



**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 deviation.

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
	Colourless 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 character considered separately, they segregate 3 : 1

i.e .	Colour	7500	Full	- 7500
	Colourless	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 No expected
		Col. Shrunken	200 ratio 1:1:1:1
		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.

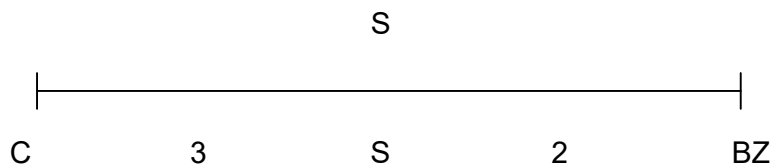
1. Genes that assort at random are non linked genes. Genes that do not segregate at random are linked genes.
2. Linked genes are arranged in a lines fashion on the chromosome. Each linked gene has a definite and constant order in its arrangement.
3. The distance between the linked genes determines the 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, thre frequency of crossing over of a pair linked genes has been found to be cosntant 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 palce. 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 centimaorgan.

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% corssing over. Experimental data revealed that the percentage of crossing over between C and BZ in 5. There 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'.

SEX DETERMINATION

Sex differentiation in living organism into male and female causes morphological, physiological and behavioral differentiation between the two sexes and this phenomenon is called sexual dimorphism. The precise form of the chromosomal differences between the sexes is not the same in different organism. Four types of sex chromosomes mechanism or heterogametes have been recognized.

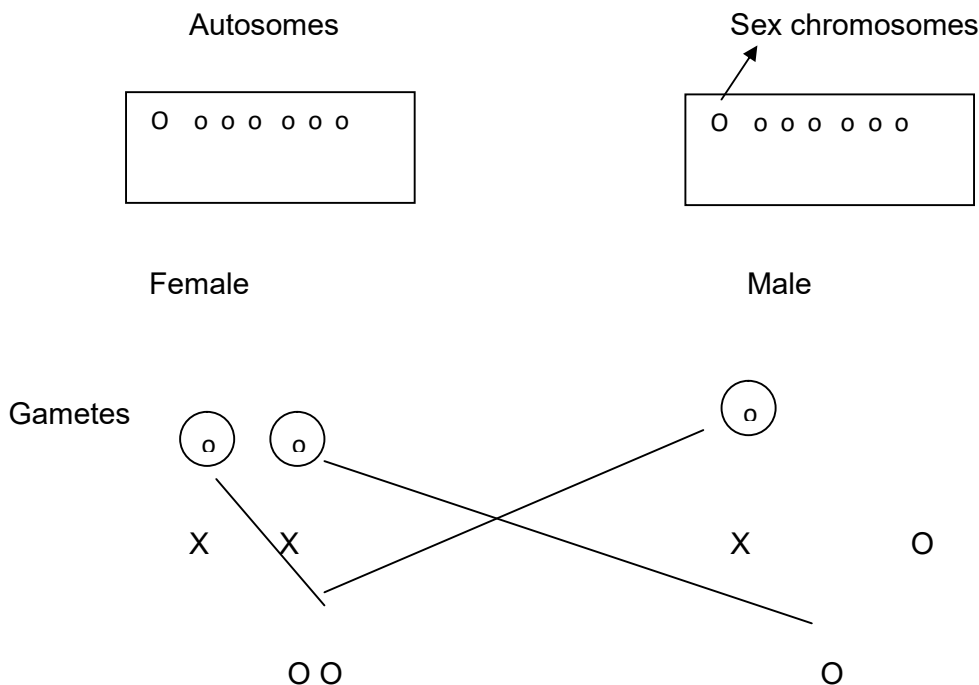
1. Sex chromosomes mechanism

a. Heterogametic male

XX - XO type

The chromosome theory of sex determination was put forward by McClung (1902) who observed that male grasshopper possessed an odd number of chromosomes in contrast to the female which possessed an even number.

In the squash bug, protenor the females have 14 chromosomes and the males have only 13 chromosomes in their somatic cells. The odd chromosome of the male thus determines the sex and hence called the sex determiner or Sex chromosome or the 'X' chromosome. The other chromosomes which are alike in females and males are called 'autosomes'. The female is 'XX' and the male is 'XO' (using 'O' to indicate the absence of 'X' chromosome).



Female

Male

XX-YY type

In many animals and plants, females and males have the same even numbers of chromosomes, but whereas in the females the members of each pair of chromosomes are alike, in the males the members of one pair of chromosomes are dissimilar in size or form.

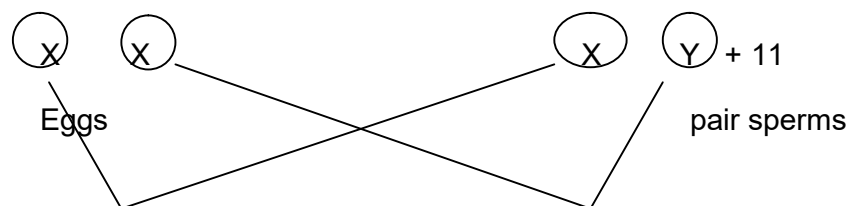
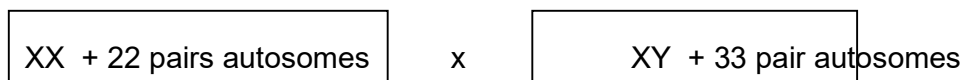
In *Drosophila*, female has four pairs of chromosomes as follows;

1. a pair of rod shaped chromosomes
2. a pair of 'V' shaped chromosomes
3. a pair of slightly longer 'V' shaped chromosomes
4. a pair of very short dot like chromosomes (XX)

In male *Drosophila*, there is only one rod shaped chromosome (X). the other member of this pair being inverted 'J' shaped (Y) Wilson, who discovered this type of chromosome arrangement in 1905 designated the unlike member of their pair in the male as the 'Y' chromosome and the other member which is like the members of one pair in the female as the 'X' chromosome.

Human beings

In human beings 46 chromosomes are present in the somatic cells. Females have 22 pairs of autosomes and two X chromosomes males have 22 pairs of autosomes and one 'X' and one very short 'Y' chromosomes (considerably smaller than the 'X' chromosome). Each egg carries 22 autosomes and an 'X' chromosome. Sperms, however are of two kinds one kind with 22 autosomes and an 'X' and the other kind 22 autosomes and a 'Y'. The sex of a child is determined at the time of fertilization by the kind of sperm that happens to meet and penetrate, the egg, an X-bearing sperm producing a girl and a Y-bearing one, a boy.





b. Heterogametic female (ZO - ZZ) type)

ZO - ZZ . The female is the heterogametic sex and the male in the homogametic one. e.g. In amoeba, Paramecium, females have 59 chromosomes and male have 60 chromosomes. The eggs are of two kind (29 and 30). All the sperms have 30 chromosomes each on fertilization an egg with 29 chromosomes gives rise to a female and an egg with 30 chromosomes gives rise to male.

ZW-ZZ type: In birds, certain insects, fishes and reptiles, the female has an unlike pair of chromosomes, Z W, and forms eggs of two sorts, one with a 'W' chromosome and the other with a 'Z' chromosome. The male has like pairs (ZZ) of chromosomes. On fertilization an egg with a 'W' chromosome and the other with a 'Z' chromosome. The male has like pairs (ZZ) of chromosomes. On fertilization, an egg with a 'W' chromosome gives rise to a female and an egg with a 'Z' chromosome gives rise to a male.

Among plants, *Fragaria elatior* is one in which the female is ZW and the male is ZZ.

Balance theory of sex determination

All individuals have genes for both sexes. To quote Bridges, both sexes are due to simultaneous action of two opposed sets of genes, one set tending to produce the characters called 'female' and the other to produce the character called 'male'. Which sex actually develops is decided by the balance i.e. by the preponderance of the female-determining or of the male determining genes. The sex chromosomes are merely vehicles of genes which help in tilting the balance in one direction or another.

Support for the balance theory of sex determination comes from the work of Bridges (1921) on *Drosophila*. Bridges observed some females of *Drosophila* with 'X' chromosomes and 3 sets of autosomes (Triploids). When he crossed them with normal (diploid) males, he found that some of the progeny had one or more chromosomes less or more than the normal flies. (i.e. aneuploids).

Bridges found intersexes, super females and super males among the progeny. Intersexes are sterile individuals intermediate between females and males super females and super males are sterile individuals which are very weak and very poor in viability.

Bridges interpreted these results as follows:- Sex in *Drosophila* is determined by the 'X' chromosomes as well as by the autosomes, the ratio of the number of 'X' chromosomes to the number of sets of autosomes being the deciding factor. In a normal (diploid) female, the $X/A = 1.00$, there being two X chromosomes and two sets of autosomes and in a normal (diploid) male the X/A value is 0.50, there being only one X chromosome and two sets of autosomes.

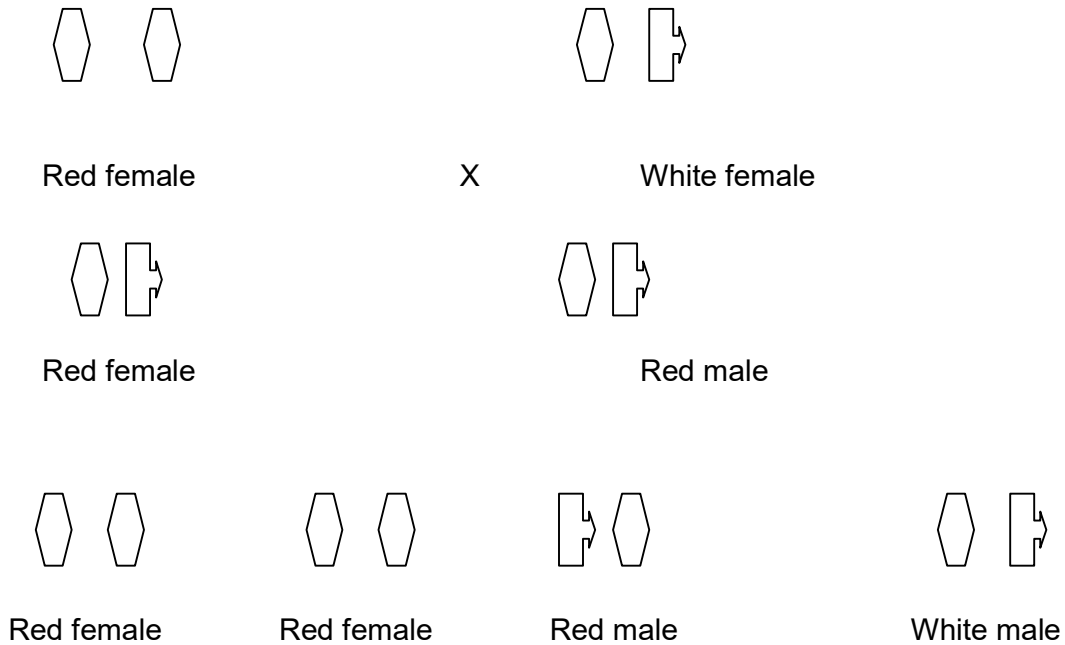
Relationship of chromosomes to sex in *Drosophila*

Chromosome constitution

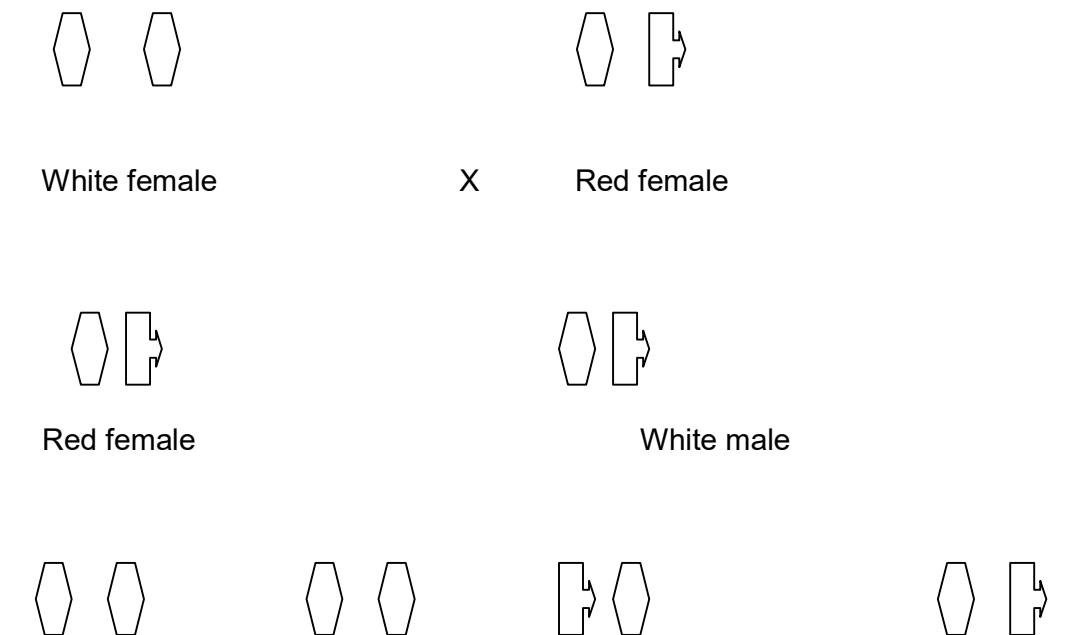
X	Y	A	X/A	Sex
3X	-	2A	1.50	Super female
3X	-	3A	1.00	Female (Triploid)
2X	-	2A	1.00	Female (diploid)
2X	1Y	2A	1.00	Female (diploid)
2X	1Y	3A	0.67	Intersex
2X	-	3A	0.67	Intersex
1X	1Y	2A	0.50	Male
1X	1Y	3A	0.33	Super male

SEX LINKAGE

Morgan crossed a red eyed female with a white eyed male and found that all F1 flies of both sexes were red eyed. In F2, 3 red and 1 white eyed. So, it is due to an allelic pair of genes of which red is dominant.



A reciprocal cross was made between white eyed female and red eyed male. It was found that among the F1 offspring, all the females were red eyed and all the males were white eyed. The results were quite unexpected firstly, because the phenotypes of F1 females and males were different.



White female

Red female

White male

Red male

The different results from the reciprocal crosses could be explained only on the assumption that the gene for eye colour is located on 'X' chromosomes and that 'Y' chromosome has no gene for colour of the eyes.

A white eyed female crossed with a red-eyed male produces red eyed females and white eyed males, this method of inheritance, is often referred to as 'criss-cross inheritance'. The F2 consisted of red eyed and white eyed individuals in equal numbers in both sexes.

Criss cross:- A sex linked gene passes from male to female then back to male.

The gene for eye colour is located on 'X' chromosome, it is called 'X' linked gene. This pattern of inheritance is called 'Sex linkage'.

There are genes located on 'Y' chromosomes and its alleles absent in X chromosome. Such genes are called 'Y linked' or Holandric genes. The gene responsible for hypertrichosis causing hairy pinna (ear lobes) in human beings is a Y linked gene.

There are certain homologous regions on X and Y chromosomes in which both the alleles of a gene may be present as in the case of bobbed bristles (b) and its allele (b+) for normal bristle. Such genes are present both in X and Y chromosomes are called XY linked genes. Eg. Colour blindness.

Sex influenced character

These characters may be expressed differently in the two sexes even when their genotypes are identical. The more influence of the sex of the individual may be sufficient to alter the phenotypic expression of a gene. The most common expression of sex influence is that dominance is reversed between the sexes. Genes determining sex influenced characters are borne on autosomes. E.g. i. Presence of horns in sheep is said to be recessive character in females but a dominant character in males.

Horned female

x

Hornless male

HH

hh



F1 Hh

In female → Hornless

In male → Horned.



	F2	1 hh	: 2 Hh	: 1 hh
Female	:	Horned	Hornless	Hornless
Male	:	Horned	Horned	
		Hornless		

Reciprocal crosses show no differences because the gene is carried by autosomes.

e.g. (2) Boldness in human being.

	Bb	X	BB
	Non-Bold ness	↓	Boldness male
		Bb	
F1	Male	→	Bold
	Female	→	Non bold
F2	BB	Bb	bb
Male	Bold	Bold	Non bold
Female	Bold	Non bold	Non bold

Boldness is recessive in female and dominant in male.

SEX LINKED CHARACTER

Sex limited inheritance is an extreme type of sex influence in which a particular phenotype can be expressed only in one sex. As genes for sex limited characters are borne on autosomes, all genotypes should occur with identical frequencies in both sexes, but the physiological frequencies between the sexes are such that certain genotypes can be expressed only in one sex.

e.g. (1) In domestic poultry, cock feathering is a character limited to the male sex.

'H' → Hen feathering is due the dominant gene.

'h' → Cock feathering is due to recessive gene.

But females with genotypes 'hh' are hen feathered. (because cock feathering is limited to the male only).

Genotypes	Phenotype	
	Female	Male
HH	Hen feathered	Hen feathered
Hh	„	Hen feathered
Hh	„	Cock feathered

Removal of the ovaries in hens with genotypes 'hh' results in cock feathering. This indicates that female sex hormone inhibits the production of cock-feathering in hens with genotype 'hh'.

e.g. (2) Yellow clover butterfly

'White' is a character limited to female limited character found only in female.

Genotype	Phenotype	
	Female	Male
WW	White	Yellow
Ww	White	Yellow
ww	Yellow	Yellow

SEX REVERSAL

In several species of plants that are normally bisexual, suppression of male or female structures has been observed in nature. The androecium getting converted into petals in ornamental plants or carpels as in carrot and cabbage or pistils as in maize, papaya and primroses has been observed. When the stamens get converted into rudimentary organ is called the 'Staminode' and a similar conversion of the pistil into non-functional rudimentary organ is called the 'pistillode'. The phenomenon in which there is suppression of one sex at the expense of the other is called 'sex reversal'. The sex reversals are mostly due to physiological and biochemical alterations involving sex hormones.

In maize, rarely it is observed that the male influence, Tassel bears seeds due to sex reversal. The recessive gene 'ba' is responsible for barren plants and another recessive gene 'ts' is responsible for tassel seed. Sex reversal in maize is due to the genetic constitution of the plants.