2.2 Recombination (Crossing over):

Definition, Types , Mechanism of crossing over, Significance

Introduction

The linkage is caused due to linked genes borne on the same chromosome.

Morgan pointed out that the phenomenon of complete linkage occurs rarely because sometimes the linked genes show the tendency to separate during meiosis and new combinations are formed.

This is due to interchange of parts between two homologous chromosomes for which the term "crossing over" is used.

In the linkage experiment with maize, it is seen that the genes for seed colour C and full seed S remain associated in the parental combination in about 96 percent but break apart in about 4 percent. This recombination of linked genes to interchange parts between homologous chromosomes is termed as crossing over.

Crossing over, in other terms, is the exchange of segments observed in homologous chromosomes between non-sister chromatids and takes place during the pachytene stage of the prophase I in the **cell division** process of meiosis and always takes place within linked genes. The recombination of linked genes that crossing over produces plays a significant role in evolution.

Recombination

Recombination is a process of producing new combinations of alleles by the recombination of DNA molecules. It is also referred to as genetic recombination, as there is an exchange of genetic material (DNA) between two different chromosomes or between different regions of the same chromosome. This process is observed in both eukaryotes and prokaryotes. It increases the genetic diversity of sexually reproducing organisms.

Definition-

Crossing over may be defined as a "mechanism of the recombination of the genes due to interchange of chromosomal segments at the time of pairing."

chromatids of homologus chromosomes during meiotic prophase (pachytene). In other words, crossing over results from exchange of genetic material between non-sister chromatids involving breakage and reunion at precise point. The term crossing over was first used by Morgan and Cattell in 1912.

Feature of Crossing Over:

The main features of crossing over are given below:

1. Crossing over takes place during meiotic prophase, i.e., during pachytene. Each pair of chromosome has four chromatids at that time.

2. Crossing over occurs between non-sister chromatids. Thus one chromatid from each of the two homologus chromosomes is involved in crossing over

3. It is universally accepted that crossing over takes place at four strand stage.

4. Each crossing over involves only two of the four chromatids of two homologus chromosomes. However, double or multiple crossing over may involve all four, three or two of the four chromatids, which is very rare.

5. Crossing over leads to re-combinations or new combinations between linked genes. Crossing over generally yields two recombinant types or crossover types and two parental types or non-crossover types.

6. Crossing over generally leads to exchange of equal segments or genes and recombination is always reciprocal. However, unequal crossing over has also been reported.

7. The value of crossover or recombinants may vary from 0-50%.

8. The frequency of recombinants can be worked out from the test cross progeny. It is expressed as the percentage ratio of recombinants to the total population (recombinants + parental types). Thus,

$$\text{Crossing over frequency (\%)} = \frac{\text{No. of recombinants}}{\text{Total progeny}} \times 100$$

Chiasma and Crossing Over:

The point of exchange of segments between non-sister chromatids of homologous chromosomes during meiotic prophase is called chiasma (pleural chiasmata).

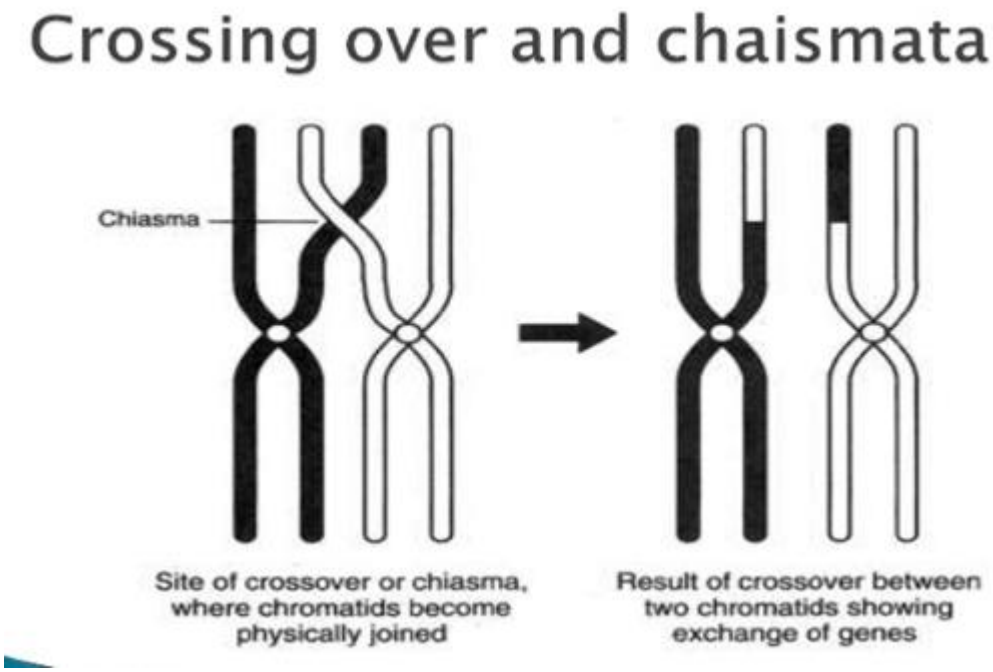
It is thought to be the place where crossing over takes place. Chiasma was first discovered by Janssens in 1909.

Depending on the position, chiasma is of two types, viz., terminal and interstitial.

When the chiasma is located at the end of the pairing chromatids, it is known as terminal chiasma and when it is located in the middle part of non-sister chromatids, it is referred to as interstitial chiasma.

Later on interstitial chiasma is changed to terminal position by the process of chiasma terminalization.

The number of chiasma per bivalent may vary from one to more than one depending upon the length of chromatids. When two chiasmata are formed, they may involve two, three or all the four chromatids.

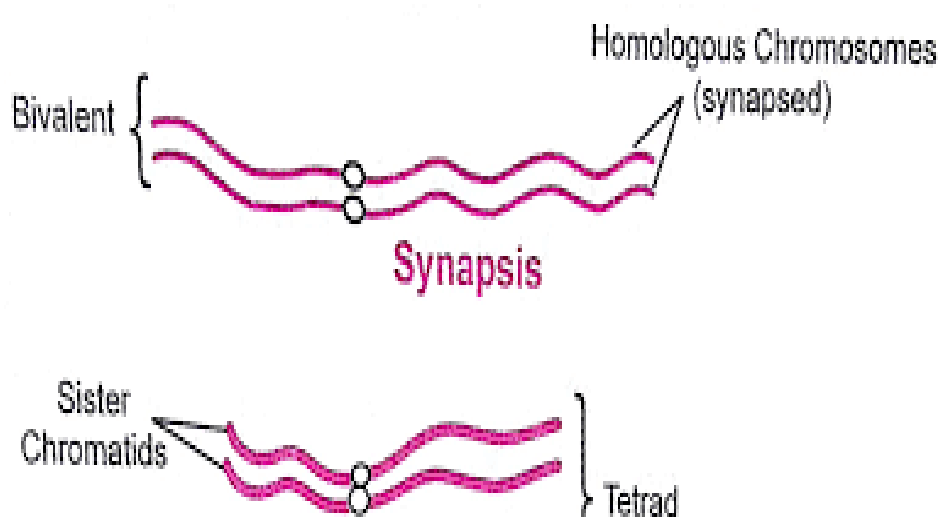


Mechanism of crossing-over:

Mechanism of crossing-over can be explained under the following heads:

(i) Synapsis:

The homologous chromosomes pair lengthwise due to a force of mutual attraction in zygote of prophase-I in meiosis.



The pairing starts at one or more points and proceeds along the whole length in a zipper fashion. The process of pairing is called synapsis. The paired homologous chromosomes are called bivalents. During synapsis, a molecular scaffold called synaptonemal complex aligns the DNA molecule of two homologous chromosomes side by side.

This pairing phenomenon is called **synapsis or syndesis.** It is of three types,

1. Procentric synapsis: Pairing starts from middle of the chromosome.

2. Proterminal synapsis: Pairing starts from the telomeres.

3. Random synapsis: Pairing may start from anywhere.

Tetrad Formation

Each homologous chromosome of a bivalent begins to form two identical sister chromatids, which remain held together by a centromere. At this stage each bivalent has four chromatids. This stage is called **tetrad stage**.

ii) Duplication of chromosomes:

Synapsis is followed by the duplication of chromosomes which changes the bivalent nature of chromosome to four- stranded stage or tetravalent. Four stranded stage (Fig. 5.48) of chromatids occurs due to splitting of homologous chromosomes into sister chromatids attached with un-splitted centromeres.

(iii) Crossing-over:

In pachytene, crossing over occurs. Non-sister chromatids of homologous pair twist over each other due to action of enzyme endonuclease. The chromatids get connected with each other at points known as chiasmata.

The crossing over can take place at several points. The number of chiasmata formed is proportional to the length of chromatids. The genes at distant loci undergo crossing-over but closely placed genes fail to cross-over and exhibit the phenomenon of linkage.

iv) Terminalization

During diakinesis of prophase-I chiasmata move towards the end of bivalent by a process called terminalization. Thus twisting chromatids separate so that the homologous chromosomes are separated completely.

At anaphase – 1 of meiosis, the homologous chromosomes separate. It is evident that one of the chromatids of each chromosome carries a portion of chromatid from its homologous chromosome. At the end of meiosis, four types of gametes are formed. Two will be of parent types and two will contain chromosomes with recombination of genes formed during crossing- over.

Types of Crossing Over:

Depending upon the number of chiasmata involved, crossing over may be of three types, viz., single, double and multiple as described below:

i. Single Crossing Over:

It refers to formation of a single chiasma between non-sister chromatids of homologous chromosomes. Such cross over involves only two chromatids out of four.

ii. Double Crossing Over:

It refers to formation of two chiasmata between non-sister chromatids of homologous chromosomes. Double crossovers may involve either two strands or three or all the four strands. The ratio of recombinants and parental types under these three situations are observed as 2:2:3:1 and 4 : 0, respectively.

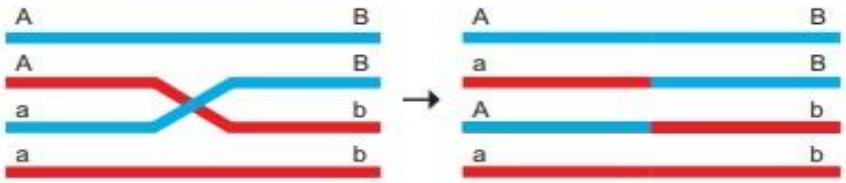
iii. Multiple Crossing Over:

Presence of more than two crossovers between non-sister chromatids of homologous chromosomes is referred to as multiple crossing over. Frequency of such type of crossing over is extremely low.

No cross over

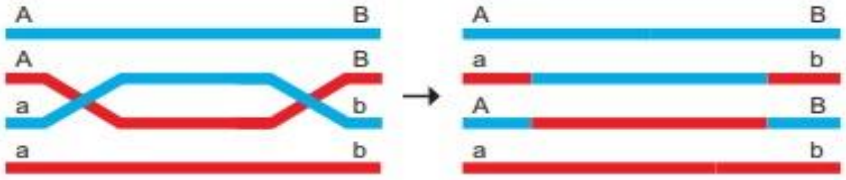
$$RF = \frac{0}{4} X100 = 0\%$$

Single cross over



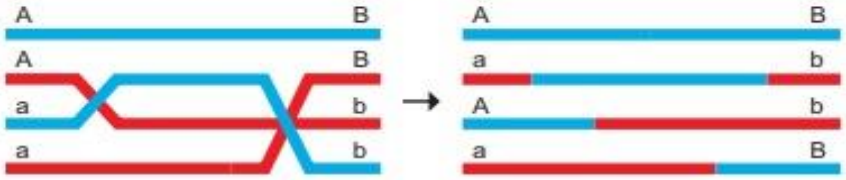
$$RF = \frac{2}{4} X100 = 50\%$$

Two strand double cross over



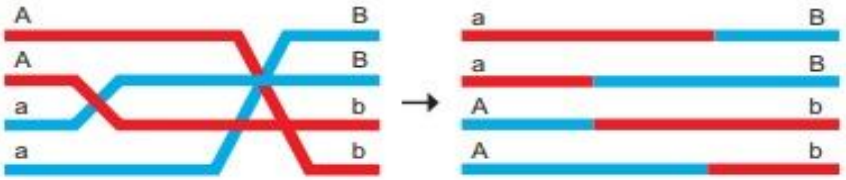
$$RF = \frac{0}{4} X100 = 0\%$$

Three strand double cross over



$$RF = \frac{2}{4} X100 = 50\%$$

Four strand double cross over



$$RF = \frac{4}{4} X100 = 100\%$$

Figure 3.11: Types of crossing over and its Recombination Frequency (RF)

Example-

In the linkage experiment with maize, it is seen that the genes for seed colour C and full seed S remain associated in the parental combination in about 96 per cent but break apart in about 4 per cent (see Fig. 5.8). This recombination of linked genes to interchange parts between homologous chromosomes is termed as crossing over.

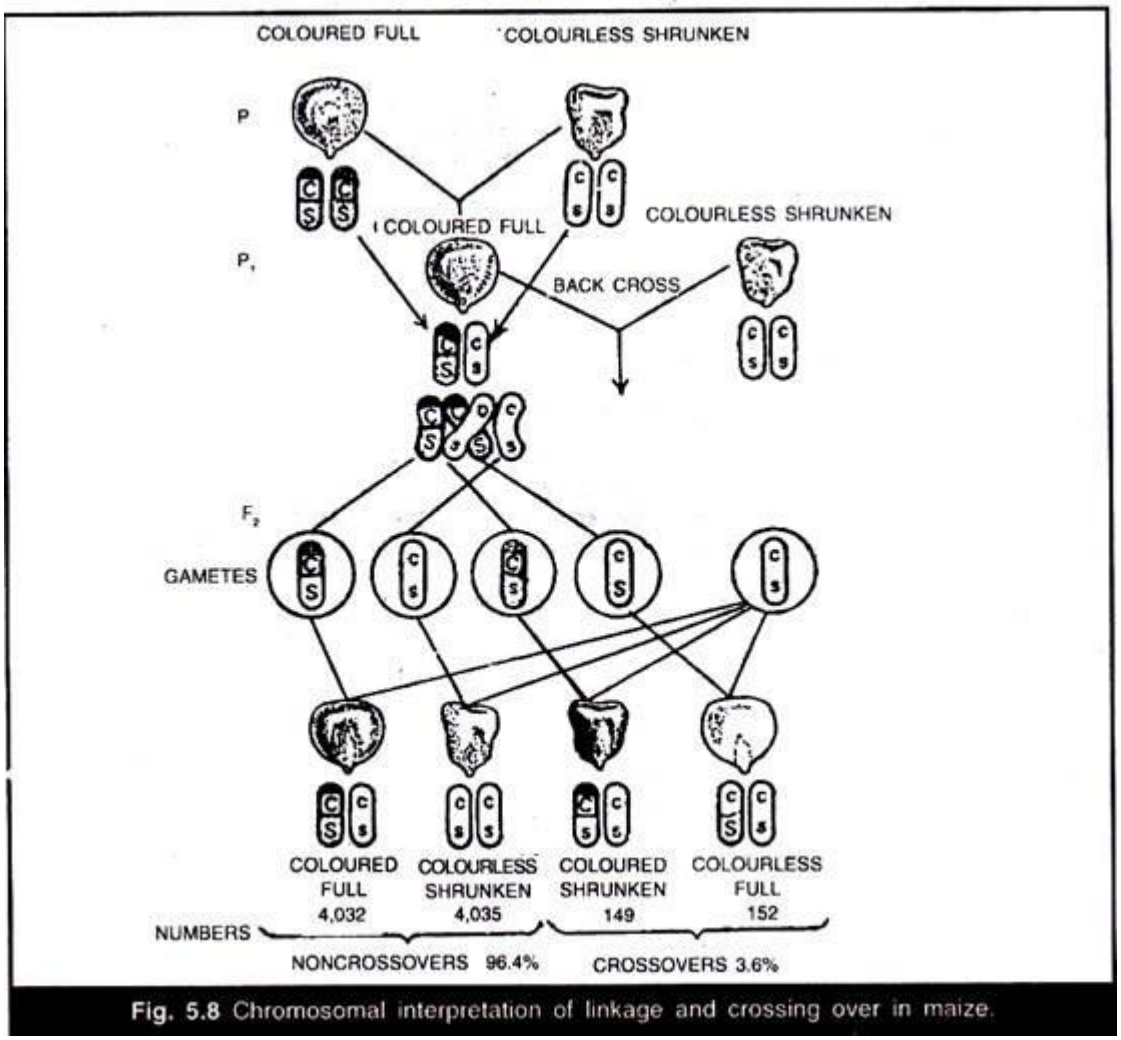


Fig. 5.8 Chromosomal interpretation of linkage and crossing over in maize.

Breakage and Reunion Theory:

This theory states that crossing over takes place due to breakage and reunion of non-sister chromatids. The two segments of parental chromosomes which are present in recombinants arise from physical breaks in the parental chromosomes with subsequent exchange of broken segments (Fig. 9.2).

The breakage results due to mechanical strains that result from the separation of paired homologous chromosomes and chromatids in each chromosome during pachytene stage. The broken ends of non-sister chromatids unite to produce chiasmata resulting in crossing over.

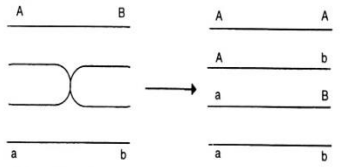
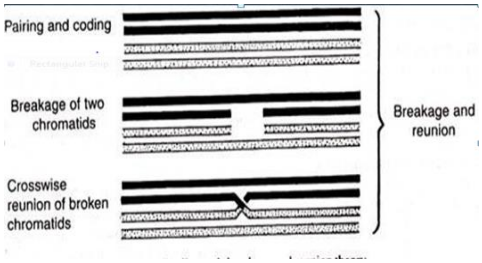


Fig. 9.2. Crossing over according to breakage and reunion theory.



Chromosome Mapping:

Chromosome map refers to a line diagram which depicts various genes present on a chromosome and recombination frequency between them. Such maps are also known as genetic maps or linkage maps. The process of assigning genes on the chromosomes is known as chromosomal mapping.

The mapping of chromosomes is done with the help of three point test cross. A three point test cross is a cross of a trihybrid (F_1 differing in three genes) with its homozygous recessive parent.

Genetic Mapping

Genes are present in a linear order along the chromosome. They are present in a specific location called **locus** (plural: loci). The diagrammatic representation of position of genes and related distances between the adjacent genes is called **genetic mapping**. It is directly proportional to the frequency of recombination between them. It is also called as **linkage map**. The concept of gene mapping was first developed by Morgan's student **Alfred H Sturtevant** in 1913. It provides clues about where the genes lies on that chromosome.

Map distance

The unit of distance in a genetic map is called a **map unit** (m.u). One map unit is equivalent to one percent of crossing over (Figure 4.). One map unit is also called a centimorgan (cM) in honour of **T.H. Morgan**. 100 centimorgan is equal to one Morgan (M). For example: A distance between A and B genes is estimated to be 3.5 map units. It is equal to 3.5 centimorgans or 3.5 % or 0.035 recombination frequency between the genes.

Genetic maps can be constructed from a series of test crosses for pairs of genes called **two point crosses**. But this is not efficient because double cross over is missed.

Three point test cross

The three point test cross provides useful information on two important aspects, viz:
(1) About the sequence of genes, and

(2) About the recombination frequencies between genes. This information is essential for mapping of chromosomes.

A more efficient mapping technique is to construct based on the results of three-point test cross. It refers to analyzing the inheritance patterns of three alleles by test crossing a triple recessive heterozygote with a triple recessive homozygote. It enables to determine the distance between the three alleles and the order in which they are located on the chromosome. Double cross overs can be detected which will provide more accurate map distances.

Significance of Crossing Over:

Crossing over occurs in all organisms like bacteria, yeast, fungi, higher plants and animals. Its importance is

- Through crossing over segments of homologous chromosomes are interchanged and hence provide origin of new characters and genetic variations. Exchange of segments leads to new gene combinations which plays an important role in evolution.

- Studies of crossing over reveal that genes are arranged linearly on the chromosomes. Linkage group and linear order of the genes help to reveal the mechanism and nature of the genes.

- Genetic maps are made based on the frequency of crossing over. Crossing over has led to the construction of linkage map or genetic maps of chromosomes
- Crossing over helps to understand the nature and mechanism of gene action.
- If a useful new combination is formed it can be used in plant breeding to improve the varieties of plants and animals.