

Notes

Programme: Bachelor of Science (Third Year – VI Semester)

Subject: Botany

Paper Code: BOC 108

Paper Title: Cytogenetics and Plant Breeding.

Unit IV: Linkage, crossing over and chromosome mapping

Module Name: Linkage, its types and significance

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Linkage

The coexistence of two or more genes in the same chromosome and their tendency to remain together in their original combination during inheritance is called linkage.

Each **chromosome** contains more than one gene. The genes for different characters may be either situated in the same chromosome or in different chromosomes. All genes present on a chromosome are said to be linked to one another.

When the genes are situated in different chromosomes, the characters they control appear in the next generation together or apart, depending on the chance alone. They assort independently according to Mendel's law of independent assortment.

Genes on different chromosomes assort independently according to Mendel's law of independent assortment.

P₁:	AA BB	X	aa bb
P₁ gametes:	(AB)		(ab)
F₁:		Aa Bb	
Test cross:	Aa Bb	X	aa bb
Gametes:	(AB) (Ab) (aB) (ab)		(ab)
F₂:	¼ Aa Bb : ¼ Aa bb : ¼ aa Bb : ¼ aa bb or 1 : 1 : 1 : 1		

But if the genes are situated in the same chromosome and are fairly close to each other, they tend to be inherited together. This type of coexistence of two or more genes in the same chromosome is known as linkage. The different genes on the same chromosome do not show independent assortment at meiosis. They show non- random assortment at meiosis.

Linked genes do not assort independently but tend to be inherited together in the same combinations as they were in parents.

P₁:	AB/AB	X	ab/ab
P₁ gametes:	(AB)		(ab)
F₁:		AB/ab	
Test cross:	AB/ab	X	ab/ab
Gametes:	(AB) (ab)		(ab)
F₂:	½ AB/ab : ½ ab/ab or 1 : 1		

Chromosomal theory of linkage by T.H.Morgan and Castle, explains the main principals of linkage.

- ✓ A chromosome contains many genes.
- ✓ The genes are arranged in a linear fashion on the chromosomes.
- ✓ These genes usually remain bounded by the chromosomal material so that they cannot be separated during the process of inheritance.
- ✓ These linked genes are inherited together from the parents to the offspring.
- ✓ The distance between the linked genes determines the strength of linkage. Closely located genes show strong linkage. Widely located genes show weak linkage.

Detection of linkage

Test cross is the most common method of detecting the linkage.

In this method, the F, heterozygous at two loci (AB/ab) is crossed to a double recessive parent (ab/ab) and the phenotypic ratio of test cross progeny is examined.

If the phenotypic ratio of test cross progeny shows 1:1:1:1 ratio of parental and recombinant genotypes, it indicates absence of linkage.

If the frequency of parental types and recombinant types deviate significantly from the normal dihybrid test cross ratio of 1:1:1:1, it reveals presence of linkage between two genes under study.

Linkage group

All the linked genes, located in a homologous pair of chromosomes constitute one linkage group.

The maximum number of linkage groups is equal to the haploid chromosome number of an organism.

For example there are ten linkage groups in corn ($2n = 20$), seven in garden pea ($2n = 14$), four in *Drosophila melanogaster* ($2n = 8$) and 23 in man ($2n = 46$).

Types of linkage

1. Complete linkage
2. Incomplete linkage

Complete linkage

The complete linkage is the phenomenon in which parental combinations of characters appear together for two or more generations in a continuous and regular fashion. In this type of linkage, genes are closely associated and tend to transmit together.

In 1919, T.H. Morgan mated gray bodied and vestigial winged ($b^+ vg/b^+ vg$) fruit flies with flies having black bodies and normal wings (bvg^+/bvg^+).

F1 progeny had gray bodies and normal long wings ($b^+ vg/bvg^+$), indicating thereby that these characters are dominant.

When F1 males ($b^+ vg/bvg^+$), were test crossed to double recessive females (bvg/bvg or black vestigial), only two types of progeny (one with gray bodies and vestigial wings, $b^+ vg/bvg$ and the other with black bodies and normal wings, bvg^+/bvg) were obtained in the ratio of 1:1, instead of four types of phenotypes.

P₁:	Gray, vestigial b^+vg/b^+vg	X	black, long bvg^+/bvg^+
P₁	(b^+vg)		(bvg^+)
gametes:			
F₁:	All gray, long b^+vg/bvg^+		
Test cross:	F ₁ male gray, long b^+vg/bvg^+	X	female black, vestigial bvg/bvg
Gametes:	(b^+vg) (bvg^+)		(bvg)
F₂:	$\frac{1}{2}$ Gray, vestigial (b^+vg/bvg) : $\frac{1}{2}$ black, long (bvg^+/bvg) or 1 : 1		

Incomplete linkage

The linked genes which are widely located in chromosomes and have chances of separation by crossing over are called incompletely linked genes and the phenomenon of their inheritance is called incomplete linkage.

The linked genes do not always stay together because homologous non-sister chromatids may exchange segments of varying length with one another during meiotic prophase. This sort of exchange of chromosomal segments in between homologous chromosomes is known as crossing over.

In *Zea mays* (maize) a case of incomplete linkage between the alleles for colour and shape of the seed has been observed by Hutchison.

When a maize plant with seeds having coloured and full endosperm (CS/CS) is crossed with another plant having recessive alleles for colourless, shrunken seeds (cs/cs), the F₁ heterozygotes are found with the phenotype of coloured, full and genotype of CS/cs.

When F₁ hybrid is test crossed with double recessive parent (cs/cs) four classes of offspring are obtained instead of two.

The test cross results are clearly showing that parental combination of alleles (e.g., CS/cs and cs/cs) are those expected from complete linkage and appear in about 96% cases, the other two are new combinations (e.g., Cs/cs and cS/cs) and appear in about 4% cases.

Thus, in 4% cases, crossing over has occurred between linked genes.

P₁:	Coloured, Full CS/CS	X	colourless, shrunken cs/cs
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P₁ gametes:	(CS)		(cs)
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F₁:	Coloured, full CS/cs
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Test cross:	Coloured, full CS/cs	X	colourless, shrunken cs/cs
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Gametes:	(CS)(cs)(Cs)(cS)		(cs)
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F₂: 48.2% Coloured, full (CS/cs); 1.8% Coloured, shrunken (Cs/cs)

48.2% colourless, shrunken (cs/cs); 1.8% colourless, full (cS/cs)

Significance of Linkage

The phenomenon of linkage reduces the possibility of variability in gametes unless crossing over occurs. i.e. Linkage reduces the chance of recombination of genes. It thus helps organism to maintain its parental, racial and other characters. For this reason, plant and animal breeders find it difficult to combine various characters. Linkage plays an important role in determining the nature of scope of hybridization and selection programmes.