GENETICS 4

LINKAGE

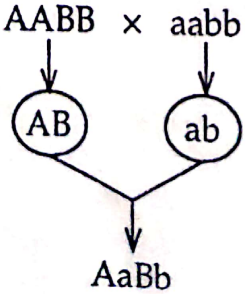
4.1 INTRODUCTION

It is universally accepted that genes are located in chromosomes. During cell division each chromosome behaves as a unit. It may, therefore, be expected that genes located in the same chromosome would move together to the same pole during cell division. As a consequence, such genes fail to show independent segregation and would to be inherited together. **This phenomenon of inheritance of genes together and to retain their parental combination even in the offsprings is known as linkage.** The genes located in the same chromosome and being inherited together are known as **linked genes.** The characters controlled by these genes are called *linked characters.*

The tendency of two or more genes to stay together during inheritance is known as linkage. Linked genes do not show independent segragation. As a consequence, the dihybrid ratios obtained in F_2 and test - cross generations are significantly different from the expected ratios of 9 : 3 : 3 : 1 and 1 : 1 : 1 : 1 respectively. The parental character combinations appear in much higher frequency than the recombinant phenotypes.

The difference between linkage and independent assortment could be understood by the following two examples :

Example (1) : Genes located on different chromosomes assort independently giving a 1 : 1 : 1 : 1 test cross progeny.



Test Cross : Aa Bb × aa bb

Gametes : (AB) (Ab) (aB) × (ab) (ab)

F_2 : Aa Bb : Aa bb : aa Bb : aa bb

1 : 1 : 1 : 1

Example (2) : Linked genes do not assort independently but tend to remain together in the same combination as they were in the parents. In the following example, the genes left to the slash line (/) are on one chromosome and those on the right are on the homologous chromosome.

Parents : AB/AB × ab/ab

(AB) (ab)

F_1 : AB/ab

Test Cross : AB/ab × ab/ab

Gametes : (AB) (ab) × (ab)

F_2 : AB/ab : ab/ab

1 : 1

4-2 DISCOVERY OF LINKAGE

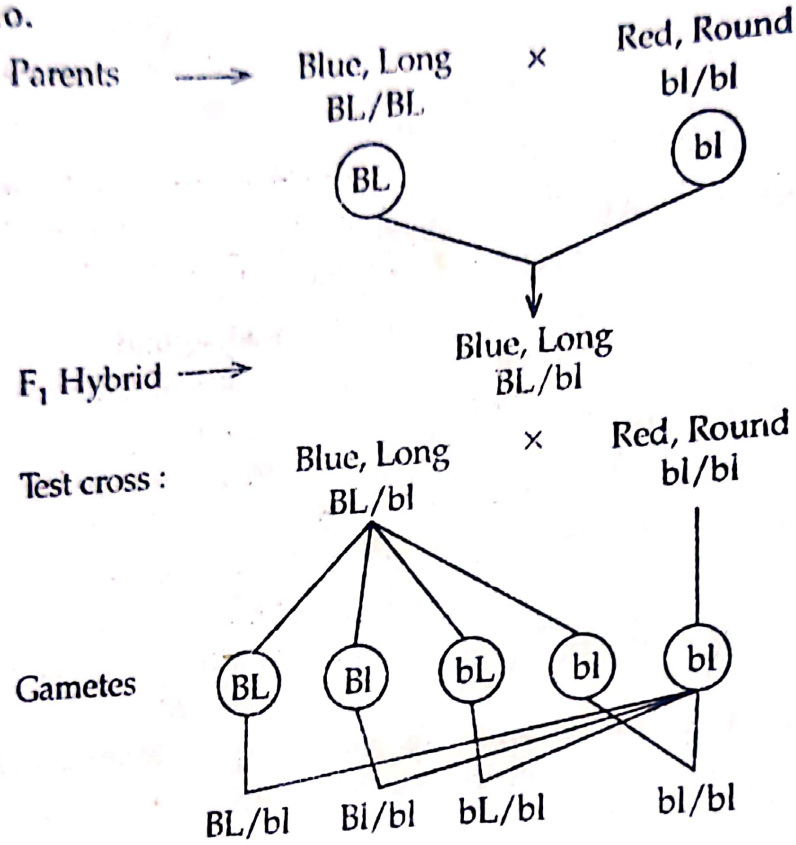
The theory of linkage was proposeded by T.H. Morgan in 1911. But, its existence was predicted even before that and was described below under different names :

1. Suttons Hypothesis : Sutton (1903) suggested that each chromosome bears more than one gene and all the genes situated in one chromosome are inherited together in the offsprings. This theory provideds a physical basis for heredity.

2. Coupling and Repulsion Hypothesis : The phenomenon of linkage was first observed by Bateson and Punnet in 1906 in pea plant. They formulated the hypothesis of 'coupling and repulsion' to explain the unexpected F_2 results of a dihybrid cross in peas.

(i) *Coupling phase* : Bateson and Punnet (1906) crossed a homozygons sweet pea (*Lathyrus odoratus*) having dominant alleles for blue/purple flowers (BB) and long pollen grains (LL) with another homozygous double recessive plant (bb ll) with red flowers and round pollen grains. All the F_1 offspring showed blue and long pollen (BL/bl).

According to law of independent assertment, the F_1 hybrid was expected to produce four types of gamets (BL/Bl/bL/bl) in equal number. Further when the F_1 hybrid was test crossed with the recessive parent (red and round pollen (bl/bl), the F_2 offspring showed a test cross ratio of 7 : 1 : 1 : 7 instead of normal 1 : 1 : 1 : 1 ratio.

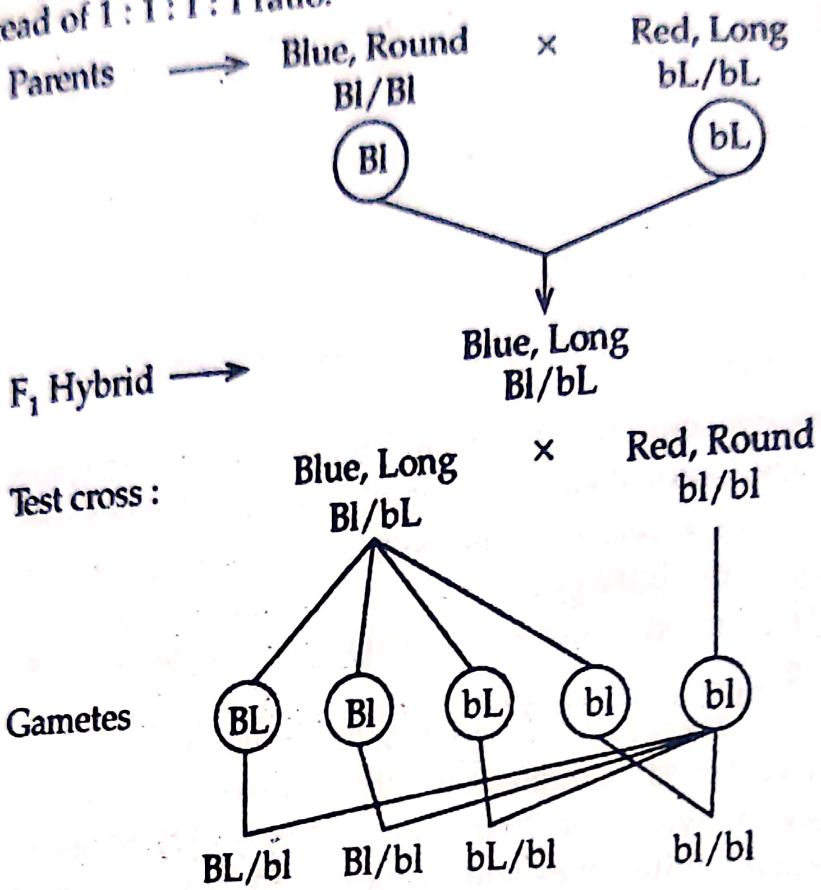


Test cross progeny :	Blue, long	Blue, Round	Red, Long	Red, Round
	7	1	1	7

The above results indicate that, the parental phenotypes (Blue, Long and Red, Round) are in greater proportion then the non - parental phenotypes (Blue, Round and Red, Long). This shows that the gametes with genes BL and bl are more common. *This tendenicy of the alleles coming from the same parent to enter the same gamete and to inherit together was termed as gametic coupling* by Bateson and Punnett.

(ii) *Repulsion Phase* : Later, Bateon and Punnet made another cross which involved the same characters but in a different combination. A pea plant bearing blue flowers and round pollen (Bl/Bl) was crossed with another pea plant having red flower and long pollen (bL/bL). The F_1 hybrids were found to be heterozygous

blue, long (Bl/bL). The F_1 hybrid when test crossed with recessive (bl/bl) parent, the test cross progeny appeared in 1 : 7 : 7 : 1 ratio instead of 1 : 1 : 1 : 1 ratio.



Test cross :	Blue, long	Blue, Round	Red, Long	Red, Round
Progeny :	1/16	7/16	7/16	1/16

The above results show that the two dominant alleles (B and L) or recessive alleles (b and l) repelled each other because they came from different parents. The gametes with genotypes Bl and bL were formed in more number. Hence, the Blue, Round and Red, Long plants were produced in more number. This peculiarity was called *Repulsion* by them.

Bateson and Punnett could not give the exact reasons for coupling and repulsion. It was MORGAN in 1910, who discovered that coupling and repulsion are essentially the two aspects of the same phenomenon called Linkage. The terms *Cis* and *Trans* were coined later (Haldane, 1942), for coupling and repulsion.

3. Morgan's concept of Linkage : T.H. Morgan (1910) while working on *Drosophila* found that coupling or repulsion was not complete. He further suggested that the two genes are found in coupling phase or in repulsion phase, because they are present on the

same chromosome (Coupling) or on two different homologous chromosomes (Repulsion). Such genes are called *linked genes* and the phenomenon of inheritance of linked genes is called *linkage* by Morgan.

Morgan further stated that the tendency of linked genes remaining together in original combination is due to their location in the same chromosome. According to him the degree or strength of linkage depends upon the distance between the linked genes in the chromosome. Morgan's concept about the linkage developed the theory of linear arrangement of genes in the chromosome. This helped the cytogeneticists in the construction of **genetic or linkage maps** of chromosomes.

4. Chromosome theory of Linkage : Morgan and Castle have formulated the Chromosome Theory of Linkage. It states that :

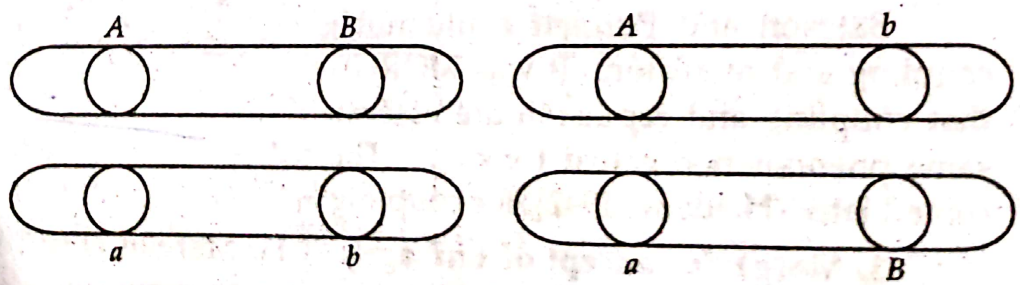
(i) Genes located in the same chromosome are inherited together and show linkage.

(ii) The linked genes are arranged in a linear fashion in the chromosome.

(iii) The degree of linkage is determined by the distance between the two genes. Linkage strength is inversely proportional to the distance between the two genes. Closely related genes show strong linkage, while genes widely located show weak linkage.

(iv) Linked genes show two types of arrangement in heterozygous individuals :

(a) *Cis - arrangement* : The dominant genes of both the pairs (A and B) are located in one member of the chromosome pair and their recessive alleles (a and b) are located in the other chromosome of the pair. This arrangement is known as *Cis - arrangement* (AB/ab). The heterozygotes with such arrangement are known as Cis - *heterozygotes*. In such cases, the genes are said to be in coupling phase.



Cis - heterozygote Trans - heterozygote

Fig. 4·1 : Cis-Trans arrangement of genes

(b) *Trans - arrangement* : The dominant gene of one pair and the recessive gene of other pair are located on one chromosome. The recessive gene of the first pair and the dominant gene of the second pair are located in the second chromosome pair (Ab/aB). This arrangement of one dominant and one recessive gene in the same chromosome of the homologous pair is know as *trans - arrangement* and the heterozygotes with such arrangement are called *trans - heterozygotes*. In such case, the genes show repulsion.

5. Linkage groups : All the genes which are located on the same chromosome constitute a *linkage group*. The number of linkage groups of a species, is equal to the haploid chromosome number of that species. This is because, the homologous chromosomes show identical genes.

Examples :

1. *Drosophila has* 4 pairs of chromosomes and 4 linkage groups.
2. Man has 23 pairs of chromosomes and 23 linkage groups.
3. Corn (*Zea mays*) has 10 pairs of chromosomes and show 10 linkage groups.

4-3 KINDS OF LINKAGE

Linkage is of two types. They are : (i) Complete and (ii) Incomplete linkage, depending upon the absence or presence of non - parental (recombinant) combinations of linked genes in the test cross progeny.

A Complete Linkage :

It is the phenomenon in which linked genes are transmitted together to the offsprings only in their original or parental combination for two or more generations. In this case, the linked genes are closely associated and do not separate to form the new or non - parental combinations. As a result, only parental character combinations are recovered in test cross progeny.

Complete linkage is a very rare phenomenon. According to BRIDGE all the genes of male *Drosophila* remain completely linked.

Example : *Complete linkage in Male Drosophila* : In *Drosophila*, grey body colour is dominant (B) over black colour (b) and long wings (V) is dominant over vestigial wings (v). When fully