LINKAGE IN *PRIMULA SINENSIS*

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Primula Sinensis is one of the few plants in which linkage between several pairs of Mendelian factors is known.¹ The work of GREGORY (1911 a, b) has indicated a relationship between these factors essentially similar to that previously established especially well in *Drosophila ampelophila*.² No such large numbers of individuals, however, were studied by GREGORY as are customary with the animal workers using such a short-cycled and easily handled type as the pomace fly. It seemed desirable, therefore, to obtain more extensive figures on a form other than *Drosophila*, in order to have sufficient data on which to base general conclusions on this most recent and important phase of genetics, —the mathematical relationships between linked factors.

Two pairs of factors are said to be linked, if, in an individual heterozygous for them, the parental combinations occur more often than the recombinations (or new combinations). Thus, when two germ-cells unite, one containing the factors for long style and red flower color, and the other those for short style and magenta flower color, an individual is formed most of the gametes of which will contain the parental combinations of factors, namely, some gametes with the factors for long style and red flower, and others with the factors for short style and magenta flower; but a smaller proportion of the gametes will contain the new combinations of factors, namely, gametes with the factors for long style and magenta flower, and others with the factors for short style and red flower. In MENDEL's experiments involving two pairs of factors, the combination and the recombination classes of gametes were equally numerous; such factors are said to show random segregation. The term "crossover" has been used to apply to new combinations between linked factors, not to the random segregation described by MENDEL.

¹A group of five pairs of linked factors is known in this plant.

²C. B. BRIDGES (1914) has interpreted GREGORY's results on the chromosome hypothesis.

Investigators in this field have found themselves divided into two camps,—those who adhere to the original reduplication hypothesis of BATESON, and those who find in the chromosomes and their behavior the basis of all Mendelian heredity. It should be a simple matter to test experimentally the hypothesis which states that the members of linked pairs of allelomorphic factors undergo so-called vegetative reductions early in the development of an individual, and that the cells containing certain haploid combinations of factors thus produced (corresponding to the gametic combinations) undergo more rapid division than cells with other combinations, the end result being the production of more gametes of certain classes (the original parental combinations) than those of other classes (the recombination classes). An attempt to test this view will be described later.

The parent plants in my experiments were grown from seed sent to me by R. P. GREGORY, to whom I wish to express my sincerest thanks. One of the parents had the three linked factors, long style (*l*), red flower (*r*), and red stigma (*s*). The other had the three allelomorphic dominants, short style (*L*), magenta flower (*R*), green stigma (*S*).³ Plants with these characters have been adequately described by GREGORY (1911 a). The F_1 , $\frac{l \ r \ s}{L \ R \ S}$, was back-crossed⁴ to the triple recessive, $\frac{l \ r \ s}{l \ r \ s}$.

Seeds for the F_1 plants used in the back-cross were planted in the greenhouse during the summer of 1914. The plants started to bloom about the middle of December. The pollinations were made during December, 1914, and January and February, 1915. During these months there were few or no pollen-carrying insects in the greenhouse. The long-styled, red-flowered, red-stigma plants were used in most cases as the female. Examination of many of these long-styled flowers showed

³The latter plant appeared pale pink, however, because it differed from the normal magenta in a pair of allelomorphs other than the pair by which normal magenta differs from the red; the pale pink factor is recessive to its allelomorph in the normal magenta (which allelomorph is also possessed by the red).

The pale pink parent was heterozygous for short and long style. I rejected the long-styled F_1 plants.

⁴This method of crossing is very desirable because the factors possessed by the hybrid gametes are shown directly by the character of the resulting offspring, since the other parent introduces no dominants to obscure the factors introduced by the heterozygote. Thus the heterozygote $Ll \times ll$ gives one-half Ll (short style) and one-half ll (long style), the gametes of Ll also being one-half short, and one-half long, style.

that they rarely, if ever, set seed without hand pollination. Moreover, the anthers of these plants did not develop properly during these months, being small, brown and hard, and sterile; they also failed to open. Plants used as female parents in crosses were nevertheless emasculated and sacked before the flowers opened, except in a few instances which were recorded. Plants used as male parents were also sacked before the flowers opened. The sterile anthers of long-styled female plants were removed generally just before pollination or several days previously. This was done by tearing the entire corolla lengthwise in two and then removing the halves, care being taken in so doing not to touch the stigma with any of the other parts of the flower. Most of the seed resulting from the back-cross was planted earlier than usual, in May and June of 1915; but the plants did not bloom before December — about the usual time of blooming. In all cases a record was made of the particular plant and capsule which produced the seed. Records were also made of the particular plant used as the pollen parent, and in certain cases also, of all the seeds resulting from the pollination with single anthers. The seed was planted in pans of sterilized soil, and the young seedlings transplanted to successively larger pots; about 800 plants were allowed to bloom in two and two-and-a-half inch pots, the rest matured in three, four and five inch pots. Individuals grown in small pots produced perfectly normal flowers (possibly a trifle smaller than those of plants in larger pots), but the number of flowers produced per plant was, of course, smaller.

An interesting feature in connection with the culture of primulas is the extreme cold in which they can thrive. The bulk of my plants was kept in cold-frames for the greater part of the winter, during which time they were probably subjected to temperatures considerably below freezing, since the outside temperature on several occasions was at or near zero Fahrenheit, and no artificial heat was used in the cold-frames.⁵ These plants were much more vigorous and produced a better bloom than similar plants cultivated in the greenhouse.⁶

⁵ Additional covering of boards or straw mats was applied at night.

It is also interesting that no watering during the entire winter was necessary, and although the soil became very dry, the plants did not droop or seem to suffer in any way. A few plants exposed by broken glass were killed by freezing.

⁶ Commercial growers as a rule transfer primulas from cold-frames to the greenhouse late in fall, but I know of no previous instance in which they were kept outdoors all winter in a climate as cold as that of New York.

Primulas demand a light, rather dry soil in a moist, cool greenhouse (45° — 60° F.). Over-watering is especially harmful to young plants before they become pot-bound; individuals so treated are sickly, yellow-leaved, with poorly developed flowers, the characters of which can not be well distinguished. Such plants must be discarded.

Whenever plants froze, failed to bloom properly, or were not included in the counts for any reason, a record of the fact was usually made.

A few further matters of technique should be mentioned. The factor for green stigma also makes the flower color, whether magenta or red, lighter. These light magentas and light reds are rather difficult to distinguish from each other at times. The flowers of poorly developed (especially over-watered) plants with green stigmas may appear light magenta, but the plant may really possess only the red factor. Any weak plants, therefore, with green stigmas and poorly developed flowers could not be included in the records, and were discarded. This would lower somewhat the number of individuals in classes 2, 3, 5, and possibly 8 (table 1 a), but as the number of such discarded individuals was very small (not over 25), these figures would not be appreciably altered. The light red and light magenta flowers of plants grown in small pots were as a rule not much, or no more, difficult to distinguish than the flowers of plants grown in larger pots. Especial care had to be exercised in not including in class 8 individuals which did not belong there, since a relatively few mistakes could alter appreciably the ratio of this class to the total. As a rule, where there was a possibility of confusion the plant was re-examined at a later period when new flowers were produced, and the two observations compared; and the individual was not recorded until there was certainty as to its proper classification. When there was any doubt as to the classification of the light individuals belonging to the larger classes 3 and 5, such plants were either re-examined later, or placed without re-examination in the class where they presumably belonged; in the latter case a note was always made of the extent to which the classification was questionable. Thus the color of twenty individuals of class 3 and of four of class 5 was somewhat doubtful. The color of fourteen individuals of class 3 and seven of class 5 was doubtful. There may have been several plants which belonged to class 8 but which were included in class 2, because all of the flowers on these plants appeared light magenta at the time the record was made, although the plants were light red genetically. This may explain partly the fact that class 8 is smaller than class 7, which it should

about equal. Moreover, a lot of about 300 plants grown in small pots is included in the records, and plants of this lot which were of uncertain color, especially such as might belong to class 8, were not classified. This again would lower somewhat the number of individuals of class 8.

The red stigma is most easily distinguished in the very young unopened flower. As the flower becomes older the stigma color becomes less distinct.

One hundred and eight plants grown in the cold-frames were killed by frost. There should be no resultant disproportionate lowering of any particular class or classes, since probably the frost had no selective action on one or more classes of plants. There were about 225 plants in small pots which I failed to count either because they had not produced a sufficiently abundant bloom at the time that I had opportunity to make counts, or because they were past their blooming period. These plants will be transferred to larger pots in an effort to induce them to bloom next winter.

The results of the back-cross are given in table 1. There are eight ✓ classes corresponding to the eight types of gametes, each class including one member of each of the three pairs of allelomorphs involved. It is desirable to report the results in this manner, as is explained below.

An examination of table 1a shows that the percentage of crossovers between the allelomorphic pairs rR and sS is 31.5 percent (column 2) + 2.52 percent (column 4) = 34.02 percent. That between lL and rR is 9.1 percent (column 3) + 2.52 percent (column 4) = 11.62 percent. When the factors are placed in the order given in table 1 (l, r, s , or L, R, S), a single crossover between the pairs of allelomorphs lL and rR , or between the pairs rR and sS results in a separation of, or crossover between, l and s (or L and S), but two simultaneous crossovers, one between lL and rR , the other between rR and sS , do not result in a separation of l and s (or L and S). The percentage of such simultaneous crossovers, or double crossovers, is 2.52 (table 1 a, column 4). If the F_1 had been homozygous for r (or R), there is no reason to doubt that essentially similar processes involving linkage would have taken place, viz., the same number of double crossovers would have taken place between the pairs of factors lL, rr (or RR), and sS ; but the parental combinations or non-crossovers l, r (or R), s , and L, r (or R), S , would have been indistinguishable from the double crossovers l, r (or R), s , and L, r (or R), S . In other words, in an individual homozygous for r (or R), but heterozygous for lL and sS , we should be unaware of the existence of double crossovers, since the factors l and s (or L and S)

TABLE I

a. *Offspring of back-cross* $\left(\frac{l, r, s}{l, r, s} \times \frac{l, r, s}{L, R, S}\right)$ *and reciprocal.*

Total number of individuals 3684.

l = long style

r = red flower

s = red stigma

L = short style

L = magenta flower

S = green stigma

	Column 1 Non-crossovers	Column 2 Single crossovers	Column 3 Single crossovers	Column 4 Double crossovers
	1. <i>l, r, s</i> 1032	3. <i>l, r, S</i> 526	5. <i>l, R, S</i> 180	7. <i>l, R, s</i> 54
	2. <i>L, R, S</i> 1063	4. <i>L, R, s</i> 634	6. <i>L, r, s</i> 156	8. <i>L, r, S</i> 39
Sum of contrary classes	2095	1160	336	93
Percent of total (3684)	56.9	31.5	9.1	2.52

b. *Offspring of* $\left(\frac{l, r, s}{l, r, s} \times \frac{l, r, s}{L, R, S}\right)$ *only* (σ heterozygous).

(Included above under a.)

	1. <i>l, r, s</i> 895	3. <i>l, r, S</i> 484	5. <i>l, R, S</i> 173	7. <i>l, R, s</i> 52
	2. <i>L, R, S</i> 934	4. <i>L, R, s</i> 569	6. <i>L, r, s</i> 152	8. <i>L, r, S</i> 33
Sum of contrary classes	1829	1053	325	85
Percent of total (3292)	55.5	32.0	9.9	2.55

c. *Offspring of* $\left(\frac{l, r, s}{L, R, S} \times \frac{l, r, s}{l, r, s}\right)$ *only* (φ heterozygous).

(Included above under a.)

	1. <i>l, r, s</i> 137	3. <i>l, r, S</i> 42	5. <i>l, R, S</i> 7	7. <i>l, R, s</i> 2
	2. <i>L, R, S</i> 129	4. <i>L, R, s</i> 65	6. <i>L, r, s</i> 4	8. <i>L, r, S</i> 6
Sum of contrary classes	266	107	11	8
Percent of total (392)	67.6	27.2	2.8	2.21

would not separate and gametes containing them would as a result be indistinguishable from the non-crossovers. Any difference which exists between the sum of the number of single crossovers between $l L$ and $r R$, and $r R$ and $s S$ on the one hand, and $l L$ and $s S$ on the other, is due to the double crossovers. These facts are directly indicated when the three factors, one from each of the three pairs of allelomorphs involved, are reported together; but if the F_1 is heterozygous for only two pairs of factors at a time (i.e., $l L$ and $r R$, or $r R$ and $s S$, or $l L$ and $s S$), then any difference in the sum of the percentages of crossovers between $l L$ and $r R$, and $r R$ and $s S$ on the one hand, and the percentage of crossovers between $l L$ and $s S$ on the other, may not represent a difference due to double crossovers, but may be due to variations in the percentages of crossovers which take place in different individuals at different times.

Geneticists are not agreed upon the explanation of linkage. BATESON'S view that the various gametic ratios are due to reduplication implies a segregation of these types in different parts of the plant. It would follow on this hypothesis in its original form that entire anthers or ovaries should contain one gametic type. To test the latter view it was only

TABLE 2

Offspring resulting from pollinations with single anthers of the heterozygous plants. The record of these individuals is included in table 1.

Number of capsule.	l r s	L R S	l r s	L R s	l R S	L r s	l R s	L r S
(1) 4.2 a 1-2	36	43	18	30	5	7	0	0
(2) 4.2 a 2-1	24	33	16	33	12	11	2	1
(3) 4.2 a 2-2	48	48	26	41	11	11	4	1
(4) 4.2 a 2-3	21	21	6	14	6	8	2	0
(5) 4.2 a 2-4	20	26	8	12	4	9	2	0
(6) 4.2 a 2-5	17	18	10	12	4	4	0	0
(7) 4.2 c 1-2	5	8	3	6	3	2	0	0
(8) 4.2 c 1-3	3	8	2	5	1	0	0	1
(9) 4.2 c 1-4	18	13	9	10	0	0	1	1

Triple recessive plants (long style, red flower, red stigma) were pollinated with these anthers. The number followed by a letter (as 4.2 a) is the label given to a particular heterozygous plant; the number following the letter designates a particular flower of this plant, and the last number designates a particular anther of this flower. Thus, anthers recorded on lines (2) to (6) (4.2 a 2-1 to 4.2 a 2-5) all came from the same flower. Each line includes all the individuals from pollinations with a single anther only.

TABLE 3

Offspring grown from seeds of single capsules of the heterozygous plants. The record of these individuals is included in table 1a.

Number of capsule.	<i>l</i>	<i>L</i>	<i>l</i>	<i>L</i>	<i>l</i>	<i>L</i>	<i>l</i>	<i>L</i>
	<i>r</i>	<i>R</i>	<i>r</i>	<i>R</i>	<i>R</i>	<i>r</i>	<i>R</i>	<i>r</i>
	<i>s</i>	<i>S</i>	<i>S</i>	<i>s</i>	<i>S</i>	<i>s</i>	<i>s</i>	<i>S</i>
173	4	9	3	4	1	0	0	1
174	4	4	0	3	1	0	0	0
175	5	4	1	0	0	0	0	0
176	6	6	2	4	1	0	0	0
177	8	6	4	3	0	0	0	0
178	7	2	3	1	0	0	0	0
180	6	5	1	1	0	0	0	0
181	4	7	0	3	0	0	0	0
182	7	8	0	5	0	0	1	0
183	5	3	1	2	0	0	0	1
184	8	3	2	4	0	0	0	0
190	4	4	0	2	0	0	0	0
191	4	5	3	1	0	0	0	0
199	5	3	2	2	0	0	0	0
200	2	5	1	1	0	1	0	0
204	5	3	4	0	0	0	0	0
205	6	5	0	0	2	1	0	0
206	8	3	0	3	1	1	0	2
207	5	3	0	4	0	0	0	0
212	6	6	1	1	0	0	0	0
216	6	3	1	6	0	0	0	0
218	2	2	0	5	1	1	0	0

Only capsules are recorded from which more than ten seeds were planted and grown to maturity.

necessary, therefore, to keep separate, seeds resulting from the single heterozygous anthers or ovaries. Table 2 gives the results obtained by using single anthers. In each instance all the expected classes are realized (except the very small class of double crossovers in some cases); and they occur in about their expected proportions. The ovaries, as shown by table 3, gave similar results, but the number of seeds that are produced by a single capsule is too small (20—40) to make the ratios significant. Suffice it to state that in no instance (22 cases in all) did any heterozygous ovary produce only one type of gamete. It follows, therefore, that reduction must take place within the anthers and ovaries, owing to some peculiarity which must occur in cell processes and cell divisions at this stage. Such peculiarities are indeed found in the sporangia, namely, at the reduction divisions. This leads us to the other explanation of linkage, based on the parallelism in the distribution of

the chromosomes and of Mendelian factors. Especially striking and complete in all its details is the identical distribution of sex-linked factors and the sex chromosomes of *Drosophila* (MORGAN 1911). Thus, for instance, the cytological evidence shows that a male transmits his sex chromosome to his daughters only, not to his sons; he also transmits a certain group of factors (sex-linked) to his daughters only, and not to his sons. The results of all crosses show that wherever the sex chromosome goes, there also these factors go. Even when, in exceptional cases, the chromosomal distribution is abnormal, there is a corresponding abnormal distribution of these sex-linked factors (BRIDGES 1916). Because of this complete association, these factors are supposed to constitute, in part, the sex chromosome. Now, all sex-linked factors have been found to be linked to each other (a linkage group). All factors in the same chromosome, in other words, are linked. The chromosome contains many distinct (i.e., separable) factors, which are considered as occupying definite loci within it, in linear arrangement (STURTEVANT 1913, 1915).

This material continuity is broken only when there is an interchange of similar portions of homologous chromosomes resulting in a new combination of factors, or a crossover.⁷ Factors that are allelomorphic are thought to occupy corresponding loci in the homologous chromosomes.

In harmony with all this observation and theory is the further fact that many other Mendelian factors which have been identified in *Drosophila* and which do not follow the sex chromosomes in their distribution to the offspring, are also never linked to those in the sex chromosome group. These non-sex-linked factors, however, form linkage groups of their own, and as the theory demands, these groups are equal in number to the pairs of chromosomes; and curiously enough, the number of identified factors in each group has so far been found to be roughly proportional to the size of the chromosomes (MULLER 1914, 1916). Finally, just as the pairs of chromosomes segregate independently of each other, so also any pair of factors in one linkage group segregates independently of any pair in all other linkage groups.

The experimental evidence that the segregation of sex-linked factors happens at the same time as the reduction of the sex chromosomes is complete. Here we are not dealing with theory, but with fact. The

⁷ This term has been substituted for recombination by MORGAN; it carries a cytological implication besides referring to the observed breeding results.

inference as to similarity in the mechanism involved extends to those cases in which the homologous chromosomes are not differentiated. In these cases, the direct evidence could not be obtained, because one chromosome can not be distinguished from the other when in association, in an individual, with a Mendelian character.

In general, the facts of linkage find a rather simple explanation on the chromosome hypothesis. When only three linked factors are involved in an experiment, it is difficult or impossible to draw conclusions, from the mathematical relationships alone, of the probable nature of the processes which are responsible for these values. Such conclusions must be based on the values afforded by many factors, all linked, in which case the various complex or special mathematical relationships may be conceived of as the result of some spatial relationship of the factors, as is believed to be true on the hypothesis of linear arrangement of the factors in the chromosomes. It would therefore be desirable to get accurate data on a reasonably large series of linked factors in *Primula* or some other easily handled plant, for the sake of comparison with the results which have been gained on *Drosophila* and which have received, in general, a simple explanation on the chromosome hypothesis.

When an individual is heterozygous for three pairs of linked factors there are various proportions of the different classes of gametes possible on *a priori* grounds. I have attempted to establish accurately the particular values given in the case of *Primula*, especially the numerical proportions of the double crossover classes recorded in column 4, table 1a.

On the simple assumption that crossovers between *l L* and *r R* do not influence those between *r R* and *s S*, the percentage of crossovers between *l L* and *r R* (11.62 percent) should be as great when crossovers take place between *r R* and *s S* (i.e., 11.62 percent of 34.02 percent = 3.95 percent) as when the latter do not occur. From table 1, column 4, it will be seen that the percentage of double crossovers follows this simple assumption of their random occurrence, the realized percentage of 2.52 percent being somewhat below the expectation of 3.95 percent. The deviation from this value may be due to the fact that class 8 (column 4, table 1a) is lower than it really should be, as was explained above. The darker-colored classes 1, 4, 6 and 7, give more reliable results. If these classes alone are considered the double crossovers form 2.87 percent of the total (i.e., $54 = 2.87$ percent of 1876). The percentage expected on the simple assumption of random occurrence of double crossovers is 2.80 percent (8.3 percent of 33.7 percent), a very close ap-

proximation to the realized percentage. These results would be explained on the chromosome hypothesis on the assumption that the factors have a linear arrangement in the chromosome in the order l, r, s (or L, R, S), and that there is no interference of crossing over between l, r and r, s (or L, R , and R, S). A double crossover, when the factors have this arrangement, does not result in the separation of the two outer factors (l and s , or L and S). The sum of the percentages of crossing over between l and r , and r and s is 45.64 percent (34.02 percent + 11.62 percent). The percentage of single crossing over between l and s is 31.5 percent + 9.1 percent = 40.6 percent. The difference between 45.64 percent and 40.6 percent is due to the double crossovers, for if the factors have a linear arrangement in the order mentioned, l, r, s (or L, R, S) a double crossover between l and s (or L and S) does not result in the separation of these factors.

This random occurrence of double crossovers occurs in *Drosophila* in cases involving rather loose linkage (i.e., a rather high percentage of crossovers). In cases involving tight linkage in this animal the number of double crossovers is below expectation. MULLER (1916) has pointed out this disparity in the latter case, and proposed the term "interference" for it. In our present state of knowledge, it is impossible to state whether one of the crossovers taking place tends to prevent the other, or whether they mutually prevent each other. In the latter case, there would be fewer total single crossovers than in the former case, other things being equal. We do not know, however, exactly what these percentages would be without interference, and therefore cannot tell how the latter operates.

On the other extreme, we are confronted with those cases in *Drosophila* in which very loose linkage is involved, and in which the number of double crossovers is far in excess of the simple expectation that one crossover does not involve the other. Between these two extremes of almost complete interference and of great excess of double crossovers there occur all intermediate values. These values are probably some function of the linkage strengths involved. Since, therefore, in different cases these values may be widely different, including all the mathematical possibilities, it is impossible to postulate with certainty any spatial relationship simply from the values given by only three pairs of linked factors.

Certain difficulties remain unsolved on the chromosome hypothesis. Cytology has not shown us clearly what the mechanism of crossing over

is, much less does it show us the cause of interference, although it suggests a number of possibilities. The loops of JANSSEN's (1905, 1909) chiasmatype seem too frequent for each to represent a crossover, and they are too short to account for the facts of interference. In this connection also we must consider some of the recent researches of BONNEVIE (1908) and of VEJDOVSKY (1911-12). The latter holds that the persistent element of the chromosome is really a long, thin, spirally wound thread or chromonema, lying within an envelope ordinarily considered the chromosome. If the factors have a linear arrangement, it must be along this chromonema. The best opportunity for the exact side-by-side juxtaposition of allelomorphs such as is demanded on the chiasmatype hypothesis would be at a stage when the chromosomes appear as long, thin threads, as in the leptotene spireme. At this stage the twists are extremely short and numerous and could hardly represent each a crossover; how one crossover would interfere with another at even short distances from it at such a stage is difficult to conceive, for such short distances themselves (say one-tenth of the length of the leptotene thread) contain numerous twists.

Finally, the different linkage values given by the two sexes in animals is an enigma. In *Drosophila* and moths no recombinations occur between linked factors in the heterozygous sex (male in *Drosophila*, female in moths). Although the details of synapsis have not been worked out in these forms, there seems to be no reason to doubt that they are essentially similar to those in *Batrachoseps*, in which the twisting of chromatin threads about each other has been observed in the heterozygous sex (the male); but it may be that crossing over occurs in the male *Batrachoseps*, as it does in the male mammal (rats, CASTLE and WRIGHT 1915).

So far as my figures go, no great dissimilarity in the linkage values given by the two sexes occurs in *Primula*. Table 1, b and c, gives these values for both the anthers and ovaries. The difference shown in the ratios is probably not significant, since the percentages of the various classes produced by the heterozygous females are based on small counts.

Some of my plants were grown at Columbia University, but most of them at the New York Botanical Garden.

SUMMARY

(1) In *Primula Sinensis* the pairs of factors studied may be arranged in the order: long or short style, red or magenta flower, red stigma or green stigma.

(2) Crossovers between the pairs of linked factors, long or short style, and red or magenta flower, respectively, take place without reference to the crossovers between the pairs of linked factors, red or magenta flower color and red stigma or green stigma, respectively; that is, there is no interference.

(3) Single anthers and single ovaries of the heterozygous individuals produce all classes of gametes. Reduction of factors must therefore accompany cell divisions occurring within many or all the anthers and ovaries.

(4) The proportions of the various gametic classes of linked factors is about the same for the anthers and the ovaries.

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