NATIONAL OPEN UNIVERSITY OF NIGERIA

FACULTY OF SCIENCES

COURSE CODE: BIO 309

COURSE TITLE: PLANT BREEDING

COURSE GUIDE

BIO309

Plant Breeding

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Published By:
National Open University of Nigeria First

Printed 2012

Reviewed 2020

ISBN: 978-058-023-9

Course Guide

Introduction

You are welcome to another course in your 300 level. BIO 309 is a 1 unit course. Plant breeding is the deliberate manipulation of the characteristics in plants giving rise to new varieties with a set of desirable qualities. Plant breeding can be accomplished through many different techniques ranging from simply selecting plants with desirable characteristics for propagation, to more complex molecular techniques.
In this course you will be given a generalized view of the concept of plant breeding and the basic things to know about plant breeding.
Being a single credit unit course (1 unit course). It is a not bulky and studying will be much easier

What You Will Learn from This Course

This course contains 9 units which cover various topics running through the definition of plant breeding, breeding methods and major farm and domestic plants and the practices used to sustain desired qualities.

Course Competencies

This course introduces you to the general concepts of plant breeding and other related factors

Course Objectives

The course sets an overall objective which must be achieved. In addition to the course objectives, each of the units has its own specific objectives. You are advised to read properly the specific objectives for each unit at the beginning of that unit. This will help you to ensure that you achieve the objectives. As you go through each unit, you should from time to time go back to these objectives to ascertain the level at which you have progressed.

By the time you have finished going through this course, you should be able to :

- Discuss the importance of plant breeding
- Discuss the cytological principles of breeding
- Explain the meaning of heterosis
- Analyse inbreeding and its consequences
- Incompatibility mechanisms
- Explain the meaning of sterility
- Evaluate the various breeding methods
- Disease and pest resistance and their inheritance
- Evaluate major farm and domestic plants and the practices used to sustain

desired qualities

Working through this Course

It is good for you to spend time studying this material. The course will be made available to you in print (hard copy), CD and online on the university website and also on your course page for your convenience. It will help you if you to do all that has been stipulated in the course units, read the recommended reference textbooks and do all the unit(s) self- assessment exercise (s) and at some points, you are required to submit your assignment (TMAs) for assessment purpose. You should therefore avail yourself of the opportunity of being present during the facilitation sessions so that you would be able to relate with your colleagues and facilitator.

Study Units

This course is divided into 9 units as follows:

1. Importance of plant breeding
2. Cytological principles of breeding
3. Heterosis
4. Inbreeding and its consequences
5. Incompatibility mechanisms
6. Sterility
7. Breeding methods
8. Disease and pest resistance and their inheritance
9. Major farm and domestic plants and the practices used to sustain desired qualities

Presentation Schedule

Presentation schedule for this course will be uploaded on the online course page.

Assessment

You are required to do your and submit your assignment (TMAs) online for assessment purpose. The questions will be uploaded on your course page. This will account for 30% of your score in the course. There will be an end of semester examination which will account for 70% of your total score in the course.

References and Further Readings

You would be required to do all that has been stipulated in the course: study the course units and read the recommended reference textbooks in each unit of the course material.

1. Chahal, G.S and Gosal, S.S., 2002. Principles and procedures of Plant Breeding, Alpha Science International, United Kingdom.
2. Kwon-Ndung, E.H. 2008. Genetics for degree students. Afaku Publishers, Abuja.
3. Holsinger, K.E., 2000. Reproductive systems and evolution in vascular plants. PNAS. June 20, vol. 97, no. 13: 7037-7042.
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5. KWV, South Africa. (2005). Setting new global standards for vine plant improvement. Vititec.
6. Franklin, F. C. H., M. J. Lawrence, and V. E. Franklin-Tong (1995). "Cell and molecular biology of self-incompatibility in flowering plants". *Int. Rev. Cytol.*

UNIT 1: IMPORTANCE OF PLANT BREEDING

1.0. INTRODUCTION

Plant breeding is the art and science of changing the genetics of plants in order to produce desired characteristics. Plant 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 centres.

2.0. Objectives

- At the end of this unit, you should be able to
- Trace the history of plant breeding
- Discuss the importance of plant breeding
- Define plant breeding terms
- Differentiate between the conventional and the modern plant breeding methods and
- Select plant breeding applications

3.0. Main Body

3.1 History and developments of Plant Breeding

Intra-specific hybridization within a plant species was demonstrated by Charles Darwin and Gregor Mendel, and was further developed by geneticists and plant breeders. In the United Kingdom in the 1880s, it was the pioneering work of Gartons Agricultural Plant Breeders. In the early 20th century, plant breeders realized that Mendel's findings on the non-random nature of inheritance could be applied to seedling populations produced through deliberate pollinations to predict the frequencies of different types.

From 1904 to World War II in Italy NazarenoStrampelli created a number of wheat hybrids. His work allowed Italy to increase hugely crop production during the so called "Battle for Grain" (1925–1940) and some varieties was exported in foreign countries, as Argentina, Mexico, China and others. After the war, the work of Strampelli was quickly forgotten, but thanks to the hybrids he created, Norman Borlaug was able to move the very first steps of the Green Revolution.

In 1908, George Harrison Shull described heterosis, also known as hybrid vigor. Heterosis describes the tendency of the progeny of a specific cross to outperform both parents. The detection of the usefulness of heterosis for plant breeding has led to the development of inbred lines that reveal a heterotic yield advantage when they

are crossed. Maize was the first species where heterosis was widely used to produce hybrids.

By the 1920s, statistical methods were developed to analyze gene action and distinguish heritable variation from variation caused by environment. In 1933, another important breeding technique, cytoplasmic male sterility (CMS), developed in maize, was described by Marcus Morton Rhoades. CMS is a maternally inherited trait that makes the plant produce sterile pollen. This enables the production of hybrids without the need for labour intensive detasseling.

These early breeding techniques resulted in large yield increase in the United States in the early 20th century. Similar yield increases were not produced elsewhere until after World War II, the Green Revolution increased crop production in the developing world in the 1960s.

After the World War II, a number of techniques were developed that allowed plant breeders to hybridize distantly related species, and artificially induce genetic diversity.

When distantly related species are crossed, plant breeders make use of a number of plant tissue culture techniques to produce progeny from otherwise fruitless mating. Interspecific and intergeneric hybrids are produced from a cross of related species or genera that do not normally sexually reproduce with each other. These crosses are referred to as *Wide crosses*. For example, the cereal triticale is a wheat and rye hybrid. The cells in the plants derived from the first generation created from the cross contained an uneven number of chromosomes and as result was sterile. The cell division inhibitor colchicine was used to double the number of chromosomes in the cell and thus allow the production of a fertile line.

Failure to produce a hybrid may be due to pre- or post-fertilization incompatibility. If fertilization is possible between two species or genera, the hybrid embryo may abort before maturation. If this does occur the embryo resulting from an interspecific or intergeneric cross can sometimes be rescued and cultured to produce a whole plant. Such a method is referred to as Embryo Rescue. This technique has been used to produce new rice for Africa (NERICA), an interspecific cross of Asian rice *(Oryzasativa)* and African rice *(Oryzaglaberrima)*.

Hybrids may also be produced by a technique called protoplast fusion. In this case protoplasts are fused, usually in an electric field. Viable recombinants can be regenerated in culture.

Chemical mutagens like Ethyl Methyl Sulphonate and Di Methyl Sulphonate, radiation and transposons are used to generate mutants with desirable traits to be bred with other cultivars in a process called Mutation Breeding. Classical plant breeders also generate genetic diversity within a species by exploiting a process called somaclonal variation, which occurs in plants produced from tissue culture, particularly plants derived from callus. Induced polyploidy, and the addition or removal of chromosomes using a technique called chromosome engineering may

also be used.

When a desirable trait has been bred into a species, a number of crosses to the favored parent are made to make the new plant as similar to the favored parent as possible. Returning to the example of the mildew resistant maize being crossed with a high-yielding but susceptible maize, to make the mildew resistant progeny of the cross most like the high-yielding parent, the progeny will be crossed back to that parent for several generations. This process removes most of the genetic contribution of the mildew resistant parent. Conventional or classical breeding is therefore a cyclical process.

With conventional breeding techniques, the breeder does not know exactly what genes have been introduced to the new cultivars. Some scientists therefore argue that plants produced by these methods should undergo the same safety testing regime as genetically modified plants. There have been instances where plants bred using conventional techniques have been unsuitable for human consumption, for example the poison solanine was unintentionally increased to unacceptable levels in certain varieties of potato through plant breeding. New potato varieties are often screened for solanine levels before reaching the marketplace

3.2 Importance of Plant breeding

It is believed 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 and that have uniformity in maturity time and other desirable qualities.

Plant breeding in certain situations may lead to the domestication of wild plants. Domestication of plants is an artificial selection process conducted by humans to produce plants that have more desirable traits than wild plants, and which renders them dependent on artificial (usually enhanced) environments for their continued existence. The practice is estimated to date back to about 9,000-11,000 years. Many crops in present day cultivation are the result of domestication in ancient times, about 5,000 years ago. In the past, domestication took a minimum of about 1,000 years and a maximum of about 7,000 years. Today, all of our principal food crops are products of domesticated varieties. Almost all the domesticated plants used today for food and agriculture were domesticated in centres of origin that have been identified as centres that host a great diversity of closely related crop wild plants or relatives, which today can also be used for improving modern cultivars by plant breeding.

A plant whose origin or selection is due primarily to intentional human activity is called a cultigen, and a cultivated crop species that has evolved from wild populations due to selective pressures from traditional farmers is called a landrace. Landraces, which can be the result of natural forces or domestication, are plants (or animals) that are ideally suited to a particular region or environment. An example are the landraces of rice, *Oryzasativa* subspecies *indica*, which was developed in South

Asia, and *Oryzasativa* subspecies *japonica*, which was developed in China and subspecies *glaberrima* which is the African rice.

3.3 Conventional plant breeding

Conventional or Classical plant breeding uses deliberate interbreeding (crossing) of closely or distantly related individuals to produce new crop varieties or lines with desirable properties. Plants are crossbred to introduce traits/genes from one variety or line into a new genetic background. For example, a mildew-resistant maize *Zea mays* may be crossed with a high-yielding but susceptible maize, the goal of the cross being to introduce mildew resistance without losing the high-yield characteristics. Progeny from the cross would then be crossed with the high-yielding parent to ensure that the progeny were most like the high-yielding parent in a process called backcrossing. The progeny from that cross would then be tested for yield and mildew resistance and high-yielding resistant plants would be further developed. Plants may also be crossed with themselves to produce inbred varieties for breeding.

Classical breeding relies largely on homologous recombination between chromosomes to generate genetic diversity. The classical plant breeder may also makes use of a number of *in vitro* techniques such as protoplast fusion, embryo rescue or mutagenesis to generate diversity and produce hybrid plants that would not exist in nature.

Traits that breeders have tried to incorporate into crop plants in the last 100 years include:

i Increased quality and yield of the crop

ii Increased tolerance of environmental pressures (salinity, extreme temperature, drought)

iii Resistance to viruses, fungi and bacteria

iv Increased tolerance to insect pests

v Increased tolerance of herbicides

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3.4 Modern plant breeding

Modern plant breeding may use techniques of molecular biology to select, or in the case of genetic modification, to insert, desirable traits into plants.

Modern facilities in molecular biology has converted classical plant breeding to molecular plant breeding

3.5 Marker assisted selection

Sometimes many different genes can influence a desirable trait in plant breeding. The use of tools such as molecular markers or DNA fingerprinting can map thousands of genes. This allows plant breeders to screen large populations of plants for those that possess the trait of interest. The screening is based on the presence or absence of a certain gene as determined by laboratory procedures, rather than on the visual identification of the expressed trait in the plant.

3.6 Reverse Breeding and Doubled Haploids (DH)

A method for efficiently producing **homozygous** plants from heterozygous starting plants which has all desirable traits. This starting plant is induced to produce doubled haploid from haploid cells, and later on creating homozygous/doubled haploid plants from those cells. While in natural offspring genetic recombination occurs and traits can be unlinked from each other, in doubled haploid cells and in the resulting DH plants recombination is no longer an issue. There, a recombination between two corresponding chromosomes does not lead to un-linkage of alleles or traits, since it just leads to recombination with its identical copy. Thus, traits on one chromosome stay linked. Selecting those offspring having the desired set of chromosomes and crossing them will result in a final F1 hybrid plant, having exactly the same set of chromosomes, genes and traits as the starting hybrid plant. The homozygous parental lines can reconstitute the original heterozygous plant by crossing, if desired even in a large quantity. An individual heterozygous plant can be converted into a heterozygous variety (F1 hybrid) without the necessity of vegetative propagation but as the result of the cross of two homozygous/doubled haploid lines derived from the originally selected plant.

IN-TEXT QUESTION

Give one contribution of George Harrison Shull to plant breeding

Answer: *He described heterosis in 1908.*

3.7 Genetic modification

Genetic modification of plants is achieved by adding a specific gene or genes to a plant, or by knocking down a gene with RNAi, to produce a desirable phenotype. The plants resulting from adding a gene are often referred to as transgenic plants. If for genetic modification genes of the species or of a crossable plant are used under control of their native promoter, then they are called cisgenic plants. Genetic modification can produce a plant with the desired trait or traits faster than classical breeding because the majority of the plant's genome is not altered.

To genetically modify a plant, a genetic construct must be designed so that the gene to be added or removed will be expressed by the plant. To do this, a promoter to drive transcription and a termination sequence to stop transcription of the new gene, and the gene or genes of interest must be introduced to the plant. A marker for the selection of transformed plants is also included. In the laboratory, antibiotic resistance is a commonly used marker: Plants that have been successfully transformed will grow on media containing antibiotics; plants that have not been transformed will die. In some instances markers for selection are removed by backcrossing with the parent plant prior to commercial release.

The construct can be inserted in the plant genome by genetic recombination using the bacteria *Agro bacteriumtumefaciens* or *A. rhizogenes*, or by direct methods like the gene gun or microinjection. Using plant viruses to insert genetic constructs into plants is also a possibility, but the technique is limited by the host range of the virus. For example, Cassava mosaic virus (CMV) only infects cassava and related species. Another limitation of viral vectors is that the virus is not usually passed on to the progeny, so every plant has to be inoculated.

The majority of commercially released transgenic plants are currently limited to plants that have introduced resistance to insectpests and herbicides. Insect resistance is achieved through incorporation of a gene from *Bacillus thuringiensis* (Bt) that encodes a protein that is toxic to some insects. For example, the cotton bollworm, a common cotton pest, feeds on Bt cotton it will ingest the toxin and die. Herbicides usually work by binding to certain plant enzymes and inhibiting their action. The enzymes that the herbicide inhibits are known as the herbicides *target site*. Herbicide resistance can be engineered into crops by expressing a version of *target site* protein that is not inhibited by the herbicide. This is the method used to produce glyphosate resistant crop plants. Genetic modification of plants that can produce pharmaceuticals (and industrial chemicals), sometimes called *pharmacrops*, is a rather radical new area of plant breeding.

3.8 Issues and concerns on modern plant breeding

Modern plant breeding, whether classical or through genetic engineering, comes with issues of concern, particularly with regard to food crops. The question of whether breeding can have a negative effect on nutritional value is central in this respect.

Although relatively little direct research in this area has been done, there are scientific indications that, by favoring certain aspects of a plant's development, other aspects may be retarded. A study published in the *Journal of the American College of Nutrition* in 2004, entitled *Changes in USDA Food Composition Data for 43 Garden Crops, 1950 to 1999*, compared nutritional analysis of vegetables done in 1950 and in 1999, and found substantial decreases in six of 13 nutrients measured, including 6% of protein and 38% of riboflavin. Reductions in calcium, phosphorus, iron and ascorbic acid were also found. The study, conducted at the Biochemical Institute, University of Texas at Austin, concluded in summary: *"We suggest that any real declines are generally most easily explained by changes in cultivated varieties between 1950 and 1999, in which there may be trade-offs between yield and nutrient content."*

The debate surrounding genetically modified food during the 1990s peaked in early 2000 in terms of media coverage and risk perception, and continues today - for example, "*Germany has thrown its weight behind a growing European mutiny over genetically modified crops by banning the planting of a widely grown pest-resistant corn variety.*".The debate encompasses the ecological impact of genetically modified plants, the safety of genetically modified food and concepts used for safety evaluation like substantial equivalence. Such concerns are not new to plant breeding. Most countries have regulatory processes in place to help ensure that new crop varieties entering the marketplace are both safe and meet farmers' needs. Examples include variety registration, seed schemes, regulatory authorizations for GM plants, etc.

Plant breeders' rights are also a major and controversial issue. Today, production of new varieties is dominated by commercial plant breeders, who seek to protect their work and collect royalties through national and international agreements based in intellectual property rights. The range of related issues is complex. In the simplest terms, critics of the increasingly restrictive regulations argue that, through a combination of technical and economic pressures, commercial breeders are reducing biodiversity and significantly constraining individuals (such as farmers) from developing and trading seed on a regional level. Efforts to strengthen breeders' rights, for example, by lengthening periods of variety protection, are on-going.

When new plant breeds or cultivars are bred, they must be maintained and propagated. Some plants are propagated by asexual means while others are propagated by seeds. Seed propagated cultivars require specific control over seed source and production procedures to maintain the integrity of the plant breeds

results. Isolation is necessary to prevent cross contamination with related plants or the mixing of seeds after harvesting. Isolation is normally accomplished by planting distance but in certain crops, plants are enclosed in greenhouses or cages (most commonly used when producing F1 hybrids.)

3.9 Steps of Plant Breeding

The following are the major activities of plant breeding;

i Creation of variation

ii Selection
iii Evaluation
iv Release
v Multiplication
vi Distribution of the new variety

3.10 Participatory Plant Breeding

The development of agricultural science, with phenomenon like the Green Revolution arising, have left millions of farmers in developing countries, most of whom operate small farms under unstable and difficult growing conditions, in a precarious situation. The adoption of new plant varieties by this group has been hampered by the constraints of poverty and the international policies promoting an industrialized model of agriculture. Their response has been the creation of a novel and promising set of research methods collectively known as participatory plant breeding. Participatory means that farmers are more involved in the breeding process and breeding goals are defined by farmers instead of international seed companies with their large-scale breeding programs. Farmers' groups and NGOs, for example, may wish to affirm local people's rights over genetic resources produce seeds themselves, build farmers' technical expertise, or develop new products for niche markets, like organically grown food.

4.0 Summary

i) Plant breeding ensure food security by developing new varieties that are higher-yielding, resistant to pests and diseases,
ii) Drought-resistant or regionally adapted to different environments and growing conditions can be established through
iii) With plant breeding crops uniformity in maturity time and other desirable qualities can be selected.
iv) Plant breeding in certain situations may lead to the domestication of wild plants.

5.0 Conclusion

Plant breeding can increasedquality and yield of the crops through the following:i) Increased tolerance of environmental pressures (salinity, extreme temperature, drought)

ii) Resistance to viruses, fungi and bacteria

iii) Increased tolerance to insect pests

iv) Increased tolerance of herbicides

6.0 Self-assessment Assignments

a Why is plant breeding important?

b Explain the role of GMOs in modern plant breeding

c Why is participatory plant breeding important?

7.0 Tutor marked assignment:

a What are the objectives of plant breeding?

b Differentiate between traditional and modern plant breeding.

8.0 References

7. Chahal, G.S and Gosal, S.S., 2002. Principles and procedures of Plant Breeding, Alpha Science International, United Kingdom.
8. Kwon-Ndung, E.H. 2008. Genetics for degree students. Afaku Publishers, Abuja.
9. Holsinger, K.E., 2000. Reproductive systems and evolution in vascular plants. PNAS. June 20, vol. 97, no. 13: 7037-7042.
10. Kohli, M.M. and Francis, M., 2000. Application of biotechnologies to wheat breeding. Proceedings of a conference at La Estanzuela, Uruguay, November 19–20, 1998. Montevideo, Uruguay: CIMMYT.
11. KWV, South Africa. (2005). Setting new global standards for vine plant improvement. Vititec.
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Unit 2 Cytological principles of plant breeding

1.0 Introduction

E. Strasburger in 1875 first discovered thread-like structures which appeared during cell division. These thread like structures were called chromosomes due to their affinity for basic dyes. The term chromosome is derived from two Greek words; chrom = colour, soma=body. This term was first used by Waldeyer in 1888.

2.0 Objectives

At the end of this unit, you should be able to

- Discuss the cytological principles of plant breeding
- Discuss the chromosomes as the basis hereditary
- Describe the structure, composition
- Explain functions of chromosomes in relation to plant breeding

2.1. Chromosomes

Of all components of cell, the chromosomes have been studied most extensively and perhaps more is known about them than any other cell organelle. The chromosome has greater constancy than any other cell component and it maintains it special qualities from one cell generation to another.
Chromosomes contributed to the division of cells and they are of prime importance as they carry the genes which are the hereditary material.

2.1.1. Chromosome number:

The number of chromosomes in a given species is generally constant. All the members of the species ordinarily have definite and generally a constant somatic and gametic chromosome number. Somatic chromosome number is the number of chromosomes found in somatic cells of a species and is represented by 2n. Generally somatic cells contain two copies of each chromosome except the sex chromosomes. Both the copies are ordinarily identical in morphology, gene content and gene order and hence known as homologous chromosomes. Gametic chromosome number is exactly half of somatic chromosome number and is represented by n. it denotes the number of chromosomes found in gametes of a species. The number of chromosomes varies greatly from 2n = 4 (n = 2) in *Haplopappusgracilis*(Compositae) to 2n = > 1200 in some Pteridophytes.

Name of the organism	Chromosome number (2n)
Rice	24
Tomato	24
Wheat	42
Onion	16
Maize	20
Garden pea	14
Cotton	52
Humans	46
Drosophila	8

2.1.2. Chromosome Size:

The size of the chromosome shows a remarkable variation depending upon the stage of cell division. The chromosomes are the longest and thinnest during interphase (resting stage) and hence not visible under light microscope. Chromosomes are the smallest and thickest during mitotic metaphase. In general, plants have longer chromosomes than animals and species having lower chromosome number have longer chromosomes than those having a higher chromosome number. Among plants, dicots in general have shorter and higher number of chromosomes than monocots. Among the higher plants, the longest mitotic chromosomes are those of *Trillium* spp., which may reach 32 μ in size. In most fungi all chromosomes are extremely minute. Chromosome size is not proportional to the number of genes present on the chromosome.

IN-TEXT QUESTION
How many chromosomes are present in a human ovum
***Answer**: 23*

2.1.3. Chromosome Morphology:

The outer covering or sheath of a chromosome is known as pellicle, which encloses the matrix. Within the matrix lies the chromatin. Flemming introduced the term chromatin in 1879. The term chromatin refers to the Feulgen positive materials observed in interphase nucleus and later during nuclear division. Chromatin readily stains with basic dyes especially Basic Fuchsin, which is specific for DNA which in turn is a major constituent of chromosomes. The chromosome morphology changes during cell division and mitotic metaphase is the most suitable stage for studies on chromosome morphology. In mitotic metaphase chromosomes, the following structural features can be seen under the light microscope.

I. Chromatid: Each metaphase chromosome appears to be longitudinally divided into two identical parts each of which is called chromatid. Both the chromatids of a chromosome appear to be joined together at a point known as centromere. The two chromatids of chromosome separate from each other during mitotic anaphase (and during anaphase II of meiosis) and move towards opposite poles. Since the two chromatids making up a chromosome are produced through replication of a single chromatid during synthesis (S)

phase of interphase, they are referred to as sister chromatids. In contrast, the chromatids of homologous chromosomes are known as non-sister chromatids.

II. Centromere: Centromere and telomere are the most stable parts of chromosomes. The region where two sister chromatids appear to be joined during mitotic metaphase is known as centromere. It generally appears as constriction and hence called primary constriction. Centromere is a localized and easily detectable morphological region of the chromosomes which helps in the movement of the chromosomes to opposite poles during anaphase of cell division. The centromere divides the chromosomes into two transverse parts called arms. The centromere consists of two disk shaped bodies called kinetochores. The kinetochores do not form part of the chromatid but lie one on each side of the chromosome such that each chromatid is having its own kinetochore. One kinetochore is attached to the spindle fibres towards one pole and the other similarly towards the other pole. Depending on position of the centromeres, chromosomes can be grouped as:

a) Metacentric: Centromere is located exactly at the centre of chromosome, i.e. both arms are equal in size. Such chromosomes assume 'V' shape at anaphase.

b) Submetacentric: The centromere is located on one side of the centre point such that one arm is longer than the other. These chromosomes become 'J' or 'L' shaped at anaphase.

c) Acrocentric: Centromere is located close to one end of the chromosome and thus giving a very chort arm and a very long arm. These chromosomes acquire ' J' shape or rod shape during anaphase.

d) Telocentric: Centromere is located at one end of the chromosome so that the chromosome has only one arm. These chromosomes are 'I" shaped or rod shaped. Normally chromosomes are monocentric having one centromere each. Acentric (without centromere) and dicentric (with two centromeres) chromosomes, if produced due to chromosomal aberrations, cannot orient properly on the equatorial plate and lag behind other chromosomes during anaphase movements. In certain organisms, centromere does not occupy a specific position, but is diffused trough out the body of chromosome. Such chromosomes, which do not have a localized centromere, are found in *Luzula* spp. and insects belonging to the order *Hemiptera*.

3. Telomere: The two ends of chromosomes are known as telomeres. They are highly stable and do not fuse or unite with telomeres of other chromosomes due to polarity effect. Any broken end of a chromosome is unstable and can join with a piece of any other chromosome. But the telomeres impart stability to the chromosome, which retains its identity and individuality through cell cycle and for many cell generations.

4. Secondary constriction: The constricted or narrow region other than that of

centromere is called secondary constriction and the chromosomes having secondary constriction are known as satellite chromosomes or sat chromosomes. Chromosome may possess secondary constriction in one or both arms of it. Chromosomal end distal to the secondary constriction is known as satellite. Production of nucleolus is associated with secondary constriction and therefore it is also called nucleolus organizer region and satellite chromosomes are often referred to as nucleolus organizer chromosomes.

5. Chromomere: In some species like maize, rye etc. chromosomes in pachytene stage of meiosis show small bead like structures called chromomeres. Chromomeres are visible during meiotic prophase (pachytene) and invisible in mitotic metaphase chromosomes. The distribution of chromomeres in chromosomes is highly characteristic and constant. The pattern of distribution being different for different chromosomes. They are clearly visible as dark staining bands in the giant salivary gland chromosomes. Chromomeres are regions of tightly folded DNA. Chromomeres of single chromosome show considerable variation in size. They may differ in size as in the case of maize or they may be of uniform size as in the case of rye.

6. Chromonema: A chromosome consists of two chromatids and each chromatid consists of thread like coiled structures called chromonema (plural chromonemata). The term chromonema was coined by Vejdovsky in 1912. The chromonemata form the gene bearing portion of chromosomes.

7. Matrix: The mass of acromatic material which surrounds the chromonemata is called matrix. The matrix is enclosed in a sheath which is known as pellicle. Both matrix and pellicle are non genetic materials and appear only at metaphase, when the nucleolus disappears.

2.1.4. Composition of chromosomes:

The material of which chromosomes are composed is called chromatin. N.Fleming introduced the term chromatin in 1879. Chromatin was classified into two groups by cytologists on the basis of its affinity to basic dyes like acetocarmine or feulgen (basic fuchsin) reagent at prophase. The darkly stained regions were called heterochromatin, while lightly stained regions were called euchromatin. This differential staining capacity of different parts of a chromosomes is known as ‘heteropycnosis’. In general heterochromatin is found in centromeric and telomeric regions and these regions of chromosome generally replicate later than the euchromatic regions of chromosomes. The genes within the heterochromatic regions are usually inactive. Most of the genome of an active cell is euchromatic and the genes with in this euchromatic region are expressed. Heterochromatin is further classified into two groups: a) Constitutive and b)Facultative

a) Constitutive heterochromatin: It is present in all cells at identical positions on both

homologous chromosomes of a pair.
b) Facultative heterochromatin: It varies in state in different cell types, at different stages or sometimes, from one homologous chromosome to another. A well known example of facultative heterochromatin is the *Barr body*, an inactivated X chromosome in somatic cells of mammalian female(XX).

Differences between Heterochromatin and Euchromatin:

	Heterochromatin	**Euchromatin**
1	Represent darkly stained regions	Lightly stained regions
2	Contains few inactive genes	Contains lot of active genes
3	Covers small region of chromosome	Larger region of chromosome
4	Usually found near centromere and telomere	Found in the middle of chromosome between centromere and telomere
5	Two types – Constitutive and facultative	Only one type
6	Late replicating	Normal replicating
7	Usually no active part in transcription	Plays active role in transcription
	30 nm fibre	3-8nm fibre

2.1.5. Karyotype and Ideogram: The general morphology (size of chromosomes, position of centromere, presence of secondary constriction and size of satellite bodies) of somatic chromosomal complement of an individual constitutes its karyotype. It can be defined as “the characteristic features by which a set of chromosomes of a species is identified”. Generally, karyotype is represented by arranging the chromosomes in descending order of size, keeping their centromeres in the same line. Thus the largest chromosome is placed on extreme left and the shortest on extreme right. The karyotype of a species can be represented diagrammatically showing all the morphological features of chromosomes. Such a

diagram is known as ideogram or ideotype.

1.2. Special types of Chromosomes

Some tissues of certain organisms contain chromosomes which differ significantly from normal chromosomes in terms of either morphology or function. Such chromosomes are referred to as special chromosomes. The following are included under this category:

1. **Giant chromosomes or polytene chromosomes:** These were first discovered by E. G. Balbiani in 1882 in *Dipteran* salivary glands and hence commonly called salivary gland chromosomes. These chromosomes replicate repeatedly but the daughter chromatids do not separate from one another and the cell also does not divide. This phenomenon is known as endomitosis or endoreduplication. It results in the formation of many stranded giant chromosomes known as polytene chromosomes and the condition is known as polyteny. Their size is 200 times or more than the normal somatic chromosomes (autosomes) and very thick. Hence they are known as giant chromosomes. These chromosomes are somatically paired and their number in the salivary gland cells always appear to be half of that in the normal somatic cells. Along the length of chromosomes, a series of dark bands are

present alternate with clear bands known as interbands. These bands have greatly helped in mapping of the chromosomes in cytogenetic studies. In the dark band region, the DNA is tightly coiled while in the interband region, DNA is less tightly coiled. The morphological expression of such sites is represented by local enlargements of certain regions called puffs. These puffs are also known as balbiani rings. Puffs are the sites of active RNA synthesis.

2. Lamp brush chromosomes: These were first observed by W. Flemming in 1882 and were described in detail in oocytes of sharks by Rukert in 1892. They occur at diplotene stage of meiotic prophase in oocytes of all animal species. Since they are found in meiotic prophase, they are present in the form of bivalents in which the maternal and paternal chromosomes are held together by chiasmata at those sites where crossing over has previously occurred. Each bivalent has four chromatids, two in each homologue. The axis of each homologue consists of a row of granules or chromomeres, each of which have two loop like lateral extensions, one for each chromatid. Thus each loop represents one chromatid of a chromosome and is composed of one DNA double helix. One end of each loop is thinner than other which is known as thickened. There is extensive RNA synthesis at thin ends of the loop while there is little or no RNA synthesis at the thick ends.

3. **Accessory chromosomes:** In many species some chromosomes are found in addition to normal somatic chromosomes. These extra chromosomes are called accessory chromosomes or B-chromosomes or supernumerary chromos omes. These chromosomes are broadly similar to normal somatic chromosomes in their morphology, but have some peculiar functional aspects. For instance, presence of several such chromosomes often leads to reduction in vigour and fertility in males. These chromosomes are generally smaller in size than the normal

somatic complement. They are believed to be generally inactive genetically. However they may not be completely devoid of genes. Origin of these chromosomes in most species is unknown.

4. **Isochromosomes:** An isochromosome is the one in which two arms are identical with each other in gene content and morphology. Such a chromosome is in essence a reverse duplication with centromeres separating the two arms. Every isochromosome is metacentric. The attached 'x' chromosome of *Drosophila* is a classical example of an isochromosome. However its origin is uncertain. There is no evidence that isochromosomes had any evolutionary significane.
5. **Allosomes / sex chromosomes:** Chromosomes differing in morphology and number in male and female are called allosomes. They are responsible for determination of sex. Eg: X and Y chromosomes in human beings and *Drosophila*. Chromosomes which have no relation with determination of sex and contain genes which determine somatic characters of individuals are called autosomes and are represented by letter 'A'.

4.0 Summary

Plants are made of chromosomes**.** The number of chromosomes in a species is constant. Somatic chromosome number is the number of chromosomes found in somatic cells of a species and two copies of each chromosome except the sex chromosomes.The size of the chromosome varieswith stage of cell division being longest and thinnest during interphase (resting stage) but smallest and thickest during mitotic metaphase. Plants have longer chromosomes than animals and species having lower chromosome number have longer chromosomes than those having a higher chromosome number. Dicots in general have shorter and higher number of chromosomes than monocots.

5.0 Conclusion

Cytological principles of plant breeding are based on the chromosomal structure, composition and function of chromosomes of the plant.

6.0 Self-assessment Assignments

1. What is a chromosome and how is it important in plant breeding?
2. Differentiate between euchromatin and hetrochromatin
3. List the special types of chromosomes and explain each

7.0 Tutor marked assignment:

1. Describe how you can distinguish chromosomes depending on position of the centromeres.

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Unit 3 :Heterosis

1.0 Introduction

Heterosis, or hybrid vigor, or outbreeding enhancement, is the improved or function of any biological quality in a hybrid offspring. It is the occurrence of a genetically superior offspring from mixing the genes of its parents.

Heterosis is the opposite of inbreeding depression. Inbreeding depression leads to offspring with deleterious traits due to homozygosity. The term heterosis often causes controversy, particularly in selective breeding of domestic animals, because it is sometimes claimed that all crossbred plants and animals are genetically superior to their parents. This is untrue, as only some hybrids are genetically superior. The inverse of heterosis, when a hybrid inherits traits from its parents that are not fully compatible, with deleterious results, is outbreeding depression.

2.0 Objectives:

By the end of this unit you should be able to:

- Discuss the genetic basis of heterosis
- Discuss the effect of Heretosis in animals

3.0. Genetic basis of heterosis

Two competing hypotheses, not necessarily mutually exclusive, have been to explain hybrid vigor. The dominance hypothesis attributes the superiority of hybrids to the suppression of undesirable (deleterious) recessive alleles from one parent by dominant alleles from the other. It attributes the poor performance of inbred strains to the loss of genetic diversity, with the strains becoming purely homozygous deleterious alleles at many loci. The overdominance hypothesis states that some combinations of alleles (which can be obtained by crossing two inbred strains) are especially advantageous when paired in a heterozygous individual. The concept of heterozygote advantage/overdominance is not restricted to hybrid lineages. This hypothesis is commonly invoked to explain the persistence of many alleles (most famously the erythrocyte-sickling allele) that are harmful in homozygotes; in normal circumstances, such harmful alleles would be removed from a population through the process of natural selection. Like the dominance hypothesis, it attributes the poor performance of many inbred strains to a high frequency of these harmful recessive alleles and the associated high

frequency of homozygous-recessive genotypes.

3.1. Hybrid corn

Nearly all field corn (maize) grown in most developed nations exhibits . Modern corn hybrids substantially outyield conventional cultivars and respond better to fertilizer.

Corn heterosis was famously demonstrated in the early 20th century by George H. Shull and Edward M. East after hybrid corn was invented by Dr. William James Beal of Michigan State University based on work begun in 1879 at the urging of Charles Darwin. Dr. Beal's work led to the first published account of a field experiment demonstrating hybrid vigor in corn, by Eugene Davenport and Perry Holden, 1881. These various pioneers of botany and related fields showed that crosses of inbred lines made from a Southern dent and a Northern flint, respectively, showed substantial heterosis and outyielded conventional cultivars of that era. However, at that time such hybrids could not be economically made on a large scale for use by farmers. Donald F. Jones at the Connecticut Agricultural Experiment Station, New Haven invented the first practical method of producing high-yielding hybrid maize in 1914-1917. Jones' method produced a double-cross hybrid, which requires two crossing steps working from four distinct original inbred lines. Later work by corn breeders produced inbred lines with sufficient vigor for practical production of a commercial hybrid in a single step, the single-cross hybrids. Single-cross hybrids are made from just two original parent inbreds. They are generally more vigorous and also more uniform than the earlier double-cross hybrids. The process of creating these hybrids often involves detasseling.

3.2. Hybrid livestock

The concept of heterosis is also applied in the production of commercial livestock. In cattle, hybrids between Black Angus and Hereford produce a hybrid known as a "Black Baldy". In swine, "blue butts" are produced by the cross of Hampshire and Yorkshire. Other, more exotic hybrids such as "beefalo" are also used for specialty markets.

Within poultry, sex-linked genes have been used to create hybrids in which males and females can be sorted at one day old by color. Specific genes used for this are genes for barring and wing feather growth. Crosses of this sort create what are sold as Black Sex-links, Red Sex-links, and various other crosses that are known by trade names.

Commercial broilers are produced by crossing different strains of White Rocks and White Cornish, the Cornish providing a large frame and the Rocks providing the fast rate of gain. The hybrid vigor produced allows the production of uniform birds with a marketable carcass at 6–9 weeks of age.

Likewise, hybrids between different strains of White Leghorn are used to

produce laying flocks that provide the majority white eggs for sale in the United States.

IN-TEXT QUESTION

What is the contribution of George H. Shull and Edward M. East to the heterosis?

***Answer**: They demonstrated Corn heterosis in the early 20th century .*

3.3. Heterosis Effect in Animals

Purebreds and inbreeds often carry genetic disease. Heterosis is a theory, where the phenomenon of crossing two inbred lines can produce descendants with superior genetic foundation. In addition to the absence of inbreeding depressing, present in inbreed and purebred dogs in general, there is some remote inbreeding in any breed. Heterosis is also produced by over dominance, i.e. better combined function of two diverse genes (alleles) on a gene site (locus), compared to two identical (but harmless) ones. This increased health and vigor does not create a superior breed, but the advantages obtained from it are what produce hybrid vigor. This goal in this scenario is not to create a new breed, but to create a happy and healthy pet.

Heterosis effect results in a healthier, more vigorous dog with a reduced chance of genetic disease. It is well known in all domestic animal breeding, hybrids, 50%-50% mixes of two different breeds, will raise the chances of having less genetic diseases because all doubling of detrimental effects will stop in the first generation. The genetic term for this is HETEROSIS EFFECT. This effect often gives non-related individuals stronger descendants than inbreeds.

Breeders who breed hybrid dogs have stated their goal was to get healthy and happy dogs without genetic problems. Most breeders crossing with the poodle are looking for a soft silky non-shedding coat good for allergy sufferers.

The purpose of these hybrids is not and should never be to develop a new breed. Once one goes beyond first generation purebred to purebred, you lose the heterosis effect, which is the goal for most hybrid breeders. The mother should always be the bigger of the two, to avoid puppies getting too big and complicating the delivery for the mother. Heterosis is said to not only occur in the first generation, but also mating to a non related hybrid of same (or other) type will also show this effect, though the aspect of the offspring will be different. The hope is that the dogs will get the benefit of the greatly demanded HETEROSIS effect, and avoid genetic diseases which are common among

purebreds and inbreeds.

4. Summary

Heterosisis the occurrence of a genetically superior offspring from mixing the genes of its parents. The genetic explanation is that there is superiority of hybrids to the suppression of undesirable (deleterious) recessive alleles from one parent by dominant alleles from the other. It is found in plants, such as corn, and the production of commercial livestock. In animals, heterosis results in a healthier, more vigorous with a reduced chance of genetic disease.

5. Conclusion

Heterosis is the method of breeding desirable traits for high agricultural yield.

6. Self-assessment Assignments

1. Describe the genetic basis of heterosis
2. Explain the concept of hybrid corn and hybrid livestock

7. Tutor Marked Assessment

1. Discuss on Heterosis in plants and animals
2. Give a concise account of how hybrid vigour is explained by two hypotheses.

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Unit 4 Inbreeding (F) and its consequences or applications

1.0 Introduction

The broad scientific definition of inbreeding is that it is the mating of individuals more closely related to each other than the average relationship within the population concerned. This statement is really only valid for large populations, since with small populations inbreeding is inevitable, even with random mating. To be more precise, an inbred person is defined as someone whose parents are related. In practice this means close direct relationship or, more usually, related through recent common ancestors, since all members of the same species are related to some extent.

2.0: Objectives

At the end of this unit you should be able to

- Define of inbreeding
- Discuss the consequences of inbreeding
- Explain coefficient of inbreeding
- Calculate inbreeding coefficient (F)
- Apply the inbreeding coefficient (F) in situations

3.0 Consequences of inbreeding

The adverse effects of inbreeding in animals are well known. The incidence of metabolic disorders, structural abnormalities and inherited disease conditions,

caused by harmful recessive genes, increases following inbreeding. Performance in several characters, particularly those concerned with reproduction and survival, declines following the mating of close relatives. This is known as inbreeding depression. These effects are mainly due to an increase in the frequency of homozygous genotypes (AA and aa) at the expense of heterozygotes (Aa), which is caused by inbreeding. It is only harmful, however, when the dominance is directional, which means that the undesirable member of a pair of genes is usually recessive. When a high proportion of these harmful genes are present in the heterozygous state (Aa) the animal is protected from their debilitating effects by the dominance of the normal gene; but when some of the heterozygotes are replaced by homozygous recessives (aa), following inbreeding, their harmful effects become manifest. Other types of gene action are sometimes responsible for inbreeding damage, but are thought to be less important.
These are: overdominance, epistatic interaction and the overall level of heterozygosity.

Overdominance occurs when the heterozygote (A_1A_2) is superior in performance to either of the two homozygotes (A_1A_1 or A_2A_2). In this situation, an increase in homozygosity following inbreeding also causes inbreeding depression.

Epistatic interaction between different pairs of genes occurs when one pair affects the expression of another pair at a different locus. With one particular type, called complementary epistasis, two dominants, one from each of two separate loci, are necessary for normal development or metabolism. Thus, AABB, AaBB, AABb and AaBb will be normal, but AAbb, aaBBAabb, aaBb and aabb will be defective. This situation arises when a metabolic pathway requires two enzymes for the essential end-product to be synthesised. Since each enzyme requires a different dominant gene for its synthesis, the absence of one or both will result in a defective individual. Inbreeding in a population with a mixture of the above genotypes will lead to a break-up of the favourable gene combinations, with more inferior genotypes, particularly aaBB, AAbb and aabb, being produced.

Finally, Lerner (1954) found evidence that some abnormal conditions in animals were not caused by single genes but by a drop in the general level of heterozygosity throughout the whole genome. His theory of developmental homeostasis suggests that for an animal to be able to cope with developmental accidents and environmental stress there is a minimum or obligate level of heterozygosity for normal development. The implication being that heterozygotes in general are more versatile because they can produce a greater variety of enzymes and other proteins. This means that the heterozygosity level per se, as well as the effects of the genes themselves, may be a contributing factor.

The opposite of inbreeding depression is known as heterosis or hybrid vigour and can result from the crossing of unrelated inbred animals or lines with different genetic backgrounds. What is lost from inbreeding is usually restored when several inbred lines are crossed randomly. Deliberate inbreeding and crossing, followed by selection between lines, is sometimes used with farm plants and animals to improve

yields. Its significance in humans is that greater mobility means that people travel further to find a spouse and are less likely to marry a person from the same locality with a similar genotype. Thus, although most of the increase in height and improved survival is the result of better nutrition and disease control, a small part may also be due to heterosis following a change in the mating system.

3.1 The coefficient of inbreeding

The coefficient of inbreeding (F) measures the probability that two genes at any locus in an individual are identical by descent from the common ancestor(s) of the two parents. This means the degree to which two alleles are more likely to be homozygous (AA or aa) rather than heterozygous (Aa) in an individual, because the parents are related. Like R,F is a relative measure, in that there will be a certain level of homozygosity within the base population; F simply estimates the increase from that initial level as a result of recentinbreeding.

The inbreeding coefficient of an individual is approximately half the relationship (R) between the two parents.This equivalence only applies to low levels of inbreeding in an otherwise outbred population.e.g.Two single first cousins normally have a relationship (R) of 1/8.If there has been no previous inbreeding, their children will have a coefficient of inbreeding of 1/16.With high levels of continuous inbreeding this relationship breaks down. e.g. some strains of laboratory rats and mice have reached an F value of 1.0, resulting from a long history of close inbreeding; but the coefficient of relationship (R) between any two members of the strain can never exceed 1.0. The mathematical reason for this is that although the basic formulae for R and F are $\Sigma(1/2)^n$ and $\Sigma(1/2)^{n+1}$, respectively, as inbreeding within a line progresses, the correction terms applied to R for inbreeding gradually become more important and start to reduce the value of R below $\Sigma(1/2)^n$. As F approaches 1.0, the correction terms for R also approach a maximum of (x 1/2); so that when F reaches 1.0 (complete homozygosity), R also becomes 1.0 and all members of the inbred line are identical.

IN-TEXT QUESTION

What is the inbreeding coefficient in

3.2. Calculating of inbreeding coefficient (F)

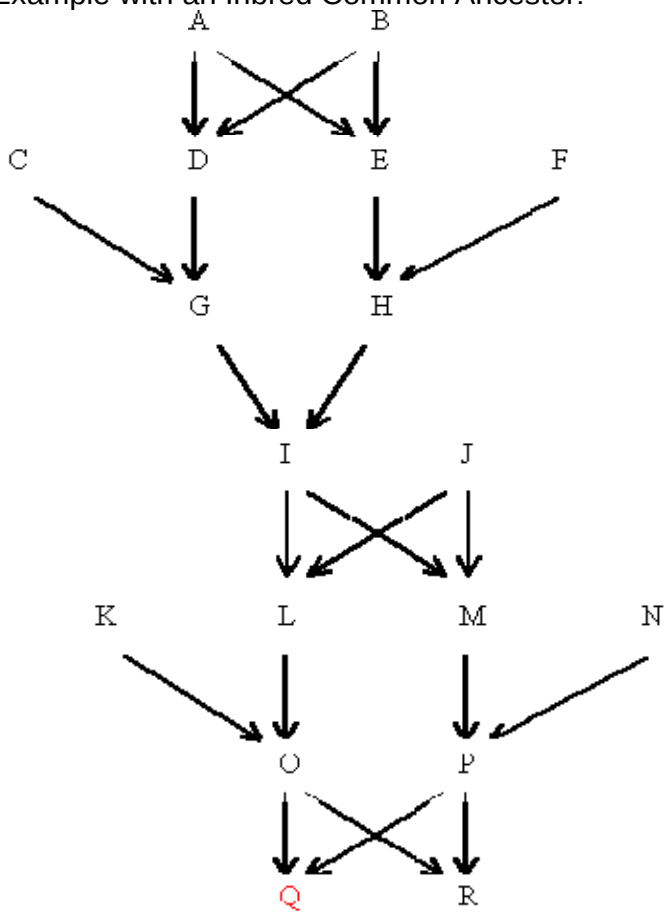
The method of calculating the F coefficient of an individual is similar to that for the coefficient of relationship (R) between two collateral relatives, and involves the tracing of paths between the two parents via a common ancestor. The formula is as follows:-

Equation 1:Method of calculating the F coefficient of an individual-

$$F_x = \sum\left[\left(\frac{1}{2}\right)^{n+1}(1+F_A)\right]$$

[1][14] Where F_X is the coefficient of inbreeding of individual X, n is the number of connecting links between the two parents of X through common ancestors and F_A is the coefficient of inbreeding of the common ancestor A. Thus, if the common ancestor is inbred, a minor calculation must be performed first to determine F_A, before the main calculation can take place.In the main calculation any coefficients of paths through inbred common ancestors can then be multiplied by $(1+ F_A)$.

Example with an Inbred Common Ancestor:



Find F_Q

The only inbred common ancestor of the two parents (O and P) is I (his parents are single first cousins).

a) First Find F_I

Common Ancestors (of parents G and H)	Paths	$(1/2)^{n+1}$	$(1+F_A)$

A	$G^{-1}D^{-2}A^{-3}E^{-4}H$	1/32	x 1.0	=	1/32
B	$G^{-1}D^{-2}B^{-3}E^{-4}H$	1/32	x 1.0	=	1/32
Therefore $F_I = \Sigma [(1/2)^{n+1}(1 + F_A)$				=	**1/16**

i.e. $F_I = 0.0625 =$ 6.25%

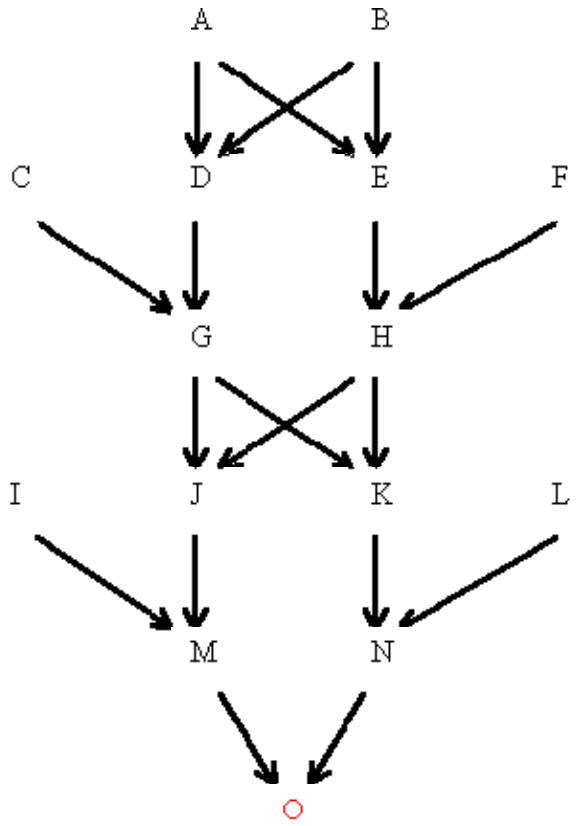
b) Main Calculation (To find F_Q)

Common Ancestors (of parents O and P)

Paths	$(1/2)^{n+1}(1+F_A)$				
I	$O^{-1}L^{-2}I^{-3}M^{-4}P$	0.03125	x 1.0625	=	0.03220
J	$O^{-1}L^{-2}J^{-3}M^{-4}P$	0.03125	x 1.0	=	0.03125
Therefore $F_Q = \Sigma[(1/2)^{n+1}(1 + F_A)]$				=	**0.06445**

i.e. $F_Q = 0.06445 =$ 6.45%

Example without Inbred Common Ancestors:



Find F_O

None of the common ancestors A, B, G or H are inbred. Therefore, no corrections are necessary.

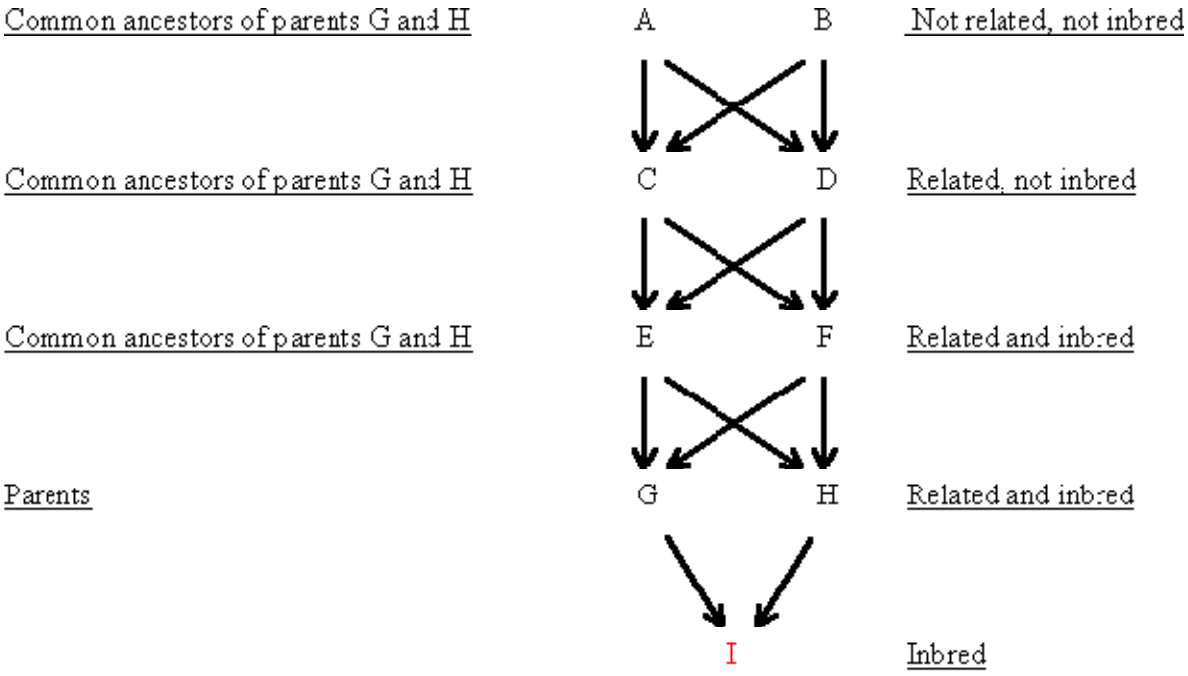
Common Ancestors (of parents M and N)	Paths	$(1/2)^{n+1}$
G	$M^{-1}J^{-2}G^{-3}K^{-4}N$	1/32 = 0.03125
H	$M^{-1}J^{-2}H^{-3}K^{-4}N$	1/32 = 0.03125
A	$M^{-1}J^{-2}G^{-3}D^{-4}A^{-5}E^{-6}H^{-7}K^{-8}N$ $M^{-1}J^{-2}H^{-3}E^{-4}A^{-5}D^{-6}G^{-7}K^{-8}N$	
B	$M^{-1}J^{-2}G^{-3}D^{-4}B^{-5}E^{-6}H^{-7}K^{-8}N$	1/512 x 4 = 0.0078125

$M-^{1}-J-^{2}-H-^{3}-E-^{4}-B-^{5}-D-^{6}-G-^{7}-K-^{8}-N$

Therefore $F_O = \Sigma(1/2)^{n+1}$ = **.0703125**

i.e. F_O = 7.03%

Close Inbreeding as used for Animals (3 generations of full sib mating):



Find F_I

Common ancestors of G and H are A, B, C, D, E and F.The only two that are inbred are E and F (related parents).Therefore, first calculate F_E and F_F (the same).

a) Find F_E and F_F

Common ancestors(of parents C and D)	Paths	$(1/2)^{n+1}$	
A	$C-^{1}-A-^{2}-D$	1/8	Therefore,
B	$C-^{1}-B-^{2}-D$	1/8	$F_E = F_F$ = 1/4 = 25%

b) Main Calculation (To Find F_I)

Common ancestors (of parents G and H)	Paths	$(1/2)^{n+1}$		$(1 + F_A)$		
E	G–1–E–2–H	$(1/2)^3$	*	1.25	=	15625
F	G–1–F–2–H	$(1/2)^3$	*	1.25	=	15625

C	$G^{-1}-E^{-2}-C^{-3}-F^{-4}-H$ $G^{-1}-F^{-2}-C^{-3}-E^{-4}-H$	$(1/2)^5$ $(1/2)^5$	* 1.0 * 1.0	= 03125 = 03125
D	$G^{-1}-E^{-2}-D^{-3}-F^{-4}-H$ $G^{-1}-F^{-2}-D^{-3}-E^{-4}-H$	$(1/2)^5$ $(1/2)^5$	* 1.0 * 1.0	= 03125 = 03125
A B	$G^{-1}-E^{-2}-C^{-3}-A^{-4}-D^{-5}-F^{-6}-H$ $G^{-1}-F^{-2}-C^{-3}-A^{-4}-D^{-5}-E^{-6}-H$ $G^{-1}-E^{-2}-D^{-3}-A^{-4}-C^{-5}-F^{-6}-H$ $G^{-1}-F^{-2}-D^{-3}-A^{-4}-C^{-5}-E^{-6}-H$ $G^{-1}-E^{-2}-C^{-3}-B^{-4}-D^{-5}-F^{-6}-H$ $G^{-1}-F^{-2}-C^{-3}-B^{-4}-D^{-5}-E^{-6}-H$ $G^{-1}-E^{-2}-D^{-3}-B^{-4}-C^{-5}-F^{-6}-H$ $G^{-1}-F^{-2}-D^{-3}-B^{-4}-C^{-5}-E^{-6}-H$	$(1/2)^7 \times 8$	* 1.0	= 06250

$F_I=\Sigma[(1/2)^{n+1}\ (1 + F_A)] =.50000$

i.e F_I =<u>50%</u>

IN-TEXT QUESTION

What does an inbreeding coefficient of 0.25 signify?

***Answer**: 0.25 is the inbreeding coefficient of a child produced by a brother and sister mating*

3.3 The Closest Form of Inbreeding

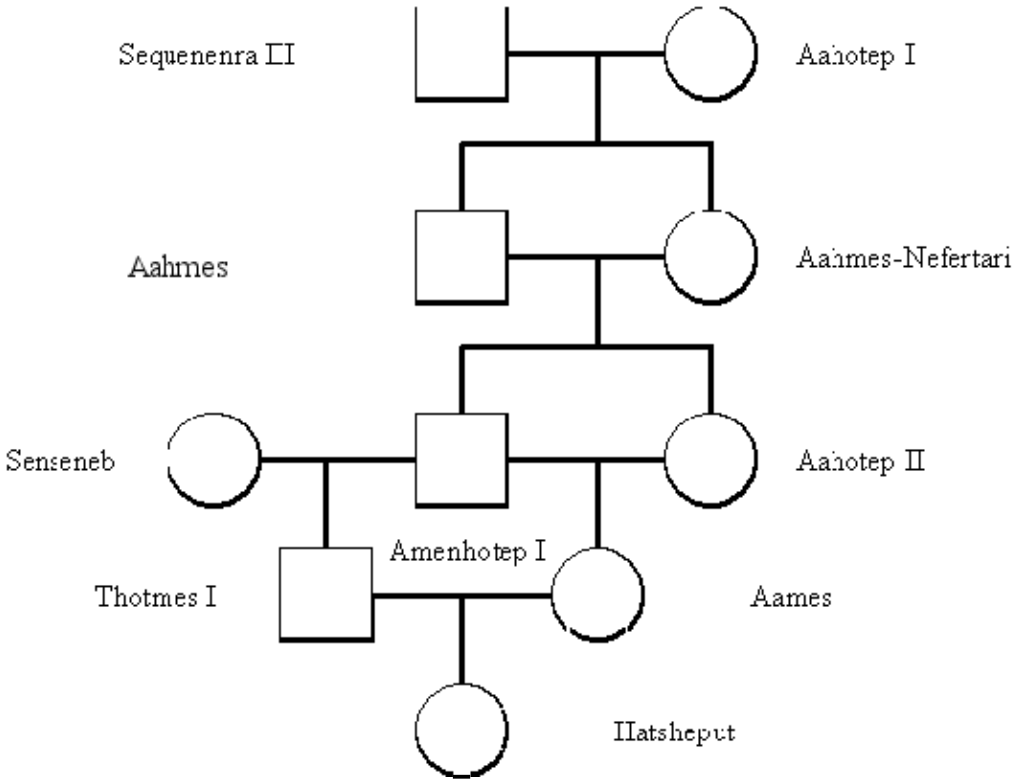
The closest form of inbreeding is self-fertilisation which normally only occurs in monoecious plants and animals which are hermaphrodites,, e.g. garden peas and slugs.The equivalent situation has been experimentally produced in turkeys where a rare form of parthenogenesis occurs.Parthenogenesis (virgin birth) is the production of viable embryos (always males in birds) from haploid infertile eggs by the artificial doubling of chromosome numbers. The embryos are highly homozygous.If one of these parthenogenetic males is mated back to his mother this is equivalent to self-fertilisation.One generation of self-fertilisation produces the same coefficient of inbreeding (F) as three generations of full sib mating, i.e. 0.5.This follows from the formula for F, which is $\Sigma(1/2)^{n+1}$ where n is the number of connecting links between the two parents via a common ancestor. With selfing, both parents are the same

individual so that the number of links (n) is 0 and, therefore $\Sigma(1/2)^{n+1} = 0.5$.

3.4 Sib Marriages in Humans

In some societies close consanguineous marriages have been encouraged.For example, the ancient Egyptians and the Incas favoured marriages of brothers and sisters of the reigning dynasty.

Marriages between Sibs and Half-sibs in the 18th Dynasty of Egypt, c. 1580 – 1350.



3.5 Application Inbreeding Coefficients

	F
a) Amenhotep I and Aahotep II	25%
b) Aames	37.5%
c) Hatsheput	25%

d) The rest of the individuals in the pedigree are not inbred, i.e. F = 0.

3.6 Double Grandchildren - The offspring of a full sib mating are sometimes referred to as double grandchildren because they only have two grandparents instead of the usual four.

3.6.1The Special Case of Directly Related Parents

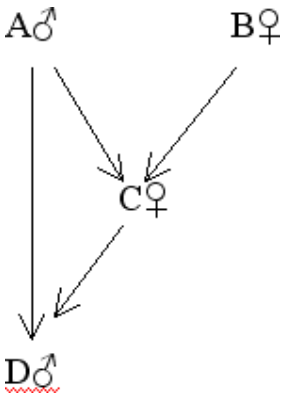
In an incestuous situation where there is a close direct relationship between the two parents, such as father-daughter, mother-son or grandparent-grandchild, they may have no common ancestors in any previous generation, even though they have a

strong genetic link. This is because one parent is the direct ancestor of the other. In these situations, despite having no common ancestors, the correction term $(1 + F_A)$

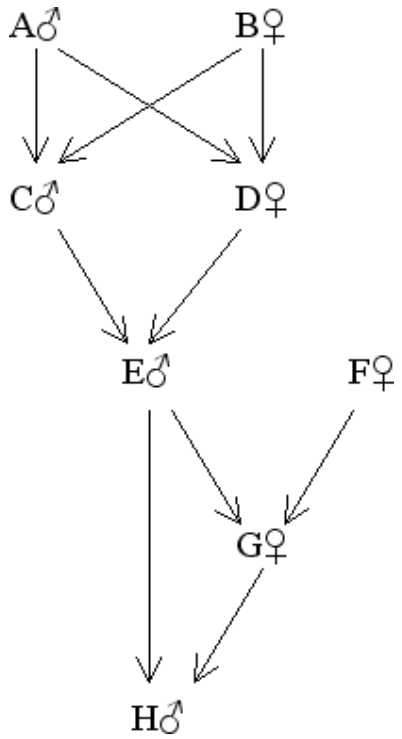
must still be applied to the path coefficient between an inbred ancestor (A) and his/her descendant partner.

A Father-daughter mating:

The reason is that, taking a father-daughter mating as an example; if the father (A) is inbred, his extra homozygosity will make it more likely that he will transmit to his grandson (D) further copies of the same alleles which his daughter (C) has already received from him. Since about one half of the genes the daughter receives from her father will also be passed on to the grandson, the latter's inbreeding coefficient (F) will rise above the normally expected level (0.25) and its value should be adjusted accordingly.



Directly Related Parents Only:



Find F_H $F_E = 0.25$

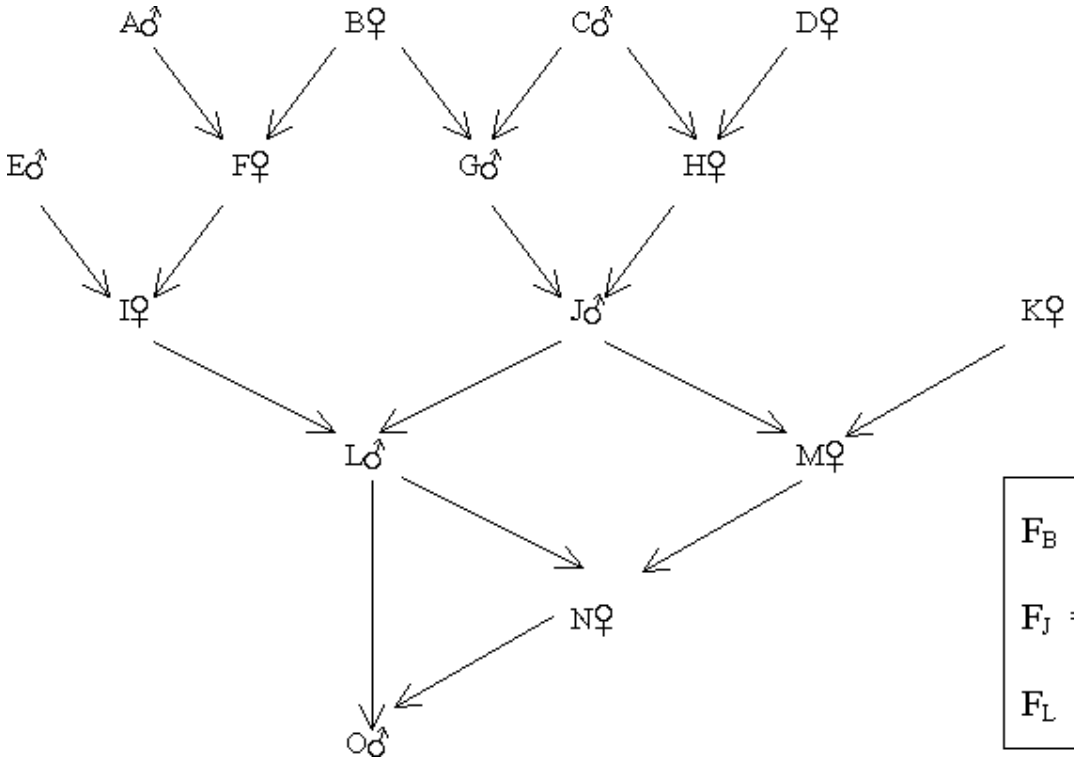
Common ancestors (of parents E and G	Path	$(1/2)^{n+1}$		$(1 + F_A)$ *		
None	E - G	$(1/2)^2$	x	1.25	=	0.3125

Therefore, $F_H = \Sigma[(1/2)^{n+1}(1 + F_A)] = 31.3\%$

However, there are cases (usually only found in animal breeding) where directly related parents do share common ancestors. If any of these common ancestors are also inbred, the correction term

$(1 + F_A)$ will be required in both situations.

Directly and Collaterally Related Parents:



$F_B = 0$

$F_J = 0.125$

$F_L = 0.03125$

Find F_O

Common ancestors (of parents L and N)	Paths	$(1/2)^{n+1}$	$(1 + F_A)$ *		
None	L - N	$(1/2)^2$	x 1.03125	=	0.2578125
J	L - J - M - N	$(1/2)^4$	x 1.125	=	0.0703125
B	L - I - F - B - G - J - M - N	$(1/2)^8$	x 1.0	=	0.00390625
					0.33203125

Therefore $F_O = \sum[(1/2)^{n+1}(1 + F_A)] =$ 33.2%

*A refers to any relevant inbred direct ancestor or common ancestor.

Alternative Methods of Calculating the coefficient of inbreeding:

An alternative method of computing F is to use the technique of 'Coancestries'.Instead of working from the present back to common ancestors we

work forward, keeping a running tally, generation by generation, and compute the inbreeding that will result from the matings now being made.This method is easier

than path coefficients for animal breeding programmes where the paths are often numerous and complex but unnecessary for normal human pedigrees.

For regular systems of inbreeding, as used in the 'inbred-hybrid' system for breeding chickens and maize, 'recurrence equations' are the only easy method for calculating F. A regular system of inbreeding is where a certain type of mating such as brother-sister, is repeated indefinitely. A recurrence equation calculates the F value of the present generation from those of recent previous ones. e.g. the recurrence equation for repeated full sib mating is:

$$F_t = 0.25 (1 + 2F_{t-1} + F_{t-2})$$

Where F_t is the coefficient of the present generation, F_{t-1} is the coefficient of the previous generation and F_{t-2} is the coefficient of the generation before that. It is important to note that recurrence equations can only be used for regular systems of inbreeding. e.g. Three generations of full sib mating:-

First generation - $F_1 = 0.25 (1 + 0 + 0) = 0.25$

Second generation - $F_2 = 0.25 (1 + 0.5 + 0) = 0.375$

Third generation - $F_3 = 0.25 (1 + 0.75 + 0.25) = 0.5$

Values of F for ConsanguinousMatings (One generation, no previous inbreeding).

Self fertilisation	1/2
Full sibs, Parent-child, Double first cousins (first degree)	1/4
Half sibs, Grandparent-grandchild, Uncle-niece, Double first cousins	1/8
First cousins	1/16
First cousins (once removed)	1/32
Second cousins	1/64
Second cousins (once removed)	1/128
Third cousins	1/256

3.7 Practical Uses of F

F is a very valuable parameter in both population and quantitative genetics.From the genealogists point of view the following are perhaps the two most interesting applications:

a) Predicting the Effects of Inbreeding Depression

A decline in performance in certain economic characters in domestic animals is well known following inbreeding. A similar depression has also been observed in humans.e.g.

Inbreeding Depression for Every 10% Increase in F:

Animal	Characteristic	Inbreeding Depression	Reference
Chickens	Hatchability	4.36%	Shoffner (1948)
	Annual egg production	9.26 eggs	Shoffner (1948)
Man	Height at age 10	2.0 cm	Falconer (1989)
	I.Q. score	4.4%	Falconer (1989)
Pigs	Body weight (154 days)	2.6 kg	Falconer (1989)
	Litter size	0.24 piglets	Falconer (1989)
Cattle	Annual milk yield	135 kg	Falconer (1989)
Sheep	Fleece weight (1 year)	0.29 kg	Falconer (1989)

Thus, 3 generations of full sib matings, as shown above, would lead to an expected decrease in egg production in chickens of 9.26 x 5 = 46.3 i.e 46 eggs, compared with other hens from the same population who were not inbred.

b) Assessing the Risk of Inheriting Genetic Defects

In a large random-mating population, where the frequency of a harmful recessive gene (a) is q, the proportions of affected individuals and 'carriers' can be estimated from the Hardy-Weinberg Lawas follows:

Aa (carriers)	aa (affected)
$2q(1 - q)$	q^2

However, if any inbreeding has occurred,Wright's Equilibrium Lawenables a further prediction to be made about the increased risk of inheriting any harmful conditions caused by homozygous recessive genes.The expected frequency following inbreeding rises to:

aa (affected)

$q^2 + Fq(1 - q)$

The following table shows how inbreeding increases the likelihood of inheriting three harmful recessive conditions in humans: phenylketonuria, albinism and alkaptonuria.The first and last of these three are serious metabolic disorders.

Effects of Inbreeding on the Frequency of Inherited Defects:

Conditions Caused by Homozygous Recessive Genes	Frequency of Recessive Gene (a) q	Random Mating		Proportion of Affected(aa) Following Inbreeding $q^2 + Fq(1 - q)$ [16]	
		Proportion of Carriers (Aa) $2q(1 - q)$ [16]	Proportion of Affected (aa) q^2	First Cousin Marriage (F = 1/16)	Full Sib Mating (F = 1/4)
Phenylketonuria	1/100	1/50	1/10,000	1/1,380	1/385
Albinism	1/141	1/70	1/20,000	1/2,000	1/550
Alkaptonuria	1/1,000	1/500	1/1,000,000	1/16,000	1/4,000

Therefore, with albinism for example, a first cousin marriage increases the risk of inheriting the condition ten-fold, and with alkaptonuria the increase following a full sib mating is 250 fold. It also comes as quite a shock to most people that, even without inbreeding, the proportion of normal people carrying phenylketonuria is as high as 1 in 50.

Inbreeding is a result of the mating of individuals which are related to one another by having one or more common ancestors. If the mated individuals are related, their offspring will to some extent be inbred.

The *coefficient of inbreeding*, is the *probability that the two genes at any locus are identical by descent*.i.e. that the two genes are copies of one of the genes carried by the common ancestor a few generations back. The coefficient of inbreeding, symbolised by *F*, is a property of an individual, but inbreeding profoundly effects the genetic composition of a population and in appropriate circumstances can lead to the formation of inbred strains in which all individuals are virtually genetically identical.

3.8 The rate of inbreeding depends on the degree of relationship

The closest relationship is that of an individual with itself, or self- fertilisation. However, the closest relationship that is usually possible with mammals is full brother x sister (known as *full-sib)* mating. Continuous mating of offspring to the younger parent (which prevents repeated backcrossing to the same individual,

which would have different genetic consequences), or a single generation of parent x offspring mating is genetically equivalent to full-sib mating.

Other regular mating systems which lead to a high level of inbreeding include half-sib and cousin matings. Repeated backcrossing, say of a transgene or a new mutation, to an inbred strain increases homozygosity as rapidly as self-fertilisation.

3.8.1 Inbreeding also arises as a result of restricted population size

In a closed colony it eventually becomes impossible to avoid the mating of related individuals. Hence even "outbred" stocks maintained as a closed colony gradually become inbred at a rate which depends on the size of the colony. Mathematical explanations of the consequences of brother x sister mating and other regular systems of inbreeding have been shown. Contrary to popular belief, avoiding brother x sister mating in a small closed, random-mated population may reduce the inbreeding of an individual but it does *not* reduce the over-all rate of inbreeding. This is because the inbreeding will be undone in a subsequent generation.

Inbreeding is always expressed relative to an arbitrary starting point at which the coefficient of inbreeding is assumed to be zero. Therefore, the magnitude of the effects of inbreeding any specific population will depend on the previous history of the stock, and the extent to which it has already been inbred.

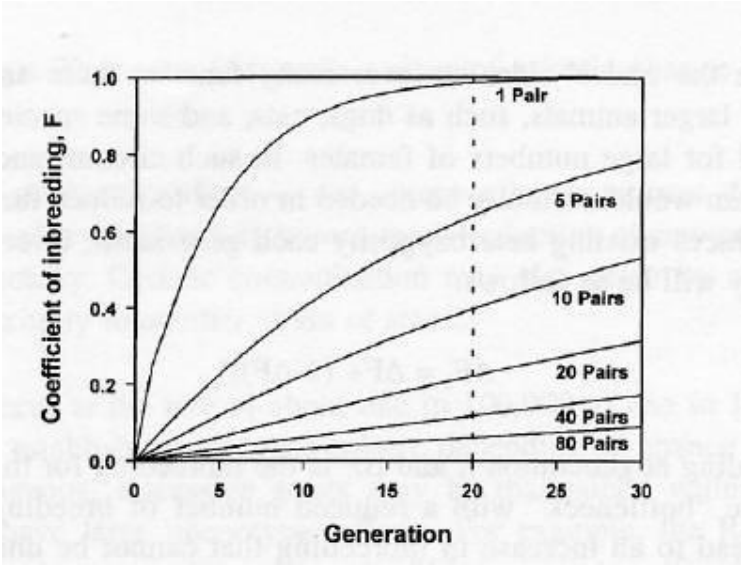


Figure showing inbreeding as a result of restricted population size. A strain is regarded as an "inbred strain" when the coefficient of inbreeding, F, is greater than 0.986, i.e. after 20 generations of sib-mating.

3.9 Full sib mating

Full sib inbreeding of a genetically heterogeneous stock doubles the total genetic

variation if all the sublines are kept. However, all the genetic variation will then be

due to differences *between*sublines, with no genetic variation within sublines. The phenotypic variation among sublines also increases. This is largely due to the "uncovering" of recessive genes and *genetic drift* in which alleles at a particular polymorphic locus become fixed in a homozygous state with plus or minus (with respect to the character) alleles being fixed largely by chance. The phenotypic variation among a set of inbred strains derived from an outbred stock is therefore substantially greater than the phenotypic variation within the starting population.

The converse of this is also true. If several inbred strains are mixed together, then the phenotypic variation in the combined population will be less than that of the individual inbred strains taken together.

The coefficient of inbreeding never quite reaches 100 per cent. Therefore, no strain is ever fully inbred. Moreover, the coefficient of inbreeding is calculated on the assumption that the reproductive performance of heterozygotes is equal to that of homozygotes, and that no mutation occurs. Both of these assumptions are incorrect, and lead to a slight overestimate of the actual level of inbreeding. On the other hand, it is assumed that the base population has a coefficient of inbreeding of zero. In practice, many inbred strains are derived from outbred stocks which may have been maintained as closed colonies with a restricted population size for many generations, as a result of which they may already be highly inbred.

3.9.1 Inbreeding depression

Inbreeding depression is a decline in reproductive performance, ability to survive and other characteristics associated with fitness as a result of inbreeding. It occurs as a result of "uncovering" deleterious recessive genes by making them homozygous and is a consequence of the evolution of dominance of loci concerned with fitness characters. The direction of the change is towards the value of the more recessive alleles. Inbreeding depression does not occur for those characters where the heterozygote is intermediate between the two homozygotes.

The degree of inbreeding depression depends on the previous history of the stock. A stock which has been kept as a closed population for many generations will already be partly inbred; hence, full-sib mating may not result in much inbreeding depression.

Inbreeding depression varies substantially among different lines. Anyone starting a new inbreeding project should do so on a sufficiently large scale to allow for extinction of a proportion of the lines during the first few generations. Once an inbred strain has been established, no further inbreeding depression should occur. Any decline in breeding performance will be due either to environmental influences (particularly disease) or in some cases to new deleterious mutations becoming fixed in the strain.

3.9.2 Inbred strains

The decision as to whether a strain is sufficiently inbred for any particular research project is largely arbitrary. The Committee on Standardized Genetic Nomenclature for Mice decided in 1952 that 20 generations of full-sib mating (or its genetic equivalent), at which time F= 98.6 per cent, is the minimum level of inbreeding required before a strain of mice can be designated as an inbred strain.

However, the coefficient of inbreeding never quite reaches 100 per cent so no strain is ever fully inbred. Moreover, the coefficient of inbreeding is calculated on the assumption that the reproductive performance of heterozygotes is equal to that of homozygotes, and that no mutation occurs. Both of these assumptions are incorrect, and lead to a slight overestimate of the actual level of inbreeding. But it is also assumed that the base population has a coefficient of inbreeding of zero. Many inbred strains are derived from outbred stocks which have been maintained as closed colonies with a restricted population size for many generations, as a result of which they may already be highly inbred.

Inbreeding is defined in terms of the probability of heterozygosity at a locus. However, all inbred strains used in biomedical research should also be isogenic, i.e. all individuals within an inbred strain should be genetically identical (apart from residual segregation due to the impossibility of achieving fully inbred strains). In fact it is isogenicity rather than homozygosity that is the most useful property of inbred strains, and the two are distinct properties which should not be confused. Isogenicity is achieved by ensuring that all individuals trace back to a common ancestral full-sib breeding pair in the twentieth or a subsequent generation. All parallel substrains should be eliminated. F1 hybrids, i.e. the first-generation cross between two inbred strains, are isogenic but not homozygous. It is unfortunate that the terms inbred and `outbred' which describe breeding methods rather than a genetic property of a group of animals, have become so widely accepted.

4.0 Summary

Inbreeding is the mating of individuals more closely related to each other than the average relationship within the population concerned. The incidence of metabolic disorders, structural abnormalities and inherited disease conditions caused by harmful recessive genes increases are results of inbreeding. Inbreeding can occur through self-fertilization and observed in monoecious plants and hermaphrodite animals and also when parthenogenesis takes place. Sibling marriages in humans, where marriage between brother and sister; or in cases where there is direct relationship with parent (mating between father and daughter) and direct and collaterally related parents. Inbreeding study is an important tool in predicting the effects of

inbreeding and assessing the risk of inheritable genetic defects. The rate of inbreeding depends on the degree of relationship between the mating partners.

5.0 Conclusion

Inbreeding occur in both plants and animals. When they occur the results is devastating. It has predictable effects and assessable risks in the populations. The rate of which depend on how closely related the reproducing individuals are.

6.0 Self Assessment Assignments

1. Write short notes on the following:
   i. Inbreeding depression
   ii. Overdominance
   iii. Epistasis
   iv. Coefficient of inbreeding (F)

2. Comment on consangeinous marriages using the sibs and half sibs marriage in the 18th dynasty of Egypt(1580-1350 BC)
3. Using 2 above, calculate the inbreeding coefficients for

   i) Amenhotep I and Aahotep II

   ii) Aames

   iii) Hatsheput

Tutor Marked Assessment

1. How can you calculate the F coefficient for an individual?

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UNIT 5 Self-incompatibility in plants

1.0 Introduction

Self-incompatibility (SI) is a general name for several genetic mechanisms in angiosperms, which prevent self-fertilization and thus encourage outcrossing. In plants with SI, when a pollen grain produced in a plant reaches a stigma of the same plant or another plant with a similar genotype, the process of pollen germination, pollen tube growth, ovulefertilization, and embryo development is halted at one of its stages, and consequently no seeds are produced. SI is one of the most important means to prevent selfing and promote the generation of new genotypes in plants, and it is considered as one of the causes for the spread and success of the angiosperms on the earth.

2.0 Objectives

At the end of this unit you should be able to :

- Define Self-incompatibility
- Discuss the mechanism of Self-incompatibility

3.0 Mechanisms of self-incompatibility

The best studied mechanisms of SI act by. These mechanisms are based on protein-protein interactions, each mechanism being controlled by a single locus termed S, which has many different alleles in the species population. Despite their similar morphological and genetic manifestations, these mechanisms have evolved independently, and are based on different cellular components; therefore, each mechanism has its own, unique S-genes.

The S-locus contains two basic protein coding regions - one expressed in the pistil, and the other in the anther and/or pollen (referred to as the female and male determinants, respectively). Because of their physical proximity, these are genetically linked, and are inherited as a unit. The units are called S-haplotypes. The translation products of the two regions of the S-locus are two proteins which, by interacting with one another, lead to the arrest of pollen germination and/or pollen tube elongation, and thereby generate an SI response, preventing fertilization. However, when a female determinant interacts with a male determinant of a different haplotype, no SI is created, and fertilization ensues. This is a simplistic description of the general mechanism of SI, which is more complicated, and in some species the S-haplotype contains more than two protein coding regions.

Following is a detailed description of the different known mechanisms of SI in plants.

3.1 Gametophytic self-incompatibility (GSI)

In **gametophytic self-incompatibility (GSI)**, the SI phenotype of the pollen is determined by its own gametophytichaploid genotype. This is the more common type of SI, existing in the families: Solanaceae, Rosaceae, Plantaginaceae, Fabaceae, Onagraeae, Campanulaceae, Papaveraceae and Poaceae. Two different mechanisms of GSI have been described in detail at the molecular level, and their description follows

The RNase mechanism

The female component of GSI in the Solanaceae was found in 1989. Proteins in the same family were subsequently discovered in the Rosaceae and Plantaginaceae. Despite some early doubts about the common ancestry of GSI in these distantly related families, phylogenetic studies and the finding of shared male determinants (F-box proteins)clearly established homology. Consequently, this mechanism arose approximately 90 million years ago, and is the inferred ancestral state for approximately 50% of all plants.

In this mechanism, pollen tube elongation is halted when it has proceeded approximately one third of the way through the style. The female component ribonuclease, termed S-RNase probably causes degradation of the ribosomal RNA (rRNA) inside the pollen tube, in the case of identical male and female S alleles, and consequently pollen tube elongation is arrested, and the pollen grain dies.

The male component was only recently putatively identified as a member of the "F-box" protein family. Despite some fairly convincing evidence that it may be the male component, several features also make it an unlikely candidate.

3.1.1 The S-glycoprotein mechanism

The following mechanism was described in detail in *Papaverrhoeas*. In this mechanism, pollen growth is inhibited within minutes of its placement on the stigma.

The female determinant is a small, extracellular molecule, expressed in the stigma; mthe identity of the male determinant remains elusive, but it is probably some cell membranereceptor. The interaction between male and female determinants transmits a cellular signal into the pollen tube, resulting in strong influx of calciumcations; this interferes with the intracellular concentration gradient of calcium ions which exists inside the pollen tube, essential for its elongation.The influx of calcium ions arrests tube elongation within 1-2 minutes. At this stage, pollen inhibition is still reversible, and elongation can be resumed by applying certain manipulations, resulting in ovule fertilization.

Subsequently, the cytosolic protein **p26**, a pyrophosphatase, is inhibited by phosphorylation, possibly resulting in arrest of synthesis of molecular building blocks, required for tube elongation. There is depolymerization and reorganization of actin filaments, within the pollen cytoskeleton. Within 10 minutes from the placement on the stigma, the pollen is committed to a process which ends in its death. At 3-4 hours past pollination, fragmentation of pollen DNAbegins,and finally (at 10-14 hours), the cell dies apoptotically.

3.1.2 Sporophytic self-incompatibility (SSI)

In **sporophytic self-incompatibility (SSI)**, the SI phenotype of the pollen is determined by the diploid genotype of the anther (the sporophyte) in which it was created. This form of SI was identified in the families: Brassicaceae, Asteraceae, Convolvulaceae, Betulaceae, Caryophyllaceae, Sterculiaceae and Polemoniaceae.

Up to this day, only one mechanism of SSI has been described in detail at the molecular level, in *Brassica* (Brassicaceae).

Since SSI is determined by a diploid genotype, the pollen and pistil each express the translation products of two different alleles, i.e. two male and two female determinants. Dominance relationships often exist between pairs of alleles, resulting in complicated patterns of compatibility/self-incompatibility. These dominance relationships also allow the generation of individuals homozygous for a recessive S allele.

Compared to a population in which all S alleles are co-dominant, the presence of dominance relationships in the population, raises the chances of compatible mating between individuals. The frequency ratio between recessive and dominant S alleles, reflects a dynamic balance between reproduction assurance (favoured by recessive alleles) and avoidance of selfing (favoured by dominant alleles).

3.1.3 The SI mechanism in *Brassica*

As previously mentioned, the SI phenotype of the pollen is determined by the diploid genotype of the anther. In *Brassica*, the pollen coat, derived from the anther's tapetumtissue, carries the translation products of the two S alleles. These are small, cysteine-rich proteins. The male determinant is termed **SCR** or **SP11**, and is expressed in the anther tapetum (i.e. sporophytically), as well as in the microspore and pollen (i.e. gametophytically).There are possibly up to 100 polymorphs of the S-haplotype in Brassica, and within these there is a dominance hierarchy.

The female determinant of the SI response in *Brassica*, is a transmembrane protein termed **SRK**, which has an intracellular kinase domain, and a variable extracellular domain. SRK is expressed in the stigma, and probably functions as a receptor for the SCR/SP11 protein in the pollen coat. Another stigmatic protein, termed **SLG**, is highly similar in sequence to the SRK protein, and seems to function as a co-receptor for the male determinant, amplifying the SI response.

The interaction between the SRK and SCR/SP11 proteins results in autophosphorylation of the intracellular kinase domain of SRK, and a signal is transmitted into the papilla cell of the stigma. Another protein essential for the SI response is **MLPK**, a serine-threonine kinase, which is anchored to the plasma membrane from its intracellular side. The downstream cellular and molecular events, leading eventually to pollen inhibition, are poorly described.

IN-TEXT QUESTION

Define Self-incompatibility (SI)

Answer: *The inability to produce zygotes after self-pollination in a fertile hermaphrodite plant*

3.1.4 Other mechanisms of self-incompatibility

These mechanisms are less abundant and have received only limited attention in scientific research. Therefore, they are still poorly understood.

3.2 Heteromorphic self-incompatibility

A distinct SI mechanism exists in heterostylous flowers, termedheteromorphic self-incompatibility. This mechanism is probably not evolutionarily related to the more familiar mechanisms, which are differentially defined as homomorphic self-

incompatibility .Almost all heterostylous taxa feature SI to some extent. The loci responsible for SI in heterostylous flowers, are strongly linked to the loci responsible for flower polymorphism, and these traits are inherited together. Distyly is determined by a single locus, which has two alleles; tristyly is determined by two loci, each with two alleles. Heteromorphic SI is sporophytic, i.e. both alleles in the male plant, determine the SI response in the pollen. SI loci always contain only two alleles in the population, one of which is dominant over the other, in both pollen and pistil. Variance in SI alleles parallels the variance in flower morphs, thus pollen from one morph can fertilize only pistils from the other morph. In tristylous flowers, each flower contains two types of stamens; each stamen produces pollen capable of fertilizing only one flower morph, out of the three existing morphs.

A population of a distylous plant contains only two SI genotypes: ss and Ss. Fertilization is possible only between genotypes; each genotype cannot fertilize itself. This restriction maintains a 1:1 ratio between the two genotypes in the population; genotypes are usually randomly scattered in space. Tristylous plants contain, in addition to the S locus, the M locus, also with two alleles.The number of possible genotypes is greater here, but a 1:1 ratio exists between individuals of each SI type.

3.3 Cryptic self-incompatibility (CSI)

Cryptic self-incompatibility (CSI) exists in a limited number of taxa (for example, there is evidence for CSI in *Silene vulgaris*, Caryophyllaceae. In this mechanism, the simultaneous presence of cross and self pollen on the same stigma, results in higher seed set from cross pollen, relative to self pollen. However, as opposed to 'complete' or 'absolute' SI, in CSI, self-pollination without the presence of competing cross pollen, results in successive fertilization and seed set; in this way, reproduction is assured, even in the absence of cross-pollination. CSI acts, at least in some species, at the stage of pollen tube elongation, and leads to faster elongation of cross pollen tubes, relative to self pollen tubes. The cellular and molecular mechanisms of CSI have not been described.

The strength of a CSI response can be defined, as the ratio of crossed to selfed ovules, formed when equal amounts of cross and self pollen, are placed upon the stigma.

3.4 Late-acting self-incompatibility (LSI)

Late-acting self-incompatibility (LSI) is also termed ovarian self-incompatibility (OSI). In this mechanism, self pollen germinates and reaches the ovules, but no fruit is set. LSI can be pre-zygotic (e.g. deterioration of the embryo sac prior to pollen tube entry, as in *Narcissus triandrus*) or post-zygotic (malformation of the zygote or embryo, as in certain species of *Asclepias* and in *Spathodeacampanulata*.

The existence of the LSI mechanism among different taxa and in general, is subject for scientific debate. Criticizers claim, that absence of fruit set is due to genetic defects (homozygosity for lethal recessive alleles), which are the direct result of self-fertilization (inbreeding depression).Supporters, on the other hand, argue for the existence of several basic criteria, which differentiate certain cases of LSI from the inbreeding depression phenomenon.

3.5 Self-compatibility (SC)

SI is not universal in flowering plants. Indeed, a great many species are **self-**compatible (SC). The best estimates indicate that approximately one half of angiosperm species are SI. Pollinator decline, variability in pollinator service, and life history traits that are associated with weediness, and the so-called "automatic advantage" of self-fertilisation, among other factors, may favor the loss of SI. As a result, mutations that break down SI (result in SC) may become common or entirely dominate in natural populations. Similarly, human-mediated artificial selection through selective breeding may be responsible for the commonly observed SC in cultivated plants. SC enables more efficient breeding techniques to be employed for crop improvement.

4.0 Summary

Self-incompatibility (SI) is a genetic mechanisms in angiosperms, which prevent self-fertilization and thus encourage outcrossing. In plants with SI, the process of pollen germination, pollen tube growth, ovulefertilization, and embryo development is halted at one of its stages, and consequently no seeds are produced.SI is one of the most important means to prevent selfing and promote the generation of new genotypes in plants.This is achieved by inhibiting the germination of pollen on stigmas, or the elongation of the pollen tube in the styles. These mechanisms are based on protein-protein interactions, each being controlled by a single locus termed S, with many different alleles in the species population.These mechanisms have evolved independently, and are based on different cellular components thus, each mechanism has its own, unique S-genes.

5.0 Conclusion

Self Incompatibility (SI) is one of the most important means to prevent selfing and promote the generation of new genotypes in plants, and it is considered as one of the causes for the spread and success of the angiosperms on the earth.

6.0 Self-assessment Assignments

1. Enumerate the role of self-incompatibility in the evolution of plants

7.0 Tutor marked assessment

1. Differentiate between gametophytic and sporophytic self-incompatibility

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Unit 6 : Cytoplasmic male sterility

1.0 Introduction

Cytoplasmic male sterility is the total or partial male sterility associated with plant

biology as the result of specific nuclear and mitochondrial interactions. Male sterility is the failure of plants to produce functional anthers, pollen, or male gametes.

2.0 Objectives

At the end of this unit you should be able to

- Explain the concept of male sterility
- Discuss cytoplasmic male sterility
- Discuss cytoplasmic-genetic male sterility
- Differentiate between cytoplasmic male sterility and cytoplasmic-genetic male sterility

3.0 Male sterility

The first documentation of male sterility came in Joseph Gottlieb Kölreuter observed anther abortion within species and specific hybrids. Cytoplasmic male sterility has now been identified in over 150 plant species. It is more prevalent than female sterility, either because the male sporophyte and gametophyte are less protected from the environment than the ovule and embryo sac, or because it results from natural selection on mitochondrial genes which are maternally inherited and are thus not concerned with pollen production. Male sterility is easy to detect because a large number of pollen grains are produced and are easily studied. Male sterility is assayed through staining techniques (carmine, lactophenol or iodine); while detection of female sterility is detectable by the absence of seeds. Male sterility has propagation potential in nature since it can still set seed and is important for crop breeding, while female sterility does not. Male sterility can be aroused spontaneously via mutations in nuclear and/or cytoplasmic genes.

Male sterility can be either cytoplasmic or cytoplasmic-genetic. Cytoplasmic male sterility (CMS) is caused by the extranuclear genome (mitochondria or chloroplast) and shows maternal inheritance. Manifestation of male sterility in CMS may be either entirely controlled by cytoplasmic factors or by the interaction between cytoplasmic and nuclear factors.

Cytoplasmic male sterility, as the name indicates, is under extra-nuclear genetic control (under the control of the mitochondrial or plastid genomes). They show non-Mendelian inheritance and are under the regulation of cytoplasmic factors. In this type, male sterility is inherited maternally. In general there are two types of cytoplasm: N (normal) and the aberrant S (sterile) cytoplasms. These types exhibit reciprocal differences.

3.1 Cytoplasmic-genetic male sterility

While CMS is controlled by an extranuclear genome often times nuclear genes can have the capability to restore fertility. When nuclear restorations of fertility genes (“Rf”) are available for CMS system in any crop, it is cytoplasmic-genetic male sterility; the sterility is manifested by the influence of both nuclear (Mendelian inheritance) and cytoplasmic (maternally inherited) genes. There are also restorers

of fertility (*Rf*) genes, which are distinct from genetic male sterility genes. The *Rf* genes do not have any expression of their own unless the sterile cytoplasm is present. *Rf* genes are required to restore fertility in S cytoplasm which causes sterility. Thus N cytoplasm is always fertile and S cytoplasm with genotype *Rf*- produces fertiles; while S cytoplasm with *rfrf* produces only male steriles. Another feature of these systems is that *Rf* mutations (*i.e.*, mutations to *rf* or no fertility restoration) are frequent, so N cytoplasm with *Rfrf* is best for stable fertility.

Cytoplasmic-genetic male sterility systems are widely exploited in crop plants for hybrid breeding due to the convenience to control the sterility expression by manipulating the gene–cytoplasm combinations in any selected genotype. Incorporation of these systems for male sterility evades the need for emasculation in cross-pollinated species, thus encouraging cross breeding producing only hybrid seeds under natural conditions.

3.2 Cytoplasmic male sterility in hybrid breeding

Hybrid production requires a female plant in which no viable male gametes are borne. Emasculation is done to make a plant devoid of pollen so that it is made female. Another simple way to establish a female line for hybrid seed production is to identify or create a line that is unable to produce viable pollen. This male sterile line is therefore unable to self-pollinate, and seed formation is dependent upon pollen from the male line.

Cytoplasmic male sterility is used in hybrid seed production. In this case, the sterility is transmitted only through the female and all progeny will be sterile. This is not a problem for crops such as onions or carrots where the commodity harvested from the F1 generation is produced during vegetative growth. These CMS lines must be maintained by repeated crossing to a sister line (known as the maintainer line) that is genetically identical except that it possesses normal cytoplasm and is therefore male fertile. In cytoplasmic-genetic male sterility restoration of fertility is done using restorer lines carrying nuclear restorer genes in crops. The male sterile line is maintained by crossing with a maintainer line which has the same genome as that of the MS line but carrying normal fertile cytoplasm.

IN-TEXT QUESTION

What is the difference between genetic male sterility and cytoplasmic male sterility?

Answer *Genetic male sterility occurs due to genome mutations, while cytoplasmic male sterility occurs due to cytoplasmic and nuclear factors*

3.3 Cytoplasmic male sterility in hybrid maize breeding

Cytoplasmic male sterility is an important part of hybrid maize production. The first commercial cytoplasmic male sterile, discovered in Texas, is known as CMS-T. The use of CMS-T, starting in the 1950s, eliminated the need for detasseling. In the early 1970's plants containing CMS-T genetics were susceptible to southern corn leaf blight and suffered from widespread loss of yield. Since then CMS types C and S are used instead.Unfortunately these types are prone to environmentally induced fertility restoration and must be carefully monitored in the field. Environmentally induced restoration is when certain environmental stimuli signal the plant to bypass sterility restrictions and produce pollen anyway. Environmentally induced restoration differs from genetic restoration in that it is rooted in external signals rather than genetic DNA.The systematic sequencing of new plant species in recent years has uncovered the existence of several novel RF genes and their encoded proteins. A unified nomenclature for the RF extended protein families across all plant species, fundamental in the context of comparative functional genomics. This unified nomenclature accommodates functional RF genes and pseudogenes, and offers the flexibility needed to incorporate additional RFs as they become available in future.

4.0 Summary

Male sterility is the failure of plants to produce functional anthers, pollen, or male gametes.Cytoplasmic male sterility is the total or partial male sterility as the result of specific nuclear and mitochondrial interactions. It is prevalent in males because the male sporophyte and gametophyte are less protected from the environment than the ovule and embryo sac, and the natural selection on mitochondrial genes which are maternally inherited and are thus not concerned with pollen production. Cytoplasmic male sterility is used in hybrid seed production

5.0 Conclusion

Cytoplasmic male sterility is used in hybrid seed production.

6.0 Self-assessment Assignments

1. Differentiate between cytoplasmic male sterility and cytoplasmic-genetic male sterility

7.0 Tutor Marked Assessment

1. Discuss the role of cytoplasmic male sterility in hybrid maize breeding

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Unit 7 Breeding methods

1.0 Introduction

The mode of reproduction of a crop determines its genetic composition, which, in turn, is the deciding factor to develop suitable breeding and selection methods. Knowledge of mode of reproduction is also essential for its artificial manipulation to breed improved types. Only those breeding and selection methods are suitable for a crop which does not interfere with its natural state or ensure the maintenance of such a state. It is due to such reasons that imposition of self-fertilization on cross-pollinating crops leads to drastic reduction in their performance.

2.0 Objectives

By the end of this unit you should be able to**:**

- Outline 4 modes of reproduction
- Explain at least 4 methods of selection of plants

3.0 Mode of reproduction

For the purpose of this study, we shall present plant breeding methods as four categories: Line breeding (autogamous crops), population breeding (allogamous crops), hybrid breeding (mostly allogamous crops, some autogamous crops), clone breeding (vegetatively propagated crops).

3.1 Self fertilizing crops or autogamous crops.

Certain restrictions caused the mechanisms for self fertilization (partial and full self fertilization) to develop in a number of plant species. Some of the reasons why a self fertilizing method of reproduction is so effective are the efficacy of reproduction, as well as decreasing genetic variation and thus the fixation of highly adapted genotypes. Almost no inbreeding depression occurs in self fertilizing plants because the mode of reproduction allows natural selection to take place in wild populations of such plants.

Critical steps in the improvement of self fertilizing crops are the choice of parents and the identification of the best plants in segregating generations. The breeder should also have definite goals with the choice of parents. Self fertilizing are easier to maintain, but this could lead to misuse of seed.

Some farm and domestic important, self fertilizing crops include rice, maize, Sorghum, Millets, cowpea beans, soy beans, groundnuts, potatoes and tomatoes, etc.

3.2 Mass selection

This method of selection depends mainly on selection of plants according to their phenotype and performance. The seed from selected plants are bulked for the next generation. This method is used to improve the overall population by positive or negative mass selection. Mass selection is only applied to a limited degree in self fertilizing plants and is an effective method for the improvement of land races. This method of selection will only be effective for highly heritable traits. One shortage of mass selection are the large influence that the environment has on the development, phenotype and performance of single plants.

A plant developed by this method will be more uniform than those developed by mass selection because all of the plants in such a variety will have the same genotype. The seed from selected plants are not added together but are kept apart and used to perform offspring tests. This is done to study the breeding behaviour of the selected plant.

Stratified mass selection for ear size over 22 cycleshas drastically altered plant phenotype in the maize population Zacatecas 58. Plants in the C22 cycle were 50 cm taller, had twice the leaf area index, reached anthesis 7 days later and had a 30% higher harvest index than C0. Differences in growth were detected early in ontogeny. The root growth of C22 exceeded that of C0 and the ratio of shoot dry mass to root dry mass was reduced by nearly 12%, from 8.0±0.2 to 7.1±0.1. Analysis of yield components revealed that C22 was superior to C0 in grain weight, number of rows per ear, number of grains per row, and total yield per unit area. Because the two genotypes were phenologically different, planting density optima are probably different for each population.

IN-TEXT QUESTION

What is autogamy?

***Answer**: It is a type of pollination in which pollen from the anthers of a flower is transmitted to the stigma of the same flower (Self- pollination)*

3.3 Selection of cross-pollinated crops

Plant species where normal mode of seed set is through a high degree of cross-pollination have characteristic reproductive features and population structure. Existence of self-sterility, self-incompatibility, imperfect flowers, and mechanical obstructions make the plant dependent upon foreign pollen for normal seed set. Each plant receives a blend of pollen from a large number of individuals each having different genotypes. Such populations are characterized by a high degree of heterozygosity with tremendous free and potential genetic variation, which is

maintained in a steady state by free gene flow among individuals within the populations.

In the development of hybrid varieties, the aim is to identify the most productive heterozygote from the population, which then is produced with the exclusion of other members of the population.

3.4 Mass selection

It is the simplest, easiest and oldest method of selection where individual plants are selected based on their phenotypic performance, and bulk seed is used to produce the next generation by mixing it. Mass selection proved to be quite effective in maize improvement at the initial stages but its efficacy especially for improvement of yield, soon came under severe criticism that culminated in the refinement of the method of mass selection. The selection after pollination does not provide any control over the pollen parent as result of which effective selection is limited only to female parents. The heritability estimates are reduced by half, since only parents are used to harvest seed whereas the pollen source is not known after the cross pollination has taken place.

3.5 Recurrent selection

This type of selection is a refined version of the mass selection procedure and differs as follows:

- Visually selected individuals out of the base population undergo progeny testing
- Individuals selected on basis of the progeny test data are crossed with each other in every possible way to produce seed to form the new base population.

3.5.1 Half-sib selection with progeny testing

Selections are made based on progeny test performance instead of phenotypic appearance of the parental plants. Seed from selected half-sibswhich have been pollinated by random pollen from the population, is grown in unreplicated progeny rows for the purpose of selection. A part of the seed is planted to determine the yielding ability, or breeding value, for any character of each plant. The seed from the most productive rows or remnant seed from the outstanding half-sibs is bulked to complete one cycle of selection.

3.5.2 Full-sib selection with progeny testing

A number of full-sib families, each produced by making crosses between the two plants from the base population are evaluated in replicated trials. A part of each full-sib family is saved for recombination. Based on evaluation the remnant seed of

selected full-sib families is used to recombine the best families.

3.6 Breeding of Asexually Propagated Crops

Asexual reproduction covers all those modes of multiplication of plants where normal gamete formation and fertilization does not take place making these distinctly different from normal seed production crops. In the absence of sexual reproduction, the genetic composition of plant material being multiplied remains essentially the same as its source plant.

Clones of mother plants can be made with the exact genetic composition of the mother plant. Superior plants are selected and propagated vegetatively; the vegetative propagated offspring are used to develop stable varieties without any deterioration due to segregation of gene combinations. This unique characteristic of asexual reproduction helped to develop a number of cultivars of fruits and vegetables including grapes, apples, pears and peaches.

3.6.1 Improving asexual plant material through selection

The selection in these crops is restricted to the material introduced from other sources, such as field plantations. The improvement of asexually propagated plants through induced mutations has distinct advantages and limitations. Any vegetative propagule can be treated with mutagens and even a single desirable mutant or a part of a mutated propagule (chimera) can be multiplied as an improved type of the original variety.

3.6.2 Selection of asexual plants

Selection, in the case of asexual plants, can be defined as the selection of the best performing plant and the vegetative propagation thereof. Because plants are not totally genetically stable, it can be expected that deviations would occur through the years. Selection is thus an ongoing process where deviants are selected or removed from the selection program. The main purpose of selection is to better the quality and yield of forthcoming plantations. Different approaches can be followed in the selection process of asexual plants, such as mass selection and clone selection from clone blocks.

In mass selection there are some factors that must be considered when selecting plants in a mother block, e.g. vineyard. Time of selection is a big factor, because you have to select when most of the characteristics of the plant are clearly showing. With asexual perennials the best time is just before harvest. For the best results the

selected plant must be evaluated during the next season, when growth-abnormalities, leave disfigurations and virus symptoms are best visualized. Mass selection is done annually on the same plant for a minimum of three years. A plant that does not conform to the requirements in any given year of the selection cycle is discarded from the program.

3.6.3 New clone development

The development and registration of new clones take place by means of local clone selection in old plantations, as well as the importation of high quality clones from abroad, for local evaluation.

A clone is the vegetative offspring of one specific mother plant; it does not show any genetic, morphologic or physiologic deviations from the mother plant. Evaluation takes place with the different selected clones after selection.Some plants reproduce by (more or less strict) self-fertilization where pollen from a plant will fertilise reproductive cells or ovules of the same plant. Other plants only (mainly) allow cross-pollination where pollen from one plant can only fertilize a different plant.

Asexual propagation (vegetative propagation) can also occur in plants (e.g. runners from sweet potato *Ipomea batatas* plant or suckers from Plantains or bananas *Musa spp.*) which gives a new plant which is genetically identical to its parent plant. All these differences change the way plant breeders work. Apomixis is the phenomenon that seeds are produced, but in an essentially asexual way, so that parent and offspring belong to one clone just as in case of 'normal' asexual propagation.

4.0 Summary

Plant breeding methods are in four categories: Line breeding (autogamous crops), population breeding (allogamous crops), hybrid breeding (mostly allogamous crops, some autogamous crops) and clone breeding (vegetatively propagated crops). To develop suitable breeding and selection methods the knowledge of the mode of reproduction is essential for its artificial manipulation to breed improved types.

5.0 Conclusion

Breeding and selection methods are suitable for a crop production to ensure food security.

6.0 Self-assessment Assignments

1. Differentiate between autogamous, allogamous and clonal crops. Give specific examples
2. Explain the breeding procedures for self pollinating and cross pollinating crops

7 .0 Tutor marked assessment

1. Write concise notes on:

    i. Recurrent selection
    ii. Mass selection
    iii. Progeny testing

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UNIT 8 Disease and pest resistance and their inheritance

8.0. Plant Breeding for Disease Resistance

1.0 Introduction

Plant breeders focus a significant part of their effort on selection and development of disease-resistant plant lines. Plant diseases can also be partially controlled by use of pesticides, and by cultivation practices such as crop rotation, tillage, planting density, purchase of disease-free seeds and cleaning of equipment, but plant varieties with inherent (genetically determined) disease resistance are generally the first choice for disease control. Breeding for disease resistance has been underway since plants were first domesticated, but it requires continual effort. This is because pathogen populations are often under natural selection for increased virulence, new pathogens

can be introduced to an area, cultivation methods can favor increased disease incidence over time, changes in cultivation practice can favor new diseases, and plant breeding for other traits can disrupt the disease resistance that was present in older plant varieties. A plant line with acceptable disease resistance against one pathogen may still lack resistance against other pathogens .

2.0 Objectives

By the end of this unit you should be able to:

Explain aspects of plant breeding for disease resistance

3.0 Plant breeding for disease resistance typically includes:

- Identification of resistant breeding sources (plants that may be less desirable in other ways, but which carry a useful disease resistance trait). Ancient plant varieties and wild relatives are very important to preserve because they are the most common sources of enhanced plant disease resistance.
- Crossing of a desirable but disease-susceptible plant variety to another variety that is a source of resistance, to generate plant populations that mix and segregate for the traits of the parents.
- Growth of the breeding populations in a disease-conducive setting. This may require artificial inoculation of pathogen onto the plant population. Careful attention must be paid to the types of pathogen isolates that are present, as there can be significant variation the effectiveness of resistance against different isolates of the same pathogen species.

- Selection of disease-resistant individuals. It is essential to note that breeders are trying to sustain or improve numerous other plant traits related to plant yield and quality, including other disease resistance traits, while they are breeding for improved resistance to any particular pathogen.

Each of the above steps can be difficult to successfully accomplish, and many highly refined methods in plant breeding and plant pathology are used to increase the effectiveness and reduce the cost of resistance breeding.

Resistance is termed durable if it continues to be effective over multiple years of widespread use, but some resistance "breaks down" as pathogen populations evolve to overcome or escape the resistance. Resistance that is specific to certain races or strains of a pathogen species is often controlled by single R genes and can be less durable; broad-spectrum resistance against an entire pathogen species is often quantitative and only incompletely effective, but more durable, and is often controlled by many genes that segregate in breeding populations. However, there are numerous exceptions to the above generalized trends, which were given the names vertical resistance and horizontal resistance, respectively, by J.E. Vanderplank.

Crops such as potato, apple, banana and sugarcane are often propagated by vegetative reproduction to preserve highly desirable plant varieties, because for these species, outcrossing seriously disrupts the preferred plant varieties. See also asexual propagation. Vegetatively propagated crops may be among the best targets for resistance improvement by the biotechnology method of plant transformation to add individual genes that improve disease resistance without causing large genetic disruption of the preferred plant varieties.

3.1 Host Range

There are thousands of species of plant pathogenic microorganisms. Only a small minority of these pathogens have the capacity to infect a broad range of plant species. Most pathogens instead exhibit a high degree of host-specificity. Non-host plant species are often said to express non-host resistance. The term host resistance is used when a pathogen species can be pathogenic on the host species but certain strains of that plant species resist certain strains of the pathogen species. There can be overlap in the causes of host resistance and non-host resistance. Pathogen host range can change quite suddenly if, for example, the capacity to synthesize a host-specific toxin or effector is gained by gene shuffling/mutation, or by horizontal gene transfer from a related or relatively unrelated organism.

3.2 Epidemics and Population Biology

Plants in native populations are often characterized by substantial genotype diversity and dispersed populations (growth in a mixture with many other plant species). They also have undergone millions of years of plant-pathogen coevolution. Hence as long as novel pathogens are not introduced from other parts of the globe, natural plant populations generally exhibit only a low incidence of severe disease epidemics. In agricultural systems, humans often cultivate single plant species at high density, with numerous fields of that species in a region, and with significantly reduced genetic diversity both within fields and between fields. In addition, rapid travel of people and cargo across large distances increases the risk of introducing pathogens against which the plant has not been selected for resistance. These factors make modern agriculture particularly prone to disease epidemics. Common solutions to this

problem include constant breeding for disease resistance, use of pesticides to suppress recurrent potential epidemics, use of border inspections and plant import

restrictions, maintenance of significant genetic diversity within the crop gene pool. Crop diversity, and constant surveillance for disease problems to facilitate early initiation of appropriate responses. Some pathogen species are known to have a much greater capacity to overcome plant disease resistance than others, often because of their ability to evolve rapidly and to disperse broadly.

In -Text Question
What does the term Host Range mean?
***Answer**: The breath of organisms a parasite is capable of infecting.*

3.3 Epidemic

In epidemiology, an **epidemic** (epi- meaning "upon or above" and demic- meaning "people"), occurs when new cases of a certain disease, in a given human population, and during a given period, substantially exceed what is "expected," based on recent experience (the number of new cases in the population during a specified period of time is called the "incidence rate"). (An epizootic is the analogous circumstance within an animal population.) In recent usages, the disease is not required to be communicable; examples include cancer or heart disease. Another example includes the infamous Black Plague of the Middle Ages.

3.3.1 Classification

Defining an epidemic can be subjective, depending in part on what is "expected". An epidemic may be restricted to one locale (an outbreak), more general (an "epidemic") or even global (pandemic). Because it is based on what is "expected" or thought normal, a few cases of a very rare disease may be classified as an "epidemic," while many cases of a common disease (such as the common cold) would not.

3.3.2 Syndemics

The term syndemic refers to interacting epidemics that increase the health burden of affected populations. Social conditions that heighten the health risk of populations (e.g. poverty, discrimination and stigmatization, and marginalization) by increasing stress, malnutrition, interpersonal violence, and the experience of deprivation, increase the clustering of epidemic diseases and the likelihood of their interacting.

3.3.3 Non-infectious disease usage

The term "epidemic" is often used in a sense to refer to widespread and growing societal problems, for example, in discussions of obesity or drug addiction. It can also be used metaphorically to relate a type of problem like those mentioned above.

3.3.4 Factors stimulating new epidemics

Factors that have been described to stimulate the rise of new epidemics include:

1. Alterations in agricultural practices and land usage
2. Changes in society and human demographics
3. Poor population health (e.g., malnutrition, high prevalence of HIV)
4. Hospitals and medical procedures

5. Evolution of the pathogen (e.g., increased virulence, drug resistance)
6. Contamination of water supplies and food sources
7. International travel
8. Failure of public health programs
9. International trade
10. Climate change
11. Reduced levels of biodiversity (e.g. through environmental destruction)
12. Bad urban planning

3.4 Breeding for pest resistance

3.4.1 Resistance Breeding Before Mendel

Wild relatives of crop plants such as beans, wheat, and maize are not uniformly resistant to insect and disease pests. This can be demonstrated in simple fashion—when selections of these wild populations are set out in plant-rows, some of them are highly susceptible, others are resistant, and some are intermediate in resistance to the common pests of the region. The first plant breeders, those women and men who domesticated crops such as beans, maize, and wheat, could save only those genotypes that had some level of resistance, i.e., those individual plants that did not succumb to pest depredation. In effect, therefore, they selected for pest resistance and thus changed the population structure of their crop species in favor of resistance genes. This change made it possible to grow the crops in monoculture, which was convenient for food production and harvest. It was also convenient for multiplication of disease and insect pests that might not be affected by the limited sample of resistance genes.

Plant breeding thus set the stage for sequential cycles of pest resistance and pest susceptibility of crop plants. We have no direct record of the consequences of this ancient ecological meddling, but myth and historical accounts tell of disastrous disease epidemics and insect outbreaks, so one can assume that from time to time large plantings of crops that were uniformly susceptible to a new kind of insect or disease fostered increases of that pest to epidemic proportions. Resistance genes were essential for crop domestication and monoculture but they did not guarantee perfect safety.

We have no record at all and little or no speculation about how the newly domesticated crops might have affected their wild relatives, which no doubt were growing in close proximity to the domesticates.

3.4.2 Resistance Breeding After Mendel

Genetics-based plant breeding, launched in the early years of the 20th century, produced new crop varieties with improved resistance to major disease and insect pests. Usually such resistance was developed as a second phase—a rescue operation—after new varieties, selected primarily for high yield, were discovered to be susceptible to a particular insect or disease. Breeders found early on that they could identify single genes (usually dominant) that conferred essentially complete resistance to the pest in question. Varieties containing such excellent resistance were developed and released for large-scale farmer use. But breeders then discovered, all too often, that the "perfect" resistance lost its effectiveness after a few seasons. They soon learnt, with the aid of entomologists and plant pathologists, that insect and disease pests are highly diverse genetically, and that almost without fail a

rare pest genotype will turn up (or perhaps be created de novo by natural mutation) that is not affected by the newly-deployed resistance gene. The new pest genotype multiplies and the crop variety's resistance "breaks down."

As years went by, breeders found that some kinds of resistance did not fail, and that such resistance often was less than complete; the plants suffered some damage but gave performance overall. This longer lasting resistance was dubbed "durable" resistance. Further, the breeders discovered that durable resistance usually (but not always) was governed by several genes rather than by one major gene. The

multifactorial kind of resistance has been called "horizontal resistance." The major-gene resistance has been called "vertical resistance."

The good news, then, was that breeders could identify and breed for durable resistance. The bad news was that the breeding was more difficult because several genes had to be transferred at one time, thus requiring larger populations for selection, as well as multiplying the usual problems with "linkage drag" (undesirable genes that are tightly linked to the desired ones). To this day, breeders use both kinds of resistance in varying proportions, according to the crop and where it is grown.

At first, breeders found and used resistance genes from the adapted, local landrace populations that also were the initial gene pool as a source of resistance genes for their new varieties. As years went by, these gene pools began to dry up and breeders looked further afield, turning to exotic (unadapted) landraces, and even to wild relatives of their crop. Sometimes they made extraordinary efforts to hybridize the domestic crop with a very distant wild relative—making a cross that could not succeed under natural conditions. Embryo rescue and even x-ray treatments were used to make "unnatural" crosses and derive breeding progeny from them. The breeders fooled around with Mother Nature; they moved genes farther than natural processes would allow.

But the breeders as a whole preferred to not breed from exotic varieties or distant and often wild relatives. They used exotic material only when there was no other choice. This preference was due not only to the difficulty of wide hybridization, but also to the fact that exotic germplasm exacerbates the problem of undesirable linkages. Few or none of the foreign genes—except the desired resistance genes—were suitable for the needs of high yielding, locally adapted varieties. But often the breeders had no choice; either they got the needed resistance genes from a distant relative, or they got nothing at all.

At about this time, breeders realized that it would be important to conserve remnant seed of landraces from all around the world, but especially from the centers of diversity of their crop. As farming worldwide grew more commercial, farmers turned more and more to professionally bred varieties that were better suited to commercial production, and in so doing they abandoned their landraces. If remnant seed of those landraces was not collected and saved in special storage facilities, the genetic base for crop breeding in the future would be drastically narrowed. Seed "banks" were needed. Through the efforts (especially in the 1960s and 1970s) of a few far- sighted plant breeders, seed banks were established in several countries and in international research centers.

So at the end of the 20th century, plant breeding for pest resistance had laid out the genetic framework of vertical and horizontal resistance, and identified important sources of new resistance genes, i.e., plant germplasm from anywhere in the world. Sources were limited, however, to the crop species itself or its relatives, either wild or cultivated. All of the introduced genes therefore came from plants.

Plant breeders selected not only for tolerance or resistance to disease and insect pests, they also selected for tolerance to abiotic stresses such as heat and drought, cool temperatures, or nutrient imbalance. Much of this selection was involuntary; in selecting varieties with top performance over many seasons and many locations the breeders necessarily selected varieties with tolerance to the prevailing abiotic

stresses of the diverse seasons and localities. In selecting for tolerance to environmental stresses, breeders necessarily changed the genetic makeup of the

crop species, altering it still further from that of the original wild species, which had been restricted to certain environmental niches. Witness teosinte (the probable parent of maize), restricted to certain habitats in Mexico as compared to maize that now is grown in nearly every country of the world except Iceland.

Global distribution of crop plants often means that they are grown with no proximity to wild relatives that might intercross with them. Teosinte is not found in Germany or China, nor for that matter in the US Corn Belt. In other cases, however, wild species with hybridization potential coexist with their cultivated crop relatives, often as weeds. Canola, sunflower, and grain sorghum are examples of crops with hybridization potential with either a related species (canola with wild mustards) or with a weedy form of the same species (sorghum with shattercane, cultivated sunflower with wild sunflower).

3.4.3 Four questions about pest resistance traits

The above discussion shows that plant breeders have changed the genetic composition of crop species to a large degree as they selected for pest resistance and also for resistance to environmental stresses. Such changes are in addition to the major phenotypic changes (e.g., non-shattering, uniform and fast germination) that were a consequence of domestication. What have been the consequences of such alterations, either on the crop species and its near relatives or on the ecosystems in which those species are grown? Experienced plant breeders have addressed this question as they responded to four queries sent to them. The questions were:

1. Have the resistance traits been stable over time?
2. Have they led to undesirable consequences with respect to weediness of the crop or its relatives?
3. What have been the major sources of pest resistance genes as used in classical breeding (e.g., same species, related species, mutation)?
4. Are there relevant differences between the resistance genes currently being engineered into plants and those that have been transferred by conventional breeding?

The summary of the responses from the breeders are stated below:

3.4.4 Have Resistance Traits Been Stable Over Time?

The breeders say that as a general rule, resistance traits governed by major dominant genes have not been stable over time, whereas those governed by several genes have been more durable. But there are exceptions to both statements. One cannot say categorically that single gene resistance will always be undependable, or that multiple factor resistance will always be durable.

It is important to remember that the phrase "stability of resistance" refers to whether or not a previously resistant variety is overcome by a particular species of disease or insect. It does not infer that individual resistance genes lose their power to hold individual pest biotypes in check. The resistance genes are stable, but new (or previously undetected) pest biotypes appear, with types of virulence that are not curbed by the now-outdated resistance genes. The variety succumbs to the disease or insect pest once again, albeit to a new race of the pest, and breeders say that the variety’s resistance was unstable.

3.4.5 Has Introduction of Conventional Resistance Genes Led to Undesirable Consequences with Respect to Weediness of the Crop or Its Relatives?

The breeders know of no undesirable consequences (such as enhanced competitive ability in a related weed species following the unintended transfer of resistance genes from crop to weed) from any introduction of resistance genes into crop plants through classical breeding. Some of the introduced genes have come from very distant relatives, but all have been derived from plants. Chances of introgression from crop species to wild relatives vary by crop. Ease of hybridization and the genetic complexity of transformation from wild to domesticated plant type (or vice versa) are major determinants for the rate and amount of introgression that might be expected. In the US, sunflower and sorghum are highly cross-compatible with related weeds and would be the most likely crops to exhibit undesired movement of pest resistance genes from crop to weed. Breeders, however, have not yet observed this kind of introgression.

3.4.6 What Are the Major Sources of Resistance Genes in Classical Breeding?

The breeders say that resistance genes from within the crop species are preferred when they can be found, because of ease of breeding with them, but they will go far afield if they have to. The practice varies with the crop; e.g., tomato breeders commonly use genes from wild relatives whereas sorghum breeders do not. The amount of genetic diversity within the crop species and its ease of breeding with alien species are major determinants of breeders' actions.

3.4.7 Are There Important Differences Between Classical and Engineered Resistance Genes?

The breeders say that engineered resistance genes now in use appear to have different modes of action than traditional resistance genes, but they point out that we know very little about structure and mode of operation of the traditional genes and so have little basis for sweeping judgments about difference. Further, we have few specifics about how a radically different genetic background might affect expression of a transgene.

Genes for herbicide resistance (the archetype example of potentially dangerous genetic transformation) are not necessarily imparted by means of genetic transformation. Such genes are found within crop species or their relatives, or have been created by means of mutation. These genes, bred into a specific crop variety, theoretically could move from the crop to cross-compatible weed species and impart unwanted herbicide resistance to the weeds. But in order to cause a new problem, resistance genes would have to introgress into weeds that had not contributed the resistance genes in the first place. This example shows how difficult it can be to decide whether or not a given resistance gene in a crop plant will increase competitiveness in weeds or make crop plants into weeds. Presence or absence of genetic engineering is not the major determining factor.

The breeders look to a future generation of engineered plant genes that will provide greater diversity and utility than genes presently available in any one crop. Genes from related taxa, from very distant taxa, or from within the crop species may be altered to provide improved resistance, but they will be plant genes rather than genes from extremely different organisms. It may be difficult to identify the point at which such new genes should be called "unnatural."

Until recently, plant breeders did not worry about how their breeding affected

weeds, or whether their crops could become weeds. Weeds were looked on as potential sources of genes for pest resistance if they could hybridize with crop

species, but almost no one thought about whether or not the population genetics of weeds could be altered by introgression from crop species. A very few students of crop evolution studied the weeds that may have been ancestors of cultivated plants. Plant taxonomists and ecologists usually ignored weeds because they weren't considered as parts of natural ecosystems.

Genetic engineering has changed all of that. If genes from far afield can be added to crop plants, giving them marvelous gains in pest resistance, tolerance of environmental stress, or enhanced seed production, one can imagine that those transgenes could enhance the power of weeds in the same ways.

The analogy may not be as simple as it sounds, however. Two concepts must be clarified and data need to be assembled before one can make firm predictions.

3.4.8 Do crop plants as a class have the same requirements for survival and luxuriance as weeds as a class?

- To consider this question one must lay out the ways in which crop plants and weeds are similar and ways in which they differ.
- Perhaps even before that, one must decide whether it is possible to make a definitive description of crop plants as a class, and another one for weeds as a class.

3.4.9 What is the functional role of resistance genes in weeds as compared to their role in crop plants?

- Will a gene that greatly enhances survival chances for a crop plant perform the same service for a weed? (Crops grow in crowded monocultures; weeds usually grow in dispersed "polycultures.")
- Will the presence or absence of genetic diversity within a crop or weed population, or among crop or weed species in a site, affect the utility of a given resistance gene? (Crop varieties usually are genetically uniform, weed populations are not.)
- Should one distinguish between dangers of imparting genes for resistance to natural restraints, such as disease or insect attack, and resistance to man-made restraints, such as herbicides?
- Do we have any reason to believe that selection for new (or previously undetected) kinds of herbicide resistance in weed species operates on different principles than selection for new (or previously undetected) kinds of virulence in disease or insect species?

The breeders, in answering the above four questions, were considering these two main points and the subsequent questions that they raise. It is possible that they did not want to classify resistance genes into only two categories—natural or engineered. Further, the breeders said we know so little about the molecular nature of resistance genes that we cannot yet categorize them in any meaningful way. It is possible they do not believe that mode of transfer or kingdom of origin is a meaningful classification.

Despite their reluctance to sort genes into "engineered-bad" and "natural-good," the breeders acknowledged that whenever we fool around with Mother Nature we get surprises, some of them bad. Therefore we need to look with caution at any novel breeding technology, predicting possible consequences as well as we can, with the

modicum of data we may have in hand.

We need to know more about the effects of genetic background on gene action. Location within a genome seems important, and the entire genetic background seems important. We have little or no understanding of these interactions.

We need to know more about the consequences of hybridization of crop species with related weeds and the potential for introgression in both directions. Jointed goatgrass hybridizes with common wheat and viable backcross offspring can be produced. Have resistance genes from wheat moved into jointed goatgrass and changed its survival potential? A similar question can be asked for sorghum and shattercane, sunflower and wild sunflower, canola and mustards, or maize and teosinte.

So we must ask ourselves, do we have data to answer either of these key questions—effect of genetic background, or consequences of hybridization—or at the least do we have enough data to let us speculate from a firmer foundation than we have at present?

In my opinion, we have fragments of data for some crops and/or their weed relatives, but rarely do we have enough for firm predictions about gene introgression or about gene action in the genome or the population.

What are the consequences of adding new pest resistance genes to a wild species, either a weed or otherwise? How plentiful and how powerful must the genes be to change the genetic balance of the wild species, make it a stronger weed, transform a non-weed into a weed, or, conversely, reduce the weed's viability as a competing population?

How about the "function" of related weeds as a reservoir of new biotypes of pest species, disease, or insects? Are the weeds more dangerous to crop plants when they lack resistance and so are a constant source of pest infection and infestation? Or are they more threatening when they contain many of the same resistance genes as carried in the crop species and therefore encourage the multiplication of new pest biotypes (biotypes that are not bothered by the weeds' resistance genes)?

The recommendation arising from these questions seems obvious. Whenever a worrisome outcome seems likely but data are too sparse for firm conclusions, scientists need to work hard to fill the void. They need to plan the right experiments, gather the needed data, and publicize the results in both public and specialist media. And the public needs to provide the fundsto support this work, since most of it will need to be done by scientists in public institutions.

Finally, sometimes the odds of a bad outcome from not doing a particular action may be much higher than the odds of a bad outcome from performing that action. Sometimes it may be better to take action with uncertain outcome than to stand still. Life always works on probabilities.

4.0 Summary

Plant diseases can also be partially controlled by use of pesticides, and by cultivation practices. Plant varieties with inherent (genetically determined) disease resistance are generally the first choice for disease control. Breeding for disease resistance has been underway since plants were first domesticated, but it requires continual effort because pathogen populations are often under natural selection for increased

virulence, new pathogens are introduced to an area, cultivation methods can favor increased disease incidence over time, changes in cultivation practice can favor new

diseases, and plant breeding for other traits can disrupt the disease resistance that was present in older plant varieties. Plant breeding for disease resistance typically includes:

- Identification of resistant breeding sources.
- Crossing of a desirable but disease-susceptible plant variety to another variety that is a source of resistance, to generate plant populations that mix and segregate for the traits of the parents.
- Growth of the breeding populations in a disease-conducive setting.
- Selection of disease-resistant individuals.

5.0 Conclusion

Plant diseases can be controlled by selecting and breeding plant resistant species

6.0 Self-assessment Assignments

1. List the components for plant breeding for disease resistance.
2. Distinguish between vertical and horizontal resistance

Tutor marked assessment

1. Identify the specific qualities required for breeding for pest resistance

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