



**FACULTY OF AGRICULTURAL SCIENCES  
AND ALLIED INDUSTRIES**

## LINKAGE AND CROSSING OVER

Bateson and Punnett discovered in 1906 that the principle of independent assortment of members of different pairs of alleles at the time of formation of gametes is not universal but has some exceptions. Thomas Hunt Morgan (1910) found similar situations in *Drosophila* to give a satisfactory explanation for such deviations.

### Linkage in maize

'C' for coloured aleurone is dominant over 'c' colourless

Sh for Full endosperm is dominant over 'sh' shrunken.

Parents (Short 'S' , 's' Col full	x	Colourless, Shrunken
CCSS	↓	ccss
	↓	
	Ce Ss	Colour full
	↓	
F2	Colour full	7300
	Colourfull shrunken	200
	Colour full	200
	Colouless shrunken	2300

F2 did not show 9: 3: 3 : 1 ratio. There were greater number of colour full, colour shrunken (parental types) than colourfull shrunken , colour full, If two characters considered separately, they segregate 3 : 1

i.e .	Colour	7500		Full	- 7500
	Colouless	2500		Shrunken-	2500

The large deviation of the observed F2 population from the expected segregation is therefore not because the members of each pair of alleles do not segregate from each other but because of the separation in one pair of alleles is not independent of the separation in the other pair of alleles.

### Test cross

Colour full	x	Colourless shrunken
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	CCSS		eess
F1	CeSs	x	eess
F2	F2	Colour full	4800
		Col. Shrunken	200
		Col. Less full	200
		Col less shrunken	4800

The data show that, the two pairs of genes have not assorted independently.

### Segregation of two pairs of genes on two pairs of chromosomes

Let us suppose that, gene 'C' is located on chromosome number 9 and 'S' on chromosome number 10 of maize. The segregation of chromosome bearing C and c is entirely independent of segregation of chromosome bearing S and s. So four types of gametes Cs, Cs, eS, eS are formed in F1 and F2 normal dihybrid ratio 9:3:3:1 and test cross 1:1:1:1

### Segregation of two pairs of genes on one pair of chromosomes

Let us suppose that, two genes C and S are located on chromosome No. 9 during meiosis only 2 gametes will be formed Cs and cs gametes.

So, Genes C and S situated on same chromosomes are said to be linked. Linkage is the association of character in inheritance due to fact that genes determining them are physically located on the same chromosomes.

### Detection of Linkage

Compare the number of individuals observed in each class with those expected on the basis of independent assortment and then to test the deviation between these two values by chi-square test.

### Linkage Group

The number of linkage groups will be equal to the haploid number of chromosomes which the species possess. Thus maize has 10 pairs chromosomes has 10 linkage groups.

### Symbol of linked genes

While representing linked gene, the two homologous chromosomes are indicated by two horizontal links.

e.g.  $\frac{CS}{cs}$                        $\frac{CS}{cs}$                       CS/cs

**Coupling**

In the condition is linked inheritance in which an individual heterozygous for two pairs of genes receives the two dominant member from one parent and the two recessive members from the other parent.

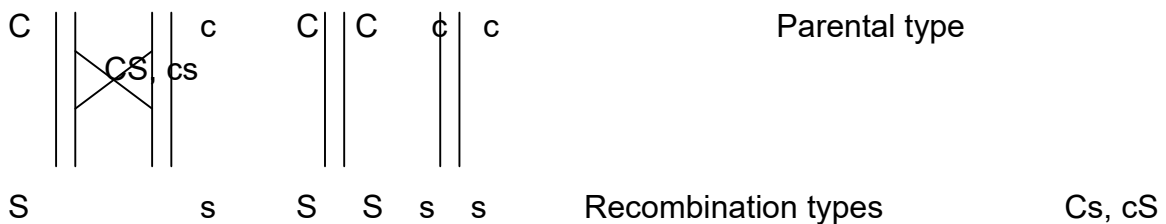
eg.                      CS / CS                      x                      cs / cs  
 ↓                      It is also said to be in C is position.  
 CS / cs

Repulsion                      CS / Cs                      x cS / cS  
 ↓  
 Cs / cS                      'Trans' position

Repulsion is the condition is linked inheritance, in which an individual heterozygous for two pairs of linked genes receives the dominant member of one pair and the recessive member of the other pair from one parent and the reverse from the other parent.

**Crossing over**

Leading to recombination of linked genes is due to the exchange of corresponding segments between the chromatids of homologous chromosomes and was first observed by Belgian cytologist Janssens in 1909.



**Linkage studies revealed the following**

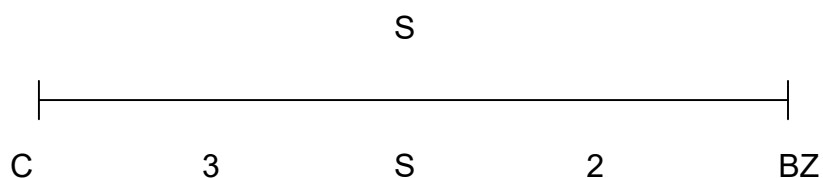
1. Genes that assort at random are non linked genes. Genes that do not segregate at random are linked genes.
2. Linked genes are arranged in a lines fashion on the chromosome. Each linked gene has a definite and constant order in its arrangement.
3. The distance between the linked genes determines the degree of strength of linkage. Closely located genes show stronger linkage that the widely located genes.
4. Linked genes do not always stay together, but are often exchanged reciprocally by cross over.

### **LINKAGE MAP (Cross over map / chromosome map or genetic map)**

Morgan postulated that genes are arranged in linear order along with length of chromosome, each gene having a fixed place on the chromosome and its allele, a corresponding position on the homologous chromosome. Under standardized environmental conditions, the frequency of crossing over of a pair linked genes has been found to be constant and Morgan put forward the hypothesis that it depends upon the distance between two genes on the chromosome. The greater the distance between the two genes, the greater in the chance that a Chiasma will occur between their loci, and the higher in the percentage of crossing over between them. If therefore, the percentage of crossing over between various genes are determined experimentally, the gene can be mapped in their order on the chromosome.

In mapping genes, a unit of distance must be used and this unit is called a map unit, which is the space within which one percent of crossing over takes place. If percent of cross over between two linked genes is 1% it means that the map distance between these two linked genes is one unit of map distance or one map unit or one centimorgan.

If the genes are in the order C, S, BZ,



The genes C and BZ show 5% crossing over. (If the gene are in the order C, BZ and Z, the genes C and BZ should show 1% crossing over. Experimental data revealed that the percentage of crossing over between C and BZ is 5. These three genes C, S and BZ on the ninth chromosome of maize and plotted as above.

### **Importance of linkage in breeding**

When there is a close linkage between desirable and undesirable characters these genes are inherited in blocks and not individually and recombination is practically nil. In such cases linkage has to be broken by 'irradiation'.