A Text Book of Genetics
Plant Breeding and Evolution

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Reg.No.U74120 MH2013 PTC 251205
Harshwardhan Publication Pvt.Ltd.
At.Post.Limbaganesh,Tq.Dist.Beed
Pin-431126 (Maharashtra) Cell:07588057695,09850203295
harshwardhanpubli@gmail.com, vaidyawarta@gmail.com
All Types Educational & Reference Book Publisher & Distributors

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❖ **Publisher :**
Harshwardhan Publication Pvt.Ltd.
Limbaganesh, Dist. Beed (Maharashtra)
Pin-431126, vidyawarta@gmail.com

❖ **Printed by :**
Harshwardhan Publication Pvt.Ltd.
Limbaganesh, Dist. Beed, Pin-431126

❖ **Page design & Cover :**
Shaikh Jahurodden

❖ **Edition: June 2019**

ISBN 978-93-89003-23-9

❖ **Price : 500/ -**

Preface

Genetics, Plant Breeding and Evolution is much awaited by the authors. This book is written according to the syllabus of undergraduate students. The present book is being humbly offered to satisfy the demand for better, exhaustive and authoritative coverage on various aspects of genetics, plant breeding and evolution. These sub branches of biology are usually form a part of the paper in most of the Universities.

The very special features of this book are, adequate and accurate illustrations, the whole matter is fertilised with good, simple information. Each and every topic in fully illustrated. Diagrams are necessary to understand the matter correctly.

We are extremely grateful to our chairman, Principal of the respective college, and authorities of BOS in Botany, Kavayitri Bahinabai Chaudhari North Maharashtra University Jalgaon.

All comments and suggestion for the improvement of book will be thankfully accepted.

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Dr.N.S.Pawar & Dr. D.S.Jain

GENETICS, PLANT BREEDING AND EVOLUTION

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CHAPTER-1 - Genetics: Definition, History and Scope (4 L)

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1.5 Scope and significance of Genetics.

Introduction: one of the most important sub division of biological sciences is cytogenetics dealing with the study of cell and hereditary potentialities. Cytogenetics is in sense a hybrid science from historical point of view. It comprises cytology and Genetics.

It is a common observation that seeds of mango trees germinate to grow into mango plants, and dogs give birth to puppies only and not into the young ones of any other animal. Humans give birth to human beings. The tendency of offspring to inherit parental characteristics is termed as 'heredity' and ***the study of science of heredity and the reasons governing the variation between the parents and their offspring, is called 'Genetics'***. Genetics also seeks to answer questions like why two offspring of same parents look different, why some people have dark, and others have fair complexion. In other words, why is there variation among individuals of the same kind? This lesson deals with heredity and the reasons behind the variation among individuals of the same species. It also includes diagnostic techniques to find out the bases for types of sex determination, inheritance of blood groups in humans, hereditary disorders and gives an insight up the human genome as amniocentesis.

It was Louis Pasteur who provided conclusive proof of discard spontaneous of living organisms. This theory that organisms arise from pre-existing ones, gave the idea of parents and offspring and perhaps also paved the way for the study of inheritance of characters from one generation to the others. While the offspring resemble their parents to a great extent, they also have some characters of their own. The fact that offspring resemble their parents is due to inheritance, while the differences encountered are due to variations. The science of genetics mainly deals with variation and inheritance of characters and their causes in living beings. The first person to experiments with hybridization was a German botanist Kolreuter, who studied the inheritance of character in a cross of two tobacco plants. he observed that the offspring resembled both the partners. The most important name in Genetics perhaps is that of Gregor Mendel, the Austrian monk. He regarded as the father of Genetics. It is he, who for the first time studied the inheritance in detail and applied mathematics to biology.

Epigenetics: new research show that you also inherit the effect of your parent's lifestyle and exospore as tag on your DNA. This called Epigenetics. These tags affects how the genes in your DNA function. For example, consider twins, identical twins are clones. They are born with same sequence of DNA. When twins are young they look the same. As twins get older, they have different environmental exposures. What they eat and their activities are not identical, this can lead to different body features such as obesity and different diseases such as heart disease, and cancer. You are especially vulnerable to epigenetic changes during critical periods like puberty and pregnancy.

Epigenetics is the study of heritable changes in gene expression (active verses inactive genes) that do not involve changes to the underlying DNA sequence-a change in phenotype without change in genotype.

HEREDITY AND VARIATION:

Whenever an infant is born in a family, the relatives begin to wonder about the resemblance of the infant's eyes, facial features, complexion, and colour of hair with those of the parents, siblings and grandparents. The source of such resemblances and differences are in the "genes" that are passed down fromparents to children and so on generation after generation. This inheritance of genes is termed 'heredity' the study of reasons of heredity is 'Genetics'. New individuals develop features according to the genes inherited by them from their parents. The transmission of characters from one generation to the next that is from parents to

offspring is known as heredity. It is further observed that siblings from same parents are unique and differ from each other except the identical twins. Such differences are termed variations. Variation means differences between parents and their offspring or between offspring of same parents or between members of the same population. Variation in a population is very important. It has survival value for the population. This is because if the environment changes, some individuals (variants) may be able to adapt to new situations and save the population from dying out. Variation arises due to mutation or sudden change in the genes. Variation also arises because genes get shifted and exchanged during meiosis at the time of formation of gametes, giving rise to new gene combinations Atfertilization, there is random mixing of paternal and maternal chromosomes with different gene combinations. Such a source of variation which is most common is called genetic recombination. Heritable Variations generally arise because of mutation and recombination.

IMPORTANT TERMS IN GENETICS

1]**Factor** : The unit of inheritance and expression of a particular character is controlled by inheritable units called factor (gene) which are present in pairs in parental cells and singly in the gametes.

2] **Gene**: A segment of DNA molecule which determines the unit of inheritance and expression of a particular character.

3] **Alleles or Allelomorphs**: Two or more alternative forms of a gene are called alleles. For example in pea plant, the gene for producing seed shape may occur in two alternative forms: smooth (S) and wrinkled (s). Genes for smooth wrinkled seeds are alleles of each other, and occupy same locus on homologous chromosomes.

4] **Trait**: is the morphologically or physiologically visible character, e.g. colour of flower, and shape of seed.

5] **Dominant trait** : Out of the two alleles or allelorrorphs of a trait, the one which expresses itself in a heterozygous organism in the F1 hybrid is called the dominant trait (dominant allele) and the one that remains masked in F1 individual but gets expressed in the next generation (F2), is called recessive. Thus, if the allelic combination in an organism is Tt, and T (tallness) expresses itself but t (dwarfness) cannot, so T is the dominant allele, and tallness is dominant on dwarfness represented by "t'.

6] **Recessive trait**: Out of the two alleles for a trait, the one which is suppressed (does not express) in the F1 hybrid is called the recessive trait (recessive allele). But the Recessive allele does express itself only in the homozygous state (e.g. tt).

7] **Genotype:** A class of individuals recognised based on its genetic constitution and breeding behaviour is called the genotype, e.g., the genotype of pure smooth seeded parent pea plant is SS and it will always breed true for smooth-seeded character, but plants having **Ss** on selfing would give rise to a population represented by 3 : 1 ratio for smooth seeded plants and wrinkled seeded plants.

8] **Phenotype**: A class of individuals recognised based on outward appearance of a trait in an individual is the phenotype, e.g. Smooth-seeded shape or wrinkled shape of seeds represent two different phenotypes.

9] **Homozygous**: An individual possessing identical alleles for a trait is termed homozygous e.g. SS is homozygous condition for smooth seeded character in garden-pea.

10] **Heterozygous**: An individual with dissimilar alleles for a trait is termed heterozygous for e.g. **Ss** represents the heterozygous condition for smooth seeded character in garden pea.

11] **Parent generations**: The parents used for the first cross represent the parent (or P1) generation.

12] **F_1 generation**: The progeny produced from a cross between two parents (P1) is called First filial or F_1 generation.

13] **F_2 generation**: The progeny resulting from self pollination or inbreeding of F_1 individuals is called Second Filial or F_2 generation.

14] **Monohybrid cross**: The cross between two parents differing in a single pair of contrasting characters is called monohybrid cross and the F_1 offspring is the Monohybrid. The phenotypic ratio of 3 dominants : 1 recessive obtained in the Heredity F_2 generation from the monohybrid crosses by Mendel was mentioned as 3:1 monohybrid ratio.

15] **Dihybrid cross**: The cross in which two parents differing in two pairs of contrasting characters are considered simultaneously for the inheritance pattern is called dihybrid cross. The phenotypic ratio obtained in the F_2 generation from a dihybrid cross is called Mendelian dihybrid ratio (9 : 3 : 3 : 1), and the F1-individual is called dihybrid (Ss Tt).

16] **Hybridisation**: Crossing organisms belonging to different species for getting desirable qualities in the offspring.
17] **Test cross**: is the Crossing of the F_1 progeny with the homozygous recessive parent. If F_1 progeny is heterozygous, then test cross always yields the ratio of 1 : 1 between its different genotypes and phenotypes.
18] **Reciprocal cross**: Is the cross in which the sex of the parents is reversed. That is if in the first cross father was dwarf and mother tall, tall, then in the reciprocal cross, dwarf parent will be female and tall parent male.

Sexuality a source of Variation- Sexuality in plants:

Plants reproduce by vegetative. Asexual and sexual methods. Vegetative method varies from plant to plant ranging from bacteria, algae, fungi, bryophytes, Pteridophytes to Angiosperms. Asexual reproduction is takes place by the producing different types of spores in algae, fungi, bryophytes and Pteridophytes.

Sexual reproduction is one of the sure method of reproduction in plants, it takes place by producing special sexual organs such as archegonia, antheridia, cones, Strobilus and well developed highly modified flowers in angiosperms. The sexual reproduction is achieved by producing the gametes, these gametes are produced by meiosis. During the meiosis, crossing over occurs, that leads to the variation in the gametes and organism in turns.

In angiosperms, flowers have great diversity in terms of size, shape mode of development, colour, fragrance and sexuality, they may be unisexual or bisexual. These features have great effect on reproduction. There are adaptation in the structure of flower for cross pollination and well as self pollination.

1.4. Historical Background:

i) Inheritance of acquired Characters and Pangenesis:

According to Lamarks (1744-1829) inheritance of the acquired characters to be transmitted in to the progenies from the generation to those in next generation. According to him, the progeny of a healthy person would also be healthy. The progeny of a weak person would be weak. According to Charles Darwin (1809-1882) whatever the characteristics are observed in individual of one generation are often met with also in individuals of the next generation.

ii) Epigenesis and Pangenesis: Concept of pangenesis was proposed by Charles Darwin in his theory of Pangenesis. He tried to describe the inheritance between parents and offspring and the process by which those units control development in offspring. He coined the term gemmules, for the hypothetical particles of inheritance thrown off by all cells of the body. The theory suggest that on organism's environment could modify the gemmules in any part of the body, and that these modified gemmules would congregate in the reproductive organs of parent to be passed on to their offspring. If an organ of organism or individual is modifies and differentiated in some way, the gemmules will also modified or differentiated accordingly for that organ. The modified gemmule now will be transmitted to its progeny through the gametes and will produce a similar modification in the corresponding organ of the progeny. This called pangenesis.

When biologists increasingly abandoned the theory of inheritance of acquired characteristics on which the pangenesis theory partially relied. Around 20thcentury, biologist replaced the theory of pangenesis with germ plasm theory and then with chromosomal theories of inheritance, and they replaced the concept of gemmules with that of genes.

Epigenetics: the Epigenetics was proposed by Waddington in 1942. It was derived from Greek word Epigenesis which originally described the influence of genetics proves on development. It is a relatively new science of the bordered field of genetics and refers to heritable changes in the gene expression or phenotype. These epigenic changes do not involve changes in the actual DNA sequence itself but rather modification in histones that comprises the chromatin and DNA methylation as well as an ever expanding array of other epigenic processes.

iii) Germplasm Theory: this theory was proposed by August Weismann, a forerunner of modern genetics. And challenged the popular belief of inheritance of acquired characters and Pangenesis. His attempts are to forward step in understanding heredity. According to this theory, the body of any individual is made up of two distinct type of tissues: (i) Somatoplasm and (ii) Germplasm.

The somatoplasm consists of body cells which are necessary for survival and functioning of the organism. These do not show any contribution in sexual reproduction. Hence, the changes which occur within

somatoplasm, strictly cannot be transmitted to the next generation. On the other hand, the germplasm produces gametes that are foundation of sexual reproduction. The changes, which in the germplasm are, therefore, transmitted to the next generation. In animal, gonads represent the germplasm and differs from somaclones. Many plants reproduce asexually while most of them develops the reproductive organs that differs from somaclones. This theory is really a very significant advancement in understanding heredity.

1.5. Scope and significance of Genetics:

In the last few decades, the science of genetics has pervaded all aspects of biology so that it has assumed a central position of great significance in biology, while on the one hand, genetics is used for a study of the mechanism of heredity and variation, on the other hand it has provided tools for the study of the fundamental biological processes examined and taught in areas, like plant physiology, biochemistry, biosystematics, ecology, plant pathology, microbiology, etc. consequently today every biologist should be bit of a geneticist. Genetics, in fact provided the modern paradigm (a prototype) for whole of biology. The science of genetics also had a tremendous impact in applied areas including medicine. Agriculture, forestry, fisheries, law and religion. Recently, Biotechnology has added further to significance of the science of genetics by introducing the genetic engineering technology, recombinant DNA technology, Tissue culture etc.

CHAPTER –2 - Mendelism and Neo-Mendelism (8 L)

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    iii) Law of independent assortment
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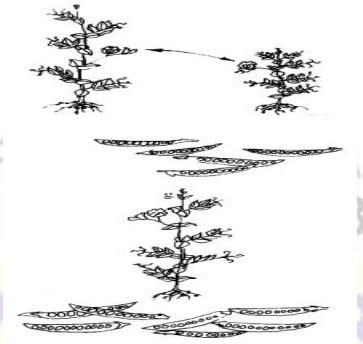
        i) 9:7 ratio (Complementary gene)
        ii) 15:1 ratio (Duplicate cumulative gene)
        iii)12:3:1 ratio (Dominant Epistatic gene)

Sir Gregor Johann Mendel (1822 to 1884) was Austrian monk who used garden pea (***Pisum sativum***) for his experiments on plant breeding and published his results in 1865. His work, however, was independently rediscovered in 1900, long after Mendel's death, by Tschermak, Correns and DeVries. But since Mendel was the first to suggest principles underlying inheritance he is regarded as the founder or **father of genetics**.

Mendel's Experiments

Mendel designed his experiments in such a way that a pure tall variety of pea plants could be crossed to a pure dwarf variety. The anthers from flowers of tall plants were removed and their stigmas dusted with pollen from flowers of dwarf plants. The reverse experiment was also carried out, that is anthers of flowes borne on dwarf plants were removed and their stigmas were dusted by pollen from flowers of tall plants. In the following spring, seeds from the new plants were collected and sown. Mendel found that all the plants of this generation called **firstfilial generation** or F1 grew to be tall plants. He allowed them to self pollinate. Again he collected the seeds. The following year, after the seeds had been sown, he found that three quarters of these plants were tall and the rest dwarf. He repeated the experiment several times and found that the ratio of tall to dwarf plants was 3 : 1



All the seeds were collected

In this way he tried to cross pea plants differing in seven such contrasting characters or **traits**. These were 1. red flowered and white flowered plants; 2. axillary flowered (flower arising in the axial of the leaf) and terminal flowered (flower arising at tip of stalk); 3. yellow seeded versus green seeded; 4. round seeded versus wrinkled seeded; 5. green pod versus yellow pod 6. Plants with inflated pods versus those with constricted pod and 7. pure tall plants versus pure dwarf plants. Plants with these contrasting characters existed in varieties that were 'self pollinating' so that generation after generation they expressed only one type of feature Crosses involving plants differing in the inheritance of **one contrasting feature only** are called **monohybrid crosses**. Mendel also tried crosses involving two contrasting features, such as tall and red flowered plants crossed with dwarf and white flowered plants. Such crosses are termed **dihybrid crosses**.

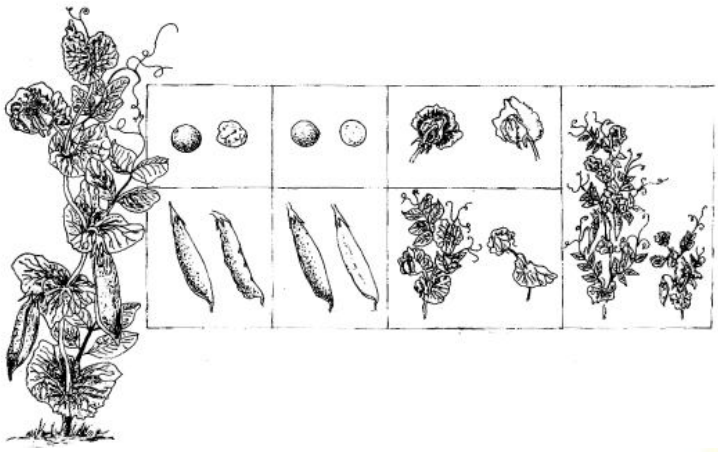
Mendel's Principles (laws) of inheritance

Based on the results of his experiments, Mendel postulated the following laws of heredity.

1. **Law of segregation or purity of gametes.** At formation of gametes, the two chromosomes of each pair separate (segregate) into two different cell which form the gametes. This is a universal law and always during gamete formation in all sexually reproducing organisms, the two factors of a pair pass into different gametes. Each gamete receives one member of a pair of factors and the gametes are pure.

Mendel's factors later came to be known as genes.

2. **Law of dominance.** During inheritance of many traits (e.g. eye colour, flower colour, seed shape) is controlled by **one pair of genes**. When the two genes of a pair are of the same kind (e.g. brown colour of eyes, red colour of flower) the condition is termed as **homozygous**. When a pair of chromosomes has the gene controlling the same feature (flower colour) in two different forms (red flower gene on one chromosome and white flower gene on another member of the pair (termed its **homologue**) the condition is termed **heterozygous.** The factors or genes for red and white flower colour are alternative forms of the same gene, that is, the gene for flower colour. Suh alternative forms of the same gene are termed as **Alleles**. The second law of inheritance maintains that when the two genes of a pair, represent contrasting characters **the expression of one is dominant over that of the other**. Thus if both genes of an allele are for tallness (represented as TT) that is **homozygous** or one gene is for tallness and another for dwarfness (Tt), that is **heterozygous**, the pea plants will be tall. The opposite of dominant gene is termed **recessive gene**. The recessive feature (e.g. dwarfness of the plant) is expressed only when both the genes of allele are in the homozygous condition (tt). The law of dominance was found to be true in both monohybrid and dihybrid crosses in cases of all the seven characteristics studied by Mendel in the garden pea.



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Parents	Male		Female
Phenotype	Tall		Dwarf
Genotype	TT		tt

Gametes T t

F_1 Generation

Tt Tall [Hybrid]

F1 Parents Male Female
Phenotype Tall Tall
Genotype Tt Tt
Gametes T t T t

Gametes	T	t
T	TT Pure Tall	Tt Hybrid Tall
T	Tt Hybrid Tall	Tt pure Dwarf

Ratio :3:1 3 Plants Tall (either TT or Tt) and one Dwarf (tt)

3. Law of independent assortment meaning whereby that in the inheritance of two features (each feature controlled by a pair of genes), genes for the two different features are passed down into the offspring **independently** i.e. the segregation of one pair of factors is independent of the segregation of the factors belonging to any other pair of factors or allelic pair.

Parents Male Female
Phenotype Yellow Round Green Wrinkled
Genotype YYRR rryy
Gametes YR ry
F_1 Generation Yellow Round [Hybrid]

YyRR

F1 Parents Male Female
Phenotype Yellow Round Yellow Round
Genotype YyRr YyRr
Gametes YR Yr yR yr

F_2 progeny worked out below.

Genes in male and female gametes	YR	Yr	yR	yr
YR	YYRR *Yellow Round*	YYRr *Yellow Round*	YyRR *Yellow Round*	YyRr *Yellow Round*
Yr	YYRr *Yellow Round*	YYrr *Yellow wrinkled*	YyRr *Yellow Round*	Yyrr *Yellow wrinkled*
yR	YyRR *Yellow Round*	YyRr *Yellow Round*	yyRR *Green Round*	yyRr *Green Round*
Yr	YyRr *Yellow Round*	Yyrr *Yellow wrinkled*	yyRr *Green Round*	yyrr *Green Wrinkled*

9 Yellow Round : 3 Yellow wrinkled : 3 Green Round : 1 Green Wrinkled

In the above chart, results show independent assortment in two pairs of genes. Y stands for Yellow colour of cotyledon, y for green colour similarly, R stands for round Shape of cotyledon, r for wrinkled, You would have noticed that the composition of genes termed **genotype** controls the outside expression which we can see, that is the **phenotype**. The ratio of progeny in the crosses is therefore, the **phenotypic ratio**. However, as more and

more scientists began to devise genetic experiments, it became clear that Mendel's laws do not hold true in all cases.

Introduction to Gene Interaction:

Mendelian genetics does not explain all kinds of inheritance for which the phenotypic ratios in some cases are different from Mendelian ratios (3:1 for monohybrid, 9:3:3:1 for di-hybrid in F_2). This is because sometimes a particular allele may be partially or equally dominant to the other or due to existence of more than two alleles or due to lethal alleles. These kinds of genetic interactions between the alleles of a single gene are referred to as allelic or intra- allelic interactions.Non-allelic or inter-allelic interactions also occur where the development of single character is due to two or more genes affecting the expression of each other in various ways.

Thus, the expression of gene is not independent of each other and dependent on the presence or absence of other gene or genes; These kinds of deviations from Mendelian one gene-one trait concept is known as Factor Hypothesis or Interaction of Genes (Table 2

Type	Ratio	Interaction
A. Allelic interaction		
1. Incomplete dominance		
(a) Monohybrids	1:2:1	Partial interaction
(b) Dihybrid	1:2:1:2:4:2:1:2:1	Partial dominance at both the gene pairs.
(c)		
2. Lethal factor	2:1/3:0	Homozygous condition causes death.
3. Multiple alleles		Occurrence of more than two allele in same locus
B. Non- Allelic Interaction		
1. Simple Interaction	9:3:3:1	New Phenotypes resulting from interaction between two dominant genes and also between two recessive genes.
2. Complementary Interaction	9:7	Two dominant genes complementary to each other in their effect.
3. Epistasis		
(a) Recessive	9:3:4	A homozygous genes is epistatic to other genes.
(b) Dominant	12:2:1	A Dominant gene is epistatic to other genes.
4. Inhibitory factor	13:3	One dominant gene inhibit the expression of others.
5. Polymorphic gene	9:6:1	One dominant gene inhibit the expression of other dominant gene.
6. Duplicate Gene	15:1	New phenotype from the interaction of two dominant gene.
		Dominant allele either pair, alone or together, are similar in phenotypic effect.
		Dominant allele of gene pair either alone or together shows similar effect.

Lethal Factor (2:1):

The genes which cause the death of the individual carrying it, is called lethal factor. Recessive lethals are expressed only when they are in homozygous state and the heterozygotes remain unaffected. There are genes that have a dominant phenotypic effect but are recessive lethal, e.g., gene for yellow coat colour in mice.But many genes are recessive both in their phenotypic as well as lethal effects, e.g., gene producing albino seedlings in barley (Fig. 7.2).

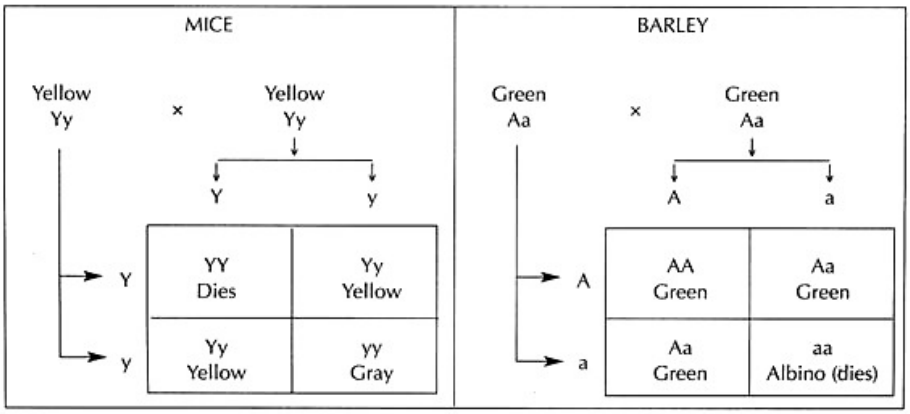


Fig. 7.2: Inheritance of lethal gene in mice and barley

Dominant lethals are lost from the population because they cause death of the organism even in a heterozygous state, e.g., epiloia gene in human beings. Conditional lethals require a specific condition for their lethal action, e.g., temperature sensitive mutant of barley (lethal effect at low temperature).Balanced lethals are all heterozygous for the lethal genes; both dominant and recessive homozygotes will die, e.g., balanced lethal system in Oenothera. Gametic lethals make the gametes incapable of fertilization, e.g., segregation distorter gene in male Drosophila.Semi-lethal genes do not cause the death of all the individuals, e.g., xentha mutants in some plants.

Non Allelic Gene Interactions:

Duplicate Recessive Epistasis [9 : 7 Ratio]:

When recessive alleles at either of the two loci can mask the expression of dominant alleles at the two loci, it is called duplicate recessive epistasis. This is also known as complementary epistasis. The best example of duplicate recessive epistasis if found for flower colour in sweet pea.

The purple colour of flower in sweet pea is governed by two dominant genes say A and B. When these genes are in separate individuals (AAbb or aaBB) or recessive (aabb) they produce white flower.

A cross between purple flower (AABB) and white flower (aabb) strains produced purple colour in F_1. Intermating of F_1 plants produced purple and white flower plants in 9 : 7 ratio in F_2 generation (Fig. 8.5). This can be explained as follows.

Here recessive allele a isepistatic to B/b alleles and mask the expression of these alleles. Another recessive allele b is epistatic to A/a alleles and mask their expression.

Hence in F_2, plants with A-B-(9/16) genotypes will have purple flowers, and plants with aaB-(3/16), A-bb-(3/16) and aabb (1/16) genotypes produce white flowers. Thus only two phenotypic classes, viz., purple and white are produced and the normal dihybrid segregation ratio 9 : 3 : 3 : 1 is changed to 9 : 7 ratio in F_2 generation.

Parents Purple Flower AABB × White Flower aabb

F_1 AaBb Purple Flower

F_2	AB	Ab	aB	ab
AB	AABB [P]	AABb [P]	AaBb [P]	AaBb [P]
Ab	AABb [P]	AAbb [W]	AaBb [P]	Aabb [W]
aB	AaBb [P]	AaBb [P]	aaBB [W]	aaBb [W]
ab	AaBb [P]	Aabb [W]	aaBb [W]	aabb [W]

P = Purple Flower, W = White Flower

Fig. 8.5. Duplicate recessive epistasis for flower colour in sweet pea. The normal dihybrid segregation ratio 9 : 3 : 3 : 1 is changed to 9 : 7 in F_2.

Dominant Epistasis [12 : 3 : 1 Ratio]:

When a dominant allele at one locus can mask the expression of both alleles (dominant and recessive) at another locus, it is known as dominant epistasis. In other words, the expression of one dominant or recessive allele is masked by another dominant gene. This is also referred to as simple epistasis.

An example of dominant epistasis is found for fruit colour in summer squash. There are three types of fruit colours in this cucumber, viz., white, yellow and green. White colour is controlled by dominant gene W and yellow colour by dominant gene G. White is dominant over both yellow and green.

The green fruits are produced in recessive condition (wwgg). A cross between plants having white and yellow fruits produced F_1 with white fruits. Inter-mating of F_1 plants produced plants with white, yellow and green coloured fruits in F_2 in 12 : 3 : 1 ratio (Fig. 8.3). This can be explained as follows.

Parents White Fruit WWgg × Yellow Fruit wwGG

F_1 WwGg White Fruit

F_2	WG	Wg	wG	wg
WG	WWGG [W]	WWGg [W]	WwGG [W]	WwGg [W]
Wg	WWGg [W]	WWgg [W]	WwGg [W]	Wwgg [W]
wG	WwGG [W]	WwGg [W]	wwGG [Y]	wwGg [Y]
wg	WwGg [W]	Wwgg [W]	wwGg [Y]	wwgg [G]

W = White Fruit, Y = Yellow fruit, G = Green Fruit

Fig. 8.3. Dominant epistasis for fruit colour in Summer squash. The normal dihybrid modified to 12 : 3 : 1 in F_2 generation.

Here W is dominant to w and epistatic to alleles G and g. Hence it will mask the expression of G/g alleles. Hence in F_2, plants with W-G-(9/16) and W-gg (3/16) genotypes will produce white fruits; plants with wwG-(3/16) will produce yellow fruits and those with wwgg (1/16) genotype will produce green fruits.

Thus the normal dihybrid ratio 9 : 3 : 3 : 1 is modified to 12:3: 1 ratio in F_2 generation. Similar type of gene interaction has been reported for skin colour in mice and seed coat colour in barley.

Duplicate Dominant Epistasis [15 : 1 Ratio]:

When a dominant allele at either of two loci can mask the expression of recessive alleles at the two loci, it is known as duplicate dominant epistasis. This is also called duplicate gene action. A good example of duplicate dominant epistasis is awn character in rice. Development of awn in rice is controlled by two dominant duplicate genes (A and B).

Presence of any of these two alleles can produce awn. The awnless condition develops only when both these genes are in homozygous recessive state (aabb). A cross between awned and awnless strains produced awned plants in F_1. Inter-mating of F_1 plants produced awned and awnless plants in 15 : 1 ratio in F_2 generation (Fig. 8.6). This can be explained as follows.

Parents — Awned Rice AABB × Awnless Rice aabb

F_1 — AaBb — Awned Rice

F_2

	AB	Ab	aB	ab
AB	AABB [A]	AABb [A]	AaBB [A]	AaBb [A]
Ab	AABb [A]	AAbb [A]	AaBb [A]	Aabb [A]
aB	AaBB [A]	AaBb [A]	aaBB [A]	aaBb [A]
ab	AaBb [A]	Aabb [A]	aaBb [A]	aabb [a]

A = Awned Rice, a = Awnless Rice

Fig. 8.6. Duplicate dominant epistasis for awn character in rice. The normal dihybrid segregation ratio 9 : 3 : 3 : 1 is changed to 15 : 1 ratio in F_2 generation.

The allele A is epistatic to B/b alleles and all plants having allele A will develop awn. Another dominant allele B is epistatic to alleles A/a. Individuals with this allele also will develop awn character. Hence in F_2, plants with A-B-(9/16), A-bb-(3/16) and aaB-(3/16) genotypes will develop awn.

The awnless condition will develop only in double recessive (aabb) genotype (1/16). In this way only two classes of plants are developed and the normal dihybrid segregation ratio 9 : 3 : 3 : 1 is modified to 15 : 1 ratio in F_2. Similar gene action is found for nodulation in peanut and non-floating character in rice.

CHAPTER – 3 - Multiple alleles (4 L)

3.1 Definition characteristics
3.2 Detection of number of alleles in a series
3.3 Isoalleles and pseudoalleles
3.4 Multiple alleles in *Nicotiana* species

Introduction

The word allele is a general term to denote the alternative forms of a gene or contrasting gene pair that denote the alternative form of a gene is called allele. These alleles were previously considered by Bateson as hypothetical partner in Mendelian segregation.In Mendelian inheritance a given locus of chromosome was occupied by 2 kinds of genes, i.e., a normal gene (for round seed shape) and other its mutant recessive gene (wrinkled seed shape). But it may be possible that normal gene may show still many mutations in pea besides the one for wrinkledness. Here the locus will be occupied by normal allele and its two or more mutant genes.Thus, three or more kinds of genes occupying the same locus in individual chromosome are referred to as multiple alleles. In short many alleles of a single gene are called multiple alleles. The concept of multiple alleles is described under the term "multiple allelism".

Dawson and Whitehouse in England proposed the term panallele for all the gene mutations at a given locus in a chromosome. These differ from the multiple factor in one respect that multiple factors occupy different loci while alleles occupy same locus.

"Three or more kinds of gene which occupy the same locus are referred to as multiple alleles." Altenburg

Characteristics of Multiple Alleles:

1. The study of multiple alleles may be done in population.
2. Multiple alleles are situated on homologous chromosomes at the same locus.
3. There is no crossing over between the members of multiple alleles. Crossing over takes place between two different genes only (inter-generic recombination) and does not occur within a gene (intragenic recombination).
4. Multiple alleles influence one or the same character only.
5. Multiple alleles never show complementation with each other. By complementation test the allelic and non-allelic genes may be differentiated well. The production of wild type phenotype in a trans-heterozygote for 2 mutant alleles is known as complementation test.
6. The wild type (normal) allele is nearly always dominant while the other mutant alleles in the series may show dominance or there may be an intermediate phenotypic effect.
7. When any two of the multiple alleles are crossed, the phenotype is of a mutant type and not the wild type.
8. Further, F_2 generations from such crosses show typical monohybrid ratio for the concerned character.

3.2 Detection of number of alleles in a series:

Using classical genetics:

Perform an allelism test. This tests whether two alleles are independently assorting, linked, or at the same locus (hence allelic). e.g.Let two alleles be dominant; each produce a different result, but are additive.

If they are on different chromosomes,

AAbb x aaBB -> expected ratio in the F2 if independent is 9:3:3:1 (A_B_,A_bb,aaB_,aabb)

If its the same locus,

A_1A_1 x A_2A_2 -> expected ratio is 1:2:1 (A_1A_1,A_1A_2,A_2A_2)

You can do the same for other models and other crosses. The point here is to test one model vs. another. Note that if you have linkage, you'll have a ratio somewhere in between - which can be very difficult to clarify if you have a quantitative trait with noise.

3.3: Importance of Multiple Alleles:

The study of multiple alleles has increased our knowledge of heredity. According to T.H. Morgan a great knowledge of the nature of gene has come from multiple alleles. These alleles suggest that a gene can mutate in

different ways causing different effects. Multiple allelism also put forward the idea that different amounts of heterochromatin prevent the genes to different degree or space.

1. Pseudo alleles:

Alleles are different forms of the same gene located at the corresponding loci or the same locus. Sometimes it has been found that non-homologous genes which are situated at near but different loci affect the same character in the same manner as if they are different forms or alleles of the same gene. They are said as pseudo alleles. These pseudo alleles which are closely linked show re-combinations by crossing over unlike the alleles.

2. Isoalleles:

Sometimes, a dominant gene occurs in two or more forms. These multiple dominant alleles will produce the same phenotypic effect in homozygous condition but their effect will show a small difference in heterozygous state.In Drosophila, thus, the gene for red eye colour is dominant over white. The red gene will produce dark red colour in the homozygous condition but in combination with the white allele the gene for red colour produces a dark red colour in flies from Soviet Russia but the same combination in the flies coming from the U.S.A. produces a light red colour. It does mean that dominant gene for red colour occurs in two forms. These are said as isoalleles.

Multiple Alleles in *Nicotiana* Species:Self-Sterility in Plants:

Kolreuter (1764) described self- sterility in tobacco (***Nicotiana longiflora***). The reason was done by East. He described that self-sterility is due to series of alleles designated as s_1, s_2, s_3 and s_4 etc. The hybrids S_1/S_2 or S_1/S_3 or S_3/S_4 are self-sterile because pollen grains from these varieties did not develop, but pollens of S_1/S_2 were effective and capable of fertilization with S_3/S_4.

The genes causing self-sterility in plants probably produce their effects by controlling the growth rate of the pollen tubes. In compatible combinations, the pollen tube grows more and more rapidly as it approaches the ovule, but in non-suitable ones, the growth of the pollen tube slows down considerably, so that the flower withers away before fertilization can take place.

Male Parent		S_1S_2		S_1S_3		S_2S_3	
Pollens		S_1	S_2	S_2	S_3	S_2	S_3
Female Parent	S_1S_3	---- Fully incompatible	---	-------	S_1S_3 S_2S_3	------	S_1S_3 S_2S_3
	S_1S_3	------	S_1S_2 S_2S_3	---- Fully incompatible	---	S_1S_2 S_2S_3	--------
	S_2S_3	S_1S_2 S_1S_3	--------	S_1S_2 S_1S_3	--------	---- Fully incompatible	---

Pseudoalleles:

Pseudoalleles refer to closely linked and functionally related genes. A cluster of pseudoalleles is known as pseudoallele series or a complex locus or a complex region.

Main characteristics of pseudoalleles are given below:

1. Pseudoalleles govern different expressions of the same character. In other words, they are functionally related.
2. Pseudoalleles are considered to occupy a complex locus which is divided into sub loci. Thus, they occupy different positions, but on the same complex locus.
3. They exhibit low frequency of genetic recombination by crossing over. In other words, crossing over occurs between pseudoalleles, but at a very low frequency.
4. They exhibit cis-trans position effect. In trans heterozygotes such mutants produce mutant phenotype, but in cis-heterozygotes they produce a wild phenotype.

Examples of Pseudoalleles:

There are several examples of pseudoalleles. The well-known examples are lozenge gene and star asteroid in Drosophila.

1. Lozenge Eye in Drosophila:

2. Star Asteroid Eye in Drosophila:

Isoalleles:

An allele which is similar in its phenotypic expression to that of other independently occurring allele is known as isoallele. In other words, isoalleles are those alleles which act within the same phenotypic range of each other.

Isoalleles are of two type as given below:

1. Mutant Isoalleles. Such alleles act within the phenotypic range of a mutant character.
2. Normal Isoalleles. Such alleles act within the phenotypic range of a wild character.

CHAPTER – 4 – Linkage and Crossing Over (6 L)

4.1 Concept and history of linkage
4.2 Coupling and Repulsion hypothesis
4.3 Linkage in maize (Hutchinson's test cross)
4.4 Definition and process of Crossing Over
4.5 Types of Crossing Over- Single and Double Crossing Over
4.6 Three point test cross

4.1 Concept and history of linkage

When two or more characters of parents are transmitted to the offsprings of few generations such as F_1, F_2, F_3 etc. without any recombination, they are called as the linked characters and the phenomenon is called as linkage.This is a deviation from the Mendelian principle of independent assortment.Mendel's law of independent assortment is applicable to the genes that are situated in separate chromosomes. When genes for different characters are located in the same chromosome, they are tied to one another and are said to be linked.

They are inherited together by the offspring and will not be assorted independently. Thus, the tendency of two or more genes of the same chromosome to remain together in the process of inheritance is called linkage. Bateson and Punnet (1906), while working with sweet pea (Lathyrus odoratus) observed that flower colour and pollen shape tend to remain together and do not assort independently as per Mendel's law of independent assortment.

Morgan's View of Linkage:

Morgan (1910), while working on Drosophila stated that coupling and repulsion are two aspects of linkage. He defined linkage as the tendency of genes, present in the same chromosome, to remain in their original combination and to enter together in the same gamete.'The genes located on the same chromosome and are being inherited together are known as linked genes, and the characters controlled by these are known as linked characters. Their recombination frequency is always less than 50%. All those genes which are located in the single chromosome form one linkage group. The total number of linkage group in an organism corresponds to the number of chromosome pairs. For example, there are 23 linkage groups in man, 7 in sweet pea and 4 in Drosophila melanogaster.

Features of Theory of Linkage:

Morgan and Castle formulated 'The Chromosome Theory of Linkage'.

It has the following salient features:

1. Genes that show linkage are situated in the same chromosome.
2. Genes are arranged in a linear fashion in the chromosome i.e., linkage of genes is linear.
3. The distance between the linked genes is inversely proportional to the strength of linkage. The genes which are closely located show strong linkage, whereas those, which are widely separated, have more chance to get separated by crossing over (weak linkage).
4. Linked genes remain in their original combination during course of inheritance.
5. The linked genes show two types of arrangement on the chromosome. If the dominant alleles of two or more pairs of linked genes are present on one chromosome and their recessive alleles of all of them on the other homologue (AB/ab), this arrangement is known as cis-arrangement. However, if the dominant allele of one pair and recessive allele of second pair are present on one chromosome and recessive and dominant alleles on the other chromosome of a homologous pair (Ab/aB), this arrangement is called trans arrangement (Fig. 5.7).

4.3 Linkage in maize (Hutchinson's test cross)

Examples of Linkage:In MAIZE:

Maize provides a good example of linkage. Hutchinson crossed a variety of maize having coloured and full seed (CCSS) with a variety having colourless and shrunken seeds (ccss). The gene C for colour is dominant over its colourless allele c and the gene S for full seed is dominant over its shrunken allele s. All the F_1 plants produced coloured and full seed. But in a test cross, when such F_1 females (heterozygous) are cross pollinated with the

pollen from a plant having colourless and shrunken seeds (double recessive), four types of seeds are produced (Fig. 5.8).

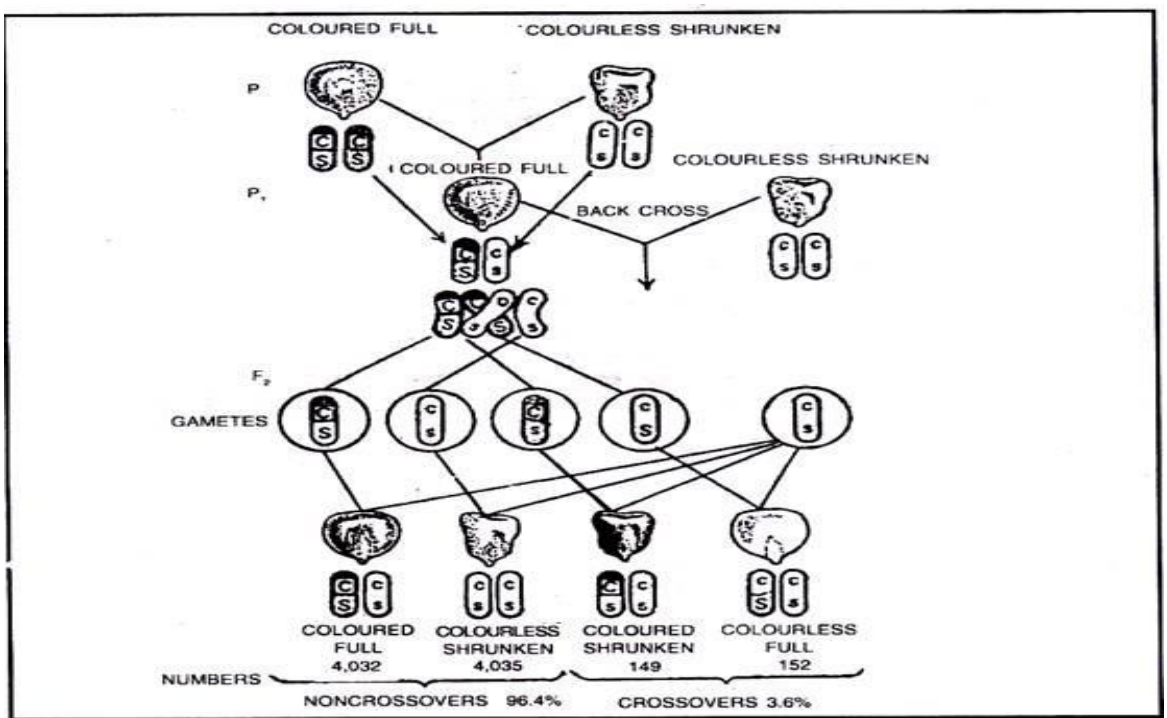


Fig. 5.8 Chromosomal interpretation of linkage and crossing over in maize.

These are:

(*i*)	**Coloured full** (CS)	– 4,032/8368	Parental combination = 96.4%
(*ii*)	**Colourless shrunken** (cs)	– 4,035/8368	
(*iii*)	**Coloured shrunken** (Cs)	– 149/8368	New combination
(*iv*)	**Colourless full** (cS)	– 152/8368	= 3.6%

From the above stated result it is clear that the parental combinations are more numerous (96.4%) than the new combination (3.6%). This clearly indicates that the parental characters are linked together. Their genes are located in the same chromosome and only in 3.6% individuals these genes are separated by crossing over. This is an example of incomplete linkage.

4.2 Coupling and Repulsion hypothesis

When two different varieties of sweet pea—one having red flowers and round pollen grain and other having blue flower and long pollen grain were crossed, the F_1 plants were blue flowered with long pollen (blue long characters were respectively dominant over red and round characters). When these blue long (heterozygous) hybrids were crossed with double recessive red and round (homozygous) individuals (test cross), they failed to produce expected 1:1:1:1 ratio in F_2 generation. These actually produced following four combinations in the ratio of 7 : 1 : 1 : 7 (7 blue long : 1 blue round : 1 red long : 7 red round) (Fig. 5.6).

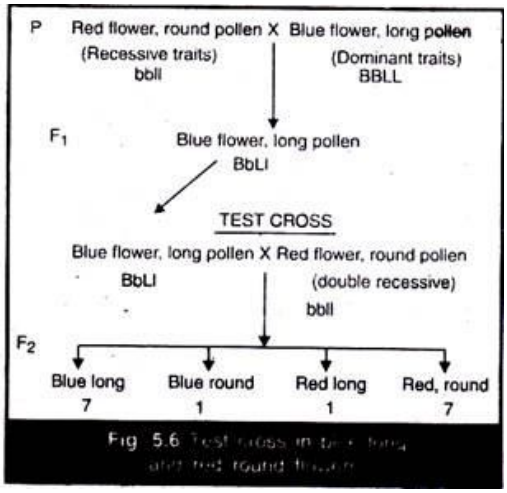


Fig 5.6

The above result of the test cross clearly indicates that the parental combinations (blue, long and red, round) are seven times more numerous than the non-parental combinations. Bateson and Punnet suggested that the genes (such as B and L) coming from the same parent (BBLL × bbll) tend to enter the same gamete and to be inherited together (coupling). Similarly, the genes (B and 1) coming from two different parents (such as BBLL x bbll), tend to enter different gametes and to be inherited separately and independently (repulsion).

Types of Linkage:

Depending upon the presence or absence of new combinations or non-parental combinations, linkage can be of two types:

(i) Complete Linkage:

If two or more characters are inherited together and consistently appear in two or more generations in their original or parental combinations, it is called complete linkage. These genes do not produce non-parental combinations.Genes showing complete linkage are closely located in the same chromosome. Genes for grey body and long wings in male Drosophila show complete linkage.

(ii) Incomplete Linkage:

Incomplete linkage is exhibited by those genes which produce some percentage of non-parental combinations. Such genes are located distantly on the chromosome. It is due to accidental or occasional breakage of chromosomal segments during crossing over.

Significance of Linkage:

(i) Linkage plays an important role in determining the nature of scope of hybridization and selection programmes.

(ii) Linkage reduces the chance of recombination of genes and thus helps to hold parental characteristics together. 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.

4.4 Definition and process of Crossing Over

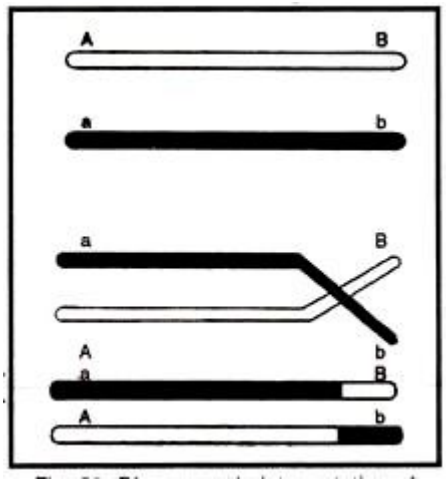
The phenomenon of complete linkage occurs rarely since the linked genes tend to separate during meiotic divisions. This mechanism of the genes as a result of interchange of chromosomal segments was termed crossing over by Morgan.

OR

Crossing over may be defined as an interchange of chromosomal parts between non-sister chromatids of a homologous pair of chromosomes resulting in the recombination of genes at Meiosis Prophase I, diplotene stage.

OR

The exchange of segments between the inner situated chromatids of homologous chromosomes is called crossing over.



The exchange of homologous segments with perfect correctness between non-sister chromatids of homologous chromosomes, responsible for recombination between linked genes is said as crossing over. It takes place during diplotene after the homologous chromosomes have undergone four-strand (4-chromatids) stage.

This produces a cross (X) like figure at the point of exchange of the chromatid segments; this figure is called chiasma, (Janssen (1909). Crossing over may take place at several points in one tetrad, resulting in the formation of several chiasmata whose number varies with the length of the chromosomes. It should be realized that chiasma is the result and not the cause of crossing over.

Although chiasma formation has been studied by several workers, detail of this process is till not definitely known. The cause leading to the breakage of the chromatids and their union, are not clear. According to recent findings chromosomal breakage and reunion may be the result of enzymatic action. The enzyme endonuclease brings about breakage and ligase is responsible for reunion.

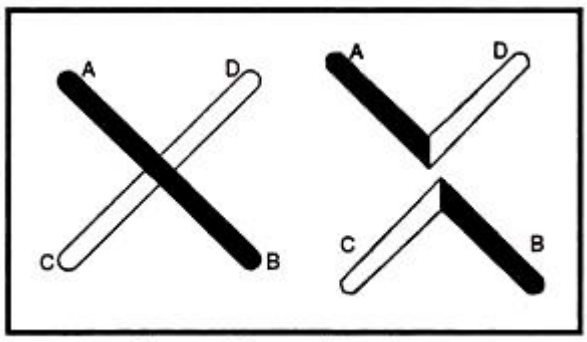


Fig. 61. Contact first theory.

Mechanism of Crossing Over:

1. Classical Theory:

This theory was proposed and advanced by Morgan and Sharp (1934) respectively, also called two-plane theory because it is assumed that adjacent loops would be present in different planes at right angles to each other. According to this theory, chiasma formation occurs when a chromatid of a chromosome comes to associate with the non-sister chromatid of a chromosome.

Generally the sister chromatids of the two chromosome of a bivalent remain attached with each other during synapsis. But in many divisions the sister chromatids separate from each other and become attached with non-sister chromatids of the homologous chromosomes thus producing chiasma.

During diplotene when the homologous chromosomes begin to separate from each other, the chromatids involved in chiasma formation are subjected to physical tension or strain (due to equational separation and reductional separation) at the point of chiasma. This may cause breakage of the two chromatid at this point, a reunion between the chromatids segments thus produced would lead to crossing over or recombination between linked genes.

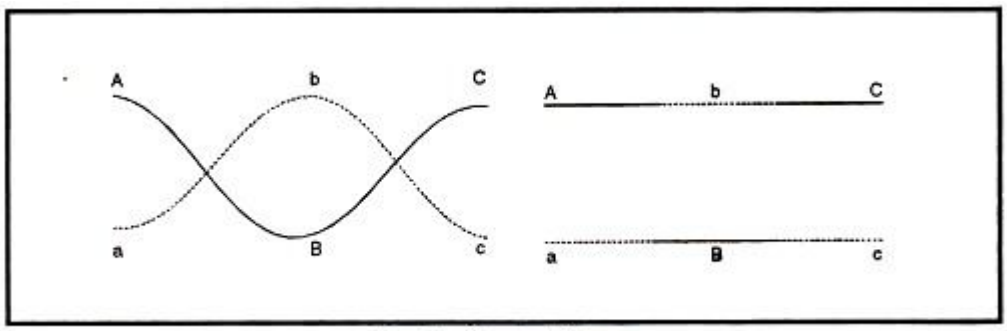


Fig. 63. Classical Theory

According to classical theory:

(i) A chiasma is formed after non-sister chromatids of homologous chromosomes become attached during synapsis.

(ii) Chiasma formation is not the result but cause of the crossing over.

(iii) Each chiasma does not lead the phenomenon of recombination or crossing over.

The above available experimental findings do not support this hypothesis and it is of only a historical significance. This theory, however, now stands rejected.

2. Chiasma Type Theory (Breakage & reunion theory):

It was firstly proposed by Janssens (1909) and later on expanded by him in 1924. Further, fully developed by Belling and Darlington. This is also said as one plane theory because in this theory, one would expect reductional separation of chromatids on either sides of a chiasma.

According to this theory, breakage in non-sister chromatids of homologous chromosomes, followed by the reunion of the chromatid segments resulting in crossing over. When the homologous chromosomes begin to move away from each other during diplotene, chiasmata are formed at those points where crossing over has taken place.

Thus (i) chiasma is the result of crossing over.

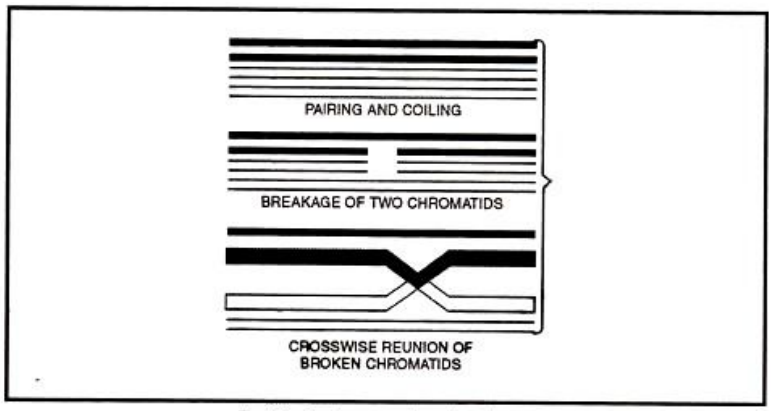


Fig. 64. Breakage and reunion theory.

(ii) Only sister chromatids are attached with each other through out the whole bivalent, where as non-sister chromatids become associated to produce chiasmata

(iii) Each chiasma is the consequence of a crossing over event, therefore

(iv) 1:1 ratio is expected between the numbering of frequencies of chiasma and crossing over.

Almost all the available evidence supports the chiasma type theory. Beadle (1932), Brown and Zohary (19-55) have strongly supported this theory since there is one to one correspondence between chiasmata and genetic crossing over explaining structure of gene maps and frequencies etc.

However, Kaufmann (1934) and Cooper (1949) objects this theory since chiasmata are also formed in some tissues of male Drosophila. Because genetic crossing over is lacking in male Drosophila, these chiasmata can not be explained by chiasma type theory. Thus, chiasma type theory seems to be a universally accepted one.

(3) Copy-Choice Theory:

This theory was proposed by J. Ledeberg (1955), according to this hypothesis, the duplication process and recombination occur simultaneously. In other words the paired chromatids duplicate by synthesizing new genes.

Then it is followed by the development of new connection between these genes. Thus the recombination's are produced by newly synthesised genes.

There are mainly two objections—one is that only two of the four chromatids are involved in crossing over. Thus two original strands remain intact while two newly formed strands would be altered by recombination. Secondly, this theory states that duplication should occur during late meiotic prophase but now evidence indicates that DNA replication occurs even before synapsis.

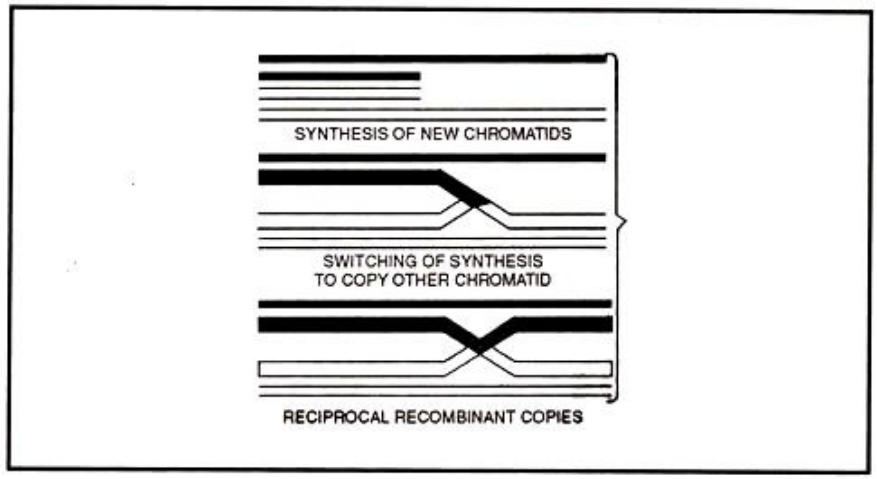


Fig. 65. Copy Choice Theory

4.5 Types of Crossing Over- Single and Double Crossing Over

Kinds of Crossing Over:

Crossing over may be single, multiple depending upon the number of chiasmata present in the chromosomes as follows:

1. Single Crossing Over:

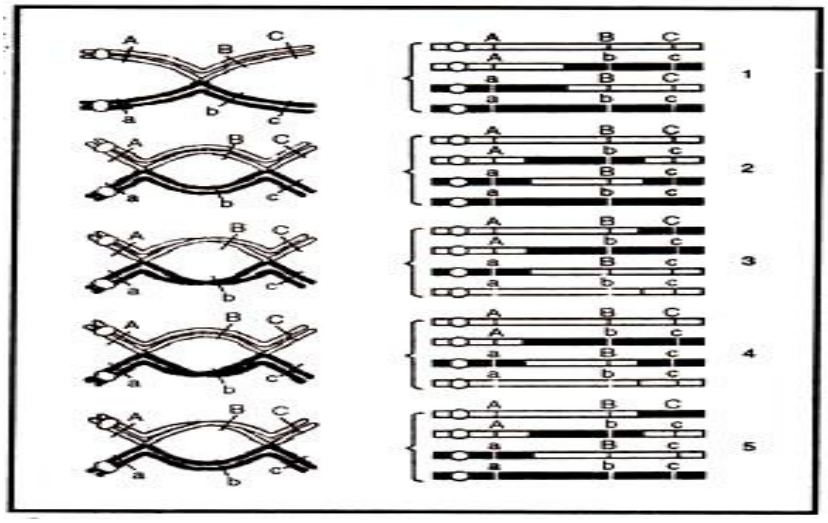
When there occurs only one chiasma or crossing over at one point in chromosome pair then it is referred to as single crossing over. The gametes which are produced by this crossing over are said as single cross-over gametes.

2. Double Crossing Over:

Occasionally or some times crossing over occurs at two points in the same chromosome pair. This is said as double crossing over. The gametes produced by this crossing over are called double cross-overs. It occurs seldom than single crossing over.

3. Multiple Crossing Over:

Crossing over may also occur at three, four or more points in the same chromosomes pair and correspondingly said as triple, quadruple, or multiple crossing over.



Factors affecting Crossing Over:

There are various genetically, physiological and environmental factors which affect the frequency of crossing over i.e., promotes or suppresses the percentage of crossing over between 2 loci.

1. Sex; 2. Mutation; 3. Age; 4. Inversion; 5. X—radiation; 6. Temperature; 7. Centromere vicinity:

Significance of Crossing Over:

(1) It has a great significance in genetics. Crossing over, a wide spread phenomenon provides a direct evidence of the linier arrangement of genes. Construction of chromosome maps and tracing linkage groups has been greatly facilitated by data obtained from the study of crossing over.

(2) It increases the frequency of variation which are vital for evolution. It causes formation of many combinations which can be acted by natural selection. The established linkage groups and linier order of genes gives much light on the nature and mechanism of genes.

4.6 Three point test cross

Chromosome Maps:

The chromosome maps represent the condensed graphic representation of the relative distance of the genes in a linkage group, expressed in the percentage recombination located and single group of chromosome. From the examples we have studied linkage and crossing over, it can be said that linkage can be taken as an exception to the second law of Mendel, and the characters of an organism are due to genes located in the chromosomes.

Moreover, genes are believed to occur in a number of linkage groups. The linkage groups correspond to the number of chromosomes. The linkage group in Drosophila melanogaster are four in number and there are four pairs of chromosomes in that fly.

In Morgan's hypothesis of crossing over it has been assumed that the genes had a linier arrangement in the chromosome. It was also thought that the distances between the two genes on the chromosome is correlated with the amount of crossing over shown by two corresponding alleles. The percentage of crossing over is directly proportional to the distance of alleles showing cross in the chromosomes.

These two facts made to represent in the form of a map which represents that:

(i) The genes are arranged in a linier row along the chromosome.

(ii) The percentage of crossing over between two genes is proportional to their distance apart.

Thus, chromosome map may be defined as a line, number of lines being equal to linkage groups on which genes are represented by points showing particular traits or characters proportional to the amount of crossing over.These chromosome maps are also referred to as cross-over maps since they are sketched by the amount of crossing over.

The percentage of crossing over is calculated by test crosses. In mapping genes a unit of distance is used. This unit used is one percent of crossing over called as Map unit or Morgan. The crossing over between linked genes may be as little as 1/10 of 1% or up to 50% depending upon their kinds.The first two chromosome maps were made in 1911 by Sturtevant and Bridges. Later in 1920, Morgan and his associates worked extensively on Drosophila and constructed chromosome maps. Then these maps were made in maize, chicks, tomato etc.

Location of Genes:

In fixing the exact position of a gene on the chromosome map, the cross-over frequency of a gene in relation to another is the criterian. The procedure adopted for constructing a chromosome map can be explained with reference to a three point test cross. A three point test cross is one in which the F_1 resulting from a cross involving three linked genes is back crossed to a triple recessive.

In Drosophila the three genes scute (sc), echinus (ec) and crossveinless (cv) are sex linked genes. Scute is condition in which many body bristles are missing, echinus means rough eyes and crossveinless indicates absence of cross veins on the wings, since these are recessive mutation, the F_1 females resulting from a cross between these recessive types and wild type resembles the wild type phenotypically. This is because the females drive one sex chromosome from their mother.

When the F_1 females are back crossed to triple recessive males, eight phenotypes are obtained as given below:

Three point test cross.

Parents $\frac{sc\ ec\ cv}{sc\ ec\ cv}$ female crossed with $\frac{+\ +\ +}{+\ +\ +}$ male

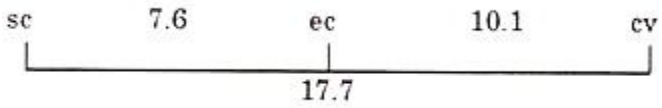
F_1 female $\frac{sc\ ec\ cv}{+\ +\ +}$ crossed with $\frac{sc\ ec\ cv}{+\ +\ +}$ male

Phenotypes obtained	Numbers	Apparent cross-over between	
		sc and ec	ec and cv
Non cross overs:			
sc ec cv	826	0	0
+ + +	820		
Single cross overs:			
+ ec cv	75		
sc + +	76	151	0
sc ec +	106		201
+ + cv	95		
Double cross overs:			
+ ec +	1	1	
sc + cv	1		1
Total	2000	152 7.6%	202 10.1%

In constructing the chromosome map the distance between the two linked genes is indicated by their cross-over frequency i.e., percentage. Since the cross-over frequency of scute in relation to echinus is 7.6%, these two genes are marked 7.6% unit apart. Again the cross-over frequency between echinus and crossveinless is 10.1%; these 2 genes are 10.1 unit apart.

In order to determine the sequence of the three genes it is necessary to find out the cross-over frequency between scute and crossveinless. The genes scute and crossveinless and the wild type alleles were introduced in to the cross by the same parent, one of these is present in the progeny without the other in 352 (151+201) cases.

To these figures the two double cross-overs may be added. The total number of cross-overs between scute and crossveinless is thus 354 or 17.7%. This is the sum and not the difference between 7.6% and 10.1. Therefore, the gene crossveinless lies beyond echinus; it means sequence is sc, ec and cv.

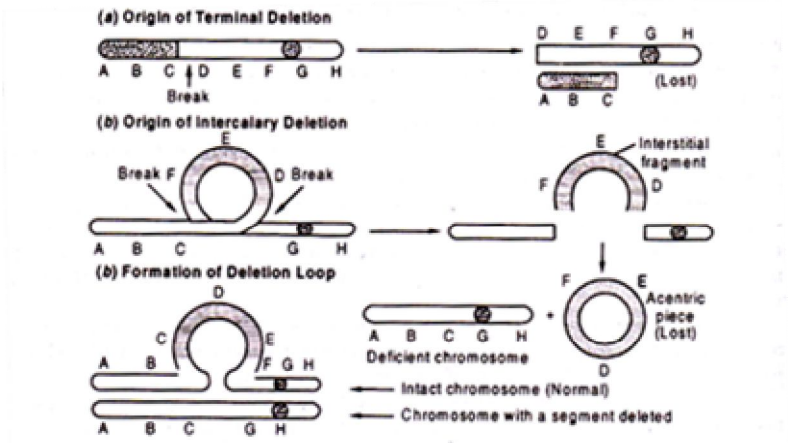


CHAPTER – 5 – Chromosomal Aberration (4 L)

5.1 Duplication and Deficiencies
5.2 Translocation and Inversion
5.3 Cytology of Translocation and Inversion.

Chromosomal Aberration: Type # 1. Deficiency or Deletion:

Chromosomes contain a number of genes on them. The genes are arranged in linear fashion. The number and also the positions of genes on a chromosome are fixed. When a chromosome is broken into several pieces, the healing (reunion) of the segments takes place and it is possible that the two ends of the fragments unite together leaving one or more acentric parts free.The acentric pieces of chromosomes as mentioned earlier disappear. The healed segments will form a chromosome that will be deficient for some of the genes, particularly those found on the lost part. Depending upon the length of chromosome segment lost in this way, the loss involves one gene or a block of genes.The loss of a section of genetic material and genetic information from a chromosome or linkage structure is termed deficiency or deletion. Deletions may be produced in several ways, such as by loss of terminal acentric fragments or interstitial segment of chromosomes Fig. 22.3).



Although in practice deletions frequently refer to losses of terminal as well as intercalary segments of chromosome, at molecular level the deletions, of course, can be so small that many mutant loci are in reality deficient for one or more nucleotides in the DNA molecule. If the deficiency is large, the chances are there that the cell may die.However, if the deficiency is small, the cells may persist. Should such a cell be fertilized egg, the net effect will be production of a dominant lethal. Homozygous deletions are usually lethal but heterozygous deletions appear as normal mutations.

Deficiency can be detected by its two characteristics, namely, genetic effects and cytological effects.

Genetic Effects of Deficiency:

1. These are primarily due to the loss of genetic information and secondarily due to qualitative changes in the genotype as well as the change of genie balance. Deficiencies have been useful in determining the exact locations of genes on the chromosomes.
2. One of the genetic effects of deficiency is pseudo-dominance. Pseudodominance occurs when the chromosome that carries the deletion of dominant allele pairs with a normal homologous chromosome carrying the recessive allele.
3. In absence of dominant alleles the recessive alleles would be expressed in phenotype as if they were dominant. This is called pseudo-dominance. If some of the corresponding genes have tendency of lethal effect in double dose, they will be lethal in single dose (recessive lethality). The chromosomes with deletion never return to a normal state.

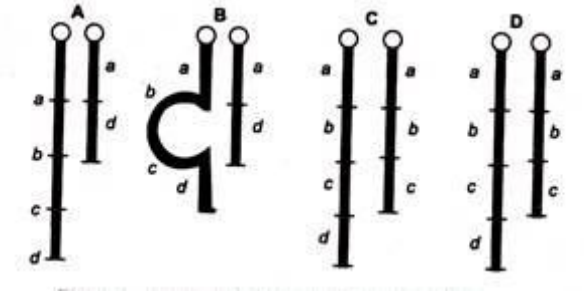
Cytological Effects:

The existence of relatively large deletions in the chromosome complements of eukaryotes may be proved cytologically

(i) By the occurrence of centric and acentric chromosome fragments in mitosis, and

(ii) By the absence of regional pairing during first meiotic prophase. If the cell is heterozygous for deletion, i.e. it has a normal chromosome and a deficient homologue, then during synapsis, the chromosomes pair precisely gene by gene all along the homologous region and in deficient region, however, the normal chromosome will not pair.

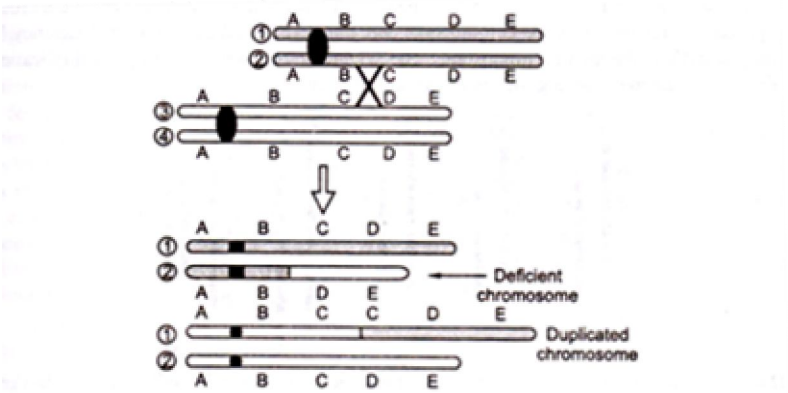
Therefore, a buckling (loop) will develop in the normal homologue at the point of intercalary deficiency (Fig.). It is, therefore, known as buckling effect. Such a configuration is called deficiency loop or compensation loop and can be observed under microscope.



Chromosomal Aberration: Type # 2. Duplications:

A structural change resulting in the doubling of genes in a section of the chromosome of prokaryotes and eukaryotes is referred to as duplication. In other words, the inclusion of extra part or duplicated gene sequence of a chromosome beyond the normal complement is called duplication.

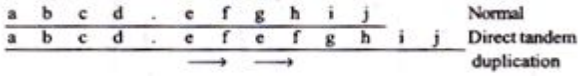
If a segment of one chromosome is incorporated in another homologous chromosome, it is called intrachromosomal duplication (Fig. 22.5), but if the duplicated chromosome segment is either incorporated into a non-homologous chromosome or occurs as a fragment in the chromosomal set it is called interchromosomal duplication (Fig.).



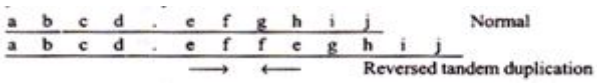
The duplicated segments contained within a single chromosome could exist in one of the following configurations depending upon the position and sequence of the duplicated genes.

(i) Direct tandem duplication in which the duplicated gene sequence lies just next to normal corresponding section and the sequence of genes with respect to centromere is the same in duplicated segment as in the normal section of the chromosome.

It will be clear from the following gene sequences in the normal and duplicated chromosomes:

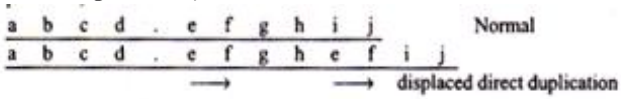


(ii) Reverse tandem duplication in which the duplicated section with reverse gene sequence lies adjacent to normal sequence as shown below:

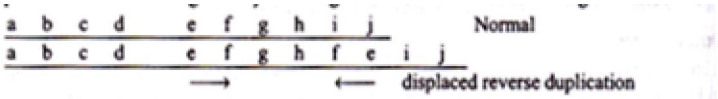


(iii) Displaced direct duplication in which the duplicated section is not adjacent or contiguous with the normal section (i.e., separated by other segment).

The duplicated and normal gene sequences may be in the same arm (intra arm) or in two different arms of the chromosome (inter arm duplication):



(iv) Displaced Reverse duplication in which the duplicated section with reverse gene sequence is separated from normal segment by other segment as shown in the following chromosomes:

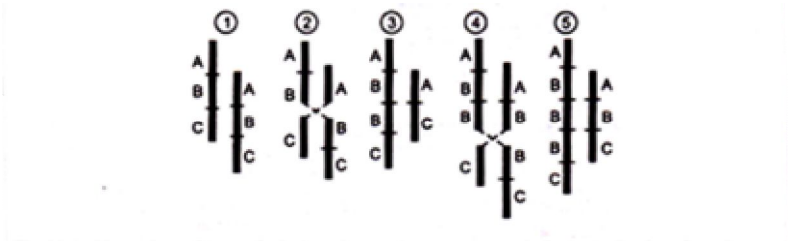


(v) Transposed duplication in which the duplicated gene sequence is attached to another position owing to inter-chromosomal duplication.

The size of duplicated segment may vary considerably. The smallest duplications that can be investigated cytologically are those of single band of polytene chromosomes. However, the whole arm of the chromosomes may be duplicated, thus giving rise to isochromosome. Where all linkage groups or chromosomes in the haploid chromosome set are doubled, this is referred to as genome mutation.

Duplication may arise in several ways. One of the most common methods is unequal crossing over, a process which produces one chromosome with duplication and another with deficiency. This is primary structural change of chromosome.

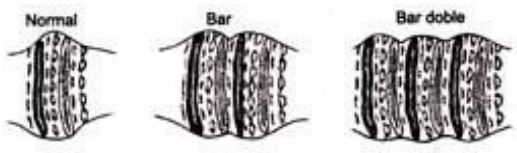
The schematic representation of gene duplication in chromosome by unequal crossing over is shown in Fig.



Duplications may also occur due to crossing over in inverted or translocated segments. (Secondary structural mutation of chromosome)

Duplications in general, are much more viable than deficiency. A heterozygous duplication has an appearance similar to deletion. Duplications sometimes appear as dominant mutations. By duplication an allele may be duplicated, triplicated or multiplicated, hence duplications may be utilized a studying the effect of various quantitative doses of members of an allelic set.

Well known example of duplication which had a significant impact on genie theory is Bar-eye mutation in Drosophila. With the discovery of chromosomal nature of this case, it was found that extra pieces of chromosome were associated with a normal X-chromosome duplicating and triplication section of it (Fig. 22.7).



The Bar-eye, a sex-linked incompletely dominant mutation responsible for the development of rod-shaped eye with reduced eye facets, appeared spontaneously in a wild type stock of Drosophila melanogaster with round eyes. Homozygous stock of Bar-eyed mutants produced flies with normal eye and flies with even more reduced eye (Double Bar) in approximately equal frequency.

These observations suggested that Bar locus was very unstable but the appearance of wild type and double bar flies in equal numbers could not easily be explained. Moreover, the two mutant phenotypes appeared in the progeny when Bar-females were crossed with normal males, and not in the progeny of Bar-males crossed with normal females.

In corn and peas, a number of duplicating factors are known. Duplications like deletions may be so small as to be molecular. Since they change the genie balance, they may produce abnormalities m body characters. Duplications are considered to play a role in origin of new genes through functional diversification of duplicated members.

Like deficiencies, duplications have diagnostic cytological and genetically effects.

Cytological Effects:

The existence of relatively small duplications in the chromosome complements of eukaryotes may be proved by the appearance of regional distortions of duplicated chromosome during pairing in first meiotic prophase or somatic pairing in specialized tissue like salivary glands of Diptera.

Crossing over in reverse tandem duplication may result into a dicentric chromosome. This can be frequently observed in maize. As the two centromeres move to opposite poles, a chromosome bridge is formed which later on breaks at any point along the bridge.

The broken ends are sticky and the replication of the broken pieces may result in two sister chromatids which may be joined together due to their sticky ends. Thus, whole chromosome arm may be duplicated giving rise to isochromosomes. In sporophytic tissues of plants, the isochromosomes are uncommon.

Genetic Effects:

The genetic effects of duplications depend on the genetic information the duplicated segments contain and the change in genie balance effected by them. In homo and heterozygous state they may cause an increase or decrease in the viability of their carriers and in extreme cases may act as lethals.

Since the duplications supply the additional genetic material and change the genie balance, they play important role in evolution at individual and population levels.

Under evolutionary conditions, small duplications may provide a basis for the mutational differentiation of genetic material and the different copies of the same gene may change in different directions without disturbing the normal functions of an organism.

The cases in which different gene pairs affect the same character (as for example, multiple factors, complementary factors) possibly arose initially after duplication of single genes. The repetition of DNA sequences frequently seen in highly evolved organisms is a direct indication to this.

Chromosomal Aberration: Type # 3. Translocation:

Chromosomes may break into two or more fragments, each with a raw end. These segments may reunite and during reunion either the pieces of the same chromosome or the pieces of the non-homologous chromosomes may be fused. Ionising radiations such as X-rays and gamma-rays are frequently used to break chromosomes for producing structural changes.

In this process, a part of the chromosome is transferred to another non-homologous chromosome within the chromosome complement.

In other words, a translocation is a chromosomal rearrangement which involves:

(i) The unidirectional transfer of a chromosome segment and its gene sequence to a different chromosome within the chromosome complement, and

(ii) The exchange of segments between non-homologous chromosomes. In this way, translocation only results into a change in the sequence and position of genes, their quantity being unaffected.

Types of Translocation:

1. Simple Non-Reciprocal Translocations or Transpositions:

In this process, a piece of one chromosome is transferred to a non-homologous chromosome.

It can be of two types:

(i)Simple translocation or Terminal transposition,

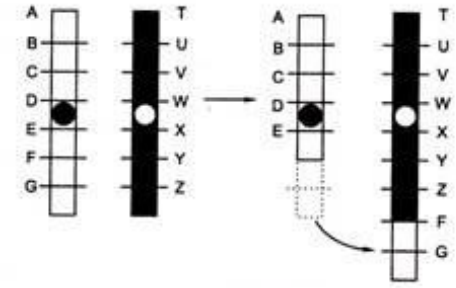
(ii) Shift translocation or Interstitial transposition.

(i) Simple Translocation:

When a chromosome breaks into two parts due to external or internal stress, one of the two segments of the broken chromosome may become attached to the natural end of the nearest chromosome which may not be its homologue. This is simple translocation.

Suppose, there are two non-homologous chromosomes A B C D E F G and TUVWXYZ. If F G part of the first chromosome is transferred to second chromosome, a new chromosome TUVWXYZFG would result as shown in Fig. 22.8. In this non-standard or translocation chromosome, F G is said to be in simple translocation state.

In the normal course, the terminal transpositions are not common because the raw ends or the telomeres of unbroken chromosomes are not sticky.



(ii) Intrachromosomal, Shift Translocation or Interstitial Transposition:

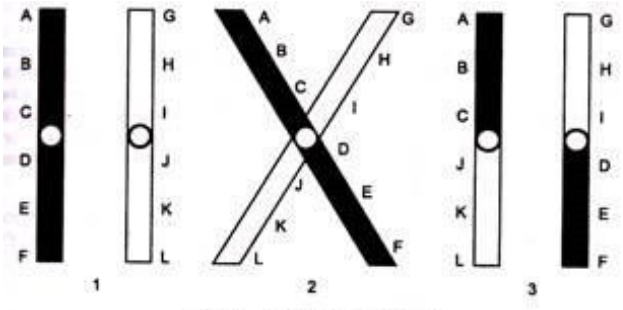
In this, an interior or interstitial segment of a chromosome that is induced by two breaks is incorporated interstitially into another non-homologous broken chromosome, the latter being induced by a single break. It is also called intercalation or insertion.

If the sequence of genes in the translocated segment is the same as that in the original segment with respect to centromere, it is referred to as encentric translocation. But if the sequence of gene loci in translocated chromosome segment is reversed it is called dyscentric translocation.

2. Reciprocal Translocation:

When a break occurs at a point where two non-homologous chromosomes touch each other, the broken end of one chromosome may become united with the broken end of second chromosome and that of second chromosome becomes attached to that of first, this is reciprocal translocation.

Suppose, there are two chromosomes A B C D E F and G H I J K L. These two after reciprocal translocation may produce chromosomes A B C J K L and G H I D E F as shown in Fig. 22.9. The reciprocal translocation is the most common type of translocation.



If there occurs two breaks in each of the two non-homologous chromosomes, the reciprocal translocation of intercalary segments may be obtained, but it is very rare.

The reciprocal translocation is like crossing over except that it involves exchange between the segments of two non-homologous chromosomes. It is sometimes called “illegitimate crossing over”.

The origin of translocations is interpreted either according to the breakage-reunion or the exchange model. The unit of translocation may be the chromosome (chromosome translocation) the single chromatid (chromatid translocation) or a segment of chromatid. The sites of translocations are called translocation points. The reciprocal translocation may be either asymmetrical (aneucentric) or symmetrical (eucentric).

The asymmetrical translocation gives rise to one dicentric and one acentric chromosomes (Fig. 22.10) and it may lead to the formation of chromosome bridge if the two centromeres of a dicentric translocation product are

distributed to opposite poles of spindle during anaphase. In symmetrical translocation, however, the products are monocentric.

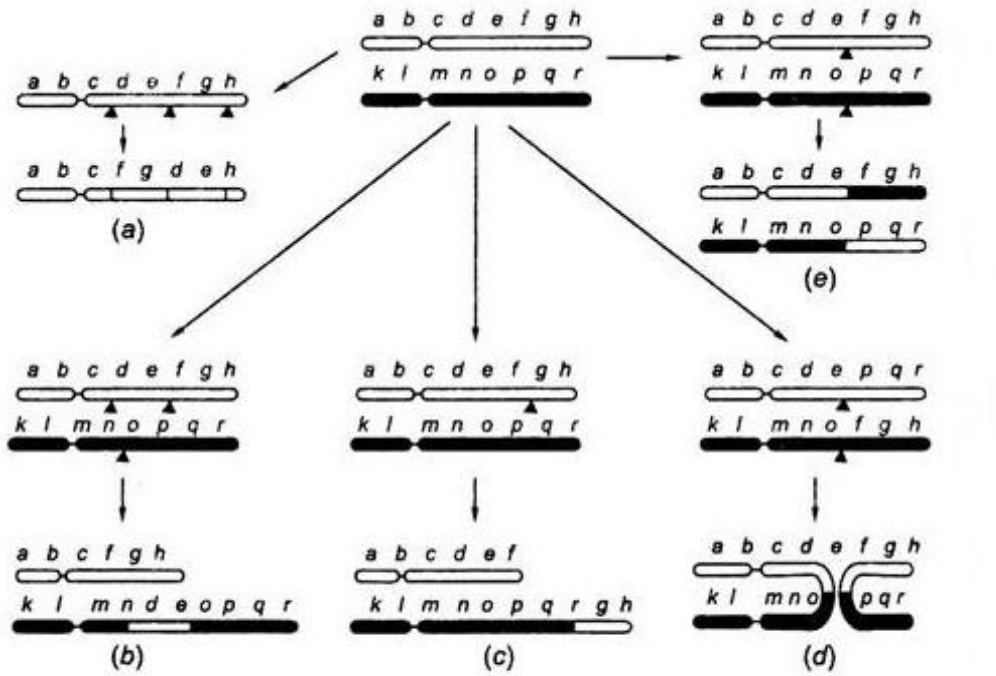


Fig. 22.10 Diagram showing several types of intrachromosomal and interchromosomal translocations (*a*) intrachromosomal transposition ("shift") of a chromosome segment; (*b*) interchromosomal transposition of a chromosome segment; the sequence d–e is transferred to a heterologous chromosome; (*c*) "terminal translocation" of the segment g–h to a heterologous chromosome (*d*) reciprocal (asymmetric) translocation (interchange) of segments f–h and p–r; (*e*) reciprocal (symmetric) translocation of segments f–h and p–r; in contrast to an asymmetric interchange the translocation products are monocentric.

1. Cytological effects
2. Genetical effects

1. Cytological Effects of Translocations:

The chromosomes of homozygous translocations generally behave as do the normal ones from which they arise, except that new linkage groups are formed. If they persist they can give rise to new chromosomal races in the population.

In the individuals heterozygous for a symmetrical reciprocal translocation (structural hybrids) two chromosomes with translocation and two normal chromosomes share a partial homology, but no two are identical.

Since synapsis is a matter of homologous regions (gene to gene pairing) and these regions are distributed over four chromosomes, in simple reciprocal translocation heterozygote, the association of all four chromosomes will be formed. Such an association will result in a cross configuration (+) at pachytene i.e., there will develop a group of four associated chromosomes (2 normal + 2 translocated).

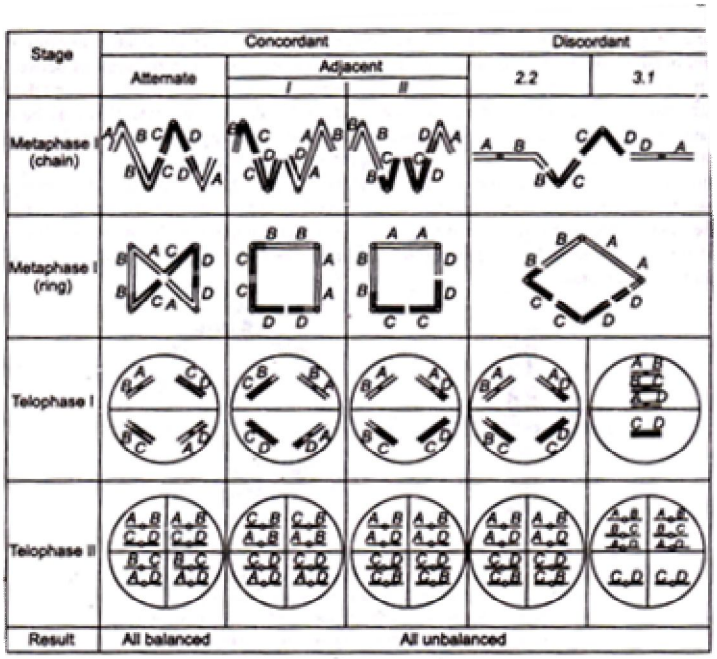


Fig. 22.14 The genetic consequences of various modes of orientation (in metaphase of the first meiotic division) of a chain-of-four or ring-of-four configuration in a karyotype heterozygous for a single reciprocal translocation

Heterozygosity for translocation reduces the crossing over frequency. The crossing over can take place in any of the four pairing segments of cross-like configuration in reciprocal translocation heterozygote but the results will vary according to the cross over site relative to centromeres and breakpoints of the translocation.

If the crossing over occurs in the regions between the centromeres and break points (i.e., interstitial region) it will result in duplicated and deficient chromosomes irrespective of adjacent or alternate distribution patterns.

This may be major cause of sterility in translocation heterozygotes. But the crossing over appears to be restricted in the interstitial regions because of inefficient synapsis between the chromosomes. If the crossing over takes place outside the interstitial regions, it does not affect the segregation patterns since one homologous section is exchanged for another.

Reduced crossing over within the translocated part is most pronounced in the vicinity of the interchange points. It is so on account of non-homologous pairing in interchange region or due to difficulty in its meiotic chromosome pairing.

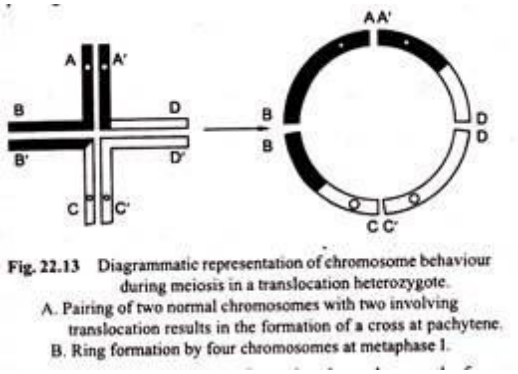


Fig. 22.13 Diagrammatic representation of chromosome behaviour during meiosis in a translocation heterozygote.
A. Pairing of two normal chromosomes with two involving translocation results in the formation of a cross at pachytene.
B. Ring formation by four chromosomes at metaphase I.

The subsequent behaviour of this cross configuration depends upon the frequency and locatior of the chiasmata and the centromere orientation. If chiasma formation takes place in all four pairing segments, a ring of four chromosomes results. The occurrence of quadrivalent rings has been observed during metaphase in Datura, peas, wheat, Tradescantia and some other plants as well as animals.

If chiasma formation fails in one of the four pairing segments, a chain of four chromosomes results. If chiasma formation takes place in two adjacent or alternate pairing segments, a chain of three chromosomes and one univalent, or two bivalents will result.

Rings and chains contain structurally normal and structurally changed chromosomes in alternating sequence. Now the distribution of the four chromosomes in ring or chain configuration at anaphase I of meiosis is determined by the orientation of centromeres. There are two common patterns of distribution, adjacent and alternate (Fig. 22.14).

(a) Adjacent distribution:

In this the chromosomes located alternately in the pairing configuration are segregated in such a way that one structurally normal and one translocated chromosome go to one pole and their counterparts, to the opposite pole. In this case both meiotic products are duplicated.

In adjacent distribution there are two events:

(i) Adjacent 1 distribution in which the centromeres of neighbouring non-homologous chromosomes segregate to same pole, and

(ii) Adjacent-2 distribution in which homologous centromeres migrate to the same pole, but it is very rare in occurrence.

(b) Alternate distribution:

In this the two normal chromosomes go to one pole and the two translocated chromosomes go to the opposite pole during anaphase I and so the gametes- formed are of two kinds; some with normal chromosomes and some with translocated chromosomes.

2. Genetic Effects of Tanslocations:

The main genetic effects of translocations are as follows:

(i) It brings about a qualitative change in the chromosomes structure or linkage group,

(ii) It brings about change in the sequences of genes in chromosomes which may eventually produce several abnormalities in body characters. This is position effect.

(iii) Semi-sterility. The translocation heterozygotes are generally semi-sterile because they produce gametes containing duplicated and deficient chromosomes as a result of typical pairing behaviours, crossing over and segregation patterns of chromosomes.

The translocation is of great importance for the individuals and the species. The most harmful effect of a reciprocal translocation is the semi-sterility it causes. It also causes severe modifications of the normal developmental pattern.

In the evening primrose (Oenothera) a number of variations are associated with translocations. This was the plant whose variability led De Vries to propose his popular mutation theory.

Chromosomal Aberration: Type # 4. Inversion:

I", is an intrachromosomal aberration characterised by inversion or reversal of a chromosome segment and the gene sequence contained therein relative to the standard chromosome or linkage group in question. It occurs in intercalary segment of the chromosome. There is no experimental evidence for occurrence of inversions in terminal segments of chromosomes.

According to the breakage reunion —model, the intercalary inversions are formed when two breaks occur in a chromosome, the middle segment between the break points (referred to as inversion points) is inverted or rotated through : and then reunion of the three segments at the sites of breakage takes place as shown below Fig. 22.16).

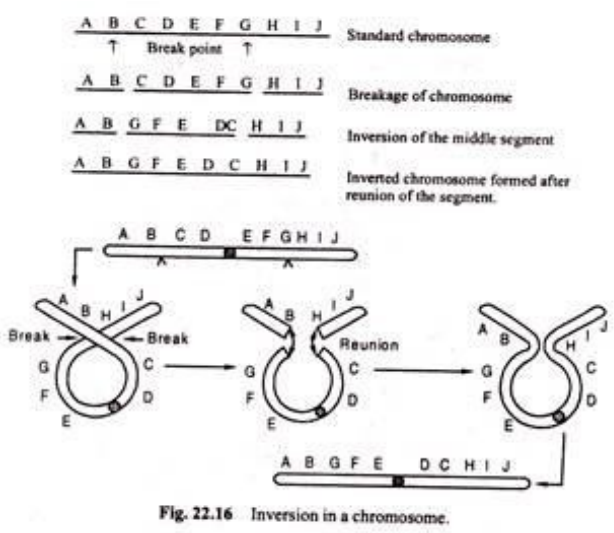


Fig. 22.16 Inversion in a chromosome.

Sometimes inverted segment or a part of it may again undergo inversion. This is called included inversion. Thus, in the above example, if the segment, GFEDC in the inverted chromosome undergoes further inversion, the result will be that the chromosome will regain original gene sequence ABCDEFGHIJ.

Types of Inversions:

The inversions are classified according to the number of inverted segments within the chromosome and the location of inversion points with respect to each other.

1. Single inversions:

When a chromosome contains a single inverted segment, it is called single inversion. Single inversions are classified according to whether or not the inverted segment of the chromosome carries the centromere.

(i) Paracentric inversion. This is the most common type of inversion which is confined to a single arm of a chromosome. In this, the inverted segment of the chromosome does not carry centromere. It is also called acentric or dyscentric orparakinetic or asymmetrical inversion (Fig. 22.17).

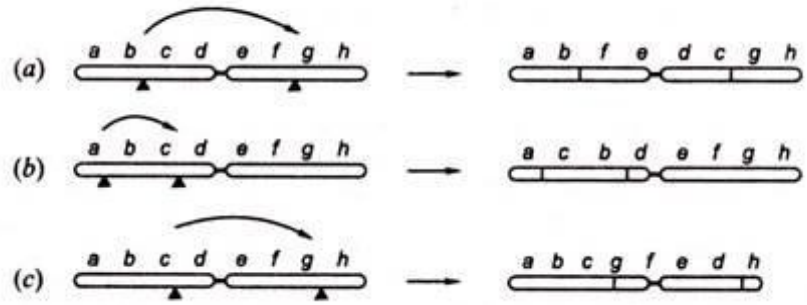


Fig. 22.17 Diagram showing various types of inversions. (*a*) pericentric; (*b*) paracentric; (*c*) pericentric which results in a change of chromosome morphology.

(ii) Pericentric inversion:

In this type of inversion, the break points are located in both the arms of chromosome so that the inverted segment includes centromere (Fig. 22.17). It is also called transcentric or eucentric or transkinetic or symmetrical inversion. If the two breakpoints involved in the formation of a pericentric inversion are equidistant from the centromere, the inverted chromosome will appear morphologically similar to normal one.

But, if the breakpoints are asymmetric (not equidistant) from the centromere, a shift of centromere from acrocentric to metacentric or vice-versa may occur, thus causing a marked change in the appearance of chromosome. This indicates that pericentric inversions might have played important role in the evolution of new karyotypes.

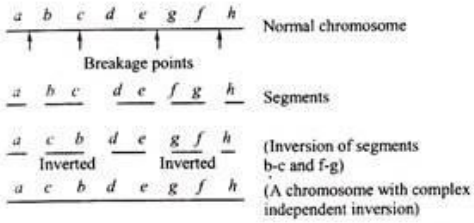
2. Complex inversions:

When a chromosome contains more than one inverted segment, it is called complex inversion.

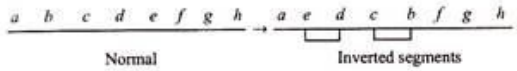
The complex inversions are classified as follows:

(i) Independent inversion:

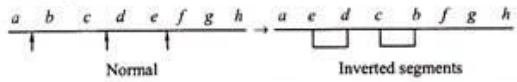
When the inverted segments are separated from one another by uninverted segment, the inversion is said to be independent inversion.



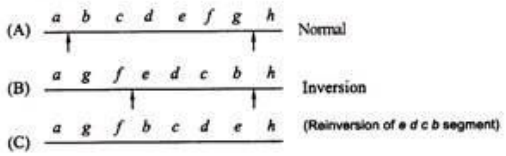
(ii) **Direct tandem inversion**. In this, two inverted segments lie adjacent to each other in the chromosome.



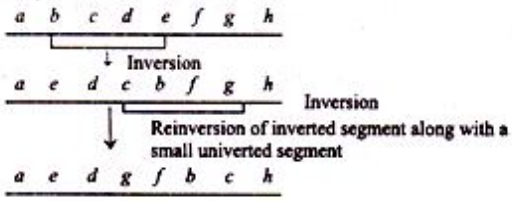
(iii) **Reversed tandem inversion**. In this, the two inverted segments are adjacent but mutually interchanged within a chromosome.



(iv) **Included inversion.** In this, the inverted segment or a part of it is inverted again within the chromosome.



(v) **Overlapping inversion**. In this a part of an inverted segment is reinverted together with a segment which remained uninverted.



Inversions may be either homozygous or heterozygous. Homozygous inversions have homologous chromosomes with identical inversions. They show normal meiotic pairing and distribution. Heterozygous inversions have one homologue with inversion and the other homologue without inversion (i.e., normal).

Inversion heterozygotes show important cytological and genetic effects. Because there is no net loss or gain of genetic material, inversion heterozygotes are perfectly viable. The pairing behaviour of inversion chromosome with standard or non-inverted homologue depends on the length of inversion and the longitudinal relationship of the inverted and uninverted chromosome segments.

If the inversion is long, chromosome pairing involves formation of characteristic loop in the normal homologous chromosome and the inversion chromosome pairs with the normal chromosome in such a way that homologous loci pair with each other. The location of the inverted segment, thus, can be recognised cytologically by the presence of an inversion loop in the paired homologues during meiosis.

If the inverted segment is so small that loop formation is not possible either the inverted segment is left unpaired or it may pair with non-homologous segment of normal chromosome. The size of the loop is a function of the size of the inversion—the larger is the inversion, the larger will be the loop.

The crossing over and chiasma formation within and outside inversion loop give rise to secondary structural changes (duplication and deletion) depending upon the type of inversion (paracentric or pericentric), the number of chiasmata and localization of chiasmata. Such structural changes result in meiotic products with unbalanced sets of chromosomes.

Single crossing over within a pericentric heterozygous inversion produces two normal meiotic products and two abnormal products—containing chromosom that are either duplicated or deficient for certain gene loci a (Fig. 22.18 B).

In plants gametes containing duplication or deficiency are generally not viable. So, pericentric inversion heterozygotes are semi-sterile, although more than 50% viable. In animals, the gametes with duplication and deficiency in chromosomes are usually normal in function, but zygote usually does not survive.

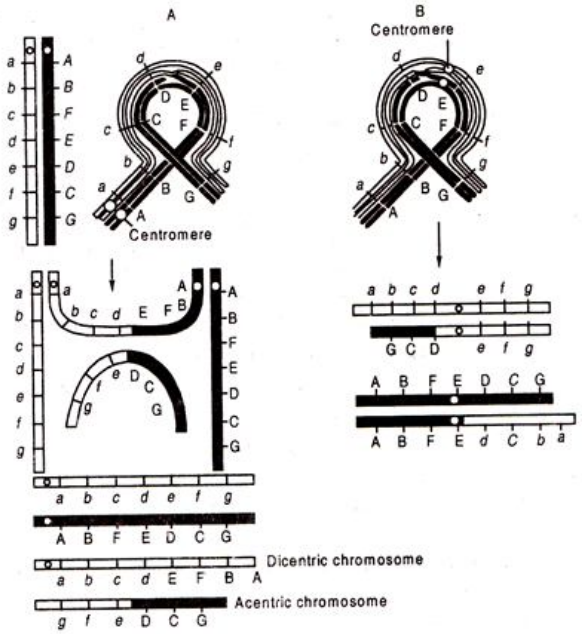


Fig. 22.18 A and B—Meiotic behaviour in Inversion heterozygotes
A. Paracentric inversion B. Pericentric inversion.

Single crossing over within a paracentric inversion has more complex consequences and it produces one chromosome with two centromere (dicentric chromosome) and one with no centromere (acentric chromosome segment).During anaphase 1 of meiosis dicentric chromosome is pulled as a bridge between two spindle poles and acentric chromosome, because it has no spindle fibre attachment, floats randomly as laggard and is eventually lost (Fig. 22.18 A).The dicentric bridge may break at any point giving rise to duplications and deficiencies in the meiotic products. Remarkably, in Drosophila and plant egg cells, the dicentric bridge may remain intact long after anaphase I. Thus, the two daughter nuclei either will be linked by dicentric bridge or will contain the fragments of the bridge if it breaks.

The fragment associated with the bridge has the effect of a deficiency and the size of deficiency determines the reduction in fertility. That is, a meiotic product or gamete lacking in one or more genes because of the loss of a segment of chromosome is likely to be non-viable and hence sterile.

In general, females heterozygous for paracentric inversion manifest no serious sterility because in most cases the chromosomes are oriented in specific direction during gametogenesis which facilitates exclusion of dicentric and acentric chromosomes from functional gametes.

When two cross overs are formed within inversion loop, the result will depend upon the number of chromatids involved. Two strand-double crossing over will yield four normal chromatids, two of which will be involved in crossing over and the other will were not. Such a condition can be detected only when appropriate genetic markers are present within the region of crossing over.

Three-strand double crossing over will yield one non-cross over chromatid, one cross-over chromatid and two acentric fragments. Four-strand double cross-over would yield two dicentric chromatids and two acentric fragments and deficiency and duplication would presumably lead to in-viability of the meiotic products or gametes or would cause death of zygote or embryo if such gametes were involved in fertilization.

It is, therefore, evident that paracentric inversions have a drastic effect on the recovery of chromatids involved in crossing over.

Another major effect of inversions is to suppress the recombination of genie loci by crossing over to maintain in the population a specific segment of a chromosome.

Crossing over does occur within the inversion, but the crossing over products do not usually contribute to the next generation either because the gametes or zygotes are inviable or because the cross over chromosomes are eliminated from non-functional megaspore in plants or polar bodies in the animals.

The presence of recessive lethal gene within inverted segment can be of added advantage in preserving structural heterozygosity because heterozygotes for lethal recessive genes will be viable and homozygous, non-viable.

In CIB stock of Drosophila, C factor which is a cross-over suppressor is found to be inverted segment of chromosome, 1 component, a recessive lethal, prevents homozygosity for CIB chromosome and B gene accounts for bar eye.

In CIB chromosome C factor is flanked on either side by two marker genes 1 and B. Muller (1928) was the first to take advantage of cross-over suppressing property o inversion heterozygote to detect sex-linked recessive lethal mutations in Drosophila induced by X rays.

The genetic evidence of inversion thus will be:

(i) Suppression of crossing over, and

(ii) Possibly; the appearance of mutation owing to position effect.

As mentioned earlier, inversion and translocation involve no loss or gain in the genes as such. Simply they bring about change in the position of some genes and no gene mutation (i.e., no change in the nature of gene) is involved in these cases.

The changed positions of genes in the chromosomes may have important consequences since continuous genes sometimes are concerned in the completion of related steps of some repetition biochemical reactions. All such alterations of gene functions due to change in the sequence of genes are referred to as **"position effects".**

Inversion homozygotes can be detected cytologically and genetically in the following ways:

(i) By detecting changed linkage relation with the help of genetic linkage studies,

(ii) By detecting the changes in chromosome morphology during mitotic metaphase.

(iii) By observing the changes in chromosome bands.

The inversion heterozygotes are detected by the following characteristics:

(i) Formation of inversion loop during the prophase I of meiosis.

(ii) Formation of dicentric chromosomal bridge, acentric fragments during anaphase I.

(iii) Development of abnormal meiotic products which may be detected by means of tetrad analysis.

(iv) Decreased fertility resulting due to production of genetically unbalanced meiotic products or gametes via crossing over.

(v) Reduced crossing-over frequency

PLANT BREEDING (26 Periods)

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6.2 Aims and Objective

6.3 Scope and Importance

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11.4 Utilization of Autopolyploidy in plant Breeding

- EVOLUTION –

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CHAPTER – 6– Introduction (2 L)

6.1 Definition and Principles
6.2 Aims and Objective
6.3 Scope and Importance

Introduction:

In India, the food grain production during the 1949-50 was 54.92 million tones it has been increased to more than 200 million tones today. Thus there is increase of about 275 % during the period of 50 years. As a result of this our nation has been become almost self sufficient in the food.

This increase in food grains production during the first "Green revolution" was due to better agricultural practices, improved crop varieties, crop management, application of chemical fertilizers, use of insecticides etc. these factors played an important role in the increasing the food production of food grains. But there are limitations for factors like chemical fertilizers, insecticides, pesticides, etc.

Similarly, there is continuous population explosion; the population in India is growing at alarming rate of more than two (2.5 %) percentage per year. With ever increasing population the problem of food grain production such as factor is improvement of crop varieties.

The improvement of crop is achieved with the technique of plant breeding. " the plant breeding is improvement in he heredity and production of new crop varieties which are superior in all aspects than the existing variety" **Plant breeding** is the art and science of changing the genetics of plants for the benefit of humankindPlant breeding can be accomplished through many different techniques ranging from simply selecting plants with desirable characteristics for propagation, to more complex molecular techniques.

Plant breeding has been practiced for thousands of years, since near the beginning of human civilization. It is now practiced worldwide by individuals such as gardeners and farmers, or by professional plant breeders employed by organizations such as government institutions, universities, crop-specific industry associations or research centers.

International development agencies believe that breeding new crops is important for ensuring food security by developing new varieties that are higher-yielding, resistant to pests and diseases, drought-resistant or regionally adapted to different environments and growing conditions.

Definition:- According to J. M. Poehlman (1959) " Plant breeding is the art and Science of changing and improving the heredity of plants".

According to D. C. Smith. (1966). The Plant breeding is an art and Science of improving the genetic pattern of plant in relation to their economic uses".

Steps of Plant Breeding

Major activities of plant breeding are following;

1. Creation variation
2. Selection
3. Evaluation
4. Release
5. Multiplication
6. Distribution of the new variety

Objectives of Plant breeding

The main aims and objectives of plant breeding are to improve the qualities of plant so that they are much desirable agronomical and economically. The specific objectives are greatly depending upon the crops under consideration. Some objectives are.

1] to evolve new variety of crops which have better yielding potency than the local crop varieties to increase the yield of desired plant product such as grains fodder, fiber oil, and so on.

2] to increase the quality of crops with regards to size color, shape, taste, nutrients contents, milling keeping and cooking etc. of grains, vegetables, flower and fruits.

3] To evolve such varieties of crops as are suitable to produce and consumer both and can need the requirement of the consumers to good extent.

4] To produce variety that is resistant o fungal bacterial disease, insects and pests.

5] To change the duration of crops maturation according to the need.

6] To develop variety with a wide range of adaptability.

7] To obtain the suitable variety for particular agronomic regions.

8] To develop variety with a wide range of adaptability.

9] To change the growth habit of crops as needs.

10] To produce new plant varieties for new seasons and new areas.

11] To determine toxic substances from the consumable part to mate them safe for human consumptions.

CHAPTER - 7 – Mode of reproduction in Relation to Breeding Methods(3 L)

7.1 Methods of Reproduction- Vegetative, Asexual and Sexual.
7.2 Mode of Reproduction – Self Pollination, Cross Pollination andGeitonogamy.

Introduction:
The mode of reproduction in crop plants may be broadly grouped into three categories: Vegetative, Apomictic and Sexual.
1. Vegetative or Asexual:
In this type of reproduction the vegetative parts of the plants act as propagule in place of seed. This mode is mostly found in all those plants where there is no seed set, long reproduction cycle and heterozygosity exists.
The following organs can act as propagule:
1. Modified Stem:
Underground modified stems like rhizome (ginger, turmeric, banana), tuber (potato), bulb (onion, garlic), corn (***Colocasia***, yam), stolon (strawberry), sucker (chrysanthemum, menthe) are used for propagation.
2. Stem Cutting:
In many of the fruit crops the artificially produced clones or stem cuttings are used as propagative material. In sugarcane the nodal portions of stems, in fruit crops like mango, litchi, lemon, grapes – the different methods like layering, grafting, budding are applied to get the stem clone.
3. Normal or Modified Root:
Normal roots of wood-apple, citrus and many such trees are used as units for propagation. Modified roots such as tuberous root (sweet potato), fasciculated root (***Dahlia***, ***Asparagus***) are used as propagule.
4. Bulbils:
In some plants the flower bud modified into globose bulb which are called bulbils can be used as multiplication unit.
Significance:
Asexual or vegetative reproduction leads to perpetuation of the same genotype with great conservation. It is very much advantageous because large number of genetically identical individuals can be obtained irrespective of the degree of heterozygosity of the genotype. At any stage of breeding programme if a breeder gets any desirable clone it can be maintained through vegetative means.
Mutation breeding, i.e., the search for desirable mutants both through natural and artificially induced mutation is very much helpful in case of vegetatively reproducing plants as the sexual reproduction can be avoided. The method of polyploid breeding is also useful as the induced bud can be used as propagule and polyploidy can be maintained without the intervention of meiotic segregational disturbances.
2. Apomixis:
Apomixis is the phenomenon where there is no normal fertilisation of the egg cell, hence no normal development of embryo from the egg cell. However, embryo may develop from an un-fertilised egg cell or from a cell other than the egg cell within the embryo sac or from the cell outside the embryo sac (Fig. 2.1).

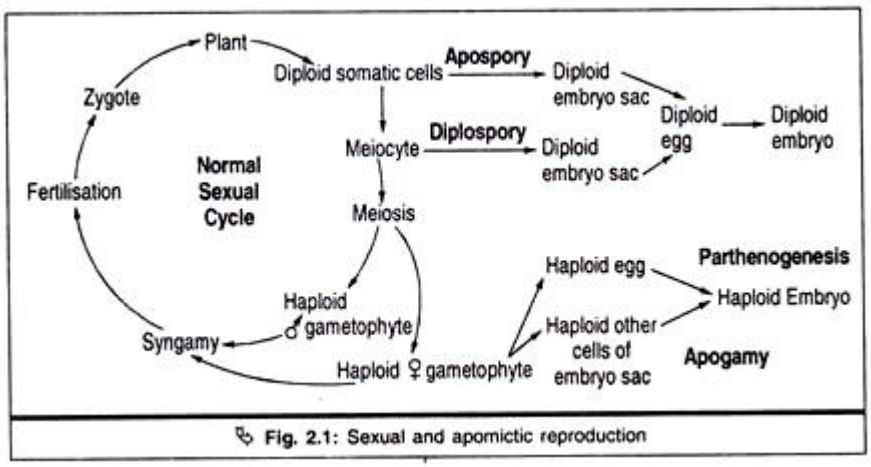


Fig. 2.1: Sexual and apomictic reproduction

The plants produced by apomixis are called apomictic which are of two types: obligate, producing only apomictic embryos, and facultative, producing both apomictic and normal embryos. This phenomenon where the substitution of sexual process occurs by asexual methods is known as apomixis (apo = away from, mixis = act of mixing), the plants are called apomictic.

Types of Apomixis:

Non-Recurrent Apomixis (Haploid Seed/Plant Formation):

Here the seed/plant develops from the un-fertilised egg cell or any other un-fertilised haploid cell of embryo sac. In this type of apomixis the first event of normal sexual cycle, meiosis takes place, the embryo sac is formed normally, but due to various reasons the fertilisation does not take place.

The reasons may be:

(i) Absence of pollen tube;
(ii) Inability of the tube to discharge its contents;
(iii) No attraction between male and female nuclei;
(iv) Early degeneration of sperms;
(v) Maturation of egg and sperm is not synchronized. ,

(a) Haploid Parthenogenesis:

Here a haploid embryo develops from an un-fertilised egg cell of the embryo sac, e.g., in Orchis maculata, Platenthera chlorantha, Cephalanthera damasonium – the pollen tube enters but fails to fertilize.

(b) Haploid Apogamy:

It is the development of haploid embryo from any haploid cell of the embryo sac other than the egg cell. In Lilium martagon, Erythraea centaurium – two pro-embryos are formed; one is from fertilized egg (zygotic cell) and another from the synergid cell (haploid cell).

Recurrent Apomixis:

Here the meiotic event does not take place either in any somatic cell or the meiocyte cell fails to undergo meiosis, thereby produces the embryo sac with diploid cells only. These diploid cells directly give rise to diploid embryos, called apospory (Fig. 2.2).

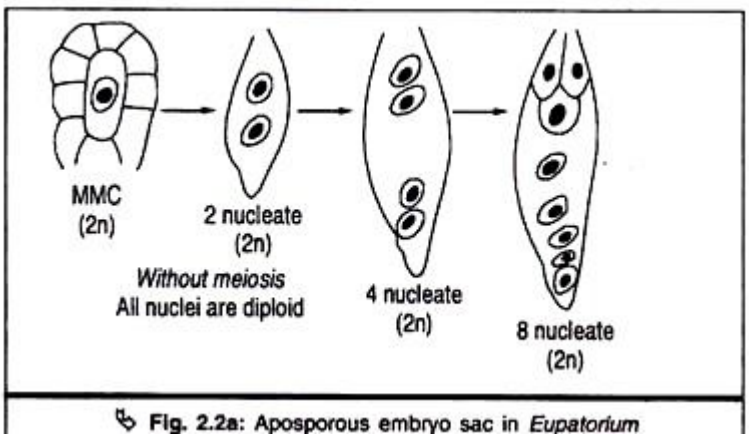


Fig. 2.2a: Aposporous embryo sac in *Eupatorium*

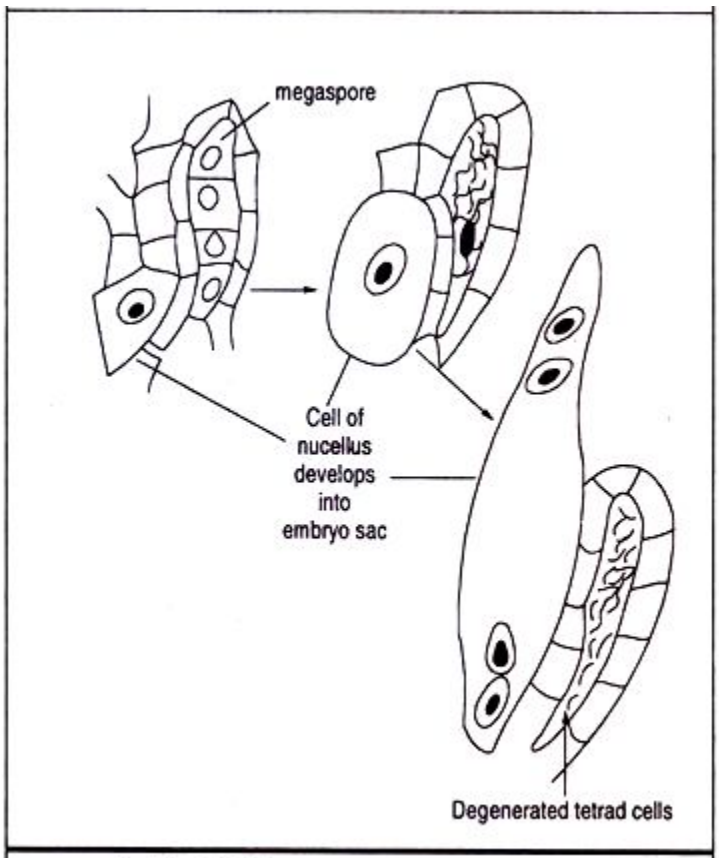


Fig. 2.2b: Aposporous embryo sac in *Hieracium*

(a) Generative Apospory:

The diploid egg cell develops into embryo without fertilisation, one particular variety of Parthenium argentatum exhibits.

(b) Somatic Apospory:

The diploid cell of nucellus or integument develops directly into diploid embryo sac and the diploid embryo is developed from the diploid un-fertilised egg cell. This phenomenon is found in Allium, Meliss, Crepis etc.

Agamospermy:

This term is used to categories the plants which has the seed habit for propagation but not through normal sexual cycle, either meiosis or syngamy or both are eliminated. This includes either the embryos which may develop from cell of the unreduced female gametophyte or directly from the diploid sporophytic cell of the ovule, such as nucellus or integuments. Diplospory, apospory and adventive embryony, all are included within this category.

Adventive Embryony:

In this case the gametophytic generation is completely eliminated. It is very much close to vegetative propagation, but the plants here retained the seed habit, i.e., the diploid embryo is developed from any diploid cell outside the embryo sac but matures into embryo within the embryo sac, zygotic embryo degenerates or competes with apomictic embryo. This kind of embryos is found in Citrus, mango, etc.

Diplospory:

Here the MMC differentiates into sexual ovules, but it does not enter into meiosis, it produces the embryo sac directly by mitotic division, all the cells within the embryo sac are diploid, and the embryos are formed.

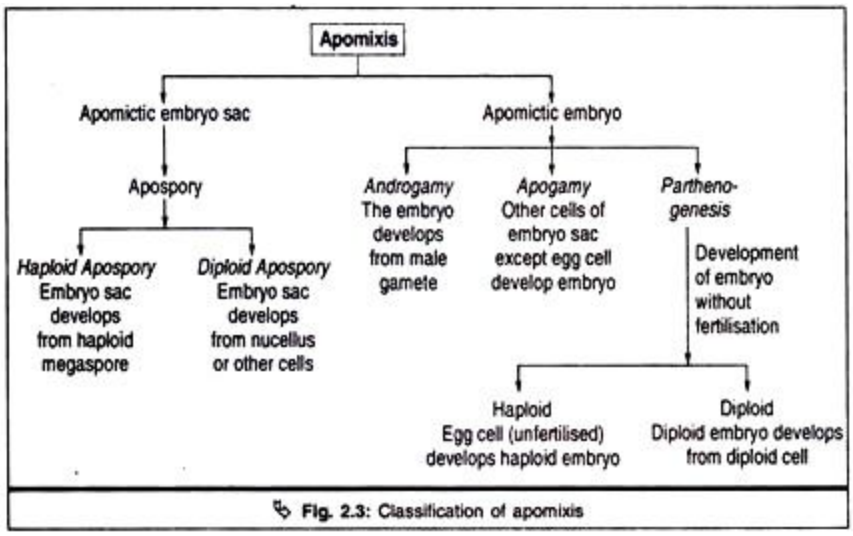


Fig. 2.3: Classification of apomixis

Significance:

Apomictic plants tend to conserve the genetic structure and are also capable of maintaining heterozygote advantages. Due to prohibition of fertilisation process, apomixis is the way for exploitation of maternal influence or perpetuation of maternal individuals or maternal properties.

The use of apomixis in plant breeding can be summarised:

1. Rapid multiplication of genetically, uniform individuals without any risk of segregation.
2. Heterosis or hybrid vigour can be utilised for recurring production of seeds of F_1 hybrids.
3. From generation to generation the maternal effect can be exploited.

3. Sexual:

This process of reproduction involves the fusion of male and female gametes and formation of seed, so it is called the process of amphimixis. Depending on the nature of pollination the plants can be categorized as self-pollinated and cross pollinated.

Sexually reproducing crop plants produce a special structure, called flower which bears the essential whorls like androecium and gynoecium. Androecium consists of stamen and gynoecium consists of carpel. The male and female gametes are produced in microspores and megaspores respectively.

Sporogenesis:

Production of microspores and megaspores is known as sporogenesis. In another lobe there are pollen sacs which contain numerous PMC (Pollen mother cell) undergoing meiosis, produces microspores or pollen, the process is called micro-sporogenesis. Inside the ovary the ovules are present in which the MMC (Megaspore mother cell) undergoes meiosis and produces 4 megaspores out of which 3 degenerate and one survives, this process is called mega-sporogenesis.

Gametogenesis:

During maturation of pollen, the microspore nucleus divides mitotically to produce generative and vegetative nucleus. The generative nucleus then divides to form male gametes or sperms. The pollen along with pollen tube and sperms is called micro-gametophyte and the production of sperms is known as micro-gametogenesis.

The nucleus of functional megaspore divides mitotically three consecutive times to produce eight nuclei, which get arranged in the embryo sac. The embryo sac contains generally one egg cell, two synergids, two central nuclei and three antipodals. All these cells are haploid and this process is called as mega-gametogenesis.

Fertilisation:

Fusion of one of the two sperms with the egg cell, to produce a diploid zygote, is known as fertilisation, and the fusion of the remaining sperm with the secondary nucleus leading to the formation of primary endosperm nucleus known as double fertilisation or triple fusion.

The zygote divides mitotically to produce ‘diploid embryo. The primary endosperm nucleus produces endosperm by mitotic division; it may be absorbed completely in legumes or may form endospermous seed in cereals.

Significance in Generating and Fixing Genotypic Variation:

Among the sexually reproduced crop plants there are two categories, self-pollinated and cross pollinated. Both the categories differ in their genetic constituent, as self-pollination leads to homozygosity whereas cross pollination tends towards heterozygosity.

In self-pollination, the genotype AA or aa will remain homozygous, whereas the genotype Aa will segregate into homozygous and heterozygous in 1: 1 ratio, as a result in each generation the homozygosity will be increased by one half and heterozygosity will be reduced by one half.

Due to cross pollination in the self-pollinated crop the heterozygosity develops, or the heterozygosity may develop in a population through natural mutation. Cross pollination is the way for developing the variations in genotype and phenotype in a population.

Heterozygosity helps in developing vigor which is known as heterosis or hybrid vigor whereas self-pollination continuously will bring in the breeding depression due to attainment of homozygosity.

In plant breeding variation of characters among the population is most wanted. The breeder will select a particular character according to the need for that crop. So the characters which will be selected should be heritable through generations.

The total mechanism of heredity is dependent upon the behaviour of chromosomes, which carry the genes. Variations are originated through chromosome rearrangement, genetic recombination, mutation, structural and numerical changes of chromosome.

In heredity the chromosomes are important, as their distribution in germ cells determine the specific heritable character to the progeny. The heritable characters may be regulated by single gene or by multiple genes. The inheritance pattern of a particular character is studied by progeny testing which is a basic procedure in plant breeding.

In a breeding programme always the superior characters are selected which may or may not be controlled by dominant gene. Depending on that the homozygosity or heterozygosity in a population is wanted, i.e., if the heritable character is controlled by dominant gene then heterozygosity is attained but if the phenotype is controlled by recessive gene then homozygosity is desirable in a population.

The genes are situated on chromosomes, the recombination phenomenon during meiotic crossing over exchanges the chromosomal segments which controls the genetic distribution. The genes are the determinants for a particular character expression. Depending on their express-ability the dominant and recessive nature are determined, the genes occur always in the alternative forms called as alleles.

Due to mutation the changes in gene may occur, which also may be heritable or non-heritable. If the change is permanent and if it alters the phenotypic characters expression and if it is heritable through succeeding generations then mutation plays an important role in plant breeding.

In plant breeding when a breeder selects any particular mode of breeding programme then it affects the genetic criteria fixation in that population as he selects a particular desirable character.

Normally in a population all the characters may be evenly distributed or the dominant characters are prevailed, but whenever a breeder is choosing for a particular criterion then the genetic constituent of that population gets changed. A particular gene gets advantage to be fixed in that population.

Suppose in a breeding programme of barley one breeder is selective for the **"white and smooth awn"** character, both of them are recessive characters, so in a dihybrid cross programme only one out of 16 plants will bear this character and then selfing of that plant will lead to homozygous population, which will change the total genetic constituent of the population.

Back-crossing is also another phenomenon of changing and fixation of genetic constituent in a population. The parent holding more desirable characters is used as recurrent parent in a back-crossing programme which develops the homozygosity due to repeated back-crossing. Back-crossing programme is more opted when the character controlled by recessive genes are wanted in a population.

In dihybrid crossing programme the homozygous recessive is only one out of sixteen, but in a back-crossing programme it is one out of four. So the large number of population is not needed to get the homozygous line.

Types of Pollination:

The transfer of pollen grains from the opened anther of the stamen to the receptive stigma of the carpel/pistil is called pollination. Each pollen grain grows and provides two male gametes for fertilisation of an ovule.

Depending upon the source of pollen grain, pollination is of three types:

1. Autogamy (Self-pollination):

It is the kind of pollination in which the pollen from the anthers of a flower is transferred to the stigma of the same flower, e.g., wheat, rice, pea, etc.

Autogamy is further classified as:

(i) Cleistogamy In some plants, flowers never open up and the anthers dehisce inside these closed flowers to ensure pollination. Thus, cleistogamous flowers are invariably autogamous as there is no chance of cross pollination. These flowers produce assured seed sets even in the absence of pollinators, e.g., Oxalis, Viola, etc.

(ii) Homogamy In this method, both the anthers and the stigma mature at the same time, e.g., Mirabilis.

2. Geitonogamy:

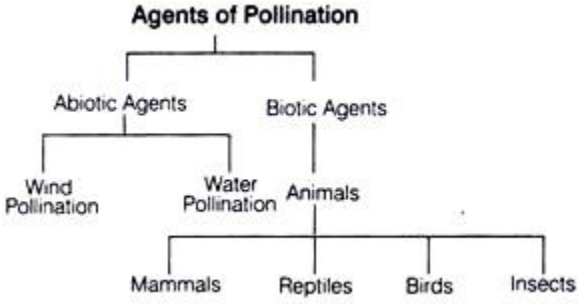
It is a kind of pollination where the pollen grains from the anther of the flower are transferred to the stigma of another flower borne on the same plant but at different branches. It usually occurs in plants, which show monoecious condition, e.g., Cucurbita.

3. Xeno-gamy (Cross-Pollination):

It involves the transfer of pollen grains from the flower of one plant to the stigma of the flower of another plant. This is the only type of pollination which brings genetically different types of pollen grains to the stigma during pollination, e.g., papaya, maize, etc.

Agents of Pollination:

The agents responsible for pollination in angiosperms have been grouped into two main categories.



Adaptations for Wind Pollination:

Wind pollination is also termed as anemophily and takes place through the wind.

i. Flowers are small, colourless, inconspicuous, nectar less and become arranged as inflorescence.

ii. The anthers are well exposed for the easy dispersal of pollen grains.

iii. Pollen grains are small, light, dry, dusty, non-sticky and sometimes even winged.

iv. The stigmas are large, hairy and feathery or branched to catch the air borne pollen grains.

v. Common examples of wind pollinated flowers are grass, sugarcane, bamboo and coconut, etc.

Adaptations for Water Pollination:

Water pollination is also termed as hydrophily and mode of pollination is water. It is quite rare in flowering plants and is limited to about 30 genera, mostly monocotyledons.

i. It is very common in plant groups such as algae, bryophytes and pteridophytes. Flowers are small, colourless, inconspicuous, odourless and nectar-less and pollen grains and stigmas are generally unwettable.

ii. The stigmas are long and sticky, e.g., Vallisneria, Hydrilla and Zostera.

iii. Not all aquatic plants use water for pollination. In a majority of aquatic plants, the flowers emerge above the level of water and are pollinated by insects or winds as in land plants, e.g., water hyacinth and lily.

iv. In Vallisneria, the female flower reach the surface of water by the long stalk and pollen grains are released on to the surface of water. They are then carried by the passive water currents.

v. In most of the water pollinated species, pollen grains are protected by mucilaginous covering.

Adaptations for Insect Pollination:

Inject pollination in also termed as entomophily.

Insect-pollinated flowers are large, colourful, fragrant and rich in nectar.

i. A number of flowers are clustered into an inflorescence to make them conspicuous.

ii. Flowers have nectar glands and are highly fragrant to attract insects.

iii. The surface of pollen grains is sticky due to exine layer and stigma is sticky due to mucilaginous layer.

iv. Nectar and pollen grains are floral rewards for the insect pollinators.

v. In some species, floral rewards are to provide safe place to lay eggs, e.g., for the tallest flower of Amorphophallus (about 6 feet in height).
vi. In plant Yucca, moth and the plant, cannot complete their life cycles without each other. The moth deposits its eggs in the locule of the ovary and the flower, in turn plant gets pollinated by the moth.
The larvae of the moth come out of the eggs as the seeds start developing.

Outbreeding Devices:

Flowering plants have developed many devices to discourage self-pollination and to encourage cross-pollination. Because the majority of flowering plants produce hermaphrodite flowers and are likely to come in contact with the stigma of the same flower. The continued self-pollination leads to chances of inbreeding depression.

Devices to prevent inbreeding are:

(i) Receptivity of pollen release and stigma is not synchronized, i.e., either the pollen is released before the stigma becomes receptive or stigma becomes receptive before the release of pollen.
(ii) In some other species, the anther and stigma are placed at different positions, so that the pollen cannot come in contract with the stigma of same flower which will prevent autogamy.
(iii) Self incompatibility is the third device to prevent inbreeding, which is a genetic phenomenon of preventing inhibiting pollen tube growth on the stigma of the same flower.
(iv) Another device to avoid self-pollination is to produce unisexual flowers, i.e., autogamy is prevented, if both male and female flowers are present on same plant, e.g., castor and maize (monoecious). Both autogamy and geitonogamy is prevented in several species like papaya, if male and female flowers are present on different plants, i.e., each plant is either male or female (dioecy).

CHAPTER - 8 - Plant Introduction and Acclimatization (3 L)

8.1 Plant Introduction – meaning and need,
8.2 Acclimatization – definition and purposes.
8.3 Procedure of plant introduction, purpose, merits and demerits.

Definition :- **Introduction:**
" The process of taking a plant in to a new locality where it was not grown earlier is called as introduction"

OR

" Introducing a plant from its growing area to the new locality with different climate is called as plant introduction"

Acclimatization :-
" The adjustment of plant of plant under the changed climatic condition of new locality is called as acclimatization"

The introduction of new crops may be in the form of seed or cutting in vegetative propagated plants. The introduction may be from different parts of the country or from outside the country. Introduction within the country is convenient but the for introduction from other country a definite procedure is required. Introduction has become a method of great importance for improvement of crop plants in the recent years, partially as a source of resistant material for the some of our crop diseases. The best example of introduction is of rust resistant strains of wheat in India.

Objectives of Introduction:-
The introduction is an important method of plant breeding and many plants in all the countries have got new crop plants b this method. The main, primary and most important objectives of plant introduction is to improve the plant wealth of country. There are many other objectives of plant introduction some of them are:

1] To obtain an entirely new crop plant _ introduction in many times done for new crop species. e.g. Maize, Tomato, soybean etc.
2] To obtain or serve as a new variety – Many introduced plant are released as superior commercial varieties. e.g. Sonora -64 wheat variety JN-1 of Rice.
3] Introduction for improvement of crop plants:- many introduced plants (varieties) are used for hybridization with local varieties to develop improved variety. e.g Pusa gold or Pusa ruby variety of tomato is cross between Meeruty and Sioux variety introduced from U.S. America.
4] To save the crop from disease and pest – Many times introduction of crop to new area is done to protect the crop from diseases and pest. e.g. Coffee was introduced in south America from Africa to prevent the losses from leaf –rust.
5] For scientific studies:- Plant introduction is also done for the studies in biosystematics, evolution, origin of species etc.
6] For Aesthetic Values:- Sometimes introduction are done for the fulfillment of aesthetic sense .

Advantages and Disadvantages:-
Plant introduction is an important method for increasing the plant wealth of the country.

Advantages.
1] It provides an entirely new crops.
2] It provides superior verieties directly of after selection or hybridization.
3] It is a very quick and economical method of crop improvement, particularly when the introduction is released directly as a variety.
4] Plant may be introduced in new disease free area to protect from damage

5] Introduction and exploration are the only means for collecting the germplasm and to protect the variability from genetic erosion.

Disadvantages:

Plant introduction is quickest method of improvement of crop plants. It is an advantageous method but it also has many disadvantages. It has been found that many disadvantages are associated with plant introduction; partially there is danger of introduction of weeds, disease, and pest along with crop plants.etc.

Weeds :- many noxious weeds e.g. Parthenium hysteriphorus,, Argemone Mexicana, Eicchornia crassipus etc.

Diseases:- many diseases also entered into India.

1] Late Blight of Potato (Causal Organism Phytopthora infestans) from Europe in 1883.

2] Coffee rust is introduced from SriLanka in 1876

3] Bunchy Top of banana in introduced from SriLanka in 1940

4] Fire Blight of Apple is introduced from England in 1940

5] Flag smut of wheat is introduced from Australia.

Insect Pest:- Some insect pests have been also introduced in India with introduction of new crops.

Potato Tuber moth come from Italy in 1900

Woody Aphis of apple and fluted scale of apple are also introduced in India from other countries.

Plant Introduction Agencies in India

A centralized plant introduction agency was initiated in 1946 at the Indian Agricultural Research Institute (IARI), New Delhi. The agency began as a plant introduction scheme in the Division of Botany and was funded by ICAR. In 1956, during the second five year plan, the scheme was expanded as the Plant Introduction and Exploration Organization. Subsequently in 1961, it was made an independent division in IARI, the Division of Plant Introduction. The division was re organized as National Bureau of Plant Genetic Resources (NBPGR) in 1976. The nature of activities and the functions of the bureau have remained the same, but the scope and scale of its activities have increased considerably. The bureau is responsible for the introduction and maintenance of germplasm of agricultural and horticultural plants. In addition to the National Bureau of Plant Genetic Resources, there are some other agencies concerned with plant introduction. *Forest Research Institute, Dehradun,* has a plant introduction organization which looks after the introduction, maintenance and testing of germplasm of forest trees. The Botanical Survey of India was established in 1890; it was responsible for the introduction, testing and maintenance of plant materials of botanical and medicinal interest. But at present, introduction and improvement of medicinal plants is being looked after by NBPGR. The Central Research Institute for various crops, e.g., tea, coffee, sugarcane, potato, Tobacco, rice etc., introduce, test and maintain plant materials of their interest. But their activities are coordinated by the NBPGR, which has the ultimate responsibility for introduction activities. Plant material may also be introduced by individual scientists, universities and other research organizations. But all the introductions in India must be routed through the NBPGR, New Delhi.

Germplasm Collections

The sum total of hereditary material or genes present in a species is known as the germplasm of that species. Therefore, a germplasm collection is the collection of a large number of genotypes of a crop species and its wild relatives. Germplasm collections are also known as gene banks (or world over the world). Further, germplasm collections furnish the richest source of variability. With the modernization of agriculture, large tracts of land have been put under pureline varieties of self-pollinated crops and hybrid varieties of cross-pollinated species. This has led to a gradual disappearance of local or land varieties ('desi' varieties) and open pollinated varieties -both reservoirs of considerable variability. Cultivation and grazing are gradually destroying many wild species and their breeding grounds. Wild relatives of crops may be eliminated by introduced species of weedy nature or even by the cultivated forms derived from them. ***The gradual loss of variability in the cultivated forms and in their wild relatives is referred to as genetic erosion.*** This variability arose in nature over an extremely long period of time and, if lost, would not be reproduced during a short period. The establishment of IBPGR to coordinate germplasm conservation activities throughout the world reflects this concern. Germplasm collections are being made and maintained to conserve as many genotype as possible.

The germplasm collections contain land varieties, various wild forms, primitive races, exotic collections and highly evolved varieties. Some of the important germplasm collections are listed below.

1. Institute of Plant Industry, Leningard. It has 1,60,000 entries of crop plants.
2. Royal Botanic Gardens, Kew, England, It has over 45,000 entries.
3. Bellsville, U.S.A., maintains germplasm collections of small grain crops.
4. The National Bureau of Plant Genetic Resources, New Delhi, is maintaining large collections of Sorghum, Pennisetum, wheat, barley, oats, rice, Maize and other agricultural and horticultural crops. For example, groundnut collection is maintained at Junagarh, Cotton at Nagpur, Potato at Simla, Tobacco at Rajahmundhry, tuber crops (other than potato) at Trivandrum etc. The Cotton collection maintained at Central Institute for Cotton Research (CICR, Nagpur) are as follo ws ; Gossypium hirsutum-4,100 entries ; G. barbadense-300 entries ; G. arboreum-1755 entries ; G.herbaceum-393 entries (1991).

Acclimatization : Generally, the introduced varieties perform poorly because they are often not adapted to the new environment. Sometimes, the performance of a variety in the new environment improves with the number of generations grown there. The process that leads to the adaptation of a variety to a new environment is known as acclimatization. Acclimatization is brought about by a faster multiplication of those genotypes (present in the original population) that are better adapted to the new environment. Thus acclimatization is essentially natural selection. Variability must be present in the original population for acclimatization to occur. Therefore, land varieties are likely to get acclimatized, while purelines are not likely to. The extent of acclimatization is determined by (1) the mode of pollination, (2) the range of genetic variability present in the original population, and (3) the duration of lifecycle of the crop. Cross-pollination leads to a far greater gene recombinations than self pollination. As a result cross-pollination is much more helpful in acclimatization than self pollination.

Plant quarantine:

Plant Quarantine: A technique for insuring disease (and pest) free plants by isolating them during a period while performing tests for latent diseases. Often used when importing new cultivars. Plant quarantine is vital to prevent the introduction of non-indigenous, potentially damaging pests and diseases of plants into a country or to eradicate them before they can become widespread and well established. Less-developed countries and other countries in transition are especially vulnerable to the damaging effects of exotic pest introductions because of often inadequate infrastructure and the fragility of their economies. The well-meaning importation of germplasm for agricultural development projects creates a further risk of introducing such quarantine pests. Without stronger phytosanitary services nations will be unable to participate in the liberalisation of world markets. Our work involves natural and social scientists from NRI and lawyers from the University's Law School.

CHAPTER - 9 - Selection (5 L)

9.1 Definition and Procedure of the following
9.2 Merits and Demerits of the following
a) Mass Selection
b) Pure line Selection
c) Recurrent Selection
d) Clonal Selection

Introduction:

Selection is basic to any crop improvement. Isolation of desirable plant types from the population is known as selection. It is one of the two fundamental steps of any breeding programme viz., 1. creation of variation and 2. Selection. There are two agencies involved in carrying out selection : one is Nature itself (Natural selection) and the other is man artificial selection. Though both may complement each other in some cases, they are mostly opposite in direction since their aims are different under the two conditions (nature and domestication). The effectiveness of selection primarily depends upon the degree to which phenotype reflects the genotype. Before domestication, crop species were subjected to natural selection. The basic for natural selection was adaptation to the prevailing environment. After domestication man has knowingly or unknowingly practiced some selection. Thus crop species under domestication were exposed to both natural and artificial selection i.e. selection by man. For a long period, natural selection played an important role than selection by man. But in modern plant breeding methods natural selection is of little importance and artificial selection plays an important role.

Basic Principles of Selection : Notwithstanding the highly complex genetic situation imposed by linkage and espistasis, there are just three basic principles of selection (Walker, 1969) :

1. **Selection operates on existing variability** : The main function of the selection exercise is to discriminate between individuals. This is possible only when sufficient variation is present in the material subjected to selection pressure. Thus, selection acts on the existing variation it cannot create new variation.

2. **Selection acts only through heritable differences** : only the selected individuals are permitted to contribute to the next genetion / progenies. Therefore, should there be greater influence of non-heritable agencies on the individuals selected; the parent progeny correlation will be greatly vitiated. Hence the variation among individuals to be selected must be genetic in nature, since it is the genetic variation that tends to close the gap between phenotype and genotype. Environmental variability cannot be of any use under selection.

3. **Selection works because some individuals are favored in reproduction at the expense of others** : As a consequence of its past evolutionary history and breeding structure, a population or a crop consists of highly genetically variable individuals with regards to such diverse phenomena as differential viability, differential maturity, differences in mating tendencies, fecundity, and duration of reproductive capacity. Hence some individuals tend to become superior to others for some or other traits desirable under domestication. These superior individuals are retained for reproduction while others discarded under selection.

Selection has two basic characteristics viz.

1. Selection is effective for heritable differences only.
2. Selection does not create any new variation. It only utilizes the variation already present in a population.

MASS SELECTION

It is the earliest method of selection. Man has always practiced mass selection consciously or unconsciously from the time of domestication. In its most basic form mass selection consists of selecting individuals on the basis of phenotypic superiority and mixing the seeds for using as planting material for next season.

Procedure for evolving variety by mass selection

First year : Large number of phenotypically similar plants having desirable characters are selected. The number may vary from few hundred to few thousand. The seeds from the selected plants are composited to rise the next generation.

Second year : composited seed planted in a preliminary field trial along with standard checks. The variety from which the selection was made should also be included as check. Phenotypic characteristics of the variety are critically examined and evaluated.

Third to sixth year : The variety is evaluated in coordinated yield trials at several locations. It is evaluated in an initial evaluation (IET) trial for one year. If found superior it is promoted to main yield trials for 2 or 3 years.

Seventh year: if the variety is proved superior in main yield trials it is multiplied and released after giving a suitable name.

Merits of Mass selection:

1. Can be practiced both in self and cross pollinated crops
2. The varieties developed through mass selection are more widely adopted than pure lines.
3. It retains considerable variability and hence further improvement is possible in future by selection
4. Helps in preservation of land races
5. Useful for purification of pureline varieties
6. Improvement of characters governed by few genes with high heritability is possible.
7. Less time consuming and less expensive.

Demerits of mass selection

1. Varieties are not uniform
2. Since no progeny test is done, the genotype of the selected plant is not known
3. Since selection is based on phenotype and no control over pollination the improvement brought about is not permanent. Hence, the process of mass selection has to be repeated not and then.
4. Characters which are governed by large number of genes with low heritability cannot be improved.
5. It cannot create any new genotype but utilizes existing genetic variability.

Achievements

Mass selection must have been used by pre historic man to develop present day cultivated cross from their wild parents. It was also used extensively before pureline selection came into existence.

Cotton : Dharwad American Cotton
Groundnut : TMV-1 & TMV-2
Bajra : pusa moti, Baja puri, Jamnagar gaint, AF3
Sorghum : R.S. 1
Rice : SLO 13, MTU-15
Potato : K122

JOHANNSEN'S PURE LINE THEORY

Characters of purelines

1. All the plants within a pureline have the same genotype
2. The variation within a pureline is environmental and non-heritable
3. Purelines are stable

Pureline selection

Pureline selection has been the most commonly used method of improvement of self pollinated crops. Almost all the present day varieties of self pollinated crops are purelines. Pureline selection has several applications in improvement of self pollinated crops. It is used to improve.

1. Local varieties
2. Old pureline varieties and
3. Introduced varieties

General procedure for evolving a variety by pureline selection

The pureline selection has three steps.

1. Selection of individual plants from a local variety or some other mixed population.
2. Visual evaluation of individual plant progenies and
3. Yield trials

1. Selection

First year : A large number of plants (200-3000) which are superior than the rest are selected from a local variety or mixed population and harvested separately (in some cases individual heads or stems may be selected). The number of plants to be selected depends upon the breeder's discretion but should be as large as possible in view of the available time, land, funds, labour etc. It is advisable to select for easily observable characters such as flowering, maturity, disease resistance, plant height etc.

II. Evaluation :

Second year: Progenies of individual plants selected in 1st year are grown separately with proper spacing (plant to row or head to row). The progenies are evaluated by taking elaborate date on visual characters such as plant height, duration, grain type, ear characters besides yield. The number of progenies should be reduced as much as possible. Disease epiphytotics may be created to test the progenies for disease resistance; poor, weak, diseased, insect attacked and segregating progenies are rejected. The superior progenies are harvested separately. If necessary the process may be repeated for one or more years.

III. Yield trials :

Third year : The selected progenies, now called as cultures are grown in replicated trial for critical evaluation of yield etc. The best local variety is used as a check and should be grown at regular intervals, after every 15 or 20 cultures for comparison. This is known as preliminary yield trial. Superior cultures based on observable characters and yields are selected. The number is drastically reduced.

Fourth & Fifth years: The superior cultures are tested against the local checks in yield trials. Observations are recorded on many characters like diseases resistance, days to flower, and days to maturity, and height of the plant ear characters, test weight and yield. The data is subjected to statistical analysis to identify really superior cultures. If necessary the trials may be extended for one more year or season. Inferior culture are rejected and a few (4-5) promising cultures are selected.

Sixth, Seventh and Eighth years: The promising cultures selected are evaluated at several locations along with strains or cultures of other breeders and local checks. One or two promising cultures are selected.

Ninth year: The best progeny identified earlier is multiplied, named and released as a variety for official release of any variety (approval from the variety releasing committee of the state or central is necessary).

Advantage of pureline selection

1. The purelines are extremely uniform since all the plants in the variety will have the same genotype.
2. Attractive and liked by the farmers and consumers.
3. Purelines are stable and long test for many years.
4. Due to its extreme uniformity the variety can be easily identified in seed certification programmes.

Limitations or disadvantages of pureline selection

1. New genotypes are not created by pureline selection
2. Improvement is limited to the isolation of the best genotype present in population. No more improvement is possible after isolation of the best available genotype in the population.
3. Selection of purelines requires great skill and familiarity with the crop.
4. Difficult to detect small differences that exist between cultures
5. The breeder has to devote more time
6. Pure lines have limited adaptability hence can be recommended for cultivation in limited area only.

Achievements : Several varieties developed by pureline selection were released in many crops. Some examples are given below

Rice : Mtu-1, Mtu-3, Mtu-7, Bcp-1, Adt-1, 3, 5, and 10
Sorghum : G 1 & 2, M 1 & 2, OO 1, 4 & 5,
Groundnut : TMV 3, 4, 7, 8 and Kadiri 71-1
Redgram : TM-1, ST-1
Chillies : G1 & G2
Ragi : AKP 1 to 7

Difference between Pure line selection and Mass Selection

Sr.	Mass Selection	Pure Line Selection
1	Used both in self and cross pollinated crops	Practiced in self pollinated crops only
2	Large number of plants are selected	Comparatively less number of plants are selected
3	The produce of the selected plants is mixed and sown as such in next year	Produce of individual plants is kept separate and progeny rows are raised next year
4	No control of pollination	Pollination is controlled
5	Variety developed is heterozygous and not uniform	Variety is homozygous homogeneous and uniform
6	Due to heterozygosity the variety deteriorates quickly	Due to homozygosity the variety lasts long
7	The method has to be repeated once in 2-3 years to purify the variety	No need to repeat
8	Wider adaptability due to heterozygosity	Narrow adaptability due to homozygosity
9	No knowledge of science is required. It is more an art.	Knowledge of science and genetics is required
10	Selection within a variety is effective	Selection with in a pureline variety is not effective
11	The variety is relatively difficult to identify	It is relatively easy to identify in seed certification programmes.

Clonal selection

Clone : A clone is a group of plants produced from a single plant through asexual reproduction. The crop plants can either be propogated by seeds or by vegetative parts. The vegetative propogation is resorted due to :

1. Lack of seed : Eg. Ginger, termiric
2. There is short viability of seed : Eg. Sugarcane
3. The seed production is very rare : Eg. Banana
4. Seeds are produced under special conditions only : Eg. Sugarcane, potato

Characteristics of Asexually propagated crops :

1. Majority of them are perennials : Eg . Sugarcane, fruit trees. The annual crops are mostly tuber crops : Eg. Potato, cassava, Sweet potato
2. Many of them show reduced flowering and seed set
3. They are invariably cross pollinated
4. These crops are highly heterozygous and show severe inbreeding depression upon selfing.
5. Majority of asexually propagated crops are polyploids : Eg. Sugarcane, Potato, Sweet, Potato
6. Many species are interspecific hybrids. Eg. Banana, Sugarcane

Characteristics of a clones :

1. All the individual belonging to a single clone are identical in genetype
2. The phenotypic variation within a clone in due to environment only
3. The phenotype of a clone is due to the effects of genotype(g), the environment(e) and the genotype x environment interaction (GxE), over the pop.mean(M)
4. Theoretically clones are immortal. They deteriorate due to viral/bacterial infection and mutations.
5. Clones are highly heterozygous and stable
6. They can be propagated generation after generation without any change.

Importance of a clone

1. Owing to heterozygosity and sterility in many crops clones are the only means of propagation.
2. Clones are used to produce new varieties.
3. Clones are very useful tools to preserve the heterozygosity once obtained. In many crops the superior plants are maintained. (Mango, orange, apple, sugarcane)

Sources of clonal selection :

1. Local varieties
2. Introduced material
3. Hybrids and
4. Segregating populations

Clonal selection :

The various steps involved in clonal selection are briefly mentioned below.

First year : From a mixed variable population, few hundred to few thousand desirable plants are selected. Rigid selection can be done for simply inherited characters with high heritability. Plants with obvious weakness are eliminated.

Second year : Clones from the selected plants are grown separately, generally without replication. This is because of the limited supply of propagating material for each clone, and because of the large number of the clones involved. Characteristics of the clones will be more clear now than in the previous generation. Based on the observations the inferior clones are eliminated. The selection is based on visual observations and on judgement of the breeder on the value of clones. Fifty to one hundred clones are selected on the basis of clonal characteristics.

Third year : Replicated preliminary yield trial is conducted. A suitable check is included for comparison few superior performing clones with desirable characteristics are selected for multilocation trials. At this stage, selection for quality in done. If necessary, separate disease nurseries may be planted to evaluate disease resistance of the clone s.

Fourth to eighth years : Replicated yield trials are conducted at several locations along with suitable check. The yielding ability, quality and disease resistance etc. of the clones are rigidly evaluated. The best clones that are superior to the check in one or more characteristics are identified for release as varieties.

Ninth year : The superior clones are multiplied and released as varieties.

Advantages :1. Varieties are stable and easy to maintain
2. Avoids inbreeding depression
3. Clonal selection, combined with hybridization generates necessary variability for several selections.
4. Only method to improve clonal crops
5. Hybrid vigour is easily utilized selection may be used in maintaining the purity of clones.

Disadvantages

1. Selection utilizes the natural variability already present in the population.
2. Sexual reproduction is necessary for creation of variability through hybridization.
3. Applicable only to the vegetatively propagative crops.

Achievements

I. Through clonal selection :

Potato : 1.Kufri Red from Darjeeling Red Round
2. Kufri Safed from phulwa
3. Bombay Green banana is a bud selection from dwarf Cavendish : pidi monthan from Monthan

II. Through hybridization :

Potato : Kufri Alankar, Kufri Kuber, Kufri Sindhuri, Kufri Kundan, Kufri Chamatkar Kufri Jyothi (late blight resistant), Kufri Sheetman (frost resistant)
Sugarcane : Co 1148, Co 1158, CoS 510, Co 975, Cos 109, Co 541
Mango : Pedda Neelam, Chinna Suwarnarekha
Bana : High gate from Gross Michel
Citrus : Robertson Navel Orange
Sweet oranges : Yuvaraj blood Red
Turmeric : Kesari, Kasturi

CHAPTER – 10 - Hybridization and Methods of Hybridization (10 L)

10.1 Definition and Types of Hybridization
10.2 Hybridization Procedure
a) Selection of Parents
b) Selfing of Parents
c) Hybridization Technique
d) Harvesting hybrid seeds and raising F1 generation
e) Trials, Multiplication and distribution
10.3 Hybrid Vigour
10.4 Methods
i) Pedigree
ii) Single cross
iii) Back cross

The mating or crossing of two plants or lines of dissimilar genotype is known as hybridization. In plants, crossing is done by placing pollen grains from one genotype, the male parent, on to the stigma of flowers of the other genotype, the female parent. It is essential to prevent self-pollination as well as chance cross-pollination in the flowers of the female parent. At the same time, it must be ensured that the pollen from desired male parent reaches the stigma of female flowers for successful fertilization. The seeds as well as the progeny resulting from the hybridization are known as hybrid or F_1. The progeny of F_1, obtained by selfing or intermating of F_1 plants, and the subsequent generations are termed as segregating generations. The term cross is often used to denote the products of hybridization, i.e. the F_1 as well as the segregating generations.

The chief objective of hybridization is to create genetic variation. When two genotypically different plants are crossed, the genes from both the parents are brought together in F_1. Segregation and recombination produce many new gene combinations in F2 and the later generations, i.e. the segregating generations.

Hybrid Varieties: In most self-pollinated crops, F1 is more vigorous and higher yielding than the parents. Wherever it is commercially feasible, F1 may be used directly as a variety. In such cases, it is important that the two parents should produce an outstanding F1.

Procedure of Hybridization

Hybridization in plant involves the following steps(i) Selection of Parents (ii) Selfing of Parents (iii) Emasculation (iv) Bagging (v) Tagging and (vi) Pollination

1) Selection of Parents- This is the first steps of hybridization. Here the two plants to be selected for crossing. They designated as male and female parents. The choice of parents mainly depends upon the objectives of breeding program. The parents should be chosen with great care. The healthy and vigorous plants are selected from the field and tested for the desired characters.

2) Selfing of parents – To create homozygosity the parents are allowed to self-pollination. The Selfing increasing the percentage of desired characters in parents.

3] Emasculation

The process of removing of anthers or stamens or killing the pollen grains of plants to be used as female parent in the cross is called emasculation. Therefore, after emasculation the flower contains only female reproductive organs. Such emasculated flower will be pollinated with pollen grains from desired male parents. In monoecious plants male flowers are removed. Emasculation may be done by following methods

1] **Hand Emasculations**: this type of emasculation is done in the large and showy flowers. The details of techniques of emasculation vary in different crops.

2] Hot or Cold Water Method-

The pollen grains are very sensitive to cold, temperature as well as alcohol. There for when the flower are small, this method is applied. The temperature as well as percentage of alcohol varies from crop to crop.

4] Bagging:- it is the covering of emasculated flower with the help of suitable bags. The bagging is performed to avoid natural pollination of emasculated flowers. The bags of parchment paper, polythene paper of paper bags are used for the bags.
5] Labeling and Tagging:- it necessary to recognize the desired plant for the further misunderstanding.

The pollen grains are very sensitive to cold, temperature as well as alcohol. There for when the flower are small, this method is applied. The temperature as well as percentage of alcohol varies from crop to crop.,
Simple Cross: In a simple cross, two parents are crossed to produce the F1. The F1 is selfed to produce F2 or is used in a backcross programme, e.g.,
A X B F1 (A X B)
Complex Cross: more than two parents are crossed to produce the hybrid, which is then used to produce F2 or is used in a backcross. Such a cross is also known as convergent cross because this crossing programme aims at converging, i.e., bringing together, genes from several parents into a single hybrid. A few examples of convergent cross are described in
Fig. 7.1. As
Three Parents (A, B, C)

A X B
F1 (A X B) X C
Complex hybrid (A X B) X C

FOUR Parents (A, B, C, D)

A X B C X D
F1 (A X B) X (C X D)
Complex hybrid (A X B) X (C X D)

Crop improvement progresses, the crop varieties would accumulate more and more favourable genes. This would lead to greater similarities between even unrelated varieties. In view of this, it may be expected that in future complex crosses would become more and more important. In breeding of highly improved self-pollinated crops like wheat and rice, complex crosses are a common practice today. Complex crosses would become routine in near future in the improvement of other self-pollinated crops with the progress in the level of their improvement.

Pre-requisites for hybridization

Breeder should have clear knowledge about the following before taking up hybridization.
1. Requirements of the tract
2. Local conditions i.e. soil, climate, Agronomic practices and market requirements
3. Existing varieties of crops both local and introduced
4. Facilities like funds, land, labour and equipment
5. Plant material i.e. germ plasm
6. Objectives: Well set objectives and planning

Hybridization procedure or steps involved in hybridization

Details of the following steps have to be covered in
Practical classes
1. Choice or selection of parents
2. Evaluation of parents i.e. by selfing and studying the progeny
3. Emasculation
4. Crossing or pollination
5. Bagging & Labelling
6. Harvesting of F_1 seed
7. Raising F1 generation

From F_2 onwards the generations are known as segregating generations and they may be handled either by pedigree method of Bulk method or backcross method for evolving new varieties.

HANDLING OF SEGREGATING GENERATIONS

Pedigree Method

In the pedigree method, individual plants are selected from F2 and subsequent generations, and their progenies are tested. During the entire operation a record of all parent off spring relationships is kept. This is known as pedigree record. Individual plant selection is continued till the progenies show no segregation. At this stage the selection is done among

the progenies, multilocation tests are conducted and released as varieties.

The pedigree may be defined as a description of the ancestors of an individual and it generally goes back to some distant ancestors. It is useful to know the relationship of two individuals and useful for selection of parents and prediction of outcome of the cross. Procedure of pedigree method

1st year : cross is made between the parents possessing desirable characters.

2nd year : Sow the F1 seed giving wide spacing so that each F1 plant produces more seeds.

Raise as many F1 plants as possible to produce large number of F2 seeds. Harvest in bulk.

3rd year : Grow 2000-10000 plants of F2 giving wide spacing for full expression of the characters in F2 generation plants. Grow parents for comparision. Depending upon the facilities and objectives of the programme about 100-500 superior plants are selected. The value of selection depend on the skill of the breeder. He has to judge which F2 plant will produce superior progeny for characters under consideration. The breeder develops this skill through close study of the crop for many generations. The selection in F2 is done for simply inherited characters like head type disease resistance etc. and selection for characters governed by many genes like yield will be reserved for later generations. The selected plants are harvested separately and given serial numbers and description entered in pedigree registers.

4th year : Progeny rows of F3 i.e. seeds of one selection plant in one row are space planted along with parents and checks. From superior progeny rows, individual plants with desirable characters are selected (about 50-100 families and about 5 plants in each family and harvested separately). Diseased, lodging and undesirable progenies are discarded.

5th year : F4 plants raised again as head to row. Desirable plants are selected from desirable rows and harvested separately.

6th year : F5 plants raised in 3 row plots i.e. seeds of each selected plant sown in 3 rows. By this time many families might have become reasonly homozygous. For comparision check variety is grown for every 3 or 5 block. Progenies are evaluated for yield and the inferior ones are rejected. The number should be reduced to 25-50. superior plants from superior

progenies are selected. Plants from each progeny are bulked.

7th year : F6 individual plant progenies are grown in multi-row plots and evaluated. Inferior progenies are rejected and superior progenies are selected. Plants of each progeny are harvested in bulk. Diseased and inferior plants from the progenies are removed.

8th year : F7 preliminary yield trial with 3 or more replications ar conducted to identify superior lines. The progenies are evaluated for many characters including yield. Standard commercial varieties must be included as checks. Two to five outstanding lines are selected and advanced to coordinated yield trials.

9^{th}, 10^{th}& 11^{th} year : selected lines are tested in several localities for 2 or 3 years for adaptation tests. Lines are evaluated for all characters mainly yield and disease resistance. A line that is superior to commercial variety in yield and other characters is selected. 11th and

12th year : Selected superior lines is named, multiplied and released as a new variety. Number of year can be reduced if generations are advanced during off seasons either in green house or under irrigated conditions. Several modifications for the above described pedigree method are followed by breeders depending upon the crop, time and availability of funds and facilities like labour, land etc.

Early generation tests :

The objective of these tests is to find out superior crosses and superior progenies in early generations i.e. in F2 and F3. we need not advance all the crossed and all selected progenies in each cross upto F8. much labour, time and cost would be saved by this early generation testing. A more reliable information about the potential crosses and progenies may be obtained by conducting replicated tests (preferably in more location) and evaluating them for yield and other characters in F2 or F3 itself. A desirable cross or progeny should have high mean yield, high genetic variance and high expected genetic advance under selection. Other crosses and progenies are rejected in the beginning i.e. F2 and F3 generations itself.

F2 progeny testing : Another modification for pedigree method. In F2 make as many single plants selections as possible. From F3 to F6 advance the progenies in bulk making selections of the progenies as a whole and discarding the inferior progenies. Thus each of the progeny is derived from the single plant selected in F2 generation. In F6 make single plant selections in each of the progeny. Compare the yields of the single plants with progenies from which they are selected. Select superior single plant progenies and advance to preliminary yield trials, multilocation tests etc. There are two advantages

1. No. of crosses can be handled simultaneously
2. Natural selection operates from F 3 to F6 since they are advanced in bulk.

Mass pedigree method : This is another modified pedigree method. Crosses are made and further generations grown in bulk or as mass until suitable season occurs for making desirable selections against drought, insect and diseases etc. The population will be exposed to the natural conditions of vagaries. From the remaining population individual plants are selected and harvested progenies are evaluated for yield and other characters in preliminary yield trials and further generations are proceeded as in pedigree method till release of variety. The advantages of both bulk and pedigree methods can be obtained and large number of crosses can be handled at a time. The disadvantage is that it takes a bit longer time.

Merits of pedigree method :

1. It gives maximum opportunity for the breeder to use his skill and judgement in selection of plants
2. It is well suited for the improvement of characters which can be easily identified and are simply inherited.
3. Transgressive segregation for yield and other quantitative characters may be recovered.
4. Information about the inheritance of characters and pe digree of lines can be obtained.
5. Inferior plants and progenies are eliminated in early generations.
6. It takes less time than bulk method to develop new variety.

Demerits of pedigree method :

1. Valuable genotypes may be lost in early generations, if sufficient skill and knowledge are lacking in the breeder, at the time of selection.
2. No opportunity for natural selection
3. Difficult to handle many crosses
4. Maintenance of records, selections, growing progeny rows etc are time consuming and laborious.

Achievements : Large number of varieties have been developed by pedigree method in many crops. A few examples are

Wheat – NP-52, 120,125, 700 and 800 series

Rice – ADT – 25, Jaya, Padma

Cotton – Lakshmi, Digvijay, Sorghum – Co 18, RS 610 etc., Tobacco – NP 222

Sorghum – Co 18, Rs 610, Tobacco – NP 222

BULK METHOD

The bulk method was first proposed by Nilsson Ehle in 1908 at Svalof. This methodis also known as **mass method** 'or' Population method of breedingIsolation of Homozygous

F2 and subsequent generations are harvested in mass as bulk to raise the next generation.

At the end of the bulking period (after attaining homozygosity) individual plants are selected and evaluated similar manner as pedigree method of breeding.

THE PROCEDURE FOR BULK METHOD

The exact procedure for the bulk method would vary depending upon the objective of breeder. The following procedure is described for the isolation of homozygous lines. The breeder may introduce various modifications in the scheme to suit his needs.

Hybridization : Parents are selected according to the objective of the breeding programme. A simple or a complex cross is then made depending upon the number of parents involved.

F1 Generation : F1 is space-planted and harvested in bulk. The number of F1 plants should be as large as possible ; usually more than 20 plants should be grown.

F2-F6 Generations : F2 to F6 generations are planted at commercial seed rates and spacing. These generations are harvested in bulk. During this period, environmental factors, disease and pest outbreaks would change, the frequencies of different genotypes in the population. Artificial selection is generally not done. The population size should be as large as possible, preferably 30,000-50,000 plants in each generation.

F7 Generations : About 30-50 thousand plants are space-planted. 1000 to 5000 plants with superior phenotypes are selected and their seeds harvested separately. Selection is based on the phenotype of plants, grain characteristics, disease reaction, etc.

F8 Generation : Individual plant progenies are grown in single or multi-row plots. Most of the progenies would be reasonably homozygous and are harvested in bulk. Weak and inferior progenies are rejected on the basis of visual evaluation. Only 100-300 plant progenies with desirable characteristics are saved. Some progenies which show segregation are generally rejected unless they are of great promise. In promising progenies, individual plants may be selected ; preliminary yield trial will be delayed for one year in such cases.

F9 Generation : Preliminary yield trial is conducted by using standard commercial varieties as checks. The progenies which are superior than the check are advanced. Quality test may be conducted to further reject undesirable progenies. The progenies are evaluated for height, lodging resistance, maturity date, disease resistance and other important characteristics of the crop species.

F10-F13 Generations : Replicated yield trials are conducted over several locations using standard commercial varieties as checks. The lines are evaluated for important characteristics in addition to yield, disease resistance and quality. If a line is superior to the standard varieties in yield trials, it would be released as a new variety.

F14 Generation : Seed of the released variety is increased for distribution to the cultivators.

MERITS OF BULK METHOD

1. The bulk method is simple, convenient and less expensive.
2. Since, each F2 plant is equally represented till F6, no chance of elimination of good genotypes in early generations.
3. Artificial or natural disease epiphytic, winter killing high temperature etc. eliminates undesirable types and increases the frequency of desirable type. Thus isolation of desirable types becomes easier.
4. Progenies select from long term bulks are superior than the selection from F2 or short term bulk.
5. Since, little work and attention is needed in F2 and subsequent generation more no. of crosses can be handled.
6. No pedigree records which saves time
7. Since large population are grown, transgressive segregants are more likely to appear and increase due to natural selection. Hence, there is a greater chance to isolate good segregants than pedigree method.

DEMERITS OF BULK METHOD

1. The major disadvantage of bulk method is that it takes a much longer time to develop a new variety. Natural selection becomes important only after F8 or F10, and bulking may have to be done upto F20 or more. Thus the time required is considerably longer, and most breeders do not use the bulk method simply for this reason.
2. In short-term bulks, natural selection has little effect on the genetic composition of populations. But short - term bulks are useful for the isolation of homozygous lines and for specific objectives as in Harlan's mass - pedigree method.
3. It provides little opportunity for the breeder to exercise his skill or judgement in selection. But in the modified bulk method, the breeder has ample opportunity for practicing selection in the early segregating generations.

4. A large number of progenies have to be selected at the end of the bulking period.
5. Information on the inheritance of characters cannot be obtained which is often available from the pedigree method.
6. In some cases, at least, natural selection may act against the agronomically desirable types.

Comparison between bulk and pedigree method.

S. No.	PEDIGREE METHOD	BULK METHOD
1	Most widely used Breeding method	Used only to a limited extent
2	Individual plants are selected in F2and subsequent generations andindividual plant progenies are grown	F2 and subsequent generations aregrown in bulk
3	Artificial selection ; artificial diseaseepidemics etc. are an integral part ofthe method	Mainly natural selection. In certaincases artificial selection may beessential
4	Natural selection does not play anyrole	N.S. determines the composition ofthe pop n at the end of the bulkingperiod
5	Pedigree Records have to bemaintained which is often timeconsuming and laborious	No pedigree records are maintained
6	Generally its taken 12-13 years torelease a new variety	Takes more than 15 years.
7	Requires close attention of breederfrom F2 onwards	It is quite simple and does not require much attention
8	Planting (spacing) the segregatinggenerations are space planted topermits effective individual plantselection	The bulk populations are generallyplanted at commercial plantingrates
	Population size is small incomparison to bulk	The population size is large

Achievements of bulk method:

The method has been used to a limited extent is Barley breeding in U.S.A. and more than 50 varieties were developed. They are : ARIVAL, BEECHER, GLACIER, and GEM. Originated from a cross : Atlas x Vaughn. The bulk was maintained for 7 to 8 months.

BACK CROSS

Breeders of early 20th century engaged in the development of disease resistant varieties observed that pureline selections with genes for resistance from intra-or interspecific hybridization were inferior to the generally acceptance superior parent in yield or quality characteristic. To overcome this problem, (Harlan and Pope (1922) suggested the back cross method by which an undesirable allele at a particular locus is replaced by the desirable allele in otherwise elite variety. In other words, B.C. procedure conserves all good characteristics of a popular adapted variety and incorporates a desirable character from another variety.

Back cross : A cross between a hybrid (F 1 or a segregating generation) and one of its parents is known as backcross.

Back cross method : In the B.C. method, the hybrid and the progenies in the subsequent generations are repeatedly back crossed to one of their parents.

Objective : To improve or correct one or two specific defects of a high yielding variety, which is well adapted to the area and has other desirable characteristics.

Recipient parent : Well adapted, high yielding variety, lacking one or two characters and hence receives these genes from other variety.

Donor parent : The variety which donates one or two useful genes.

Recurrent parent : Since the recipient parent is repeatedly used in the backcross programme, it is also known as the recurrent parent.

Non-recurrent parent : The donor parent, on the other hand, is known as the non-recurrent parent because it is used only once in the breeding programme (for producing the F1 hybrid).

REQUIREMENTS OF A BACK CROSS PROGRAMME

1. Existence of a good recurrent parent variety which requires improvement is some qualitatively inherited character or a quantitative character with high heritability.
2. A suitable donor parent must be available possessing the character or characters to be transferred in a highly in tense form.
3. High expressivity of the character under transfer through several back crosses in the genetic back ground of the recurrent parent.
4. The character to be transferred must have high heritability-preferably determined by one or few genes.
5. Simple testing technique for detecting the presence of the character under transfer.
6. Recovery of the recurrent genotype in a reasonable number of back cross generations.

CHAPTER – 11 - Polyploidy (3 L)

11.1 Meaning and types
11.2 Role of Polyploidy in crop evolution. E.g. Wheat, *Raphano Brassica, Nicotiana.*
11.3 Utilization of Allopolyploidy in Plant Breeding.
11.4 Utilization of Autopolyploidy in plant Breeding

Role of Polyploidy in Evolution: - Polypoidy is commonly met within plant world. In animals, it is indeed rare. About one half of total species of flowering plants are polyploides (Stabbins 1950).

Polyploides has played an important role in evolution of new varieties and species in nature. Angiosperms and Pterdophytes have very high number of polyploides species in nature. More than 35% angiosperms are polyploides. It is generally noted that with the increase in chromosome number the adaptability and variabilities of species increase progressively.

Autopolyploidy has limited contribution in the evolution of plant species e.g. Potato (4n),Sweet Potato (6n) ,Banana(3n),Coffee(4n),Ground Nut(4n) and Tomato (4n). Allopolyploidy has played vital role in the evolution of species. It is estimated that about 1/3 of flowering plants are polyploides and most of them are Allopolyploides.

EVOLUTION OF WHEAT ----

The origin bread wheat (*Triticum astivum*) has been most extensively investigated. The common bread wheat (*Triticum astivum*) is Hexaploid species (2n=6x=42) having three different sets of genome (AA BB DD) which seem have been contributed by three different diploid species (Sears,Kihara,Percival etc.) . The species of wheat (*Triticum)* fall in to the following three categories diploids,Tetraploids, and Hexaploids.

The possible evolutionary history of hexaploid wheat as follows.

T. monococcum X Aegilops speltoides
2n=14(AA) 2n=14(BB)

F1=2n=14 AB (Hybrid Sterile)

Aegilops squarrasu XAABB(2n=28)TetraploidEmmer wheat(T.dicocum)
2n=14 DD AB
N=7 D n=14

F_1 ABD (21)
2n=21

Spontaneous chromosome doubling

AABBDD Hexaploid Wheat (Amphidiploid)
(2n = 6x=42) Triticum astivum

The genome D present in bread wheat is supposed to have derived from grass Aegilops squrossa (2n=14). The different varieties of wheat with higher chromosome number have appereantly arise from this type and other related grasses through hybridization followed by chromosome doubling. J. Percival is of the opinion that bread wheat (T.aestivum) originated through hybridization emmer wheat (2n=14) and goat grass (2n=14). These investigator double the chromosome number by Colchicine. The resultant Hybrid with 42 chromosome number.

NICOTIANA:- The allopolyploids can be utilized as bridge species. An amphidiploids is utilized as bridge in transfer of desirable character of one species to the other related species.

When hybrid between the cultivated species to which the desirable character is to be transfer and wild species (Donor) from which the desirable character is to be transfer is sterile. In such cases the

chromosome number of F1 sterile is sterile. In such cases, the chromosome number of F1 sterile hybrid is doubled to produce amphidiploids which is generally fertile and can be crossed with recipient species. The progeny of the cross between recipient species and amphidiploids would have 2n chromosome of recipient species and one genome from donor species. This progeny can be back crossed with recipient species. This to addition of gene into recipient species .

This can be clear from the following example of Synthetic allohexaploid *Nicotiana digulata* as bridge for transfer of resistance against Tobacco Mosaic Virus from *N. sylvestris* to *N. tobacum.*

N. sylvestris (2n= 24) X N. tobacum (2n= 4x = 48)
(resistant against TMV)
n=12 n = 24
↓
Hybrid (Sterile) (2n = 36)
↓
Artificial Doubling of Chromosome
↓
N. tobacum X Synthetic amphidiploids (2n = 72)
2n = 4x = 48 (N. Digulata) Back cross
N= 24 n= 36
↓
Hybrid
↓
Back crossed to Nicotiana tobacum

Pentaloid progeny with 2n chromosomes of ***Nicotianatobacum*** and are one genome of ***Nicotiana sylvestris*** so sufficiently fertile.

Use of Allopolyploidy in creation of New Species :-

One of the best examples of application of polyploidy breeding is *Raphanobrassica.*In 1928 a Russian Geneticist **Korpernchenkov** obtain an interesting amphidiploid from an intergeneric cross between ***Raphanus sativa*** and ***Brassica oleracea.***He combined the root characteristics of raphaanus sativus with other features of Brassica oleracea. The chromosome number of Raphanus sativus as well as Brassica oleracea are 2n = 18. The F_1 Hybrid obtained from the cross also has 2n = 18 but nine (9) from each. The F_1 having characteristics of radish as well as cabbage both, hence called as Raphanobrassica (cabbage). It has hardlines of Brassica oleracea and quick growth as well as disease resistance of Raphanus sativus.

Raphanus sativus X Brassica oleracea
2n = 18 2n = 18
n= 09 n = 09
↓
2n F_1 Hybrid (Sterile 2n = 18)
↓
Spontaneous chromosome doubling
↓
Raphanobrassica (36) Fertile(2n =36)

EVOLUTION –

CHAPTER – 12 – Introduction to Evolution (5 L)

12.1 Meaning of Evolution
12.2 Theories of Evolution –
i) Lamarkism and Neo-Lamarkism
ii) Darwinism and Neo-Darwinism
iii) Mutation theory of Hugo de Vries
iv) Synthetic theory

1. Lamarck's Theory:

Jean Baptiste Lamarck (1744-1829), a French naturalist, made several valuable contributions to biological science, including the coining of the term 'biology' and using the same in its true sense. He studied comparative anatomy and planned a tree of life for explaining the phylogenetic relationship among organisms.He believed in the fundamental unity of living things and in a progressive development of forms and functions in all organisms. But the most important contribution of Lamarck —his theory of evolution—was framed in 1801 and published in the 'Philosophic Zoologique' in 1809, that is the year in which Charles Darwin was born.

Lamarckism:

The essence of the Lamarckian theory or Lamarckism may be summarised as follows:

(1) Necessity in the organism may give rise to new structures or may lead to the disappearance of certain parts. Lamarck expressed this as the law of use and disuse. According to Lamarck an organ which is used extensively by the organism would enlarge and become more efficient, while disuse or lack of use of a particular organ would lead to its degeneration and ultimate disappearance.

For example, the webbed toes of aquatic birds such as swans developed due to constant stretching of the skin at the bases of the toes in some ancestral form which lived on land. The necessity of the web of skin arose when the ancestors migrated into the water in search of food. This led to constant use and stretching, thereby a change was induced and a paddle-like foot evolved.

Similarly, the ancestors of the snakes were lizard-like creatures with 1 two pairs of limbs and the modern snakes lost their limbs by constant disuse while passing through narrow crevices. Thus by differential use and disuse of various parts, an organism could change a good deal; that is, the organism acquires certain new characteristics.

Fig. 195. Jean Baptiste Lamarck (1744-1829).

(2) The second part of Lamarck's theory postulated that acquired traits induced by use or disuse of organs were transmitted to the offspring; this is the law of inheritance of acquired characters. Lamarckism explains evolution of the modern giraffe in the following way.

There was a short-necked ancestral stock which used to feed on tree leaves. It stretched its neck further up, to reach higher levels, when the leaves lower down were finished. Due to constant stretching the neck length increased a little and his new trait was inherited by the offspring.

The latter in turn kept on stretching their necks and this was continued for many generations. Each successive generation would acquire the gains of the previous generation by inheritance, and would itself add a bit to the neck length. In the course of time, the long-necked modern giraffe evolved out of the short-necked ancestral form.

Criticism of Lamarckism:

The first part of Lamarck's theory, that is, the law of use and disuse is acceptable. For example, moderate exercise taken regularly builds big muscles, or a limb put up on splints and not used for a long time undergoes atrophy. But the second part of Lamarckism, that is, inheritance of acquired characters, is not acceptable.

It implies that a man who has developed large muscles by lifelong exercise will beget children with big muscles. Lamarckism was chiefly opposed by Weismann (1834- 1914) who postulated that germ cells are not affected materially by changes in the body cells.

In spite of the laborious research of neo-Lamarckists such as Guyer, Smith and Cope, Lamarckism is untenable. Acquired characters are phenotypic variations. They cannot affect the genes. As such they cannot be transmitted to the offspring.

Neo-Lamarckism:

Although Lamarck's doctrine of inheritance of acquired characters was strongly refuted and rejected, yet a few biologists accepted the theory in modified way. The prominent among them were cope (1840 -1897), Giard (1846 -1908), Packard Spencer and Mc Bridge.

According to Neo-Lamarckism the adaptation is the universal feature of living beings. It arises as a result of interaction between the structure, function and environment. The changed or fluctuating environmental conditions can alter the habit and structure of the organisms.

So, the organisms acquire new adaptation in response to new environmental conditions and consequently variations among plants and animals may result. These variations become established gradually in the heredity of the race.

This is the modified version of Lamarckism or Neo-Lamarckism because it does not follow the general perfecting tendency in evolution and stresses mainly on the direct action of environment on organic structure.

According to some Neo Lamarckians, the fur development on the skin of some animals as adaptation against cold weather is the consequence of changed environment from warmer to colder state.
On the other hand, if the environment comes to the normal state again, the fur would also disappear. Neo-Lamarckians have discarded natural selection as the sole mechanism of evolution. They are of the opinion that the interaction between the structure, function and environment is the only cause of evolution. Today no evolutionist supports the Neo-Lamarckism.

Fig. 196. Charles Robert Darwin (1809-1882).

2. Darwin's Theory of Evolution:

The name of Charles Robert Darwin (1809-1882) is a proverb in the history of science. This illustrious grandson of Erasmus Darwin was born in 1809 and his date of birth coincided with that of Abraham Lincoln. In his early life Darwin, like all other scientists of his time, believed in Lamarckism.
As a young man he joined the naval expeditionary ship 'H.M.S. Beagle' and undertook a circumglobal voyage for five long years. He spent his time in collecting numerous specimens of plants and animals from different parts of the world. After returning home Darwin spent 20 years in studying his collections.
At this time he was greatly influenced by the publications of Lyell and Malthus. By studying Lyell's 'Principles of Geology' Darwin learnt about the changing Jonas of the earth, and about the fossils which were known i: that time. The famous essay on population published by Malthus taught Darwin about overpopulation and consequent competition for food and shelter.
Having completed his study, Darwin was preparing his theory of natural selection for explaining the mechanism of organic evolution when he received an essay from a younger scientist, Alfred Russell Wallace (1823-1913), who was working independently on the flora and fauna of Malayan archipelago. To his amazement Darwin found that Wallace's views on the origin of species coincided with his own theory.
The natural selection theory was first published as a paper under joint authorship in 1858. Two renowned scientists of that time, Lyell and Hooker, presented the paper at the meeting of the Linnean Society and Darwin was conspicuous by his absence. In the following year, that is in 1859, Darwin published his classical work in the form of a book—**"On the origin of species by means of natural selection."**

Essence of Darwinism:

Darwin's theory is based on intrinsic analysis of facts in a scientific spirit by induction and deduction.

The following is the essence of Darwinism:

(1) Prodigality of Production:

The plants and animals have a tendency to increase in geometric progression, but the habitable space and the food supply remain constant. Darwin calculated that starting from a pair of elephants, the herd will increase to about 20,000,000 in 1000 years, and elephants are the slowest breeders producing 4 to 6 calves in their life-time. Such enormous prodigality in production results in struggle for existence.

(2) Struggle for Existence:

This means a keen competition amongst the living forms for food and shelter.

It operates in a threefold way:

(a) Interspecific, that is, struggle in between different species of organisms,
(b) Intraspecific, that is, struggle between members of the same species, and
(c) Environmental, that is, struggle against the changes of the environment.

(3) Variation:

Darwin observed that no two living forms were exactly alike. Diversity tends to appear even among members belonging to the same species. Darwin paid particular attention to small, fluctuating and continuous variations which appeared randomly.
According to him these continuous variations help the organism to win the struggle for existence. Large, discontinuous variations, which appeared suddenly, were considered by Darwin as mere 'sports of nature', and therefore ignored.

(4) Survival of the Fittest:

The organisms possessing suitable variations which helped them to win the struggle for existence were better adapted to their environment. They survived and propagated their variations to the next generation. The others with unsuitable variations perished.

(5) Natural Selection:

This is the most important deduction of Darwin. Natural selection is the process by which individuals possessing favourable variations enjoy a competitive advantage over the others.

They are better adapted to their environment, and therefore they survive in proportionately greater numbers and produce more offspring. The rest with disadvantageous variations fail to adapt properly to their environment and therefore eliminated by natural selection.

The favourable variations which are the cause of success are handed down to the offspring by inheritance. Thus the number of the favoured individuals increase rapidly, and if natural selection operates for a long time, those favourable variations which have attained the survival value are intensified successively from generation to generation, until the original ancestral forms are thoroughly changed into a new species.

For example, Darwinism explains the evolution of the modern giraffe in the following manner. The original ancestral forms were short-necked, leaf-eating animals. Darwin assumed that as a result of individual variation, some of them had slightly longer or shorter necks in comparison with the population's average neck-length.

The longer-necked forms were better adapted to get at foliage's situated a bit higher up. Consequently they were better fed than the shorter-necked fellows, and they produced proportionately greater numbers of offspring.

As a result of natural selection the proportion of the longer-necked population would be doubled in the next generation. This is repeated in successive generations until the entire population would be transformed into individuals with slightly longer necks.

Individual variation would occur in the new population and actual neck-lengths would vary more or less on either side of an average. Long necks would again be favoured in a second round of natural selection and then in successive rounds, until the modern giraffe with very long neck evolved out of the short-necked ancestral stock.

Criticism of Darwin's Theory:

In spite of strong evidences and critical scanning of facts, Darwinism suffers from certain serious drawbacks.

A few objections to Darwinism are briefly discussed as follows:

(1) Variations were accepted by Darwin to be the chief tool in the process of evolution of new species, and he believed that small continuous variations of fluctuating type were inherited by the offspring. Unfortunately Darwin had no knowledge about the real cause of variation.

At this time the science of genetics was unknown, and the laws of inheritance were unexplored. Most of the fluctuating variations considered by Darwin to be important factors in his theory of natural selection are not genotypic and as such they are not inherited.

(2) Darwin, like Lamarck, believed in the inheritance of acquired characters—a fact which is not proved by genetics.

(3) Darwin's natural selection mainly operates in one direction, and often leads to over specialisation and ultimate extinction. The canine teeth of the sabre-toothed tiger and the antlers of the Irish elk increased progressively in size because the characteristics in both the cases were favoured by natural selection.

But ultimately, the structures became so large that instead of being helpful they became hindrance in the struggle for existence, and led to the extinction of the species.

(4) Natural selection theory fails to account for the degeneracy which is very often observed in the parasitic forms.

(5) The essence of Darwinian natural selection is the elimination of the unsuitable forms. Hence it is better to name it as the 'theory of natural rejection'.

(6) Darwin actually observed large, discontinuous variations or mutations to occur in nature. He rejected them as they occurred less frequently. But mutations are genotypic variations and they have now been recognised as important factors in the origin of new species.

In spite of its weakness Darwinism is still accepted as one of the important factors in evolution. Thanks to the untiring efforts of Thomas Henry Huxley (1825-1895), the great champion of natural selection, and others, such as August Weismann, the theory has been firmly established.

Neo-Darwinism

Previous (Neo-Confucianism)
Next (Neo-Hegelianism)

Neo-Darwinism, also called the **modern evolutionary synthesis**, generally denotes the integration of Charles Darwin's theory of evolution by natural selection, Gregor Mendel's theory of genetics as the basis for biological inheritance, and mathematical population genetics. Although this was not the historical meaning of the term neo-Darwinism, it has been the popular and scientific use of the expression since the synthesis of the 1930s. (See Origin of the term neo-Darwinism.) Other terminology used synonymously with neo-Darwinism are *modern synthesis*, *evolutionary synthesis*, and *neo-Darwinian synthesis*.

Neo-Darwinism has been one of the most significant, overall developments in evolutionary biology since the time of Darwin. Bowler (1988) stated that there is "a sense in which the emergence of the modern synthetic theory can be seen as the first real triumph of Darwinism."

Essentially, neo-Darwinism introduced the connection between two important discoveries: the units of evolution (genes) with the mechanism of evolution (natural selection). By melding classical Darwinism with the rediscovered Mendelian genetics, Darwin's ideas were recast in terms of changes in allele frequencies. Neo-Darwinism thus fused two very different and formerly divided research traditions, the Darwinian naturalists and the experimental geneticists. This fusion took place roughly between 1936 and 1947.

While the modern synthesis remains the prevailing paradigm of evolutionary biology, in recent years it has both been expanded and challenged as a result of new developments in evolutionary theory. In particular, concepts related to gradualism, speciation, natural selection, and extrapolating macroevolutionary trends from microevolutionary trends have been challenged.

Major figures in the development of the modern synthesis include Thomas Hunt Morgan, Ronald Fisher, Theodosius Dobzhansky, J. B. S. Haldane, Sewall Wright, William D. Hamilton, Cyril Darlington, Sergei Chetverikov, E. B. Ford, Julian Huxley, Ernst Mayr, George Gaylord Simpson, and G. Ledyard Stebbins.

3. De Vries' Theory:

The mutation theory was published in 1901 by the Dutch botanist, Hugo De Vries (1848-1935). His theory is mainly based on his experiments on a plant called evening primrose,

Oenothera lamarckiana:

De Vries found that certain strikingly different forms appeared suddenly among a population of normal type of evening primrose. He called them mutants. A mutant is a variant which arises abruptly among normal forms. A mutant always breeds true, that is, it produces offspring like itself.

The term mutation or psaltation is applied to a sudden large change or discontinuous variation in organisms, and this can be inherited. According to the mutation theory, mutations are the real cause for the evolution of a new species.

Numerous mutants may be produced in nature. They are then subjected to natural selection .which determines the types that would survive. The mutants which survive in the struggle for existence are responsible for the origin of new species.

Criticism:

(1) Mutation often produces monsters which have no evolutionary significance.
(2) Mutations occur infrequently and they therefore cannot be regarded as the sole factor in evolution.
(3) Mutation theory accepts natural selection as the controlling agent in evolution.

4. Modern Theory of Evolution:

This is the product of recent researches in cytology, embryology, and genetics. In the opinion of modern scientists, the heritable characters of an individual rest upon particles of nucleoproteins or genes in the

chromosomes of the gametes. Any variation in the characteristics of an individual, whether continuous or discontinuous, must come through changes in the genes.

Such changes that suit well with the environment are advantageous, and individuals possessing advantageous changes get the better chance of living and multiplying. This will continue for successive generation until a final form comes into existence, differing profusely from the ancestral type.

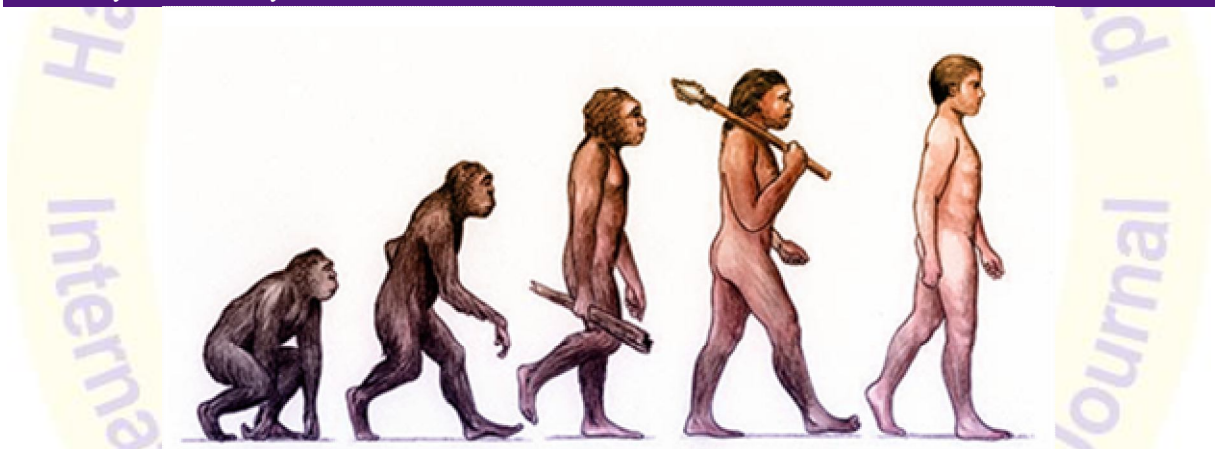
Natural selection acting as a screen leads to differential survival and differential reproduction. In the present outlook about the origin of species, Darwin's struggle for existence may not be in the form of a competition, but the selective value has been found to be more important in differential survival of different variations.

The modern theory explains the evolution of the giraffe in the following way: Every generation of the short-necked ancestral stock must have included a few mutant types, with shorter or longer necks than the average neck-length of the population.

The longer-necked individuals are in a more advantageous position. In the subsequent generation they will produce more longer-necked forms. This will go on through several generations in which changes in the gene would produce mutants, and natural selection acting as a screen would again and again eliminate the short-necked individuals, until the appearance of the modern giraffe with very long neck.

This modern theory is known as the synthetic theory. Several investigators of the synthetic school, such as Haldane, Ford, Waddington, Miller, Dobzhansky, and others have contributed their bit in its shaping. It is nothing but a completely re-modelled natural selection theory minus its weaknesses.

Modern Synthetic Theory of Evolution



The Modern Synthetic theory of Evolution explains the evolution of life in terms of genetic changes occurring in the populations that leads to the formation of new species. It also explains about the genetic population or mendelian population, gene pool and the gene frequency. The concepts coming under this synthetic theory of evolution includes the genetic variations, reproductive and geographical isolation and the natural selection.

The Modern Synthetic populations, of Evolution, describes the merging of the Darwinian evolution with the Mendelian genetics, resulting into a unified theory of the evolution. This theory is also referred as the Neo-Darwinian theory. Synthetic theory of Evolution was introduced to us by few legendary evolutionary biologists naming T. Dobzhansky, J.B.S. Haldane, R.A. Fisher, Swall Wright, G.L. Stebbins, Ernst Mayr in the years 1930 and 1940.

The Modern Synthetic theory of Evolution showed a number of changes as to how the evolution and the process of evolution are conceived. The theory gave a new definition about the evolution as "the changes occurring in the allele frequencies within the populations, " which emphasizes on the genetics of evolution.

The modern synthetic theory includes the scientific evidence from the genetics. It explains the concepts which occur when the allele frequency of the population changes. According to this theory, when the changes are great enough, there is a formation of new species. A species is a group of individuals which are capable of interbreeding and producing a fertile offspring.

Factors of Modern Synthetic Theory of Evolution

There are some factors describing the modern theory of synthetic evolution which are as explained below-

In addition to these reactions, the other factors affecting the working of the process are Migration of the individuals from one form of the population to other, hybridization between the races of species increase the genetic variability of the population.

1. **Recombination or Variation**

Recombination of the new genotypes from the existing genes. The gene combinations having same individuals with two kinds of alleles, mixing of the chromosomes during sexual reproduction of two parents produce new individuals, an exchange of the chromosomal pairs of alleles during the meiosis which is called as crossing over produce the new form of gene combinations. Chromosomal mutations like deletion, inversion, duplication, translocation, polyploidy result in the recombination.

2. **Mutation**

The changes that occur in the gene due to phenotypic effect differential as the mutation. This produces a various number of changes that may be harmful. Many of the mutant forms of genes are recessive to the normal genes in a homozygous condition. These mutations cause variations in offsprings.

3. **Heredity**

The transmission occurring in the variations from the parents to their offsprings is a primary mechanism in the evolution. The organisms which possess hereditary properties are favoured in the struggle for the existence. By this, the offsprings benefit from the characteristics of parents.

4. **Natural selection**

Natural selection produces a change in the frequency of the genes from one generation to the other favoring the differential form of the reproduction. The natural selection process creates an adaptive relation between the environment and the population through various combinations of genes.

5. **Isolation**

It is one among the significant factor responsible for the synthetic theory of evolution. The isolation helps in preventing the interbreeding of related organisms which is a reproductive form of isolation.

CHAPTER- 13- Speciation (3 L)

13.1 Species and Races
13.2 Concepts of Species
13.3 Methods of Speciation – Allopatric, parapatric, sympatric mode of speciation, Chromosomal speciation

Concept of Biological Species | Biology

The concept of biological species was advanced by Mayer (1957) and gained general acclaim through the advocacy of Stebbins, Clausen, Grant and others in botanical taxonomy. This concept underscores reproductive isolation which is, in turn, a by-product of genetic divergence.

The biological species, according to Grant (1957), is defined as "a community of cross fertilising individuals linked together by bonds of mating and isolated reproductively from other species." In short, a biological species is formed by "groups of interbreeding natural populations that are reproductively isolated from such other groups."

In this concept, two aspects are stressed:

(i) Interbreeding between members of the same species and

(ii) Reproductive isolation between the members of different species.

Since the bulk species of the angiosperms are outbreeding, this aspect allows a good quantity of gene exchange between populations and accounts for the variability within species; this aspect contributes little by way of isolation. Inbreeding, on the other hand, reduces variability by curtailing gene exchange and aids in spreading homozygous population under the condition that there are no harmful influences for the homozygosity.

Continued self- fertilization will create deleterious effects on the genetic makeup of populations. Under fluctuating or unreliable conditions, selfing has proved helpful over interbreeding by ensuring pollination which leads to rapid growth in the population.

This has been demonstrated in populations of *Agrostis tenuis* and ***Anthoxanthum odoratum*** which can tolerate heavy metals. In this case, autogamy is a contrivance for metal tolerance by insulating these populations against gene exchange from non-tolerant forms.

However, selfing can evolve for reasons other than isolation. In *Armeria maritima*, the high degree of self-fertility in metal tolerant populations compared to the normal ones is not subject to gene exchange from non-tolerant populations and has probably evolved in response to low density in colonising state.

Portulaca is another example where autogamy has led to the production of several pure line populations which are isolated to such an extent from one another that each one of them has been assigned a separate binomial.

Interspecific incompatibility, one of the corner stones of the biological species concept, is an isolating mechanism between species that has been facilitated by evading fertilisation in the prezygotic phase.

This is evident in ***Linum, Lycopersicon, Nicoticina, Petunia*** and *Solatium*. One of the main causes of this incompatibility of the related species in the lack of correlation between the length of the pollen tube and length of the style. ***Kostoff*** (1943) listed 68 interspecific crosses in ***Nicotiana*** which failed in view of the pollen tubes not being able to reach the ovules.

In such crosses, generally the maternal styles are very long for the pollen tube to travel the path to the ovules. However, such crosses with those species possessing shorter pollen tube as females are reportedly fruitful.

Still another type of infertility has been recorded in the genus Datura where the pollen tube grows faster in the style of the same species and frequently bursts in the styles of other species. In comparison with the rate of domestic pollen tube growth, that of the alien pollen differs from one recipient to another.

Discordant evolution of genotype and phenotype poses an entirely different problem. Genotype does not undergo divergence and phenotype does in polymorphic species, whereas genotype diverges and phenotype

remains the same in cryptic species. Such cases frequently confuse many practicing plant taxonomists and correct decisions are difficult to arrive at. In evolution, the basic unit is a breeding population.

A fundamental tenet of the biological species concept is the criterion of reproductive isolation. In asexually reproducing organisms, where there are neither breeding populations nor reproductive isolation, interbreeding is not relevant. Among angiosperms, several genera exhibit the phenomenon of apomixis. As a consequence, the biological species concept cannot be applied to these cases.

The problem is so acute that "the most satisfactory solution in taxonomic practice seems to be a dualistic one …. It consists in defining the term species biologically in sexual organisms and morphologically in asexual ones". While agreeing with this statement, Maheshwari (1967) proposed the terms 'biospecies' and 'phenospecies' respectively for them.

Although the value of the concept lies in population biology and involves fertility tests; such tests have been limited to a few selected individuals and the results then applied to the entire population. In allopatric populations, these tests can be performed only under experimental conditions and are of mere academic interest because gene exchange does not take place in natural populations.

Furthermore, local breeding populations differ considerably in their genetic properties and may have various kinds of kinship with such other populations. Among higher plants, there are many natural interspecific and inter-generic crosses which present formidable problems to the evolutionary taxonomists.

During the last three decades, the concept has stirred the imagination of biologists. In the domain of botany, the concept has remained largely conceptual rather than operational. Even Mayr (1957) admitted the hazards in applying the concept to animal organisms. Heywood (1974) observed that the "general acceptance of a concept is, of course, a different matter from acceptance in practice".

Even the so called experimental studies which the concept itself encouraged lead to the interference that most species are not evolutionary units held together by gene flow and that efforts to accommodate all variations into units so defined are misguided. Simultaneously, the validity of the concept has been challenged on operational grounds by numerical taxonomists.

Sokal and Crovollo (1970) jumped to the conclusion that the biological species concept is "neither operational nor heuristic are of practical value". They went to the extent of suggesting that this concept be abandoned in favour of the phenetic species concept which is the most suitable one to be associated with the taxonomic category 'species'.

History of Species Concept:

The species, as we know, is the fundamental unit of taxonomic hierarchy. Davis (1978) called them 'Building bricks' in Biological classification. In biological phenomenon biosystematics concept is the oldest one. It is the lowest category of hierarchy which is consistently used and recognized by all the botanists. According to Stebbins (1977) is the basic unit of evolutionary process.

It starts with the great Philosopher Plato who proposed concept of eidos or species and believed that all objects are shadows of the 'eidos'. Mayr (1957) suggested that variations in species are found arid presented on typological species concept.

Principle of logical division by Aristotle based in part upon Plato's idea was the basis of Taxonomy serving as schema upon which "species concept" is based. Species was considered to be a relative term applicable to various levels in a classification scheme.

A logical relationship was also established between genus and species. Then species was defined on a priori basis and regarded as unchanging and fixed. After the knowledge of a number of organisms, people started facing difficulty as there are species which belong to different genera.

In biological taxonomy, **race** is an informal rank in the taxonomic hierarchy, below the level of subspecies. It has been used as a higher rank than strain, with several strains making up one race.[1][2] Various definitions exist. Races may be genetically distinct populations of individuals within the same species,[3] or they may be defined in other ways, e.g. geographically, or physiologically.[4] Genetic isolation between races is not complete, but genetic differences may have accumulated that are not (yet) sufficient to separate species.[5] The term is recognized by some, but not governed by any, of the formal codes of biological nomenclature.

Race: Races are defined according to any identifiable characteristic, including gene frequencies.[7] "Race differences are relative, not absolute".[7] Adaptive differences that distinguish races can accumulate even with substantial gene flow and clinal (rather than discrete) habitat variation.[8]

Chromosomal race

A population distinguished by having a unique karyotypes, i.e., different chromosome numbers (ploidy), or different chromosome structure.[7]

Geographical race

A distinct population that is isolated in a particular area from other populations of a species,[9] and consistently distinguishable from the others,[9] e.g. morphology (or even only genetically[3]). Geographic races are allopatric.[7]

Physiological race

A group of individuals that do not necessarily differ in morphology from other members of the species, but have identifiably different physiology or behaviour.[10] A physiological race may be an ecotype, part of a species that is adapted to a different local habitat, defined even by a specific food source.[11] Parasitic species, often tied to no geographic location, frequently have races that are adapted to different hosts,[10][12] but difficult to distinguish chromosomally.[13]

In botany, where *physiological race* (mostly used in mycology[12]), *biological race*, and *biological form* have been used synonymously,[10][14][15] a physiological race is essentially the same classification as a *forma specialis*,[10] except the latter is used as part of the infraspecific scientific name (and follows Latin-based scientific naming conventions), inserted after the interpolation "f. sp.", as in "*Puccinia graminis* f. sp. *avenae*"; while the name of a race is added after the binomial scientific name (and may be arbitrary, e.g. an alphanumeric code, usually with the word "race"): "*Podosphaera xanthii* race S".[13]

A physiological race is not to be confused with a *physiologic race*, an obsolete term for cryptic species.[12] Neither biological form nor *forma specialis* should be confused with the formal botanical taxonomic rank of *forma* or form, or with the zoological term form, an informal description (often seasonal) which is not taxonomic.

The term *race* has also historically been used in relation to domesticated animals, as another term for *breed*;[3] this usage survives in combining form, in the term landrace, also applied to domesticated plants. The cognate words for *race* in many languages (Spanish: *raza*; German: *Rasse*; French: *race*) may convey meanings the English word does not, and are frequently used in the sense of 'domestic breed'.[16]

Essay on Speciation of Organism!

Individuals of a species are similar and they can breed among themselves. At the same time, there are some small, but significant, differences (variations) between the individuals of a species.

Heritable variations are transmitted to the offspring. These variations are important as they produce changes in the characters of that particular species.

This leads to microevolution or evolution on a small scale with the emergence of new varieties or new subspecies.To understand how such small variations lead to the formation of a new speeds, let us take the beetle's example again. Suppose there are beetles spread over a large area. If the population of beetles gets divided into two subpopulations by a barrier (say, a river or a mountain) then it will be difficult for the members of one subpopulation to go to the other side for mating.

Therefore, exchange of genetic material, or gene flow, between them will decrease. They will be restricted to mate within their own subpopulations. In other words, they will be forced to inbreed, or mate with closely related individuals in their own isolated subpopulations.

In this process, the recessive mutant genes of each parent have a much greater chance of coming together. The genes will now be expressed giving benefit or harm to the offspring. These new characters, or variations, may be selected by nature and may lead to the formation of a new species.

The new generations differ so much from the original population that they can no longer interbreed to produce fertile offspring. This leads to speciation, that is, the formation of one or more species from an existing species.

After a few years, if a male beetle from one isolated area and a female from another area are brought together, they may or may not mate with each other. If they mate but are unable to reproduce, then they have become two different species. If they are able to reproduce, then they are still the same species.

Over many generations, different variations are accumulated in each subpopulation. Suppose, for example, in one area with a beetle subpopulation, crows are scarce due to the presence of eagles. And in another area, crows are present in large numbers.

Natural selection will not select the green variety of beetles in the first area as there are no crows to eat the beetles. But the green variety will be selected in the second area as the crows will eat the other beetles there. Thus, natural selection may operate differently on the same variations in subpopulations of different areas. Nature will select those variations that help to adapt better in a particular environment.

Over a period of time, the processes of genetic drift and natural selection will cause the two isolated subpopulations to become more and more different from each other.

Microevolution is generally a consequence of gene mutation. But larger changes in the genetic make-up, like change in the number of chromosomes, may not allow the germ cells of two subpopulations to fuse together. This prevents interbreeding and causes the emergence of new species.

Speciation due to inbreeding, genetic drift and natural selection will be applicable to all sexually reproducing organisms. Geographical isolation does not play any role in the speciation of asexually reproducing organisms. It also does not play any major role in the speciation of self-pollinating plants.

Related Articles:

Main Types of Speciation | Evolution | Biology

Speciation is the method of formation of new species. A species can be defined as one or more populations of interbreeding organisms that are reproductively isolated in nature from all other organisms. As natural selection adapts populations occupying different environments, they will diverge into races, subspecies, and finally separate species. When populations no longer interbreed, they are thought to be separate species.

Speciation is of two types:

Type # 1. Allopatric Speciation:

Allopatric speciation is the evolution of species in a population that occupy different geographical areas. Geographic isolation is often the first step in allopatric speciation. Other isolating mechanism may also operate that further restrict reproduction between populations. An example of allopatric speciation is the Darwin's finches. The finches varied from each other mainly in shape and size of beak and colour of the feathers or plumage.

According to Darwin, the species in the South American mainland were the original species from which different forms migrated to different islands of the Galapagos and became adapted to the environmental conditions of these islands. The adapted forms eventually became the new species (Fig. 34).

In the case of the finches, geographical isolation led to the development of reproductive isolation and thereby to the origin of new species.

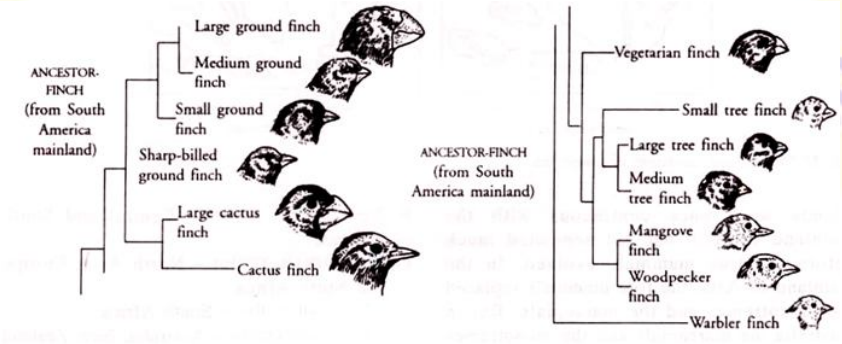


Fig. 34 Divergence of the Galápagos finches from ancestral colonisers from the South American mainland.

Type # 2. Sympatric Speciation:

Speciation within a population that occupies the same geographic environment by either ecological isolation (differing habitats) or by chromosomal aberrations as seen in plants is known as sympatric speciation. Sympatric speciation happens when members of a population develop genetic differences that prevent them from reproducing with the parent type.

Polyploidy in plants and hybridisation are two methods of introducing reproductive isolation. Polyploidy is the phenomenon when organism has more than two sets of chromosomes – 3n, 4n, 5n and so on.

Polyploidy is a mechanism that can lead to the formation of new species very rapidly. Polyploidy does not occur in animals naturally.

This mechanism is best understood in plants, where failure to reduce chromosome number results in polyploid plants that reproduce successfully only with other polyploids. Reproduction with their parent population (the diploids) produces sterile offspring. For example, the wheat variety, Triticum aestivum is a hexaploid that has been developed by polyploidy.

Origin of Species: Modes and Mechanisms

In this article we will discuss about the modes and mechanisms of origin of species.

Modes of Origin of Species:

The main modes of speciation are:

1. Sympatric speciation:

This is the origin of species without geographic isolation. Sympatric species originate by instantaneous development of isolating mechanisms within a deme. Once reproductive isolation is established each population follows its own evolutionary course and forms sympatric species.

2. Allopatric speciation:

This is also known as geographic speciation. Geographically isolated populations are known as allopatric. Such isolation provides the opportunity for each population to evolve along its own lines.

3. Stasipatric speciation:

This is the origin of species through chromosomal rearrangements. An ancestral species gives rise to a number of descendents species through chromosomal rearrangements such as centric fusions, centric fissions, inversions and translocations.

4. Instaneous speciation:

This is also called as cytocatalytic speciation. It is the origination of a single (e.g. alloploid) individual which is reproductively isolated from the species to which its parents belong. It is reproductively and ecologically capable of establishing a new population.

5. Saltational speciation:

This is the origin of species by multiple structural changes of the karyotype.

Mechanism of Origin of Species:

There are two distinct ways in which new species arise from the preexisting one:

1. Splitting of species
2. Transformation of species

1. Splitting of species:

Suppose species A is ancestral. During the course of evolution, it will give rise to species B and specie C.

2. Transformation of species:

In this type of evolution only one species exists at a time. As for example, species A evolves into species B and B into C and so on.

According to Simpson, there are two types of transformations:

(a) Phyletic evolution:

This involves the sustained directional changes in the average characters of a population. This is caused either due to adaptations to shifting environment or due to increasing specializations for a particular environment or improved adaptation in a constant environment This results in the origin of new genera and families.

(b) Quantum evolution:

It involves rapid shift or sudden changes in the organization of a population to a new equilibrium, distinctly different from the ancestral forms and adapted to occupy new conditions. This results in the origin of higher taxonomic groups such as orders and classes. That is, quantum evolution is macro and mega evolution operating above species level.

Glossary of terms

Accession: A distinct, uniquely identified sample of seeds, plants, or other germplasm materials that is maintained as an integral part of a germplasm collection.
Adapatedness: The degree or capacity of an individual to survive in a local environment and to transmit its genotype to the next generation.
Additive gene effect: The effect of an allele expected after it has replaced another allele at a locus. Agrobacterium: A type of soil-inhabiting bacteria that is capable of introducing DNA from plasmids in the bacteria into the genome of plant cells. Often used in the genetic transformation of plants.
Allele: One of several alternate forms (DNA sequences) that resides at the same locus on the chromosome and controls the same phenotype (although with potentially differing effects).
Allogamy: Alternative term for cross-pollination.
Alloploid (or allopolyploid): An individual with somatic cells that contain more than two sets of chromosomes, each of which derives from a different species.
Amino acid: A building block of proteins. Each protein consists of a specific sequence of amino acids (with the sequence of amino acids determined by the sequence of the underlying DNA). There are 20 types of amino acid molecules that make up proteins.
Amphidiploid (or amphiploid): An alloploid with the complete chromosome complements of two diploid species. Aneuploid: An individual with a chromosome number that is not the exact multiple of the basic number for the species.
Antisense: The complementary strand of a coding sequence (gene); often an expressed copy of an antisense sequence is transformed into a cell or organism to shut off the expression of the corresponding gene.
Apomixis: Asexual reproduction in plants through the formation of seeds without fertilization (agamospermy). Asexual reproduction: The reproduction process that does not involve the union of gametes.
Autoploid (or autopolyploid): An individual with more than two complete sets of the basic number of chromosomes for the species.
Average effect of a gene: The change in mean value of the population produced by combining a gene with a random sample of gametes from the original population.
Backcross: A cross of an F1 to either parent used to generate it.
Base collection: A comprehensive collection of germplasm accessions held for the purpose of long-term conservation.
Base pair (bp): Two nitrogenous bases (adenine and thymine or guanine and cytosine) held together by weak bonds. Two strands of DNA are held together in the shape of a double helix by the bonds between base pairs.
Bioinformatics: A broad term to describe applications of computer technology and information science to organize, interpret, and predict biological structure and function. Bioinformatics is usually applied in the context of analyzing DNA sequence data.
Biopharming: The use of genetically transformed crop plants and livestock animals to produce valuable compounds, especially pharmaceuticals. Also called pharming.
Bioremediation: The use of biological organisms to render hazardous wastes non-hazardous or less hazardous.
Biotechnology: A set of biological techniques developed through basic research and now applied to research and product development.
Breeding: The science and art of manipulating the heredity of an organism for a specific purpose.
Breeding line: A genetic group that has been selected and bred for its special combinations of traits.
Breeding value: The mean genotypic value or the progeny of an individual expressed as a deviation from the population mean.

Bt (Bacillus thuringiensis): A naturally occurring bacterium that produces a protein toxic to certain lepidopteran insects.
Callus: A cluster of undifferentiated plant cells that have the capacity to regenerate a whole plant in some species.
Cell: The fundamental level of structural organization in complex organisms. Cells contain a nucleus (with chromosomes) and cytoplasm with the protein synthesis machinery, bounded by a membrane.
Cell culture: A technique for growing cells under laboratory conditions.
Central dogma: The underlying model for describing gene structure and function. It states that genes are transcribed in the nucleus into messenger RNA molecules, which are then translated into proteins on ribosomes.
Certified seed: The progeny or increase from a breeder or foundation seed and approved by a certifying agency.
Chimera: An individual consisting of cells of two or more types.
Chromosome: A condensed structure found in the cell nucleus that contains the genes of that cell.
Clonal propagation: The reproduction of plants through asexual means, such as cuttings, grafts, or tissue culture.
Cloning: Asexually producing multiple copies of genetically identical cells or organisms descended from a common ancestor.
Codon: A triplet of nucleotides in a DNA or RNA molecule that codes for one of the 20 amino acids in proteins, or for a signal to start or stop protein production. Each gene that codes for protein is a series of codons that gives the instructions for building that protein.
Combining ability: The performance of a line with others in a cross.
Complementary: The opposite or "mirror" image of a DNA sequence. A complementary DNA sequence has an A for every T, and a C for every G. Two complementary strands of single-stranded DNA will join to form a double-stranded molecule.
Complementary DNA (cDNA): A single-stranded DNA molecule that is complementary to a specific RNA molecule and synthesized from it. Complementary DNAs are important laboratory tools as DNA probes and for isolating and studying individual genes.
Conserved sequence: A base sequence in a DNA molecule (or an amino acid sequence in a protein) that has remained essentially unchanged throughout evolution.
Crossing over: The breaking during meiosis of one maternal and one paternal chromosome, the exchange of corresponding sections of DNA, and the rejoining of the chromosomes. Cultivar: A product of plant breeding that is released for access to producers.
Deoxyribonucleic acid (DNA): The molecule that encodes genetic information. DNA is a double-stranded molecule held together by weak bonds between base pairs of nucleotides. The four nucleotides in DNA contain the bases: adenine (A), guanine (G), cytosine (C), and thymine (T). In nature, base pairs form only between A and T and between G and C; thus the base sequence of each single strand can be deduced from that of its partner.
Diploid: A full set of genetic material consisting of paired chromosomes, one chromosome from each parental set. DNA chip: A high density array of short DNA molecules bound to a solid surface for use in probing a biological sample to determine gene expression, marker pattern, or nucleotide sequence of DNA/RNA. See also Microarray.
DNA probe: A single-stranded DNA molecule used in laboratory experiments to detect the presence of a complementary sequence among a mixture of other singlestranded DNA molecules. Also called gene probe.

DNA profile: The distinctive pattern of DNA restriction fragments or PCR products that can be used to identify, with great certainty, any person, biological sample from a person, or organism from the environment.

DNA replication: The use of existing DNA as a template for the synthesis of new DNA strands. In humans and other eukaryotes, replication occurs in the cell nucleus. DNA sequencing: Determining the order of nucleotides in a specific

DNA molecule. Domestication: The process of bringing wild plants under cultivation to produce crops under the supervision of humans.

Dominant: A phenotype that is expressed in an organism whose genotype may be either homozygous or heterozygous for the corresponding allele.

Double helix: The shape that two linear strands of DNA assume when bonded together. Doubled haploid: An individual that is produced by doubling its gametic (n) chromosome number into 2n.

Electrophoresis: A method of separating substances, such as DNA fragments, by using an electric field to make them move through a "gel" at rates that correspond to their electric charge and size.

Embryo rescue: The removal and culture of an immature embryo to produce a plant, often following a wide cross.

Enhancement: The process of improving a germplasm accession by breeding while retaining the important genetic contributions of the accession.

Enzyme: A protein that acts as a catalyst, speeding the rate at which a biochemical reaction proceeds but not altering the direction or nature of the reaction. GLOSSARY OF TERMS 727

Epistasis: The interaction of genes at different loci; the situation in which one gene affects the expression of another.

Eukaryote: Cell or organism with a membrane-bound, structurally discrete nucleus and other well-developed subcellular compartments.

Functional genomics: The field of study that attempts to determine the function of all genes (and gene products), largely based on knowing the entire DNA sequence of an organism.

Gamete: Mature male or female reproductive cell (sperm or ovum) with a haploid set of chromosomes. **Gene**: The fundamental unit of heredity; a bundle of information for a specific biological structure or function.

Gene cloning: Isolating a gene and making many copies of it by inserting the DNA sequence into a vector, then into a cell, and allowing the cell to reproduce and make many copies of the gene.

Gene expression: The process in which a cell produces the protein, and thus the characteristic that is specified by a gene's nucleotide sequence.

Gene library: A collection of DNA fragments (carried on vector molecules) that, taken together, represents the total DNA of a certain cell type or organism.

Gene regulation: The process of controlling the synthesis or suppression of gene products in specific cells or tissues.

Gene splicing: Joining pieces of DNA from different sources using recombinant DNA technology.

Genetic code: The language in which DNA's instructions are written. The code consists of triplets of nucleotides (codons), with each triplet corresponding to one amino acid in a protein structure or to a signal to start or stop protein production.

Genetic engineering: The manipulation of genes, composed of DNA, to create heritable changes in biological organisms and products that are useful to people, living things, or the environment.

Genetic erosion: The loss of genetic diversity caused by either natural or man-made processes.

Genetic marker: A genetic factor that can be identified and thus acts to determine the presence of genes or traits linked with it but not easily identified.

Genetic stocks: Accessions that typically possess one or more special genetic traits that make them of interest for research.
Genetic vulnerability: The condition that results when a crop or a plant species is genetically and uniformly susceptible to a pest, pathogen, or environmental hazard.
Genetically modified (GM) organism: An organism whose genetic makeup has been changed by any method, including natural processes, genetic engineering, cloning, mutagenesis, or others.
Genetics: Study of the patterns of inheritance of specific traits.
Genome: The complete set of chromosomes found in each cell nucleus of an individual. Genomics: The field of study that seeks to understand the structure and function of all genes in an organism based on knowing the organism's entire DNA sequence, with an extensive reliance on powerful computer technologies.
Genotype: The specific combination of alleles present at a single locus in the genome.
Germ cells: The sex cell(s) of an organism (sperm or egg, pollen or ovum). They differ from other cells (somatic) in that they contain only half the usual number of chromosomes. Germ cells fuse during fertilization to begin the next generation.
Germplasm: The sum total of all hereditary material in a single (interbreeding) species.
Green Revolution: An aggressive effort between 1950 and 1975 where agricultural scientists applied modern principles of genetics and breeding to improve crops grown primarily in less developed countries.
Haploid: A cell or organism with a single genome.
Heterozygosity: The presence of different alleles at one or more loci on homologous chromosomes.
Heterozygous: Situation where the two alleles at a specific genetic locus are not the same.
Homologous: Stretches of DNA that are very similar in sequence, so similar that they tend to stick together in hybridization experiments. Homologous can also be used to indicate related genes in separate organisms controlling similar phenotypes.
Homologous chromosomes: A pair of chromosomes containing the same linear gene sequences, each derived from one parent.
Homozygous: Situation where the two alleles at a specific genetic locus are identical to one another.
Hybrid: The progeny of a cross between two different species, races, cultivars, or breeding lines.
Hybridization (or crossing): The process of pollen transfer from the anther of the flower of one plant to the stigma of the flower of a different plant for the purpose of gene transfer to produce an offspring (hybrid) with a mixed parental genotype.
Hybridization: Bringing complementary single strands of nucleic acids together so that they stick and form a double strand. Hybridization is used in conjunction with DNA and RNA probes to detect the presence or absence of specific complementary nucleic acid sequences.
In vitro: Performed in a test tube or other laboratory apparatus. In vivo: In the living organism. Inbreeding: The breeding of individuals that are related.
Isoenzyme (isozyme): Different chemical forms of the same enzyme that can generally be distinguished from one another by electrophoresis.
Landrace: A population of plants, typically genetically heterogeneous, commonly developed in traditional agriculture from many years of farmer-directed selection, and which is specifically adapted to local conditions.
Linkage: The proximity of two or more markers (e.g., genes, RFLP markers) on a chromosome.
Linkage map: A map of the relative positions of genetic loci on a chromosome, determined on the basis of how often the loci are inherited together. Distance is measured in centimorgans (cM).
Locus: The position on a chromosome where the gene for a particular trait resides; a locus may be occupied by any one of several alleles (variants) for a given gene.

Meiosis: The process of two consecutive cell divisions in the diploid progenitors of sex cells. Meiosis results in four rather than two daughter cells, each with a haploid set of chromosomes.
Messenger RNA (mRNA): The ribonucleic acid molecule that transmits genetic information from the nucleus to the cytoplasm, where it directs protein synthesis.
Microarray: A large set of cloned DNA molecules spotted onto a solid matrix (such as a microscope slide) for use in probing a biological sample to determine the gene expression, marker pattern, or nucleotide sequence of DNA/RNA.
Microsatellite: A repeated motif of nucleotides, usually only two or three bases in length, where the number of repeats frequently differs between different members of a species.
Mitosis: The process of nuclear division in cells which produces daughter cells that are genetically identical to each other and to the parent cell.
Molecular marker: An identifiable physical location on a chromosome (e.g., restriction enzyme cutting site, gene) whose inheritance can be monitored.
Multiline: A mixture of isolines, each of which is different for a single gene conditioning different forms of the same trait. Mutagen: A substance that induces mutations.
Mutation: A permanent change in the genetic material involving either a physical alteration in the chromosome or a biochemical change in the underlying DNA molecule.
Nitrogenous base: A nitrogen-containing molecule having the chemical properties of a base. Nucleic acid: A large molecule composed of nucleotide subunits.
Nucleotide: A subunit of DNA or RNA consisting of a nitrogenous base (adenine, guanine, thymine, or cytosine in DNA).
Nucleus: Membrane-bound structure in the cell that contains the chromosomes (genetic material). The nucleus divides whenever the cell divides.
Pathogen: A specific biological causative agent of disease in plants or animals. Pedigree: A record of the ancestry of an individual of family.
Phenotype: A biological characteristic or trait possessed by an organism that results from the expression of a specific gene. Physical map: A map of the locations of identifiable landmarks on DNA (e.g., restriction enzyme cutting sites, genes), regardless of inheritance. Distance is measured in base pairs.
Plasmid: A small, self-replicating molecule of DNA that is separate from the main chromosome. Because plasmids are easily moved from cell to cell or to the test tube, scientists often cleave them with restriction enzymes and insert foreign DNA, and then transfer the recombinant DNA plasmid molecule (as a vector) into other cells.
Pollination: The transfer of pollen from the anthers to the stigma of a flower. Polymerase chain reaction (PCR): A technique to amplify a specific DNA sequence in vitro using a DNA replicating enzyme, specific oligonucleotide primers, and repeated cycles of heating and cooling. PCR often amplifies the starting material many thousands or millions of times.
Polymorphism: The simultaneous occurrence of two or more distinct forms in a population in a frequency that cannot be accounted for by the balance of mutation and selection.
Polyploidy: An individual with more than two sets of chromosomes characteristic of the species. Primer: Short pre-existing polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase.
Probe: Single-stranded DNA or RNA molecules of a specific base sequence, labeled either radioactively or immunologically, that are used to detect the complementary base sequence by hybridization.
Prokaryotes: Organisms whose genetic material is not enclosed by a nucleus. Promoter: A DNA sequence preceding a gene that contains regulatory sequences controlling the rate of RNA

transcription of that gene. In effect, promoters control when and in which cells a given gene will be expressed. **Protein**: A molecule composed of amino acids arranged in a special order determined by the genetic code. Proteins are required for the structure and function of all living organisms.

Pure line: The progeny of a single homozygous individual produced by repeated selfing. Recessive: A phenotype that is expressed in organisms only if it is homozygous for the corresponding allele.

Recombinant DNA: A hybrid DNA molecule produced in the laboratory by joining pieces of DNA from different sources.

Recombinant DNA technologies: Procedures used to join together DNA segments in a cell-free system (an environment outside a cell or organism). Under appropriate conditions, a recombinant DNA molecule can enter a cell and replicate there, either autonomously or after it has become integrated into a cellular chromosome.

Recombination: The process by which progeny derive a combination of genes different from that of either parent. In higher organisms, this can occur by crossing over.

Recurrent selection: A breeding method whereby plants are repeatedly selected and intercrossed to increase the frequency of favorable alleles.

Regeneration: The process of growing an entire plant from a single cell or group of cells.

Reporter gene: A gene sequence that is easily observed when it is expressed in a given tissue or at a certain stage of development.

Restriction enzyme: An enzyme that recognizes a specific nucleotide base sequence (usually four to six base pairs in length) in a double-stranded DNA molecule and cuts both strands of the DNA molecule at every place where this sequence occurs.

Restriction fragment length polymorphism (RFLP): The presence of two or more variants in the size of DNA fragments produced by a restriction enzyme. These different sized fragments result from an inherited variation in the presence of a restriction enzyme's target sequence. RFLPs are used for gene mapping and DNA profiling.

Ribonucleic acid (RNA): A molecule that translates the instructions encoded in DNA to build proteins. **Ribosomes**: Small cellular components composed of specialized ribosomal RNA and protein; site of protein synthesis.

Selection (field): The process of discriminating among genetic variability to advance a fraction to the next generation or breeding cycle.

Selection (in vitro): A method to retain specific cells (or clones of cells) expressing a specific trait, such as antibiotic or herbicide resistance, while killing off all other cells that do not express that trait.

Somatic cell: Cells in the body that are not involved in sexual reproduction (that is, not germ cells).

Southern blotting: Transfer by absorption of DNA fragments separated in electrophoretic gels to membrane filters for the detection of specific base sequences by radiolabeled complementary probes.

Tissue culture: Growing cells, tissues, or tissue fragments (from complex, multicellular organisms) on a nutrient medium in a dish, test tube, or flask.

Totipotent: A cell that is capable of regenerating an entire adult organism by itself. Trait: A distinguishing characteristic or quality of an organism.

Transcription: The transfer of information from specific sequences in a DNA molecule to produce new strands of messenger RNA, which then carry this information from the nucleus to the cytoplasm (where the messenger RNA is translated into protein).

Transformation: Introduction of an exogenous DNA molecule into a cell, causing it to acquire a new phenotype (trait).

Transgenic: An organism that has been transformed with a foreign DNA sequence.

Translation: Synthesis of protein using information contained in a messenger RNA molecule.

Vector: A type of DNA molecule, usually a plasmid or virus, that is used to move recombinant DNA molecules from one cell to another.

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