Topic: Linkage
B.Sc. Botany (Sub.) I
Group: B

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Mendel's law of independent assortment is applicable both to genes and chromosomes. During meiosis, the maternal and paternal members of each pair of chromosomes are distributed independently to the gametes. It is for this reason that genes carried in different chromosomes undergo independent assortment and produce the ratios of differentiating characters which Mendel discovered and explained so successfully.

It has been found that in most individuals the number of genes exceed the number of pairs of chromosomes. For example, in Drosophila hundreds of genes have been studied yet there are only four pairs of chromosomes. About 400 pairs of genes are known in maize, yet there are only 10 pairs of chromosomes.

Stern has estimated that the total number of pairs of genes in man is not less than 5000 or more than 1,20,000 but man has only 23 pairs of chromosomes. Thus, it is clear that numerous pair of genes must be located on each pair of chromosomes and genes located in the same chromosome will not be assorted independently.

So, Mendel's second law is not universal but is limited to genes in different chromosomes.

Coupling and Repulsion Theory

Bateson and Punnett in 1906 discovered that independent assortment of factors does not take place always as assumed by Mendel in some cases. This difference from the law of independent assortment was first studied by them in sweet peas. In a cross between purple long and red round the F_2 progeny did not give the 9:3:3:1 ratio as expected.

On the other hand, purple long and red round were more numerous than expected where as the purple round and red long were less in frequency. Likewise, when a purple round variety was crossed with a red long variety, the parental combinations appeared more frequently in the F_2 than the new combinations.

On the basis of the above results Bateson and Punnett formulated a coupling & repulsion theory. They back crossed the hybrid purple long (PpL1) with recessive parent (ppll) and got the phenotypic ratio of about 7 purple long to 1 red long to 1 purple round to 7 red round. It is clear from this that the hybrids produced gametes of types PL and pl

about 7 times as frequently as those of types PL and pl.

Hence Bateson and Punnett suggested that these dominant determiners of two pairs must in some way be coupled, so that they tended to pass in the same gametes at gametogenesis. This tendency of same pair of characters (PP or LL) to unite together and to reappear hand to hand in next generation was termed Coupling by them.

DATA SHOWING LINKAGE (coupling)

F_2	Purple long (PL)	Purple round (Pl)	red long (pL)	red round (pl)	Total
Observed	4831	390	393	1338	6952
Expected (9:3:3:1)	3910.5	1303.5	1303.5	434.5	6952
Difference	+920.5	—913.5	—910.5	+903.5	

DATA SHOWING LINKAGE (repulsion)

F_2	PL Purple long	Pl Purple round	pL Red long	pl Red round	Total
Observed	226	95	97	1	419
Expected (9:3:3:1)	235.8	78.5	78.5	26.2	419
Difference	—9.8	+16.5	+18.5	—25.2	

Secondly, they crossed the purple round peas (PPll) with red long (ppLL). The F_1 hybrid was again heterozygous (PpLl) purple long. When this hybrid was back crossed with recessive

parent (ppll), the F_2 ratio was 1 purple long to 7 purple round to 7 red long to 1 red round.

Now it is clear that gametes PI and pL appeared seven times more than PL and pl gametes (This is just opposite to the previous experiment). This tendency of unlike pairs (PI and pL) to remain together and to avoid union with their dominant and recessive partners is termed as Repulsion.

In fact, the nature of coupling and repulsion was not completely understood by Bateson and Punnett. No satisfactory explanation of coupling and repulsion was given until Morgan and his associates Muller, Bridges, Sturtevant and others discovered that coupling and repulsion are essentially two aspects or facts of the same phenomenon, linkage.

T.H. Morgan (1910) postulated by his extensive experiments on Drosophila that those genes which are located on the same chromosome are linked and pass together from generation to generation while those chromosomes on other hand become freely assorted or segregated during gametic formation.

Furthermore, Morgan advanced the basic idea that the degree of strength of linkage depends upon the distance between the linked genes in the chromosome. This proved very fruitful idea and led to the construction of genetic or linkage maps of chromosomes. This tendency of genes to live together in the same chromosome during hereditary transmission is called linkage.

Linkage is the consequence of the concerned genes being located in the same chromosome. Linked genes do not show independent segregation, as a consequence, the ratios found 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 in the case of two linked genes.

This effect of linkage is more clearly noticeable in a test cross generation. The frequency of parental characters combination are clearly more than expected while those of new or non-parental character combinations are lower.

Linkage of two types

i. Complete linkage:

Complete linkage is the phenomenon in which two or more parental characters are inherited together and uniformly appear through two or more generations. In complete linkage genes are closely associated and tend to transmit together. This is due to the fact that there is no break in the male genes combinations in the chromosomes. It is found in male Drosophila.

It is clear from the above cross that there is no breakage of chromosomal segments. Because of this reason in male Drosophila only two types of gametes are formed BV and by which on mating with gamete; 'bv' produces only parental type progenies like grey long 'BbVv' and black vestigial 'bbvv' in F_2 generation.

ii. Incomplete linkage

It involves the accidental or occasional breakage of chromosomal segments. This arrangement is called crossing over, It was first of all noticed by Morgan in white eyed and

miniature winged Drosophila flies.

In cross between grey long (BBW) X black vestigial (bbvv), the F_1 hybrid is grey long (BbVv). The F_1 hybrid is female and produces gametes of four kinds. Two gametes will show the linked gene and no chromosomal change (non-crossovers) and other two will show chromosomal interchange. Thus, non-cross over gametes formed without chromosomal interchange are in 82% ratio and cross-over gametes formed as a result of crossing over are 18%.

If we cross the F_1 hybrid to a black vestigial male (Bb Vv X bbvv), the F_2 will show 82%' offspring of parental ratio i.e., 41% grey long and 41% black vestigial and 18% offspring of new cross-over ratio, 9% grey vestigial and 9% black long.

Theories of Linkage

- **Theory of differential multiplication**

This theory was proposed by Bateson (1930) to explain the phenomenon of linkage. According to this theory, the set of gametes possessing parental combinations multiply

more rapidly than the set having non- parental combinations after the segregation of characters during gamete formation. This results in the formation of a greater number of gametes with parental combinations.

This theory has no cytological basis hence has been condemned by other cytologists. We know from our knowledge of gametogenesis, that after segregation, only a single division comes before the gametes are formed. Moreover the theoretical results do not agree with the statistics obtained.

- **Chromosomal theory of linkage**

This theory was proposed by Castle and Morgan. They claimed that genes situated in the same chromosomes are inherited together i.e., they are linked while those located in different chromosomes are inherited freely or independently i.e., they are not linked. The extent of linkage is correlated with the distance between the genes in the chromosomes—closer the genes, stronger the linkage & vice- versa.

The linkage of genes, according to this theory, is linear. An important distinguishing

Feature is that genes are located in the chromosomes longitudinally in linear fashion. The chromosome theory of linkage is well supported by other cytologists and is widely accepted.

Linkage in Maize

A good example is the results obtained by Hutchinson who crossed a variety of maize having seeds that were coloured and full to one with colourless and shrunken seeds.

In other experiments it had been shown that colour gene "C" was a simple dominant over colourless 'c' where as full endosperm, gene 'S' is dominant over shrunken 's'. Accordingly the parents were CCSS and ccss and the F_1 as expected, had coloured full seeds that must have the genotype CcSs.

If C and S assort (segregate) independently in accordance with Mendel's second principle, these plants should produce four types of gametes CS, Cs, cS, cs in equal numbers.

TABLE
Results of Hutchinson's test-cross in maize

Test cross	Coloured, full CcSs	×	Colourless, shrunken ccss	
Progeny	Coloured, full CcSs 4032	Coloured, shrunken Ccss 149	Colourless, full ccSs 152	Colourless, shrunken ccss 4035
	Parental	Recombinants		Parental

TABLE
Results of Hutchinson's reciprocal cross and the subsequent test cross in maize

Parents	Colourless, full ccSS	×	Coloured, shrunken CCss	
F_1	Coloured, full CcSs			
Test-cross	Coloured, full cS/Cs	×	Colourless, shrunken cs/cs	
Test-cross progeny	Coloured, full CS/cs 638	Coloured, shrunken Cs/cs 21,379	Colourless, full cS/cs 21,906	Colourless, shrunken cs/cs 672
	Recombinant	Parentals		Recombinant

Parentals = 43,285 = 97.06 per cent
Recombinants = 1310 = 2.94 per cent

The easiest way to test this gametic ratio is to make a test cross of F_1 to the double recessive cross which according to the expectation stated above, would produce four classes of progeny in the ratio of 1:1:1:1. When the cross was made, however, this expectation was not realized.

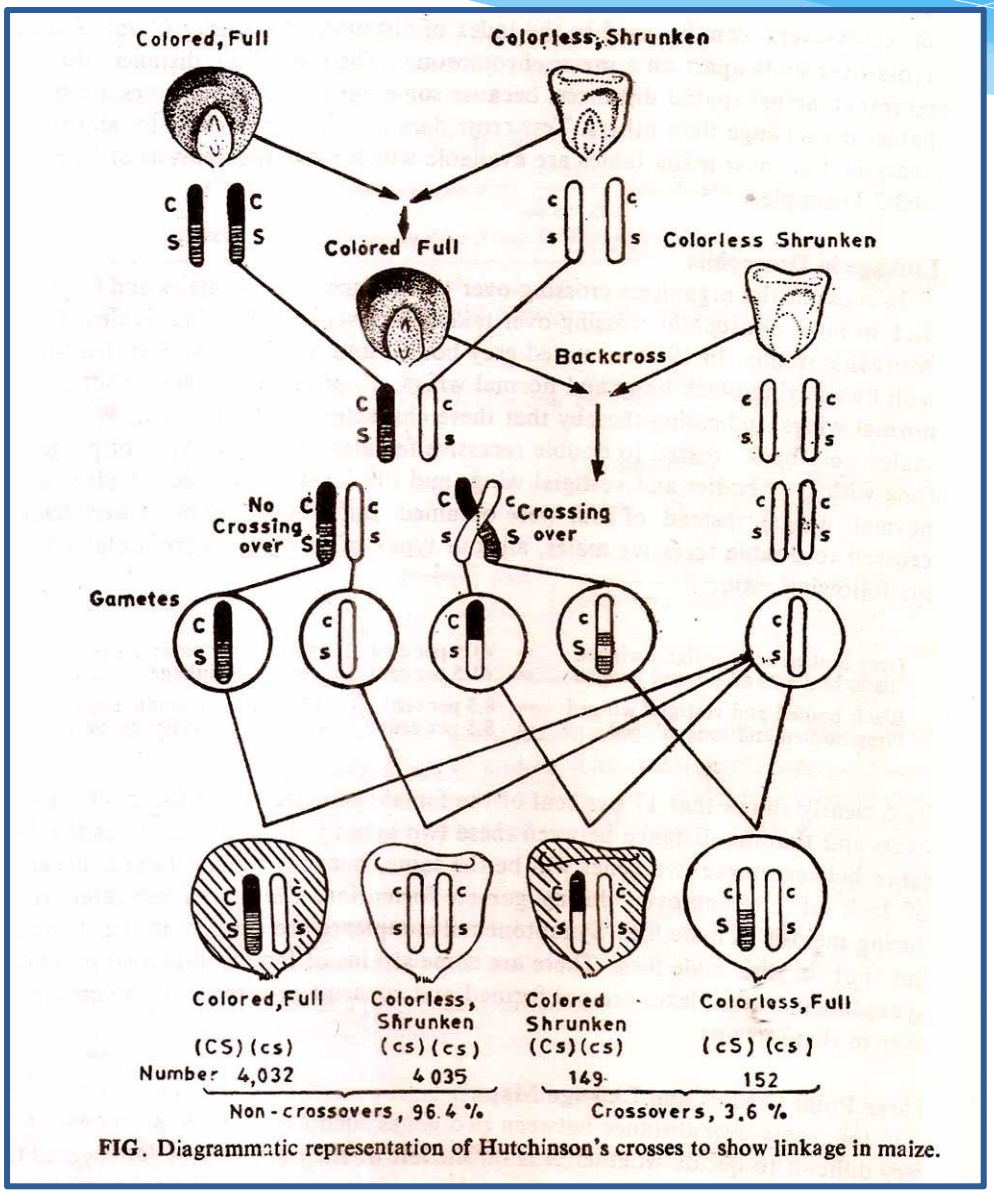

FIG. Diagrammatic representation of Hutchinson's crosses to show linkage in maize.