

3. Inversions: Inversions would involve two breaks followed by reunion of interstitial segment in a reverse order i. e., the segment rotates by 180° . Gene sequence in an inverted segment is exactly the opposite of that in its normal homologous pair.

(Let us imagine that a chromosome 1-2-3-4-5-6-7-8 gives rise to another chromosome having the order 1-2-6-5-4-3-7-8. the segment 3-4-5-6 has rotated here at 180° giving an inverted order of genes 6-5-4-3)

Inversions can be of two types depending upon whether centromere is involved or not in inversions.

(a) Paracentric inversions and (b) Pericentric inversions.

3. Differentiate between paracentric inversion and pericentric inversion

Paracentric inversion	Pericentric inversion
1. Inverted segment do not include centromere and hence involves only one arm of the chromosome	1. Inverted segment include centromere. Since centromere is involved, both arms of the chromosome are involved in this type of inversion (pericentric means surrounding the centromere or on the periphery of centromere).
2. Crossing over within the inversion loop results in the formation of a dicentric bridge (chromatids having two centromeres) and acentric fragment at anaphase-1	No dicentric bridge (chromatids having two centromeres) and acentric fragment are formed at anaphase-1
3. The crossover products (meiotic products or gametes) are non viable due to chromosomal deletions	The crossover products (meiotic products or gametes) are non viable due to chromosomal deletions and duplications

Why paracentric inversions are called crossover suppressors?

The products of single crossing over will not function and the only crossover products recovered will be double cross overs, the observed frequency of recombination between any two genes of interest will be considerably reduced. Due to this reason, inversions (especially paracentric inversions) are often called crossover suppressors. This reduction in crossing over is not the actual reduction in cytological crossing over, but is the result of lack of recovery of the products of single cross overs (that is gametes of single cross overs are non-viable). This property of inversion has been utilized in the production of CIB stock used by Muller for the detection of sex-linked lethal mutations in Drosophila melanogaster.

Cytology of inversions: When both the members of a homologous pair have similar type of inversion, it is called inversion homozygote. Meiosis is normal in inversion homozygotes and hence produce viable gametes. When only one chromosome of a homologous pair has inversion it is called inversion heterozygote. Due to an inverted segment in one of the two homologous chromosomes, the normal kind of pairing is not possible in an inversion heterozygote. In order to enable pairing of homologous segments, a loop is formed by each of the two chromosomes. This kind of configuration will be observed in both paracentric as well as pericentric inversions. However, the products of crossing over and the subsequent stages of meiosis will differ in these two kinds of inversions.

However, in pericentric inversion, if the two breaks are not situated equidistant from the centromere, this will result in the change in shape of the chromosome. For instance, a metacentric chromosome may become sub-metacentric and vice-versa.

Genetic consequences of inversions

1. Simple inversions do not have primary effects other than change in chromosome shape.
2. **A peculiar kind of position effect occurs due to suppression of the transcription of Gene. This situation occurs when genes in euchromatin region come near to centromere due to inversion, the genes gets heterochromatinized and transcription is suppressed in the genes.**
3. **The general property of both types of inversions is the absence of normal linear pairing of homologous chromosomes in the region of inversion.** These pairing problems together with lack of recovery of single crossover gametes in an inversion heterozygotes contribute to reduction in the observed frequency of recombination between any two genes of interest. Due to this reason, **inversions are often called crossover suppressors**. The general property of inversion is the lack of recovery of viable gametes that has been utilized in the production of CIB stock used by Muller for the detection of sex-linked lethal mutations in *Drosophila melanogaster*.
4. **Heterozygosity will be maintained from generation to generation.**
5. Gametes (crossover products) obtained from paracentric inversion will have terminal deletions and gametes of pericentric inversions have deletions and duplications. Therefore gametes or

crossover products or meiotic products are non viable and cannot be recovered in inversion heterozygote. **In plants there will be sufficient pollen sterility.**

4. Shifts: Shifts are altered forms of inversions. In this type of aberrations, the genes are in the right order but a segment is shifted either to the right or to the left.

II. Interchromosomal aberrations : These are of the following types.

1. Translocation : Integration of a chromosome segment into a non-homologous chromosome is called translocation. It involves shifting of one part of chromosome to another non-homologous chromosome. The phenomenon of translocation was discovered by C.B. Bridges in 1923 in *Drosophila* and by Hugo de Vries in *Oenothera lamarckiana*.

Translocation is of two types

1. Simple translocation: In simple translocation, the terminal segment of chromosomes is integrated at one end of a non-homologous chromosome. However, they are rare.

2. Reciprocal translocation: If two non-homologous chromosome exchange segments which need not be of same size, it results in reciprocal translocation. Production of reciprocal translocation requires a single break in each of the two non-homologous chromosomes followed by reunion of the chromosome segments thus produced. An individual having reciprocal translocation may be either a translocation homozygote or a translocation heterozygote. When both the chromosomes from each pair are involved, it produces translocation homozygote and when only one chromosome from each pair of two homologues is involved, it gives rise to translocation heterozygote.

In a translocation homozygote, the two homologues of each of the two translocated chromosomes are identical in their gene content. As a result, they form normal bivalent and there is no detectable cytogenetic aberration (peculiarity). Gametes are viable.

In a translocation heterozygote, one member from each of two homologous pairs is involved in reciprocal translocation, while the remaining chromosomes of the two homologous pairs are normal. **Due to the pairing between homologous segments of chromosomes, a cross-shaped (+) figure involving four chromosomes will be observed at pachytene.** These four chromosomes at metaphase I will form a quadrivalent and follow mandels' law of segregation.

The three modes of segregation in a translocation heterozygote are as follows:

1. Alternate
2. Adjacent I
3. Adjacent II

1. **Alternate** : In this case, alternate chromosomes having non-homologous centromeres will orient towards the same pole. As a result, the two normal chromosomes move to one pole (chromosome 1 & 4), while the two translocated ones move to the opposite pole (chromosome 2 & 3). Such a segregation can take place only when the cross shaped figure of four chromosomes is twisted to form a figure of 'oo'. **Only the gametes formed due to alternate segregation are viable.**

2. **Adjacent-I**: In adjacent I orientation, adjacent chromosomes having non-homologous centromeres will orient towards the same pole. In the figure, chromosome 1 & 3 move to one pole while chromosomes 2 & 3 to another pole. Thus a ring of four chromosomes will be observed.

3. **Adjacent – II**: In adjacent II orientation, the adjacent chromosomes having homologous centromeres will orient towards the same pole, which is a rare occurrence. In the figure, chromosome 1 & 2 move to one pole while chromosomes 3 & 4 to another pole. In this case also a ring of four chromosomes will be observed.

In both Adjacent-I and adjacent-II disjunctions, one normal and one translocated chromosome move to the opposite poles. Adjacent-I and adjacent-II segregations will form gametes which would carry duplications or deficiencies and as a result gametes or zygotes formed are non-functional or sterile. Therefore, in a plant having translocation in heterozygous condition, there will be considerable pollen sterility as well as reduced yields.

Genetic significance of translocation heterozygotes:

1. The presence of translocation heterozygosity can be detected by the occurrence of semi-sterility and low seed set. Presence of 50% reduction in viable gametes or zygotes is an important diagnostic for translocation heterozygote.
2. Some genes which earlier assorted independently (that is, present on separate chromosomes) tend to exhibit linkage relationship.
3. The phenotypic expression of a gene may be modified when it is translocated to a new position in the genome.

4. The presence of translocation heterozygosity can be detected by the occurrence of semi-sterility and low seed set. This can then be confirmed at meiosis by quadrivalent formation. Functional gametes will be formed only from alternate disjunction, which will give rise to three kinds of progeny *viz.*, normal, translocation heterozygotes and translocation homozygotes in 1:2:1 ratio.

Role of structural chromosomal aberrations in plant breeding

1. Deletions are important cytological tools for mapping genes on chromosomes and eventually useful in the identification of chromosomes
2. Utilization of vigour as in case of duplication.
3. Useful in genome analysis.
4. Useful for the transfer of desirable characters through translocation. For instance, due to semi sterility or half-sterility of translocation heterozygotes, insect pests can be controlled by introducing translocations into wild populations.
5. They have evolutionary significance.

Isochromosome: Isochromosome is the one in which both the arms are identical in both gene content and morphology. It arises when the centromere divides in wrong plane yielding two daughter chromosomes each of which carries the information of one arm only but present twice.

Important notes for your understanding:

- Adjacent-1 and alternate segregation occurs equally and hence half of the gametes are incapable of contributing to the next generation, a condition known as semisterility or half sterility.
- Deletion and inversion (both paracentric and pericentric inversions) show some reduction in fertility, but exact 50% reduction in the viability of gametes or zygotes is an important diagnostic of translocation heterozygote.
- Both deletions and inversions in heterozygous state show characteristic loop.
The main diagnostic feature of inversion heterozygote is inversion loop, reduction of recombinant frequency and reduced fertility due to non-viable gametes.