# AN EXPERIMENTAL AND THEORETICAL STUDY OF CHROMATID CROSSING OVER[1]

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Received February 17, 1933

## INTRODUCTION

The term "crossing over" is used to denote the exchange of pieces or segments between homologous chromosomes. There are many facts which indicate that the exchange of parts or segments occurs during the first meiotic prophase when the two homologous chromosomes are in intimate association. Prior to 1916 crossing over was thought to take place between the two paired chromosomes before they had divided equationally. BRIDGES, however, in that year, from his study of non-disjunction of the X chromosome of *Drosophila melanogaster* came to the conclusion that each chromosome was split equationally when crossing over occurred. Later L. V. MORGAN (1925), ANDERSON (1925) and BRIDGES and ANDERSON (1925) in a beautiful series of experiments substantiated BRIDGES' earlier conclusion; and ANDERSON (1925) and BRIDGES and ANDERSON (1925) further demonstrated that only two of the four strands crossed over at any one level. This was true for both diploids and triploids. REDFIELD (1930, 1932) working with triploid Drosophila found that the II and III chromosomes likewise crossed over when each chromosome was split equationally. ANDERSON used the phrase "four strand crossing over" to denote the divided condition of the chromosomes at the time crossing over took place in diploids. This term should not be applied to triploids, since it infers diploidy, even though only two of the three chromosomes (four chromatids) are involved in any one point of crossing over. The terms "double strand" or "chromatid crossing over" could be used for both diploids and polyploids since they refer only to the presence of the equational split.

In addition to the chromosomes of *D. melanogaster*, the X chromosomes of *D. simulans* (STURTEVANT, 1929) and *D. virilis* (DEMEREC, unpublished) have been genetically proved to cross over at a double strand stage. RHOADES (1932) presented data which proved that the *pr*-$v_2$ chromosome in Zea, the fifth largest in the monoploid complement, crossed over after, or at the time, the equational split occurred. WHITING and GILMORE (1932) reached a similar conclusion for one chromosome of Habrobracon in their study of impaternate daughters from virgin females. As far as the writer is aware, these are the only cases where chromatid or double strand crossing

[1] Paper No. 194 from the Department of Plant Breeding, Cornell University, Ithaca, New York.

over has been genetically demonstrated. (LINDEGREN recently [1933] demonstrated chromatid crossing over in the fungus Neurospora.) There are certain data (BLAKESLEE and others 1923, FROST 1931) in plants which can be interpreted as the result of double strand crossing over, but since other explanations are possible they can not be said to prove that double strand crossing over occurred.

In recent years many cytological papers by various investigators have dealt with the nature of the tetrad present in the first meiotic division of diploid organisms. They have attempted to discover the cytological mechanism by which genetic crossing over is effected through their study of the nature and origin of chiasmata. There is much controversy regarding many salient points, but most of the investigators agree that only two of the four chromatids in each chiasma are involved in the actual exchange of partners.

STERN (1931) and CREIGHTON and MCCLINTOCK (1931) have proved that genetic crossing over is accompanied by an actual exchange of parts between the chromosomes. Later (1932) CREIGHTON and MCCLINTOCK presented cytological evidence that crossing over in Zea takes place between chromatids. Zea thus becomes the first organism in which chromatid crossing over has been demonstrated both genetically and cytologically.

The occurrence of chromatid crossing over in such diverse forms as Drosophila, Habrobracon, and maize suggests that it may be a wide spread or universal phenomenon. However, WETTSTEIN'S data on Funaria, where he found only two types of spores among the quartets from sporophytes which were heterozygous for linked factors, indicates that crossing over in Funaria takes place between undivided chromosomes and not between chromatids.

## DOUBLE STRAND CROSSING OVER IN ZEA

In diploid organisms where the four chromatids which comprise the tetrad are normally distributed to the quartet of cells arising from each meiocyte and where it is impossible to recover the four resulting cells from any given meiocyte it is impossible to tell genetically whether crossing over occurs in a single or double strand condition. It was only through such aberrant behavior as non-disjunction which results in two of the four chromatids going to a single member of the quartet that the occurrence of double strand crossing over was genetically proven in diploid Drosophila. In trisomic and polyploid individuals where the number of homologous chromosomes present in metaphase I makes it possible for some members of the quartet to regularly receive more than one chromosome it is possible to test for the occurrence of double strand crossing over.

For this study in Zea the *pr-v*$_2$ trisome, which involves the fifth largest

chromosome, was used since these trisomic plants differ markedly in appearance from their disomic sibs and an accurate classification into the two classes is possible.

The writer, in 1932, published a preliminary note on the genetical demonstration of double strand crossing over in Zea. This paper will present more extensive data upon this subject.

The factor pair *Pr:pr* differentiates between purple and red aleurone color and the factor pair $V_2$:$v_2$ is responsible for green and virescent seedling color. These two pairs of genes give a recombination value of 41 percent as shown by the data in table 1. The crossover value or map distance

TABLE 1

*Control data for percent of recombinations between pr and $v_2$ in diploids. Pr $V_2$ pr $v_2$ × pr $v_2$.*

| PEDIGREE | PURPLE ALEURONE GREEN SEEDLING | PURPLE ALEURONE VIRESCENT SEEDLING | RED ALEURONE GREEN SEEDLING | RED ALEURONE GREEN SEEDLING |
|---|---|---|---|---|
| 1831–1840 | 438 | 267 | 288 | 375 |

40.6 percent of recombinations.

is much greater than this since undetected double crossovers reduce the percent of recombinations.

Trisomic plants of $\frac{Pr \quad V_2}{Pr \quad V_2}$ constitution were

$\frac{pr \quad v_2}{}$

pollinated by double recessive individuals. The ensuing seeds were classified into purple and red aleurone classes and when planted the seedlings classified as green or virescent. Classification into trisomic and disomic types was made just before anthesis.

If crossing over among the members of the trivalent occurred between undivided chromosomes and not between chromatids there should be no cases of trisomic plants homozygous for *pr* or $v_2$. If, however, crossing over took place between chromatids the occurrence of trisomic plants homozygous for the two loci is expected. Diagram 1 shows how a trisomic plant homozygous for $v_2$ may arise. Similarly if a crossover had taken place between *pr* and the spindle insertion, a trisomic homozygous for *pr* would be possible. The data in table 2 show 61 trisomic individuals homozygous for the $v_2$ gene. There were nine plants among the 553 individuals arising from red aleurone (*pr*) seed which were trisomic. Only two of the 15 pedigrees listed in table 2 failed to throw exceptional trisomic types.

The constitution of the trisomic plants was *AACCRr* with respect to the aleurone factors affecting color. Since the male parents were *AA*

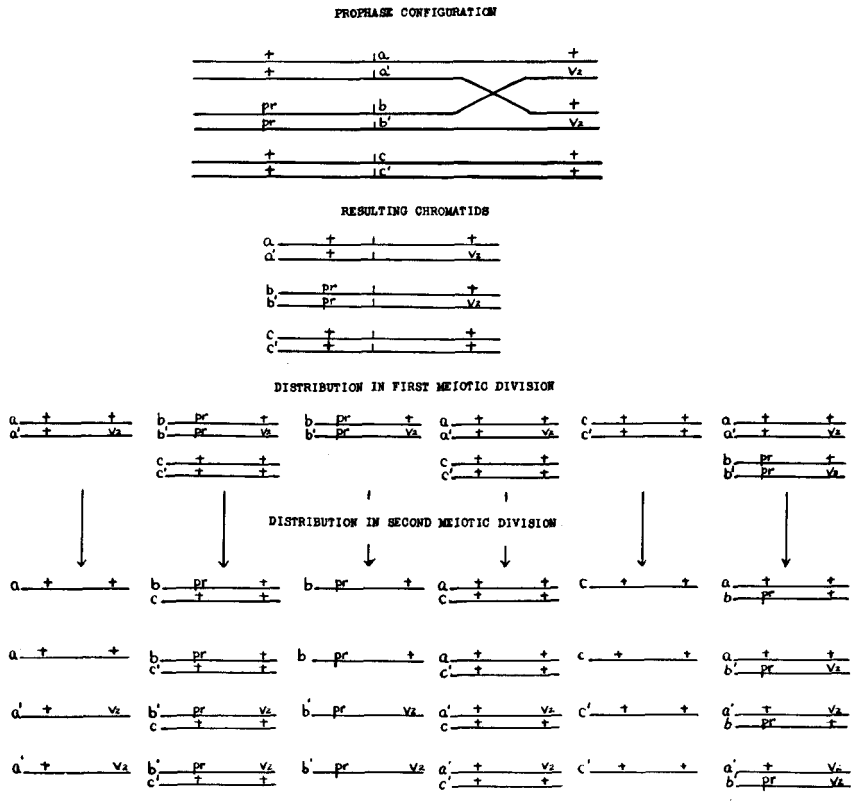


DIAGRAM I

Diagram illustrating how a trisomic plant homozygous for $v_2$ may arise through chromatid crossing over. The combination in the lower right hand corner will give rise to the exceptional trisomic type.

*CCRR* it was expected that all the seeds would have colored aleurone and could be classified as purple or red. Surprisingly enough approximately 50 percent of the seeds had colorless aleurone. Subsequent investigation showed that two of the *r* genes were dominant over a single *R* gene. This *r* allelomorph has been designated $r^{rw}$ (the superscript *r* to represent its effect upon plant color and the superscript *w* to represent its effect upon aleurone color). This behavior is analogous with the floury-flinty endosperm situation. Although the *Pr:pr* constitution of these colorless seeds could not be told without testing, they were planted since data on the $v_2$ locus could be had.

Since approximately only one-half of the seeds could be classified for aleurone color the total number of trisomic plants homozygous for *pr* should be twice 9, or eighteen. This is a legitimate procedure since the *R* locus is in another chromosome. Five of the nine *pr* trisomes were also

TABLE 2

*Data on cross of* $\frac{Pr \quad V_2}{Pr \quad V_2}$ *trisomes by double recessive male parents.*
$\frac{}{pr \quad v_2}$

| PEDIGREE | CULTURE | ALEURONE | 2N GREEN | 2N $v_2$ | 2N+1 GREEN | 2N+1 $v_2$ |
|---|---|---|---|---|---|---|
| 1482 (1)×1055 | 1620 | 235 *Pr* | 79 | 23 | 72 | 4 |
| | 1621 | 279 wh. | 95 | 47 | 73 | 3 |
| | 1622 | 59 *pr* | 24 | 27 | 0 | 0 |
| 1482 (2)×1055 | 1623 | 20 *pr* | 2 | 12 | 0 | 0 |
| | 1624 | 146 wh. | 55 | 38 | 19 | 0 |
| | 1625 | 115 *Pr* | 49 | 12 | 24 | 0 |
| 1482 (3)×1055 | 1626 | 157 *Pr* | 41 | 15 | 65 | 2 |
| | 1627 | 43 *pr* | 15 | 25 | 0 | 0 |
| | 1628 | 132 wh. | 46 | 32 | 28 | 3 |
| 1482 (4)×1055 | 1629 | 40 *pr* | 9 | 27 | 0 | 2 |
| | 1630 | 169 *Pr* | 65 | 17 | 50 | 2 |
| | 1631 | 175 wh. | 74 | 32 | 40 | 3 |
| 1482 (5)×1055 | 1632 | 231 *Pr* | 93 | 21 | 68 | 5 |
| | 1633 | 237 wh. | 78 | 50 | 53 | 2 |
| | 1634 | 59 *pr* | 20 | 24 | 0 | 1 |
| 1482 (6)×1055 | 1635 | 41 *pr* | 15 | 20 | 0 | 0 |
| | 1636 | 133 *Pr* | 57 | 13 | 38 | 1 |
| | 1637 | 201 wh. | 76 | 28 | 52 | 0 |
| 1482 (7)×1055 | 1638 | 186 *Pr* | 65 | 15 | 70 | 3 |
| | 1639 | 51 *pr* | 16 | 28 | 0 | 0 |
| | 1640 | 171 wh. | 69 | 36 | 33 | 3 |
| 1482 (8)×1055 | 1641 | 185 *Pr* | 65 | 24 | 43 | 1 |
| | 1642 | 65 *pr* | 14 | 30 | 1 | 0 |
| | 1643 | 268 wh. | 84 | 50 | 60 | 6 |
| 1482 (9)×1055 | 1644 | 36 *pr* | 9 | 23 | 0 | 1 |
| | 1645 | 146 wh. | 50 | 27 | 48 | 1 |
| | 1646 | 124 *Pr* | 44 | 11 | 50 | 1 |
| 1482 (10)×1055 | 1647 | 194 *Pr* | 87 | 19 | 57 | 3 |
| | 1648 | 56 *pr* | 21 | 24 | 0 | 0 |
| | 1649 | 253 wh. | 106 | 50 | 48 | 1 |
| 1482 (11)×1055 | 1650 | 60 *pr* | 12 | 28 | 2 | 1 |
| | 1651 | 228 *Pr* | 62 | 10 | 66 | 3 |
| | 1652 | 281 wh. | 99 | 46 | 49 | 1 |
| 1582 (12)×1055 | 1653 | 34 *pr* | 8 | 8 | 0 | 0 |
| | 1654 | 170 wh. | 52 | 34 | 21 | 0 |
| | 1655 | 121 *Pr* | 23 | 15 | 28 | 0 |
| 1482 (13)×1055 | 1656 | 34 *pr* | 7 | 20 | 1 | 0 |
| | 1657 | 131 *Pr* | 50 | 12 | 46 | 1 |
| | 1658 | 179 wh. | 55 | 37 | 55 | 2 |
| 1482 (14)×1055 | 1659 | 227 *Pr* | 82 | 27 | 71 | 1 |
| | 1660 | 266 wh. | 116 | 47 | 50 | 4 |
| | 1661 | 64 *pr* | 21 | 36 | 0 | 0 |
| 1482 (15)×1055 | 1662 | 34 *pr* | 12 | 8 | 0 | 0 |
| | 1663 | 111 wh. | 38 | 14 | 20 | 0 |
| | 1664 | 126 *Pr* | 50 | 4 | 38 | 0 |

homozygous for $v_2$. These individuals might have arisen through non-disjunction at any one of the four divisions following the first meiotic division. But the normal frequency of non-disjunction during these divisions is so low that this interpretation can be disregarded. The $v_2$ trisomes from purple aleurone seed all proved to be $\frac{Pr \quad v_2}{pr \quad v_2}$ in constitution. The male pronucleus brought in a single $\frac{pr \quad v_2}{}$ chromosome so the egg must have been $\frac{Pr \quad v_2}{pr \quad v_2}$ in constitution.[1] The origin of eggs of this type is possible only through chromatid or double strand crossing over. The same argument holds for those *pr* trisomes of $\frac{pr \quad V_2}{pr \quad v_2}$ constitution. Here the egg must have been of $\frac{pr \quad V_2}{pr \quad v_2}$ constitution and this combination is possible only through chromatid crossing over. The genotypic constitutions of all the exceptional trisomic plants are presented in table 3. This table

TABLE 3

*Genotypic constitutions of exceptional trisomes listed in table 2.*

| PLANT | GENOTYPIC CONSTITUTION | $2N+1$ BY ROOT TIP COUNTS | $2n+1$ BY ALEURONE OR SEEDLING RATIOS | $2n+1$ BY APPEARANCE |
|---|---|---|---|---|
| 1620 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1620 (3) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1620 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1620 (B) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1621 (1) | $v_2$ $v_2$ $v_2$ | " | — | " |
| 1621 (2) | $v_2$ $v_2$ $v_2$ | " | — | " |
| 1621 (A) | $v_2$ $v_2$ $v_2$ | " | — | " |
| 1626 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1626 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1628 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1628 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1628 (3) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1629 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | — | " |
| 1629 (2) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | — | " |
| 1630 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1630 (3) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1631 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1631 (2) | $v_2$ $v_2$ $v_2$ | " | — | " |
| 1631 (3) | $v_2$ $v_2$ $v_2$ | — | — | " |

[1] Extensive tests made by the writer show that pollen carrying an extra *pr*-$v_2$ chromosome rarely, if ever, functions in competition with haploid pollen since of a total of 1845 plants from the cross of a disome by a trisome there were no trisomic plants.

TABLE 3 (*Continued*)

| PLANT | GENOTYPIC CONSTITUTION | $2N+1$ BY ROOT TIP COUNTS | $2n+1$ BY ALEURONE OR SEEDLING RATIOS | $2n+1$ BY APPEARANCE |
|---|---|---|---|---|
| 1632 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1632 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1632 (5) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1632 (6) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1632 (7) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | — | — | " |
| 1633 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1633 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1634 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | — | " |
| 1636 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1638 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1638 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1638 (B) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1640 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1640 (B) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1640 (C) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1641 (1) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1642 (2) | *pr pr pr* $V_2$ $v_2$ $v_2$ | — | " | " |
| 1643 (3) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | " | — | " |
| 1643 (2) | $v_2$ $v_2$ $v_2$ | " | — | " |
| 1643 (B) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1643 (C) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1643 (D) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1643 (E) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1644 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | — | — | " |
| 1645 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1646 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1647 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1647 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1647 (3) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | — | — | " |
| 1649 (1) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1650 (1) | *pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1650 (2) | *pr pr pr* $V_2$ $v_2$ $v_2$ | " | " | " |
| 1650 (3) | *pr pr pr* $V_2$ $V_2$ $v_2$ | " | " | " |
| 1651 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1651 (2) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1651 (4) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1652 (1) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1656 (1) | *pr pr pr* $V_2$ $v_2$ $v_2$ | " | " | " |
| 1657 (2) | *Pr* ? *pr* $v_2$ $v_2$ $v_2$ | — | — | " |
| 1658 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | — | " | " |
| 1658 (B) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1659 (1) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1660 (A) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1660 (B) | *Pr pr pr* $v_2$ $v_2$ $v_2$ | " | " | " |
| 1660 (C) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1660 (D) | $v_2$ $v_2$ $v_2$ | — | — | " |
| 1660 (1)* | *pr pr pr* $V_2$ $v_2$ $v_2$ | " | " | " |

* From table 4.

TABLE 4

*The genotypic constitution for the pr locus in non-virescent trisomes from colorless aleurone seeds.*

| PEDIGREE | NUMBER OF PLANTS OF *Pr Pr pr* CONSTITUTION | NUMBER OF PLANTS WITH *Pr pr pr* CONSTITUTION | NUMBER OF PLANTS WITH *pr pr pr* CONSTITUTION | TOTAL |
|---|---|---|---|---|
| 1621 et cetera to 1663 | 62 | 106 | 1 | 169 |

shows that two of the $v_2$ trisomes from colorless seed were also homozygous for *pr*. One hundred and sixty-nine non-virescent trisomes from colorless seed were either selfed or backcrossed by *A C R pr* plants. In either case a 1:1 ratio for colored:colorless aleurone resulted. One of these 169 plants was homozygous for *pr*. Therefore it is apparent that the doubling of the number of *pr* trisomes was justified in order to find the approximate number of *pr* trisomes in the total population.

The genotypic constitutions of the exceptional trisomic types listed in table 3 were determined by crossing with the appropriate testers. For example, the constitutions of the $v_2$ trisomes with respect to the *pr* locus were determined by selfing and out-crossing with *A C R pr* individuals. Plant 1626–1 was a trisomic $v_2$ plant from purple seed. That it had the constitution $\frac{Pr \quad v_2}{pr \quad v_2}$ is shown by the following tests: (1) It was a trisome by root tip counts and appearance. (2) When self-pollinated it gave 177 *Pr*:95 *pr* seeds which is close to a 2:1 ratio. (3) When used as the male parent on *A C R pr* silks it gave 62 *Pr*:122 *pr*, a good 1:2 ratio. (4) It was homozygous for $v_2$ as shown by its appearance and when it was crossed with $v_2$ plants gave only $v_2$ individuals in the $F_1$. Another example is as follows: Plant 1630–2 was a trisomic $v_2$ plant from purple seed. When selfed it gave 39 *Pr*:17 *pr* seeds and when used as the male parent in a backcross gave 118 *Pr*:234 *pr* seeds. It was trisomic by appearance and root tip counts, and tests showed it to be $v_2$. These results are typical of those obtained for the other exceptional trisomes and they seem to make possible the statement that chromatid crossing over in Zea is a proven fact.

While the writer feels that a perfectly accurate classification into trisomes and disomes can be made by appearance alone, an attempt was made to secure root tip counts for all of the exceptional trisomic plants. These counts have been included in table 3.

Among the trisomic individuals listed in table 2 there were 4.1 percent of them homozygous for $v_2$. If the locus of $v_2$ is far enough removed from the insertion region so that its distribution is at random with respect to the insertion region the percentage of trisomic plants homozygous for $v_2$

should be 6.7. It would seem therefore that the locus of $v_2$ was some distance (crossover distance—not physical distance) from the spindle fiber. If 18 be accepted as the approximate number of *pr* trisomes, this gives a percentage of 1.2. The locus of *pr* then should be much closer to the insertion region than is the locus of $v_2$ since the frequency with which a gene becomes homozygous is a function of its crossover distance from the spindle fiber.

Five of the nine *pr* trisomes were also homozygous for $v_2$ while four were non-virescent. If *pr* and $v_2$ were closely linked and on the same side of the spindle fiber they would be expected to appear together in the exceptional trisomic types. But since the two loci are far apart (41 percent recombinations) there should be no tendency for the *pr* trisomes to be $v_2$, irrespective of whether or not they are in the same arm of the chromosome. One of the four green *pr* trisomes was of $\frac{pr \quad V_2}{pr \quad V_2}$ constitution. The egg was therefore $\frac{pr \quad V_2}{pr \quad v_2}$ in constitution. This suggests that *pr* and $v_2$ are on opposite sides of the insertion region since a much simpler type of prophase configuration will give the above combination if *pr* and $v_2$ are in different arms than if they are in the same arm. This is in agreement with the genetic map of this chromosome which places the gene $bm_1$ between *pr* and $v_2$ and McCLINTOCK (1932) believes $bm_1$ to be near the insertion. The cytogenetic data of the writer on a reciprocal translocation involving this chromosome also places *pr* much nearer the insertion than is $v_2$.[2]

## THE ORIGIN OF A 32 CHROMOSOME PLANT

In the winter of 1931–32 a planting of seed of exactly the same cross as reported in this paper was made for the purpose of demonstrating the occurrence of chromatid crossing over. Since it was not considered possible to identify all of the trisomic plants in the seedling stage these data have not been included in table 2. They were, however, the basis for the statement by the writer in 1932 that crossing over occurred in Zea between chromatids. One of the $v_2$ plants from a purple seed in these cultures was classified as a trisome. Root tip counts in several clear figures showed that this plant had 32 chromosomes. If the pollen contributed 10 of these chromosomes there is left a total of 22 chromosomes as the contribution from the egg. The plant was clearly $v_2$ as progeny tests showed later,

[2] Data recently obtained from a study of this translocation give, in conjunction with McCLINTOCK's placing of the $bm_1$ locus, the following order: $bm_1$—insertion region—*pr*—$v_2$.

so it is possible to say that an n+1 megaspore, with two chromosomes carrying the recessive $v_2$ gene as a result of chromatid crossing over, in some way doubled its number of chromosomes to 22. Whether this occurred through non-disjunction of the entire chromosome set during the formation of the embryo sac or through fusion of the egg nucleus with a synergid it is impossible to state. The fact remains, however, that a doubling of the chromosome number occurred during the gametophytic generation.

## TRISOMIC RATIOS

If a trisomic plant of *Pr Pr pr* constitution is pollinated by recessive pollen a 5:1 ratio of *Pr*:*pr* is expected if 50 percent of the eggs are n+1. Since only 31 percent of the progeny from a plant trisomic for the *pr*–$v_2$ chromosome are trisomes the theoretical ratio of *Pr*:*pr* is 3.35:1. If, however, we assume that crossing over occurs in a double strand stage and that the locus of the factor under observation is sufficiently far from the spindle fiber region so that it assorts at random with respect to the spindle fiber, the theoretical ratios are markedly changed. With 50 percent of trisomes and chromatid crossing over with randomness a 4:1 ratio of *Pr*:*pr* is expected instead of a 5:1 ratio with "chromosome" crossing over. Since only 31 percent of the plants are trisomes a ratio of approximately 3:1 (25.1 percent recessives) for *Pr*:*pr* is expected with chromatid crossing over and random assortment. It follows that the genetic ratio for a given factor pair in triploid individuals depends in part upon the location of the gene with respect to the point of spindle fiber attachment. That is, the further removed (crossover value) the locus of the genetic factor is, the greater the effect, up to the ratio expected with random assortment, will be upon the ratio of dominants to recessives. In other words if the locus of a factor is close to the insertion region its genetic ratio will be little affected by the occurrence of chromatid crossing over while a progressively greater disturbance in the genetic ratio will occur the further removed the gene lies from the insertion region. Thus the theoretical gametic ratio in duplex trisomic individuals with 31 percent of the progeny trisomes will be 3:1 with chromatid crossing over and random assortment while it will be 3.35:1 with "chromosome" crossing over. Therefore, the ratio of dominants to recessives in the progeny of triploid individuals should indicate whether the gene in question is close or far removed from the insertion region.

Since we have calculated the theoretical ratios expected on the various assumptions let us see what the observed ratios were for the two factor pairs reported in this paper. The percentage of *pr* seeds among a total progeny of 14,160 was 22.7 and the percentage of $v_2$ plants in a total of 4856 individuals was 24.9. The expected percentage of recessives from a

duplex trisomic individual with 31 percent of its progeny trisomes and "chromosome" crossing over, or with chromatid crossing over and the location of the gene near the insertion, should be 23 (3.35:1 ratio). This suggests that *pr* should be close to the insertion region. With 31 percent of trisomes and chromatid crossing over with random assortment the expected percentage of recessives should be 25.1. There were 24.9 percent of $v_2$ plants which indicates that the locus of $v_2$ is far enough removed from the insertion so that an approach to a random assortment is realized. The observed percentages of *pr* and $v_2$ agree very well with the position of these loci with respect to the insertion region as determined from the frequency of homozygous trisomic types.

The difference between 25.1 percent and 23.0 percent, the two extremes, is small and a large amount of data would be necessary to permit any definite conclusions as to the locus of a gene. If 50 percent of the functioning eggs were n+1 the difference in the percentage of recessives would be greater since 16.7 percent would be expected with chromosome crossing over as contrasted to 20 percent with chromatid crossing over and random assortment.

## CROSSING OVER IN TRIPLOIDS

A theoretical discussion of the effect of double strand crossing over on crossover values in triploids and trisomics will be taken up in this section.

Represent the three homologous chromosomes present in a triploid or trisome as a, b, and c and let c carry the recessive genes. Crossing over can occur between a and b, a and c, and b and c with equal frequencies. Crossing over between a and b cannot be detected since both chromosomes carry the normal allelomorphs but crossing over between a and c, and b and c lead to detectable crossovers. Therefore, it can be argued that the amount of actual crossing over is 3/2 the observed amount (REDFIELD 1930). If there is a random distribution of the three chromosomes the proportion of crossover to non-crossover chromosomes should be the same in both the haploid and diploid eggs. REDFIELD (1930, 1932) apparently assumed this for she multiplied the observed crossover values determined from the diploid progeny for the factor 3/2. If we make a similar calculation for the *pr*-$v_2$ region from the data in table 2 we find that the observed recombination value among the disomic offspring is 26.2 percent. The corrected value would be 39.3 percent which agrees very well with the recombination value of 40.6 percent found in the diploid controls. Since only the diploid offspring were used in the calculation, a similar recombination value, if crossing over is the same in mega- and microsporocytes, should be found if the trisomic plants were used as the male parent in a backcross with double recessive individuals. Here all the offspring can be used since none

of the n+1 pollen succeeds in effecting fertilization. A corrected recombination value, using the factor 3/2, of 41.0 percent was found.

In the discussion above it has been assumed that crossing over between a and c, and b and c lead to detectable crossovers. Let us examine the consequences of crossing over between b and c. For simplicity, we will assume that we are dealing with a rod-shaped chromosome and that the location of the two genes under observation is near the terminal insertion region. Represent the genes as *x* and *y* and the normal allelomorphs by the conventional + sign. The constitution of the triploid before crossing over takes place is:

| | |
|---|---|
| + | + a |
| + | + a′ |
| + | + b |
| + | + b′ |
| *x* | *y* c |
| *x* | *y* c′ |

Crossing over occurs between chromosomes b and c but involves chromatids b′ and c. The constitution following the crossing over is:

| | |
|---|---|
| + | + a |
| + | + a′ |
| + | + b |
| *x* | + b′ |
| + | *y* c |
| *x* | *y* c′ |

If the distribution of the three chromosomes is at random in the metaphase of the first meiotic division (arbitrarily assumed to be reductional for the spindle region) there are six combinations possible at the end of the first division. They are as follows:

| (1) | | (2) | | (3) | | (4) | | (5) | | (6) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| + | + a | | | + | + a | | | + | + b | | |
| + | + a′ | | | + | + a′ | | | *x* | + b′ | | |
| | | + | *y* c | | | + | + b | | | + | + a |
| | | *x* | *y* c′ | | | *x* | + b′ | | | + | + a′ |
| + | + b | | | + | *y* c | | | + | *y* c | | |
| *x* | + b′ | | | *x* | *y* c′ | | | *x* | *y* c′ | | |

The next division is equational for the spindle region so 12 of the resulting 24 combinations have 2 chromosomes represented and the other 12 have a single chromosome. But 4 of the 12 single chromosome types are crossover chromosomes and 8 are non-crossovers and 8 of the 24 chromosomes in the "two chromosome" combinations are crossover strands. That is, instead of every crossover between b and c leading only to detectable cross-

over chromosomes we find that only one-third of the recovered chromosomes are crossovers whereas in diploids one-half of the recovered strands, from every crossover point, are crossovers. Therefore, in place of using the factor 3/2 to obtain the actual amount of crossing over it is necessary to use the factor 2.25.

If the factor 2.25 is the correct one to use and the factor 3/2 used by REDFIELD is wrong, then her comparisons between triploid and diploid crossing over must be revaluated since her triploid values were obtained by multiplying the observed crossover values by 3/2.

In a comparison of crossing over in triploids and diploids it is necessary to state the basis upon which the comparison is to be made. In diploids the frequency of crossover points in a short region is always twice the map distance since only one-half of the strands exchange segments at the crossover point. Therefore, instead of saying that genes A and B are 10 map units apart it would be equally proper to say that 20 cells out of every 100 have a crossover point between the loci A and B. We can then express map distances in terms of the number of crossover points as well as the percentage of crossover chromosomes among the progeny. In diploids a map distance of 10 means a crossover point frequency of 20 percent. If we wish to compare crossing over in a certain region in triploids with that in diploids we must keep in mind that what we really want to measure is the frequency with which crossover points occur in that region. We know that in triploids only two of the three chromosomes are synapsed at a given level, with the third chromosome acting as an univalent (cytological observations on plant sporocytes), while the Drosophila genetic data show that crossing over occurs between only two of the three chromosomes at any level. Therefore, in a short region we can have only one crossover point in triploids and only one in diploids. If we wish to compare the total amount of crossing over for a given region in triploids with that in diploids we must bear in mind that what we have to measure is the frequency with which crossover points actually occur in that region rather than the frequency with which crossover strands are found in the progeny. Since the proportion of crossover chromosomes recovered from a crossover point in triploids is not the same as in diploids, as shown on page 546, this difference must be taken into account. The writer believes that the proper way to "compare the actual amount of crossing over in triploids with that in diploids" is to compare the actual frequency of crossover points in the two forms rather than the resulting frequencies of types observed in the progeny. In other words, if we are to reach a real understanding of crossing over, we should study the mechanism involved and not confine our attention to the results of its action. It is upon these grounds that it is suggested that REDFIELD failed to use the proper correction factor, since

she explicitly stated that she was making the corrections to obtain the actual amount of crossing over in triploids.

All of the foregoing calculations have been based on the assumption that there was a random distribution of the three chromosomes in the first meiotic division. What would be the consequences if there should be a correlation, either positive or negative, between crossing over and disjunction? The data presented in this paper do not aid in solving this question but the Drosophila triploid data can be utilized. BRIDGES and ANDERSON (1925) studied crossing over in the X chromosome of triploid Drosophila. The three X chromosomes carried mutant genes so situated that the identity of a considerable portion of any of the recovered strands could be established. Approximately 41 percent of the progeny from a triploid mother are diploid females whose two X chromosomes come from their mother. These females are XXY in constitution and are called exceptional daughters since both of their X chromosomes came from their mother. These exceptional daughters were mated and the constitution of their X chromosomes determined from their male offspring. The analysis of the genotypic constitution of the exceptional daughters permitted a calculation of the amount of crossing over which occurred in the triploid mothers. These crossover values were then compared with the values found for the same regions in the diploid controls.

*Comparison between triploid and diploid crossing over for the X chromosome (after* BRIDGES *and* ANDERSON *1925)*

| REGION | TRIPLOID CROSSOVER VALUE | DIPLOID CROSSOVER VALUE | RATIO $\frac{T}{D}$ |
|---|---|---|---|
| 1 | 14.3 | 6.9 | 2.07:1 |
| 2 | 11.3 | 22.8 | 0.50:1 |
| 3 | 3.9 | 10.1 | 0.39:1 |
| 4 | 8.2 | 16.2 | 0.51:1 |

For the rightmost regions (nearest the spindle fiber) the ratio of triploid to diploid crossing over was about 1:2, while for the leftmost region the ratio was approximately 2:1. These ratios point to a real difference in the amount of crossing over in triploid and diploid females. But it is important to remember that the triploid values were calculated from those eggs which had received two maternal X chromosomes.

REDFIELD (1930, 1932) studied crossing over in the II and III chromosomes in triploid females. The amount of crossing over in the triploids was based on the constitution of those eggs which received a single chromosome from the mother. The calculated amounts of crossing over, using the correction factor 3/2, in the triploid for the various regions studied are compared below with the crossover values for the diploid control females.

*Comparison of triploid and diploid crossover values for the II chromosome (after* REDFIELD *1932)*

| REGION | TRIPLOID CROSSOVER VALUE | DIPLOID CROSSOVER VALUE | QUOTIENT $\frac{T}{D}$ |
|---|---|---|---|
| *al-dp* | 8.3 | 10.0 | 0.83 |
| *dp-b* | 16.2 | 27.2 | 0.59 |
| *b-pr* | 7.4 | 5.7 | 1.30 |
| *pr-c* | 27.1 | 19.2 | 1.41 |
| *c-px* | 13.0 | 22.1 | 0.59 |
| *px-sp* | 4.4 | 5.7 | 0.77 |

*Comparison of triploid and diploid crossover values for the III chromosome (after* REDFIELD *1930)*

| REGION | TRIPLOID CROSSOVER VALUE | DIPLOID CROSSOVER VALUE | QUOTIENT $\frac{T}{D}$ |
|---|---|---|---|
| *ru-h* | 19.5 | 25.3 | 0.77 |
| *h-th* | 14.9 | 15.3 | 0.97 |
| *th-st* | 1.2 | 0.4 | 3.00 |
| *st-cu* | 21.2 | 5.6 | 3.79 |
| *cu-sr* | 14.6 | 14.0 | 1.04 |
| *sr-es* | 6.1 | 8.9 | 0.69 |
| *es-ca* | 18.0 | 34.3 | 0.52 |

The location of the spindle fiber in the II chromosome is slightly to the right of *pr* while the spindle fiber is situated between *st* and *cu* in the III chromosome. Therefore, we see that in REDFIELD'S experiments where her calculations of triploid crossing over are based on the constitution of those eggs which received a single chromosome the calculated amount of crossing over near the insertion region in triploids is higher than for the corresponding regions in diploids. The relative amount of crossing over in triploids in the distal regions of the II and III chromosomes is less than in the diploid controls. These results are the converse of those found by BRIDGES and ANDERSON. Since REDFIELD'S calculations were based on those eggs which received a single strand while BRIDGES and ANDERSON'S were obtained from those eggs which received two strands it seemed plausible to the writer that there might be a direct relationship between crossing over in triploids and the distribution of the members of the trivalent group. Especially did this seem likely since ANDERSON'S (1929) data showed that non-disjunction of the two X chromosomes in diploid females was more likely to happen if there was little or no crossing over between the two chromosomes. To tell if there is a correlation between crossing over and disjunction in triploids it is best to study both those eggs which receive a single strand and those which receive two strands. Unfortunately the published data do not permit such a direct comparison but the data of BRIDGES and ANDERSON on the types of association in the two chromosome combinations do permit some tentative conclusions to be drawn.

We will for the present confine our interest to the rightmost regions

(nearest the spindle fiber) studied by BRIDGES and ANDERSON. Assume that a crossover occurs between chromosomes a and b near the insertion region. We know that only one of the chromatids from chromosome a and only one chromatid from chromosome b are involved in the crossover. The two chromatids from chromosome c are not involved in any crossover in this region (BRIDGES and ANDERSON). The identity of the six strands following the crossing over is as follows: a a

b a′

a′ b

b′ b′

c c

c′ c′

If we assume that crossing over near the insertion region has no effect on the distribution of the chromosomes, then six types of combinations are possible at the end of the first meiotic division (we are arbitrarily assuming that reduction occurs at the first division since it is immaterial whether the first or second division is reductional for the insertion region). After the second (equational) division 24 combinations are expected with equal frequencies. The "two chromosome" combinations containing crossover strands can be classified into the following types of association:

| *Types of association* | | *Frequency* |
|---|---|---|
| crossover | b a | 4 |
| dissimilar non-crossover | c c | |
| crossover | b a | 2 |
| similar non-crossover | b b | |
| complementary crossover | b a | 1 |
| complementary crossover | a b | |

The single chromosome combinations are composed of 4 crossover to 8 non-crossover strands and the percentage of crossover strands is 33.3 among the single strands. There are twelve "two chromosome" combinations which comprise a total of 24 strands. Eight of these are crossover chromosomes so the percentage of crossover strands is here also 33.3. Therefore if the distribution of the three chromosomes (six chromatids) is not influenced by crossing over near the insertion region the same amount of crossing over should be found in both types of eggs.

But assume that crossing over near the insertion region does have an effect on the distribution of the chromosomes and, since ANDERSON'S 1929 data gives such an indication, further assume that if two chromosomes undergo crossing over near their insertion regions they always pass to

different poles. As before the identity of the six strands following the postulated crossover is:

| | |
|---|---|
| a | a |
| b | a′ |
| a′ | b |
| b′ | b′ |
| c | c |
| c′ | c′ |

But since the mode of disjunction has been determined by the previously occurring crossover we have only four instead of six combinations at the end of the first division. And instead of 24 combinations only 16 are expected at the end of the second division. The "two chromosome" combinations containing crossover strands can be resolved into the three types of association:

| | | *Frequency* |
|---|---|---|
| crossover | b a | 4 |
| dissimilar non-crossover | c c | |
| crossover | b a | 0 |
| similar non-crossover | b b | |
| complementary crossover | b a | 0 |
| complementary crossover | a b | |

There are 16 strands in the "two chromosome" combinations and 4 of these are crossover chromosomes which is a percentage of 25.0. Among the single strand combinations the number of crossover strands is 4 out of a total of 8 or a percentage of 50.0. Obviously if there is a correlation between crossing over near the insertion and distribution, it makes a great difference in the observed crossover values which class of eggs are studied. With complete correlation and using those eggs which received two chromosomes the amount of crossing over would be only one-half that which would be found if the eggs with only one chromosome were used. BRIDGES and ANDERSON found the amount of crossing over in the rightmost region in the triploid mother was only one-half that in the diploid. Their calculations were based on those eggs which received two chromosomes. REDFIELD, working with eggs which received a single chromosome, found the amount of crossing over in the regions near the spindle fiber to be from one and one-half to more than three times as much as in the diploid controls. It would seem that such differences might have some relation to crossing over and the manner of disjunction.

In table 12 of the paper by BRIDGES and ANDERSON (1925) are listed the various associations of crossover chromosomes from triploid females. As stated before if there is no correlation between crossing over

and disjunction there should be for regions near the insertion region a ratio of $4\frac{b\ a}{c\ c}:2\frac{b\ a}{b\ b}:1\frac{b\ a}{a\ b}$ combinations. With complete correlation the ratio should be $4\frac{b\ a}{c\ c}:0\frac{b\ a}{b\ b}:0\frac{b\ a}{a\ b}$. The data of BRIDGES and ANDERSON for their rightmost region, the right end of which is approximately ten units from the fiber, show $23\frac{b\ a}{c\ c}:1\frac{b\ a}{b\ b}:3\frac{b\ a}{a\ b}$ combinations. This is far from the 4:2:1 ratio expected with random disjunction and strongly supports the idea that there is a positive correlation in triploids between crossing over near the fiber and disjunction to opposite poles. In fact the correlation may be complete for regions very near the fiber as the deviation from the 4:0:0 ratio for the rightmost region may well be due to the fact that it was some 10 units from the end. Their data also show that for the leftmost region the approximation to a $4\frac{b\ a}{c\ c}:2\frac{b\ a}{b\ b}$ ratio is very close, which suggests that the effect of crossing over on disjunction is dissipated progressively away from the fiber. This would be expected.

If there exists a positive correlation between crossing over and disjunction the association of strands in the diploid eggs would be such that the percentage of exceptional daughters homozygous for a recessive gene whose locus is near the fiber end would be low, approaching zero as a limit. But since the effect of crossing over on disjunction becomes less away from the spindle fiber attachment point the percentages of exceptions homozygous for genes in the distal end should increase progressively. Only 1.1 percent of the exceptional daughters in BRIDGES' and ANDERSON'S data were homozygous for point V (*f*, *B*, +), approximately 10 units from the fiber, while 11.5 percent of them were homozygous for point I (*y*, *sc*, +), which is about 70 units from the fiber attachment point. RHOADES (1931) in a study of homozygosis in diploid females with attached X's, where crossing over cannot affect disjunction since that is predetermined, found 19.0 percent of the exceptional daughters homozygous for yellow (*y*) and about 5 percent of homozygosis for forked (*f*). The ratio of homozygosis for *y* and *f* in the attached X data is 3.8:1 while it is 10.4:1 in the triploid data. It is possible that this difference is due, in part at least, to the correlation between crossing over and disjunction in triploids. The marked differences in coincidence values in triploids and diploids found by BRIDGES and ANDERSON should also affect the frequencies of homozygosis.

Although the relation of crossing over to disjunction is admittedly more complex in V shaped chromosomes than in rod shaped it seems to the writer that the regional differences in crossing over between triploids and

diploids reported by REDFIELD and by BRIDGES and ANDERSON cannot be accepted until the possible relationship between crossing over and disjunction has been considered, and if the writer is correct in his argument, until the proper factor for undetected crossovers has been used. The correction factor for the distal regions in REDFIELD'S data should then be 2.25 instead of 1.5. We must assume, however, that there is for these regions no effect of crossing over on disjunction. For those regions near the insertion and where a strong correlation between crossing over and disjunction presumably exists the correction factor is 1.5. The difference in the correction factors for the distal and proximal regions is due to the correlation between crossing over and disjunction which results in a higher percent of crossovers in the proximal regions going to the haploid eggs. The correction factors for intermediate regions lies somewhere between these two values.

The above correction factors are to be used when only one of the three chromosomes is marked by mutant genes. If all three of the chromosomes are properly populated with mutant genes so that crossing over can be detected between all of the three homologues, different correction factors must be used. The correction factor for regions near the insertion becomes 1.0 while for distal regions, where no correlation exists between crossing over and disjunction, the correction factor should be 1.5. These correction factors are to be used when those eggs which receive a single chromosome are studied. If, as BRIDGES and ANDERSON did, those eggs which receive two chromosomes are studied, and all three of the chromosomes are marked by mutant genes, the correction factor for regions near the insertion should be 2.0 and for the distal regions it should be 1.5. If these correction factors are applied to BRIDGES' and ANDERSON'S data the amount of crossing over near the insertion is approximately the same in triploids as in diploids, while the amount of crossing over in the leftmost region of the X chromosome becomes even greater in triploids than in diploids.

The corrected percent of recombination of 39.3 for the *pr*–$v_2$ region was determined from the diploid offspring listed in table 2 of this paper but the correction factor used in obtaining this value was 1.5. As pointed out in a preceding section it is in close agreement with the percent of recombination found in the disomic controls and would seem to permit the conclusion that the amount of recombination in this region was approximately the same in trisomes and disomes. But if the factor 1.5 is not the one to use, as the writer argues, the corrected value of 39.3 is incorrect and a recalculation must be made using the proper correction factor. Since $v_2$ is some distance from the insertion region the correction factor should probably be much nearer 2.25 than 1.5.

## ADDENDUM

Recently MATHER (1933) attempted to calculate the frequency of chiasmata in triploid Drosophila. He used crossover values from REDFIELD'S data which were based upon the constitution of the diploid offspring. His calculations led him to conclude that there was an excess of crossover chromosomes among the diploid progeny. To account for this calculated excess of crossovers he postulates that in triploids the three homologous chromosomes are associated as a trivalent group in two-thirds of the cases and in the remaining one-third as a bivalent and an univalent. Since crossing over can only occur between the members of the bivalent, and the univalent will pass at random to either pole, this would lead to an excess of crossovers among the diploid progeny.

The writer agrees with MATHER that there is an excess of crossovers among the diploid progeny. He does not, however, entirely agree with MATHER'S explanation of their occurrence although it is both possible and probable that some of the excess crossovers are caused by the formation of some bivalents and univalents instead of trivalent groups. But before accepting MATHER'S explanation the following facts should be mentioned:

(1) The excess of crossovers among the diploid offspring could be at least partially accounted for by the correlation between crossing over near the insertion and disjunction.

(2) The data of BRIDGES and ANDERSON (1925) and REDFIELD (1932) show that the two types of double crossovers (recurrent and progressive) occur with approximately equal frequency. This suggests that the frequency with which the three homologous chromosomes have failed to synapse so as to form a trivalent group at metaphase I is low (assuming the occurrence of a univalent is due to its failure to pair with the other two homologues in the meiotic prophases).

(3) MATHER'S assumption of univalents being formed in $33\frac{1}{3}$ percent of the cases is not universally valid since the frequency of trivalents at metaphase I in maize plants trisomic for the $pr-v_2$ chromosome is approximately 90 percent.

## SUMMARY

1. The occurrence of chromatid or double strand crossing over in Zea was genetically demonstrated by the determination of the genotypic constitution of certain trisomic types.

2. The frequencies of homozygosis for *pr* and $v_2$ indicate that $v_2$ is much further removed from the insertion region than is *pr*.

3. The effect of chromatid crossing over upon genetic ratios in triploids and trisomes is discussed.

4. Genetic proof was obtained for the occurrence of the doubling of the entire chromosome set in the gametophytic generation.

5. The genetic data obtained by BRIDGES and ANDERSON, and REDFIELD for triploid Drosophila is discussed with reference to a possible correlation between crossing over in triploids and disjunction. Certain data of BRIDGES and ANDERSON are presented in support of a positive correlation between crossing over and disjunction.

6. REDFIELD'S treatment of her triploid data is discussed and the suggestion is made that she failed to use the proper correction factor for undetected crossing over. It is further suggested that the triploid data of BRIDGES and ANDERSON should also be corrected.

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