smallest chromosomes were included in the ring. The small size and rather characteristic appearance of chromosome 10 served to identify it.

In the course of further work on these interchanges, more detailed studies are made at the mid-prophase or pachytene stage. At this stage it is possible to recognize each of the chromosomes. These prophase studies thus serve to verify the chromosome identifications. Likewise the identifications are verified when genetic data are obtained showing linkage of the semisterility with genes of the corresponding linkage groups.

DATA

Table 1 presents a summary of the data from diakinesis examinations of the crosses of the new interchanges with the testers. The chromosome configurations or groupings are indicated by "4+4" for two rings or chains of four chromosomes each plus six pairs, and by "6" for a ring or chain of six chromosomes plus seven pairs. Under the column marked "satellite" a plus sign indicates that the satellited chromosome (No. 6) is included in the ring as shown by the attachment of the ring to the nucleolus. Under "No. 10" a plus sign indicates that chromosome 10 is involved in the interchange, as determined by examination of the free chromosomes, usually in crosses with tester T8-9. In each case this can also be shown by elimination. Where the chromosomes involved have also been identified by means of mid-prophase studies or by means of linkage tests, the chromosomes so identified are listed in the last two columns.

TABLE 1

Chromosome configurations in crosses of new interchanges with known interchange testers.

INDEX NO.	TESTER								SATEL- LITE	NO. 10	CHROMO-	IDENTI-	IDENTI-
	T1-2	T8-9	T1-7	T4-8	T3-9	T5-7	T4-5	T2-3			SOMES IN- VOLVED	FIED BY LINK- AGE	FIED CY- TOLOGI- CALLY
11	6	4+4		4+4		6	4+4	4+4	—		1-7	1,7	
12	6	4+4	6	4+4	6		4+4	6	—		1-3	1,3	
13	4+4	6	4+4	6	6		6		—		4-9	9	4,9
14	4+4	4+4	4+4	6	4+4	6			—		4-5	4,5	
15	4+4	4+4	4+4	4+4			4+4	6	—	+	3-10	3,10	
16	4+4	6	4+4	6	4+4	4+4	4+4	4+4	—	+	8-10	8,10	8,10
17	6	4+4	6	4+4	4+4		4+4	6	—		2-7	2	2,7
18	4+4	4+4	4+4	4+4	6	4+4	4+4		—	+	3-10	3,10	
19	6	4+4	4+4	4+4	6	4+4	4+4		—		2-3	2	2,3
20	4+4	4+4	4+4	4+4		6	6	4+4	—	+	5-10	5	
21	4+4	6	4+4	6	4+4	6	6	4+4	—		5-8	5,8	
22	4+4	6	4+4	6	4+4	4+4	4+4	4+4	—	+	8-10	8,10	
23	4+4	4+4		4+4			4+4	4+4	+	+	6-10	6,10	6,10
24	6	4+4	6	4+4		6	6	4+4	—		1-5		
25	6	4+4	6	4+4	4+4	6	4+4	6	—		2-7	2,7	
26	4+4	4+4		4+4		4+4			—	+	3-10		
27	4+4	4+4	6	4+4	6		4+4	6	—		3-7	3,7	
28	4+4	4+4		4+4		6	6	6	—		3-5	3,5	
29		4+4	6	4+4	4+4	4+4		6	—		1-2		
30	4+4	4+4	4+4	4+4		4+4	4+4		+		3-6	6	
31	4+4	6		4+4			4+4	6	—		3-9	3,9	
32	6	4+4	6	4+4		6		4+4	—		1-5	5	
33	6		4+4	4+4			4+4	6	—		2-6	2,6	2,6
35	6	6	6	4+4	6	4+4	4+4	4+4	—		1-9	9	
36	4+4	4+4	4+4	6	4+4	4+4			+		4-6		
37	4+4			6		4+4	6		+		4-6	4,6	4,6
38		6		6	6	4+4	4+4	6	—		3-8		
40	6	4+4	6	4+4	4+4	6	6	4+4	—		1-5		
41	6	4+4		4+4	4+4	4+4	4+4	6	+		2-6	6	
42	6	4+4		6			6	6	—		2-4	2	
43	6	6	6	4+4	6	4+4			—		1-9		
52	4+4	4+4	4+4	4+4	6	6	6		—		3-5	3	
58	6	4+4	6	4+4	6	4+4			—		1-3	3	
61	4+4	4+4	4+4	6	4+4		6	4+4	—	+	4-10		
62	4+4	6	4+4	6	4+4	4+4	4+4	4+4	—	+	8-10	8,10	
64	6	4+4	6	4+4	4+4	4+4	4+4		—	+	1-10	1	
66	4+4	4+4	4+4	6	4+4	6		4+4	—		4-5	4,5	
69	6	4+4	6	4+4	4+4	6	4+4	6	—		2-7	2,7	2,7
70	4+4	4+4	4+4	6	4+4	4+4	6		+		4-6	4,6	4,6
73	6	4+4		4+4	4+4	6	4+4	4+4	—		1-7		
74	6	4+4	6	4+4		4+4	4+4	6	—		1-3		
75	6	4+4	4+4		4+4	6			—		2-5	2	
76	6	6	4+4	4+4			4+4		—		2-9	9	
77	6	6	6	4+4	6				—		1-9		
78	6	6	4+4		4+4		4+4	6	—		2-8		
79	4+4	6	4+4	6	6	4+4	6	4+4	—		4-9		
80	6	4+4	4+4	4+4	4+4	4+4			+		2-6		

TABLE 1 (Continued)

Chromosome configurations in crosses of new interchanges with known interchange testers.

INDEX NO.	TESTER								SATEL- LITE	NO. 10	CHROMO-	IDENTI-	IDENTI-
	T1-2	T8-9	T1-7	T4-8	T3-9	T5-7	T4-5	T2-3			SOMES IN- VOLVED	FIED BY LINK- AGE	FIED CY- TOLOGI- CALLY
83	4+4		4+4	6	6		4+4	4+4	—		8-9		
84	4+4	6		6	4+4	4+4		4+4	—	+	8-10	8	
85	4+4	4+4	4+4		4+4		6		—	+	4-10	10	
87	6	4+4	6	4+4	6	4+4			—		1-3		
88		4+4	4+4	6	4+4	4+4	6	6	—		2-4		
90	6	4+4	4+4	4+4	6	4+4	4+4		—		2-3	3	
94	4+4	6	4+4	4+4	6	4+4			—	+	9-10	9, 10	
101	6	4+4	4+4	6	4+4	4+4	6	6	—		2-4		
103	6	4+4		4+4	4+4	6	4+4	4+4	—		1-7		1, 7
111	4+4	6	4+4	6	4+4				+		6-8	6, 8	6, 8
118	6	4+4	4+4	4+4	6	4+4	4+4		—		2-3		
119	4+4	6	4+4	4+4	6				+		6-9	6, 9	6, 9
122	6	4+4	6	6	4+4	4+4	6	4+4	—		1-4		
129	6	4+4	4+4	6	4+4		6	6	—		2-4	2, 4	
133		4+4	4+4	4+4	6	4+4		6	—	+	3-10		
136	4+4	4+4	6	4+4	4+4		6	4+4	—		5-7		
137	4+4	4+4	6	6	4+4	6	6	4+4	—		4-7		

In addition to the above interchanges there were obtained from the X-rayed cultures a number of partial sterile lines which did not consistently show rings or chains of chromosomes at diakinesis. These range from fairly good semisteriles to low steriles and to types with part of the pollen small and often incompletely filled. One such culture has been studied (CLARKE and ANDERSON 1934) and shown to be an interchange involving the satellite of chromosome 6 and the end of the long arm of chromosome 3. It is probable that many of the others are also interchanges occurring so near the ends of the chromosomes that a chromosome ring is either not formed or is so loosely held together that it most frequently separates into two "pairs."

CATALOG OF KNOWN INTERCHANGES IN MAIZE

The following list is arranged in the order of the chromosomes involved. It has been aimed to include as far as possible all interchanges where the chromosomes involved are known. In assigning the order of interchanges involving the same chromosome combinations, priority has in general been followed for previously published cases. Within the writer's own material an attempt has been made to list them in their order of convenience or usefulness, with clear-cut semisteriles preceding low steriles. References are given for all except those described in this paper. Some incidental information on these interchanges may be found in papers on

other subjects (BRINK 1932, BRINK and COOPER 1932b, BURNHAM 1934b). A number of papers dealing with the production (SPRAGUE 1930, STADLER 1931, BEADLE 1932b) or cytology (McCLINTOCK 1931b, 1933) of chromosome aberrations mention interchanges not included in this catalog.

SYMBOL	OLD NAME OR NUMBER	REFERENCES
T1-2a	Semisterile-1	BRINK 1927, BRINK and BURNHAM 1929, BRINK and COOPER 1931, 1932a, COOPER and BRINK 1931
T1-2b	29	
T1-3a	12	
T1-3b	58	
T1-3c	74	
T1-3d	87	
T1-4	122	
T1-5a	24	
T1-5b	32	
T1-5c	40	
T1-6a	Semisterile-5	COOPER and BRINK 1931, BRINK and COOPER 1932a
T1-6b	Low sterile	BURNHAM 1932a
T1-7a	Semisterile-3	BURNHAM 1930
T1-7b	11	
T1-7c	73	
T1-7d	103	
T1-9a	35	
T1-9b	77	
T1-9c	43	
T1-10a	6466	ANDERSON and CLOKEY 1934
T1-10b	64	
T2-3a	Semisterile-7	BURNHAM, unpublished
T2-3b	19	
T2-3c	90	
T2-3d	118	
T2-4a	42	
T2-4b	88	
T2-4c	101	
T2-4d	129	
T2-5a	Semisterile-4	RHOADES 1931, 1933
T2-5b	75	
T2-6a	—	BURNHAM 1932b
T2-6b	6471	ANDERSON and CLOKEY 1934
T2-6c	33	
T2-6d	41	
T2-6e	80	
T2-7a	17	
T2-7b	25	
T2-7c	69	
T2-8	78	
T2-9a	6460	ANDERSON and CLOKEY 1934
T2-9b	76	
T2-10	6473	ANDERSON and CLOKEY 1934

SYMBOL	OLD NAME OR NUMBER	REFERENCES
T3-5a	6468	ANDERSON and CLOKEY 1934
T3-5b	28	
T3-5c	52	
T3-6a	30	
T3-6b	125	CLARKE and ANDERSON 1934
T3-7a	6474	ANDERSON and CLOKEY 1934
T3-7b	27	
T3-8a	6477	ANDERSON and CLOKEY 1934
T3-8b	38	
T3-9a	6465	ANDERSON and CLOKEY 1934
T3-9b	31	
T3-10a	15	
T3-10b	18	
T3-10c	133	
T3-10d	26	
T4-5a	6472	ANDERSON and CLOKEY 1934
T4-5b	6462	ANDERSON and CLOKEY 1934
T4-5c	14	
T4-5d	66	
T4-6a	37	
T4-6b	70	
T4-6c	36	
T4-7	137	
T4-8	6467	ANDERSON and CLOKEY 1934
T4-9a	13	
T4-9b	79	
T4-10a	61	
T4-10b	85	
T5-6	6452	ANDERSON and CLOKEY 1934
T5-7a	Semisterile-6	BURNHAM unpublished
T5-7b	6475	ANDERSON and CLOKEY 1934
T5-7c	136	
T5-8	21	
T5-9	—	BURNHAM 1934a
T5-10	20	
T6-8	111	
T6-9a	6470	ANDERSON and CLOKEY, 1934
T6-9b	119	ANDERSON 1934
T6-10	23	
T8-9a	Semisterile-2	BURNHAM 1930, 1934c, McCLINTOCK 1930, 1931a, CREIGHTON and McCLINTOCK 1931, BEADLE 1932a
T8-9b	83	
T8-10a	16	
T8-10b	22	
T8-10c	62	
T8-10d	84	
T9-10	94	
—	m-sterile	BRINK and COOPER 1932c

DISTRIBUTION OF INTERCHANGES

The interchanges following X-ray treatment reported by ANDERSON and CLOKEY (1934) and the ones reported in this paper form a fairly random sample of those which consistently form rings or chains at diakinesis. They may be used for comparing the frequency with which each chromosome becomes involved in interchanges. These frequencies are summarized in table 2. Each chromosome is well represented. The frequencies are in

TABLE 2
Comparison of frequencies of interchanges after X-ray in the different chromosomes.

CHROMOSOME	ANDERSON	STADLER	TOTAL	EXPECTED
1	15	1	16	21.0
2	15	3	18	17.1
3	15	5	20	16.6
4	13	3	16	16.1
5	11	5	16	16.1
6	10	2	12	13.1
7	9	2	11	13.1
8	9	2	11	12.9
9	10	3	13	11.6
10	13	2	15	9.5

reasonably close proportion to the lengths of the different chromosomes. The probability of a deviation as great as that observed is about 0.7, showing a close fit. Most of the deviation is due to chromosome 1 being low and chromosome 10 being high.

ISOLATION AND VIABILITY OF HOMOZYGOUS INTERCHANGES

In order to obtain stocks homozygous for each of the interchanges, the method used by BRINK and BURNHAM (1929) has been followed. The heterozygous interchange (semisterile) plants are self-pollinated or crossed to other semisterile plants from the same source. One half of the progeny obtained are semisterile, the other half, normal. The normals are of two types, ordinary normals and homozygous interchanges. These are not distinguishable in appearance but may be distinguished by outcrossing to known standard stocks. Each plant tested is also selfed or crossed to a related semisterile. In practice it was found useful to cross to a semisterile in an outcross family in order to avoid too much inbreeding.

Of the 64 interchanges reported in this paper 39 have already been obtained in homozygous condition as have also all but one of the 14 reported by ANDERSON and CLOKEY (1934). The balance are cases where tests have not yet been made, or only a few plants have been tested. All those adequately tested have been shown to be viable as homozygotes. This is in

marked contrast to the results obtained in *Drosophila*. In maize the elimination for chromosome unbalance is far more stringent in the haploid gametophyte generation than in the diploid sporophyte. This is shown by the failure of deficiencies from X-rays to be transmitted beyond the immediate generation in which they appear (STADLER 1931, McCLINTOCK 1931b) and also by the early elimination of the duplicate-deficient spores from the semisteriles. The elimination is more severe in the male gametophyte than in the female as shown by the differential transmission of trisomic types in reciprocal crosses. It is anticipated that a small proportion of interchanges will be transmitted less freely through the male than through the female. A few of those listed have indicated such behavior but the data are not as yet sufficient.

The interchanges thus far described in maize have been rather simple types, relatively free from complications and not involving more than two chromosomes. The contrast with *Drosophila* translocations is quite marked. This serves to emphasize the selective elimination in the gametophyte generation. Presumably the interchanges recovered in maize are only a small proportion of those which occur, an indefinite but large proportion being weeded out by this selective elimination.

SUMMARY

Sixty-four additional chromosomal interchanges in maize are described. Evidence is presented to establish the chromosome constitution of each.

A catalog list is given of the known chromosomal interchanges in maize.

The relative frequency of interchanges following X-ray treatment is tabulated for the ten chromosomes. The distribution is approximately proportional to the relative lengths of the chromosomes.

All the interchanges adequately tested are viable in homozygous condition, indicating that selection is more stringent in the haploid gametophyte than in the zygote.

APPENDIX

Sources of interchanges from X-ray treatment

All of the interchanges from the writer's treated material came from four lots of seed exposed 50 or 60 minutes 8 inches from the tungsten target of a Coolidge tube operated at 50 kilovolts and 5 milliamperes with a one-millimeter aluminum screen. Within each lot, the interchanges are listed in the order of planting of the original seed. In three cases two different interchanges were obtained from the progeny of a single plant. These are bracketed together.

Lot 1. Pedigree 5411-9×5409-11

Sixty-minute treatment.

94 (9-10)	16 (8-10)	
6452 (5-6) A and C 1934	12 (1-3)	
101 (2-4)	125 (3-6)	C and A 1934
103 (1-7)	58 (1-3)	
11 (1-7)		

Fifty-minute treatment.

42 (2-4)	
43 (1-9)	79 (4-9)

Lot 2. Pedigree 5534-11×5547-6

Sixty-minute treatment.

{ 13 (4-9)	19 (2-3)
{ 61 (4-10)	69 (2-7)
14 (4-5)	20 (5-10)
17 (2-7)	15 (3-10)
62 (8-10)	35 (1-9)
64 (1-10)	36 (4-6)
66 (4-5)	70 (4-6)
18 (3-10)	

Fifty-minute treatment.

27 (3-7)	80 (2-6)
28 (3-5)	30 (3-6)
29 (1-2)	31 (2-9)

Lot 3. Pedigree 5538-3×5543-5

Sixty-minute treatment

111 (6-8)	74 (1-3)
37 (4-6)	22 (8-10)
21 (5-8)	136 (5-7)
73 (1-7)	

Fifty-minute treatment

83 (8-9)	84 (8-10)
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Lot 4. Pedigree 5539-9×5433-21

Sixty-minute treatment.

{ 32 (1-5)	24 (1-5)
{ 118 (2-3)	137 (4-7)
119 (6-9)	40 (1-5)
38 (3-8)	25 (2-7)

23 (6-10)	{ 41 (2-6)
77 (1-9)	{ 78 (2-8)
75 (2-5)	26 (3-10)
76 (2-9)	
Fifty-minute treatment.	
85 (4-10)	88 (2-4)
87 (1-3)	90 (2-3)

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