COURSE GUIDE

CRP 512
CROP EVOLUTION AND ADAPTATION

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INTRODUCTION

CPR 512: Crop Evolution and Adaptation is a two-credit unit course for students offering B. Agriculture in the School of Agricultural Science. The course consists of Four (4) modules that are divided into16 units. These units will educate the student that evolution is the force that shapes the living world. He will also be informed that countless different kind of plants pack the earth and each species is itself composed of a wide range of morphologies and adaptations.

The course material has been developed to suit undergraduate students in Agriculture at the National Open University of Nigeria (NOUN) by using an approach that provides the student with requisite knowledge in crop evolution and adaptation. A student who successfully completes the course will know that in its simplest sense, evolution is a change in gene frequency over time. He will also understand that genetic variability is produced by mutation and then shuffled and sorted by the various evolutionary forces. The student will also comprehend the fact that the way organisms evolve is dependent on their genetic characteristics and the type of environment the live in and get adapted to.

The Course Guide tells you briefly what the course is about, what course materials you will be using and how you can work your way through these materials. It suggests some general guidelines for the amount of time you are likely to spend on each unit of the course in order to complete it successfully. It also gives you some guidance on your tutor-Marked assignments. Detailed information on Tutor-Marked Assignment is found in the separate assignment file which will be available in due course.

WHAT YOU WILL LEARN IN THIS COURSE

On successful completion of these modules, you should be able to:

1. State and explain the theory of evolution.
2. Understand and describe the process and mechanics of evolution.
3. Explain the Role of hybridization, recombination and natural selection in crop evolution.
4. Describe isolation mechanism and its contribution to plant speciation.
5. Enumerate different types of speciation and explain the part it plays on the evolution of plant.
6. Discuss the concept of primary and secondary centers of origin of cultivated plants.
7. Know the Origin of commonly cultivated crops
8. Explain the concept of genetic variations and its effect in the population

9. Understand genetic drift and its role in speciation

COURSE AIMS

The course is designed to enable student understand the concept of evolution and the role it plays in shaping crop plants with a wide range of morphologies and adaptations. It will also provide student with the knowledge of adaptation as a dynamic evolutionary process that fits organisms to their environment, enhancing their survival and reproduction in nature.

COURSE OBJECTIVES

The aims of the course stated above can only be realised through a set of objectives. Each unit of this course also has its specific objectives that are enumerated at the beginning. You will need to go through and have a grasp of the objectives before you start working through the unit. You are encouraged to refer to them periodically to check on your progress in learning and assimilating the content. On completion of a unit, you may re-examine the objectives to ensure that you learning has taken place and knowledge was acquired. This will enable your track your progress and assess if the requirement of the unit has been met. Consequent on the above and in line with stated aim, the course has the following specific objectives:

1. Explain the theory of evolution.
2. Know the process and mechanics of evolution.
3. Describe the Role of hybridization, recombination and natural selection in crop evolution.
4. Understand isolation mechanism and its contribution to plant speciation.
5. State different processes of speciation and explain the part it plays on the evolution of plant.
6. Distinguish between primary and secondary centers of origin of cultivated plants.
7. Understand and describe the Origin of commonly cultivated crops
8. Comprehend the concept of genetic variations and its role evolution
9. Know genetic drift and its role in speciation

WORKING THROUGH THE COURSE

To successfully complete this course, you are required to read the study units, reference books and other materials that will guide and assist you achieve the objectives of course. Each unit contains self-assessment exercises in addition to Tutor- Marked Assignment (TMA). The TMA will eventually form part of your continuous assessment; therefore, you will be required to submit the assignment for assessment. At the end of the course there will be a final examination. This course should take about 15 weeks to complete and some components of the course are outlined under the course material subsection.

COURSE MATERIALS

The major components of the course are:

1. Course Guide
2. Study Units
3. Textbooks and References
4. Assignment File
5. Presentation Schedule

STUDY UNITS

The course is divided in to four modules each of which contains four units. Each unit should take you two to three hours to work through. Each unit has a table of contents, introduction, specific objectives, and summary. The following are the study units contained in this course:

Module 1 Evolution and Adaptation

Unit 1 Definition and Concept of Evolution and Adaptation
Unit 2 Theory of Evolution
Unit 3 Evolution by Natural Selection
Unit 4 Evidence of Evolution

Module 2 Evolution of Crop Plants

Unit 1 Mechanism of Crop Evolution
Unit 2 Forces of Evolution
Unit 3 Role of Speciation in the Evolution of Crop Plants
Unit 4 Role of Hybridization in Crop Evolution

Module 3 Origin of Cultivated Crops

Unit 1 Plant Genetic Variation in a Population
Unit 2 Origin of Commonly Cultivated Crops
Unit 3 Centers of Agriculture
Unit 4 Domestication of Plants

Module 4 Crop Adaptation

Unit 1 Evolutionary Adaptation
Unit 2 Adaptation of Crops to Environment
Unit 3 External Factors Regulating Crop Adaptation
Unit 4 Adaptive Response of Crop to Environment

TEXTBOOKS AND REFERENCES

Every unit contains a list of references and Further Readings. Try to get as many as possible of those textbooks and materials listed. The textbooks and materials are meant to deepen your knowledge of the course.

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ASSIGNMENT FILE

In this file, you will find the details of the work you must submit to your tutor for marking. The marks you obtain will form part of your total score for this course.

ASSESSMENT

There are two components of assessment for this course. The Tutor Marked Assignment (TMA) and the End of Course Examination. Your assessment will be based on Tutor-Marked Assignment (TMA) and a final examination which you will write at the end of the course.

TUTOR-MARKED ASSIGNMENT (TMA)

There are many assignments in this course and you are expected to do all of them. You should follow the schedule prescribed for them in terms of when to attempt the homework and submit same for grading by your Tutor.
Assignment questions for the 15 units in this course are contained in the Assignment File. You will be able to complete your assignments from the information and materials contained in your set books, reading and study units. However, it is desirable that you demonstrate that you have read and researched more widely than the required minimum. You should use other references to have a broad viewpoint of the subject and also to give you a deeper understanding of the subject. When you have completed each assignment, send it, together with a TMA form, to your tutor. Make sure that each assignment reaches your tutor on or before the deadline given in the presentation file. If for any reason, you cannot complete your work on time, contact your tutor before the assignment is due to discuss the possibility of an extension. Extensions will not be granted after the due date unless there are exceptional circumstances. The TMAs usually constitute 30 per cent of the total score for the course.

FINAL EXAMINATION AND GRADING

The final examination for this course will take two hours and have a value of 70 per cent of the total course grade. The examination will consist of questions which reflect the types of self-assessment exercises and tutor-marked problems you have previously encountered. All areas of the course will be assessed. Take time to revise the entire course before the examination. The examination covers information from all parts of the course.

PRESENTATION SCHEDULE

Your course materials give you important dates for attending tutorials and the timely completion and submission of your Tutor-Marked Assignment. Do remember that you are required to submit all your assignments by the due date. You should guard against falling behind in your work.

COURSE MARKING SCHEME

The following table lays out how the actual marking scheme is broken down.

Table 1: Course Marking Scheme

Assessment	**Marks**
Assignments 1 – 4	Three assignments count 10% each = 30% of course marks
Final Examination	70% of overall course marks
Total	100% of course marks

HOW TO GET THE MOST FROM THIS COURSE

In distance learning, the study units replace the conventional university lecturer. This is one of the great advantages of distance learning; you can read and work through specially designed study materials at your own pace, and at a time and place that suit you best.

Each of the study units follows a common format. The first item is an introduction to the subject matter of the unit and how a particular unit is integrated with the other units and the course as a whole. Next is a set of learning objectives. These objectives let you know what you should be able to do by the time you have completed the unit. You should use these objectives to guide your study. When you have finished the unit, you must go back and check whether you have achieved the objectives. If you make a habit of doing this you will significantly improve your chances of passing the course.

FACILITATORS/TUTORS AND TUTORIALS

There are 20 hours of tutorials (ten 2-hour sessions) provided in support of this course. As soon as you are allocated a tutorial group, you will be notified of the dates, times and location of tutorials, together with the name and phone number of your tutor.

Your tutor will mark and comment on your assignments; he/she will keep a close watch on your progress and on any difficulties you may encounter and provide assistance to you during the course. You must mail your tutor-marked assignments to your tutor well before the due date (at least two working days are required). They will be marked by your tutor and returned to you as soon as possible.

Do not hesitate to contact your tutor by telephone, e-mail, or via the discussion board if you need help. The following might be circumstances in which you would find help necessary.

Contact your tutor if:

- you do not understand any part of the study unit
- you have difficulty with the assignments/ exercises

- you have a question or problem with your tutor's comments on any assignment or with the grading of an assignment.

You should try your best to attend tutorials. This is the only chance to have face to face contact with your tutor and to ask questions. You can raise any problem encountered in the course of your study. To gain the maximum benefit from the tutorials, prepare a list of questions before hand, you will learn a lot from participating actively in the discussions.

MAIN COURSE

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MODULE 1 EVOLUTION AND ADAPTATION

Unit 1 Definition and Concept of Evolution and Adaptation
Unit 2 Theory of Evolution
Unit 3 Evolution by Natural Selection
Unit 4 Evidence of Evolution

UNIT 1 DEFINITION AND CONCEPT OF EVOLUTION AND ADAPTATION

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5.0 Summary
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7.0 References/Further Reading

1.0 INTRODUCTION

Evolution is the force that shapes the living world. Countless different kind of plants and animals pack the earth and each species is itself composed of a wide range of morphologies and adaptations. These species are continually being modified as they face the realities of their particular environments. Evolution means change, change in the form and behavior of organisms between generations. The forms of organisms, at all levels from DNA sequences to macroscopic morphology and social behavior, can be modified from those of their ancestors during evolution.
Evolution is the process by which nature selects, from the genetic diversity of a population, those traits that would make an individual more likely to survive and reproduce in a continuously changing environment. Evolution stresses the relatedness of all life rather than its differences.

Adaptation is defined as dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also defined as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection. Adaptation is related to biological fitness, which governs the rate of evolution as measured by change in gene frequencies.

2.0 OBJECTIVES

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

- define evolution
- describe the concepts of evolution
- define adaption.
- discuss the concept of adaptation and give examples of organism’s adaptation to environment.

3.0 MAIN CONTENT

3.1 Definition of Evolution

Evolution means change in living things by descent with modification. Evolution is the change in inheritable traits in a population over generations. Change in traits is caused by changes in the genes (in DNA) that code for those traits.

Evolution means change, change in the form and behaviour of organisms between generations. The forms of organisms, at all levels from DNA sequences to macroscopic morphology and social behavior, can be modified from those of their ancestors during evolution.

3.2 Concepts of Evolution

The concept of evolution stresses the processes of change between generations within a population of a species. When the members of a population breed and produce the next generation, one can imagine a lineage of populations, made up of a series of populations through time. Each population is ancestral to the descendant population in the next generation: A lineage is an “ancestor–descendant” series of populations. Evolution is then change between generations within a population lineage.

Evolution is the process by which nature selects, from the genetic diversity of a population, those traits that would make an individual more likely to survive and reproduce in a continuously changing environment. Over many years and many generations, the full diversity of life on earth is expressed. Evolution is one of the most fundamental organising principles of the biological sciences and as such is the single most dominant theme in biology today.

Evolution stresses the relatedness of all life rather than its differences and its important because:

1. it provides a framework (unifying principle) for the way that we study and understand the living world and
2. it's a way of bringing together many diverse aspects of life's tremendous complexity

3.3 Definition of Adaptation

Adaptation is a defined as dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also defined as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection.
In biology, adaptation has three related meanings. Firstly, it is the dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness. Secondly, it is a state reached by the population during that process. Thirdly, it is a phenotypic trait or adaptive trait, with a functional role in each individual organism, which is maintained and has evolved through natural selection.

3.4 Concepts of Adaption

Adaptation is related to biological fitness, which governs the rate of evolution as measured by change in gene frequencies. Often, two or more species co-adapt and co-evolve as they develop adaptations that interlock with those of the other species, such as with flowering plants and pollinating insects.

One of the "characteristics of life" is that organisms adapt to their environment as it changes from year to year example:

1. same species of plant adapts to dryer conditions in one part of its range and wet conditions in another
2. same species of plant or insect may have one generation in northern part of its range or two, even three, generations in the southern part of its range.
3. virtually every bacterial pathogen has become at least somewhat resistant to antibiotics over the past 60 years

Over time, these populations may change in their appearance and other visible characteristics and will surely change in their genetic structure example:

1. For example many unrelated species often adapt in similar was when subjected to the same environmental conditions

Over long periods of time these changes could be significantly different from what you started with yet, no one has ever witnessed the origin of a major new animal or plant group, as is reported to take approximately 10,000's or millions of years. We do however have an increasing amount of fossil data that shows the evolution of one species from another, step by step and today with molecular techniques we can actually observe and measure the rate of evolution in many species. There is generally no controversy surrounding evolution within the scientific community.

3.5 Basic Genetic Concepts

Crops are plants that are grown and utilised for economic gain. In order to understand the diversity among crop species, and how they evolve, adapt and were domesticated and improved through breeding, we need to know how important characteristics are transmitted from one generation to the next. In part of this lecture we will review some basic terms and concepts in Genetics, which is the study of inheritance and variation among organisms.

Gene:- The fundamental physical and functional unit of heredity, which carries information from one generation to the next.

Locus:- a specific place on a chromosome where a gene is located.

Allele:- one of the different forms of a gene that can exist at a single locus. The form of the gene is determined by its DNA sequence. When an individual has different forms of an allele at a locus, it is a heterozygote. When its alleles are the same, it is a homozygote.

Central dogma of biology:- DNA from alleles at a genetic locus is transcribed into RNA, which in turn is translated into proteins. Structural proteins are used to construct the cells, and enzymatic proteins provide the basis for cellular machinery.

Genotype:- The sum total of all the alleles at all the loci in an organism, Considered as a measure of 'breeding value' for evolution and crop improvement efforts. The term is also used to refer to the specific alleles that an individual possesses at a particular locus. One allele comes from the male parent, and one from the female parent.

Phenotype:- The external and observable expression of the genes, and the result of genes interacting with the environment. The appearance of individuals,

Phenotype (P) = Genotype (G) + Environment (E) + (GXE)

An individual's phenotype can be viewed as the sum of the effects due to genes, the effects of the environment, and interactions between the genes and the environment (GXE).

Heritability:- The proportion of total phenotypic variance at the population level that is contributed by genetic variance. If a trait is largely determined by environmental factors, then the heritability will be low. Traits that are largely controlled by genes have a high heritability and consequently are more likely to change in response to selection.

In higher plants, chromosomes occur in cells in homologous pairs. Members of a pair contain the same loci, but may have different alleles at any given locus. One chromosome from each pair came from the male parent, and one from the female parent. Each plant species has a characteristic number of chromosomes in its cells.

Genome:- The entire complement of genetic material in a chromosome set. The number of chromosomes in one nuclear genome is designated 'n', which is equivalent to the haploid number.

Diploid species have one set of homologous chromosome pairs, so their total number of chromosomes is 2n. Some species are polyploid which means that they have multiple sets of n chromosomes (triploids are 3n, tetraploids are 4n, etc.).

Populations:-A population is a community of individuals that share a common gene pool. It is 'a breeding group' of individuals that may intermate. The genetic constitution of a population is described by the array of gene frequencies and alleles that are present at each locus.

SELF-ASSESSMENT EXERCISE

Define evolution and explain the concepts of evolution

Define adaption and discuss the concept of adaptation with specific examples.

4.0 CONCLUSION

In this unit, we define evolution as a change, change in the form and behaviour of organisms between generations, a change in inheritable traits in a population over generations and a change in living things by descent with modification. It was also demonstrated that Evolution is the process by which nature selects, from the genetic diversity of a population, those traits that would make an individual more likely to survive and reproduce in a continuously changing environment. Similarly, you have learned the fact that one of the "characteristics of life" is that organisms adapt to their environment as it changes from year to year or from generation to generation.

The unit also defines adaptation as dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. We also understand that adaption could be a phenotypic or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection. You have also been informed that one of the "characteristics of life" is that organisms adapt to their environment as it changes from generation to generation.

5.0 SUMMARY

Evolution means change in living things by descent with modification. Evolution is the change in inheritable traits in a population over generations. Change in traits is caused by changes in the genes (in DNA) that code for those traits. Evolution means change, change in the form and behavior of organisms between generations. The concept of evolution stresses the processes of change between generations within a population of a species. When the members of a population breed and produce the next generation, one can imagine a lineage of populations, made up of a series of populations through time. Each population is ancestral to the descendant population in the next generation. Evolution stresses the relatedness of all life rather than its differences.

Adaptation is a defined as dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also defined as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection. One of the "characteristics of life" is that organisms adapt to their environment as it changes from year to year. Over time, these populations may change in their appearance and other visible characteristics and will surely change in their genetic structure.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define and explain the term evolution.
2. Explain the concept of evolution and adaptation.
3. Define adaption and give two examples of organism's adaptation to environment.

7.0 REFERENCES/FURTHER READING

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UNIT 2 THEORY OF EVOLUTION

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    3.2 Various Theories of Evolution
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1.0 INTRODUCTION

In the early modern period, European naturalists, working in centralized botanical gardens and national zoos, investigated an unprecedented variety of animal and plant specimens. After series of systematic investigation of the fossil remains of various organisms and compare these with living organisms. They then come to the conclusion that there was evidence to suggest that there was a large-scale biological change going on among species of animal and plants.

Although there was a lot of disagreement about how these changes had taken place, and what they implied, by Darwin's time, most naturalists accepted that there had been some changes in biological species. However, even if we accept that there has been change in species throughout the history of the earth, we might have several different theories about how this change occurred.

All of the theories advanced before Darwin argued for some kind of directed change – in some sense responding to, and hence directly influenced by, the environment and the actions of organisms. Darwin tried to distinguish his theories from these by arguing that evolutionary changes were based only on naturally occurring processes – processes that are still occurring around us now. This unit describes the history of evolution as a scientific theory and discusses the various theories of evolution proposed by different scientist.

2.0 OBJECTIVES

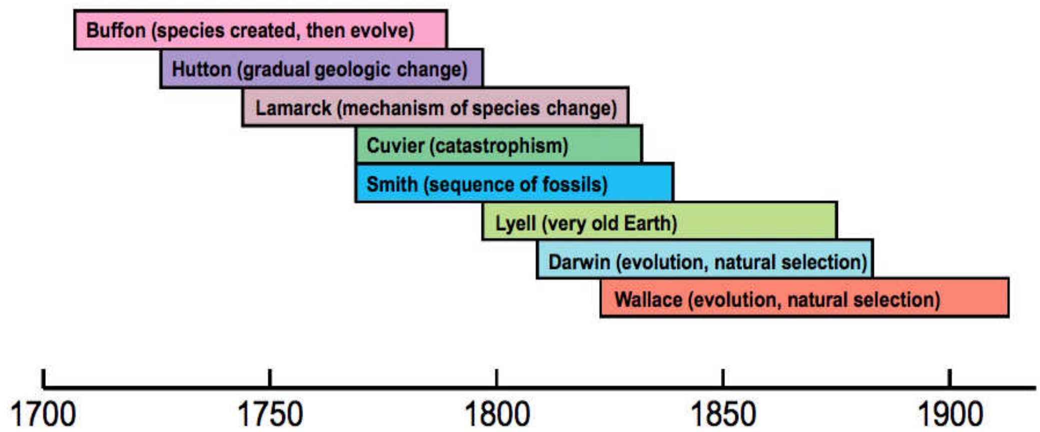
By the end of this unit, you should be able to:

- explain the history of Evolution as a Scientific Theory
- describe the Various Theories of Evolution

3.0 MAIN CONTENT

3.1 History of Evolution as a Scientific Theory

Theories are evidence-supported explanations for natural phenomenon. To exist, theories must have abundant evidence from many well-tested hypotheses. Theories grow from evidence! Theorizing without evidence is not Science. While many people associate evolution with Darwin, other scientists were talking about organic change long before Darwin published his theory of natural selection.



The history of evolution can be traced to the historic rise of evolutionary biology that can be sketched in four main stages:

1. Evolutionary and non-evolutionary ideas before Darwin.
2. Darwin's theory (1859).
3. The eclipse of Darwin (*c*. 1880–1920).
4. The modern synthesis (1920s to 1950s).

Many thinkers before Darwin had discussed the possibility that species change through time into other species. Lamarck is the best known. But in the mid-nineteenth century most biologists believed that species are fixed in form. Darwin's Theory of Evolution by Natural Selection explains Evolutionary Change and Adaptation. Darwin's contemporaries mainly accepted his idea of Evolution, but not his explanation of it by Natural Selection.

Darwin lacked a theory of heredity. When Mendel's ideas were rediscovered at the turn of the twentieth century, they were initially thought to count against the Theory of Natural Selection. Fisher, Haldane, and Wright demonstrated that Mendelian heredity and natural selection are compatible; the synthesis of the two ideas is called neo-

Darwinism or the synthetic Theory of Evolution. During the 1930s and 1940s, neo-Darwinism gradually spread through all areas of biology and became widely accepted. It unified genetics, systematic, paleontology, and classic comparative morphology and embryology.

3.2 Various Theories of Evolution

Aristotle (384-322 B.C.) viewed the living world as fixed and unchanging. All living things could be arranged in a ladder from inferior to superior, with humans on top. Aristotle's views influenced thought for over 2000 years.

George Louis LeClerk, Compte de Buffon (1707 - 1788) sought a naturalistic explanation for fossils. Buffon devised one of the first theories of organic change. However, Buffon's ideas were grounded in logic rather than in evidence from the natural world, as much science was at the time.

Buffon suggested that organisms had a basic form, the "interior mold," which could be shaped by the environment.

James Hutton (1726 - 1797) and Charles Lyell (1797 - 1875). These two naturalists are best known for the theory of Uniformitarianism, proposed by Hutton and expanded by Lyell. Uniformitarianism states that the physical laws that now shape the earth have always done so, and that the past can be understood by studying the present. Both suggested that the Earth is very old.

Georges Cuvier (1769 - 1832) was a student of Buffon, but disagreed about organic change. Cuvier was an anatomist. He pointed out that animals had features that helped them survive. If those features changed, wouldn't that be harmful? Cuvier studied fossils and identified several new animals based on fossils. However, he had his own explanation for fossils.

Jean-Baptiste de Lamarck (1744 - 1829) was also a student of Buffon. Like Buffon, Lamarck sought a naturalistic explanation for the diversity of modern organisms and the animals seen in the fossil record. Lamarck used the theory of Inheritance of Acquired Characteristics, a widely-held belief at the time, to explain change in organisms. Blacksmiths, for example, were thought to pass their well-developed right arms on to their sons. Lamarck's Organic Theory of Development Organisms are shaped by their environment. Change is goal-directed -- organisms have an internal drive to become more and more complex.

Charles Darwin (1809 - 1882) and Alfred Russell Wallace (1823 - 1913) Darwin and Wallace, working separately, devised a model for organic change that was based on their observations of living and fossil organisms over many years. Natural Selection was the first evidence-based mechanism for evolution that was proposed.

Darwin and Wallace observed that change did not happen equally to all members of a population, as Buffon and Lamarck thought. Instead, Darwin and Wallace proposed that selection happens each generation. Some individuals have traits that help them survive and reproduce, while others have traits that put them at a disadvantage. Over generations, the number of individuals with favourable traits increases while those with unfavourable traits decrease.

SELF-ASSESSMENT EXERCISE

> Enumerate the four main stages of evolutionary history that are linked to the rise of evolutionary biology.
> Describe the Various Theories of Evolution

4.0 CONCLUSION

In this unit, we explained that theories are evidence-supported explanations for natural phenomenon and that to exist; theories must have abundant evidence from well-tested hypotheses. We have understood that the history of evolution can be traced to the historic rise of evolutionary biology that can be sketched in four main stages. We have also seen that many thinkers before Darwin had discussed the possibility that species change through time into other species. But that in the mid-nineteenth century most biologists believed that species are fixed in form. Similarly we know that Darwin's Theory of Evolution by Natural Selection explains Evolutionary Change and Adaptation, however his contemporary scientist mainly accepted his idea of Evolution, but not his explanation of it by Natural Selection.

We were informed in this unit that various theories of evolution have been developed by scientist including; Aristotle (384-322 B.C.), George Louis LeClerk, Compte de Buffon (1707 - 1788), Buffon, James Hutton (1726 - 1797) and Charles Lyell (1797 - 1875), Georges Cuvier (1769 - 1832), Jean-Baptiste de Lamarck (1744 - 1829) and Charles Darwin (1809 - 1882) and Alfred Russell Wallace (1823 - 1913).

5.0 SUMMARY

Scientific theories are evidence-supported explanations for natural phenomenon and to exist; theories must have abundant evidence from many well-tested hypotheses. Theories grow from evidence thus proposing a theory without evidence is unscientific. While many thinkers before Darwin believed that species change through time into other species, in the mid-nineteenth century however most biologists believed that species are fixed in form. Darwin's Theory of Evolution by Natural Selection explains Evolutionary Change and Adaptation.

Darwin proposed the Theory of Natural Selection while Mendel developed a theory of heredity. These two ideas were merged to gather and called neo-Darwinism or the synthetic Theory of Evolution. During the 1930s and 1940s, neo-Darwinism gradually spread through all areas of biology and it unified genetics, systematic, paleontology, and classic comparative morphology and embryology. Various theories of evolution have been developed by scientist including; Aristotle (384-322 B.C.), George Louis LeClerk, Compte de Buffon (1707 - 1788), Buffon, James Hutton (1726 - 1797) and Charles Lyell (1797 - 1875), Georges Cuvier (1769 - 1832), Jean-Baptiste de Lamarck (1744 - 1829) and Charles Darwin (1809 - 1882) and Alfred Russell Wallace (1823 - 1913).

6.0 TUTOR-MARKED ASSIGNMENT

1. Discuss the history of Evolution as a Scientific Theory
2. Describe the history of evolution in four stages linked to evolutionary biology.
3. Explain the theories of evolution as proposed by:
   - Jean-Baptiste de Lamarck (1744 - 1829)
   - Charles Darwin (1809 - 1882) and Alfred Russell Wallace (1823 - 1913)

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UNIT 3 EVOLUTION BY NATURAL SELECTION

CONTENTS

1.0 Introduction
2.0 Objectives
3.0 Main Content
3.1 Natural Selection
3.1.1 The Effects of Selection on Populations
3.1.2 Response to Selection
3.1.3 Speciation
3.2 Condition for Natural Selection
3.3 The Theory of Evolution by Natural Selection
3.4 Darwin, Natural Selection & Evolution
3.5 Darwin Concept of Evolution by Natural Selection
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

The theory of evolution by natural selection as developed by Darwin and Wallace is a theory about the mechanism by which evolution occurred. The theory states that biological change takes place with two basic characteristics; Variation and Struggle for existence. Evolution by natural selection stress the fact that for living organism, there are no traits that are better in any absolute sense – there are only traits that are better suited for a particular set of circumstances. Within a species, individuals specialise at exploiting the environment in various ways, and over long periods this specialisation creates divergence.

Darwin concept of evolution by natural selection was developed and published in a book "The Origin of Species, in 1859. The concept of his theory for the evolution of plants and animal species is as follows: 1) Artificial select of preferred character from Plant and animal carried over many generation produce very different types of animals (varieties of the same species). 2) A similar selection occurs in nature and 3) Individual organisms and species are all in a struggle for existence. The struggle referred to as the "survival of the fittest."

Excess fecundity, and consequent competition to survive in every species, provides the preconditions for the process Darwin called Natural Selection that requires four conditions: 1) Reproduction 2) Heredity 3) Variation in Individual Characters among the members of the population and 4) Variation in the fitness of organisms (heritable character). If these conditions are met for any property of a species, Natural Selection automatically results.

This unit discusses the theory of evolution by natural Selection, explains Darwin's concept of evolution by natural selection and describes the condition necessary and sufficient for natural selection to occur.

2.0 OBJECTIVES

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

- define natural selection
- explain the concept of evolution by natural selection
- describe the condition for natural selection

3.0 MAIN CONTENT

3.1 Natural Selection

Living things produce more offspring than the finite resources available to them can support, so they face a constant struggle for existence. The individuals in a population vary in their phenotypes, and some of that variation is due to genetic differences. Fitness is the relative ability of an individual to survive and transmit its genes to the next generation. A population undergoes selection when certain alleles are found at greater frequency in a new generation because they imparted greater fitness to the parent. The forces of natural selection act on phenotypes but evolution occurs only if there is a change in the genotypes in a population.

There are several ways that fitness can be achieved:

1. Survival or mortality selection - ability to survive to a reproductive age
2. Mating success or sexual selection - in plants, for example, this could refer to the likelihood that a female flower will receive male pollen
3. Family size or fecundity selection - number of offspring produced.

Evolution involves two related phenomena:

1. Adaptation - refers to genetically determined characteristics that enhance an individual's ability to cope with its environment.
2. Speciation - a single species can give rise to two or more descendant species when isolated by geography or ecologically divergent space.

Evolution may be caused by a 'lack of fit' between a population and its environment. A species evolves when gene frequencies change and the species moves to a higher level of adaptation for a specific ecological niche.

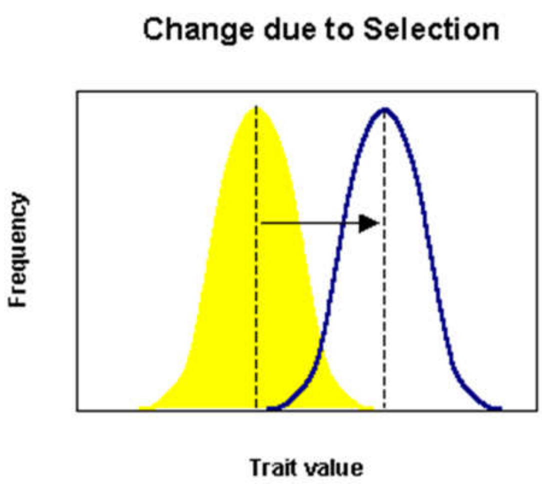
If environmental conditions are constant for a long period of time, a population may reach equilibrium, where optimum fitness is attained and there is little change in gene frequencies from one generation to the next.

Changes in environment may result in 'lack of fit' of a static population. Many factors, biotic and abiotic, can act to change fitness. The maintenance of adaptation requires that natural selection operate constantly in every generation to maintain the fit of a population to its environment.

3.1.1 The Effects of Selection on Populations

Directional selection

When one extreme of a population is favored over another, selection will tend to move the mean of the population in that direction. Changes may be small between one generation and the next, but will accumulate over time. Examples include traits such as yield, fertility, stress tolerance, and disease tolerance.

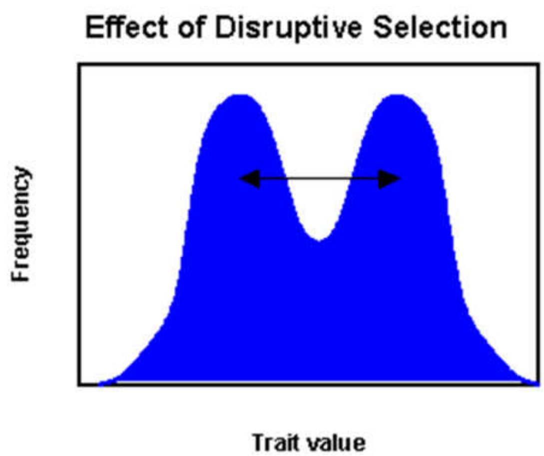


Stabilising selection

Natural selection often works to weed out individuals with extreme phenotypes. Stabilising selection reduces variation in a population and favors individuals with an average phenotype over the extremes. This mode of selection is often referred to as optimising selection. Examples in plants include maturity, seed size, and plant height.

Disruptive selection

Disruptive selection acts against the individuals in the middle of the range of phenotypes and tends to favour individuals in the extremes. In the long term, disruptive selection can create two distinct gene pools from a single gene pool. Such a force is required for the origin of new species.



3.1.2 Response to Selection

Heritability (h^2) measures how well offspring resemble their parents, or the amount of additive genetic variance (σ_A^2) as a proportion of the total variance among phenotypes (σ_P^2):

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

The selection differential is an indicator of selection intensity:

s = mean after selection – mean before selection

If expression of a trait is due to a large number of polygenic loci, then Response to selection is a function of both the heritability of a trait (i.e., additive genetic variance) and the strength of selection on the trait (selection differential).

Response = h^2 x s

With either low heritability or weak selection, response to selection is slow. Conversely, with a high heritability and high selection pressure, response to selection will be rapid.

<u>Artificial selection</u>

Modern food crops would not have evolved under 'natural conditions or processes' without man's selection and interference. The process of domestication has led to striking changes in morphological traits of plants. This is continuing through modern plant breeding.

Plant breeding is a means by which artificial selection is imposed on plant populations to change morphological traits, increase tolerance to biotic and abiotic stress, and improve agronomic performance.

3.1.3 Speciation

A species is a group of organisms that are capable of interbreeding freely with each other. They do not interbreed with other species even when they have the opportunity (or if they do mate the offspring are sterile).

How do new species originate? What is the mechanism? There are two theories proposed:

1. Phyletic gradualism - change due to natural selection is gradual and progressive (Darwin's view)
2. Punctuated equilibrium - sudden changes punctuate long periods of little change. (Gould and Eldridge). Small, isolated populations may evolve more rapidly.

The formation of two or more species often requires geographical isolation of subpopulations of the species. Only then can natural selection or perhaps genetic drift produce distinctive gene pools.

In general, a stimulus like an environmental change causes the evolution into a new species. The organism must either:

1. Adapt to changing conditions if possible
2. Survive by changing habits or migrating into another area
3. Go extinct.

3.2 Condition for Natural Selection

Excess fecundity, and consequent competition to survive in every species, provides the preconditions for the process Darwin called Natural Selection. The argument, in its most general form, requires four conditions:

1. Reproduction. Entities must reproduce to form a new generation.

2. Heredity. The offspring must tend to resemble their parents: roughly speaking, “like must produce like.”
3. Variation in Individual Characters among the members of the population. If we are studying natural selection on body size, then different individuals in the population must have different body sizes.
4. Variation in the fitness of organisms according to the state they have for a heritable character.

If these conditions are met for any property of a species, Natural Selection automatically results. And if any are not, it does not. This also implies that when the four conditions apply, the entities with the property conferring higher fitness will leave more offspring, and the frequency of that type of entity will increase in the population.

3.3 Theory of Evolution by Natural Selection

The theory of evolution by natural selection is a theory about the mechanism by which evolution occurred in the past, and is still occurring now. The basic theory was developed by both Darwinand Wallace, however, Darwin gave a much fuller argument. The theory states that biological change takes place with two basic characteristics:

1. Variation: Random variations occur in the traits of individual organisms and are passed on to their offspring.
2. Struggle for existence: There is an existential competition that insures advantageous traits are preserved and disadvantageous traits are eliminated.

A key result of evolution by natural selection is that it forces us to look at various binaries such as advantage and disadvantage, superior and inferior from a local perspective. This means that there cannot be traits that are better in any absolute sense – there can only be traits that are better suited for a particular set of circumstances.

Within a species, individual’s specialise at exploiting the environment in various ways, and over long periods this specialisation creates divergence. For example a group of birds with longer beaks might prefer worms, while a group with stronger beaks might prefer nuts. Or being attractive to, and interacting with, mates of the opposite sex is an exploitation of local circumstances.

3.4 Darwin, Natural Selection & Evolution

Charles Darwin published his book "The Origin of Species" in 1859. He presented two major arguments:

1. The theory of evolution - all species alive today is descendants from earlier species. Life is continually changing.
2. The mechanism of evolution is natural selection or survival of the fittest. Changes occur gradually over time.

His findings generated a storm of criticism, some of which continues to the present. The concept of evolution was disturbing to people because it seemed to contradict the literal interpretation of the story of creation in the Bible, and because it implied that humans had evolved from some apelike ancestor. From a scientific standpoint, Darwin's ideas ran counter to the prevailing paradigm of fixed species that had been proposed by Carolus Linnaeus in the 1700's. Today, the question we ask is not so much whether evolution occurs, but how does it occur?

3.5 Darwin Concept of Evolution by Natural Selection

After an intensive and detailed observation of the variation existing among plans and animal species, Darwin spent over a year developing the argument which he published in a book "The Origin of Species, in 1859. The concept of his theory for the evolution of plants and animal species is as follows:

1. Plant and animal breeders artificially select preferred characteristics from domestic populations (maize, rice, pigeons, cows, dogs, etc.) in which there are a lot of random variation. When this process is carried over many generation these small differences produce very different types of animals (varieties of the same species).

2. A similar selection occurs in nature. The nature of species is that the demarcation between different species and different varieties is difficult. A well-marked variety is an "incipient species" – that is, newly forming, or emerging.

3. Individual organisms and species are all in a struggle for existence. Life is a complex struggle resulting "natural selection." The struggle referred to as the "survival of the fittest."

The core of Darwin's Theory of evolution by natural selection includes:

1. Nature varies, randomly.
2. Some of variations are more advantageous than others.
3. Because there is a struggle for existence, any advantage will be important, however slight.
4. In the long run, those organisms that have a slight innate advantage will survive more often than those that do not, passing on their advantages to their offspring.

Through this mechanism, Darwin argued that a population will change by the accumulation of small, but favorable advantages, over vast periods of time. Again, he referred to artificial selection, calling natural selection "unconscious artificial selection." But notice that nature does not chose preferred traits in the way that a breeder does.

SELF-ASSESSMENT EXERCISE

Define natural selection and explain the concept of evolution by natural selection
Describe the necessary conditions for natural selection

4.0 CONCLUSION

We learn from this unit that the theory of evolution by natural selection was developed by Darwin and Wallace as a theory that explain the mechanism by which evolution occurred. We were also informed that the theory states that biological change takes place with two basic characteristics; Variation and Struggle for existence. It was also stated that evolution by natural selection stress the fact that for living organism, there are no traits that are better in any absolute sense – there are only traits that are better suited for a particular set of circumstances or environment.

This unit also thought us that Darwin concept of evolution by natural selection was developed and published in a book "The Origin of Species, in 1859. We also know that the core of Darwin's Theory of evolution by natural selection was that nature varies, randomly with some of variations being more advantageous than others. Due to a struggle for existence, any advantage will be important, however slight. Consequently, those organisms that have a slight innate advantage will survive more often than those that do not, passing on their advantages to their offspring.

The unit further highlighted that excess fecundity, and competition to survive in every species, provides the preconditions for the process Darwin called Natural Selection which requires four conditions: 1) Reproduction 2) Heredity 3) Variation in Individual Characters among a population and 4) Variation in the fitness of organisms (heritable character). Conclusively natural selection automatically occurs when these conditions are satisfied.

5.0 SUMMARY

The theory of evolution by natural selection is a theory about the mechanism by which evolution occurred in the past, and is still occurring now. The basic theory was developed by Darwin and Wallace. The theory states that biological change takes place with two basic characteristics: a) random variations in the traits of organisms passed on to their offspring and b) struggle for existence. Therefore, within a species, individuals specialise at exploiting the environment in various ways, and over long periods this specialisation creates divergence.

Darwin concept of the theory of evolution by natural selection explains that: 1) Artificial select of preferred character from Plant and animal carried over many generation produce very different types of animals (varieties of the same species). 2) A similar selection occurs in nature and 3) Individual organisms and species are all in a struggle for existence that is referred to as the “survival of the fittest.”

Excess fecundity, and competition to survive in every species, provides the preconditions for the process Darwin called Natural Selection which requires four conditions: 1) Reproduction 2) Heredity 3) Variation in Individual Characters among a population and 4) Variation in the fitness of organisms (heritable character).

6.0 TUTOR-MARKED ASSIGNMENT

1. State the theory of evolution by natural selection and its key takeaway.
2. Discuss the Darwin’s concept of evolution by natural selection.
3. Explain the core of Darwin’s Theory of evolution by natural selection.
4. Outline the four conditions required for natural selection.

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UNIT 4 EVIDENCE OF EVOLUTION

CONTENTS

1.0 Introduction
2.0 Objectives
3.0 Main Content
3.1 Evidence for Evolution
3.1.1 Direct Observation on Small Scale
3.1.2 Homology
3.1.3 The Order of the Main Groups in the Fossil Record
3.2 Evidence for Selection
3.2.1 Artificial Selection
3.2.2 Selection Acts on Variations
3.2.3 Selection does not Cause New Variations.
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

A number of evidence showed that species have evolved from a common ancestor, rather than being fixed in form and created separately. On a small scale, evolution takes place in nature, such in breeding agricultural varieties. Natural variation can cross the species border, and new species can be made artificially, as in the process of hybridization and polyploidy by which many agricultural and horticultural varieties have been created. There are three main types of evidence for evolution that include: a) direct observation on the small scale; b) Homology; and c) the order of the main groups in the fossil record.

Evolution is described as the change in inherited traits in a population over generations. However, evidence of evolution that include fossils, molecular data, and other evidence indicates that the genetics of a population do evolve over time. Natural Selection, the one mechanism for evolution, is well-supported by evidence. The facts put forward as evidence for the existence of selection in nature includes the following: a) artificial Selection; b) selection acting on variations and c)Selection not cause new variations. This unit explains and identifies the three main types of evidence for evolution. It further enumerates and discusses the facts presented as evidence for the existence of selection in nature.

2.0 OBJECTIVES

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

- list and explain the evidence for evolution.
- enumerate and describe the evidences for the existence of selection in nature.

3.0 MAIN CONTENT

3.1 Evidence for Evolution

A number of lines of evidence suggest that species have evolved from a common ancestor, rather than being fixed in form and created separately. On a small scale, evolution can be seen taking place in nature, such as in the color patterns of moths, and in artificial selection experiments that are used in breeding agricultural varieties. Natural variation can cross the species border, for example in the ring species of Salamanders, and new species can be made artificially, as in the process of hybridization and polyploidy by which many agricultural and horticultural varieties have been created.

In summary there are three main classes of evidence for evolution, they include those from:

1. Direct observation on the small scale;
2. Homology; and
3. The order of the main groups in the fossil record.

3.1.1 Direct Observation on Small Scale

Observation of evolution on the small scale, combined with the extrapolative principle of uniformitarianism, suggests that all life could have evolved from a single common ancestor. The small-scale observations work most powerfully against the idea of species fixity; by themselves, they are almost equally good evidence for evolution and for transfornism. They show, by uniformitarian extrapolation, that evolution could have, in theory, produced the whole history of life.

3.1.2 Homology

Homologous similarities between species (understood as similarities that do not have to exist for any pressing functional reason), suggest that species descended from a common ancestor. Universal homologies such as the genetic code found in all living things suggest that all species are descended from a single common ancestor. The more recently discovered molecular homologies, such as the universal genetic code, extend the argument to the whole of life a and favor evolution over both transformism and creationism

3.1.3 TheOrder of the Main Groups in the Fossil Record

Stronger arguments for large-scale evolution come from classification and the fossil record. The fossil record provides some direct evidence of the origin of new species. The order of succession of major groups in the fossil record is predicted by evolution, and contradicts the separate origin of the groups. The geological succession of the major groups and most classic morphological homologies strongly suggest that these large groups have a common ancestor.

3.2 Evidence for Selection

Evolution is the change in inherited traits in a population over generations. However, Fossils, molecular data, and other evidence shows that the genetics of a population do change over time. Natural Selection, one mechanism for change, is well-supported by evidence. To construct his theory, Darwin had to gather and examine evidence to discover whether selection happens in nature. Research continues to refine our ideas of how selection happens and what effects it has on species. The facts put forward as evidence for the existence of selection in nature includes the following:

3.2.1 ArtificialSelection

Darwin knew from his studies of pigeon breeding that selection can change organisms, sometimes rapidly.

Figure 14-13a Biology: Life on Earth, 8/e
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Figure 14-13b Biology: Life on Earth, 8/e
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Human selection created many breeds of dogs from wild dogs or wolves as humans chose to breed those animals with traits that the humans wanted.

3.2.2 SelectionActs on Variations

Studies have shown that guppies living in ponds with few predators are more brightly coloured than those living with many predators.

In both populations there are guppies with genes for bright colors. Why are dull colours favoured in ponds with many predators? Why are bright colours favoured in ponds with few predators?

3.2.3 Selection does not Cause New Variations

Studies on Anole lizards showed that long, fast-moving legs were favored where trees had thicker branches, while shorter, more agile legs were favored where trees were flimsier.

If lizards from places where trees had thin branches were moved to a place where trees had thick branches, those with the longest legs survived better. Each generation had more individuals with longer legs because the genes for longer legs *were already in the population.*

SELF-ASSESSMENT EXERCISE

List and explain the evidence for evolution.
Enumerate and describe the evidences for the existence of selection in nature.

4.0 CONCLUSION

Information presented in this unit indicated that a number of evidence showed that species have evolved from a common ancestor, rather than being fixed in form and created separately. We also came to know that evolution takes place in nature on a small scale, example in breeding agricultural varieties. We were thought in this unit that natural variation can cross the species border, and new species are then created artificially, as in the process of hybridisation and polyploidy by which many agricultural and horticultural varieties have been developed. It was shown that the three main types of evidence for evolution are: a) direct observation on the small scale; b) homology; and c) the order of the main groups in the fossil record.

This unit further described evolution as the change in inherited traits in a population over generations. It went on to state that evidence of evolution including fossils, molecular data, and other evidence indicates that the gene of a population do evolve over time. It was also explained in this unit that the mechanism for evolution (which is natural selection) is well-supported by evidence. In addition we were informed that the evidence for the existence of selection in nature are: a) artificial selection; b) selection acting on variations and c) selection not causing new variations.

5.0 SUMMARY

Evidence suggests that species have evolved from a common ancestor, rather than being fixed in form and created separately. On a small scale, evolution can be seen taking place in nature, example in breeding agricultural varieties. When natural variation crosses the species border, new species can be made artificially such as in the process of hybridization and polyploidy. This process results in the creation of many agricultural and horticultural varieties.

There are three main types of evidence for evolution that include: a) direct observation on the small scale; b) Homology; and c) the order of the main groups in the fossil record. Fossils records, molecular data, and other evidence showed that the genetics of a population can change over time. Natural Selection, one mechanism for change, is well-supported by evidence. The evidence for the existence of selection in nature are: a) artificial selection; b) selection acting on variations and c) selection not causing new variations.

6.0 TUTOR-MARKED ASSIGNMENT

1. List and explain in each case the evidence for evolution and transfornism.
2. Enumerate and discuss the facts put forward as evidence for the existence of selection in nature.

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MODULE 2 EVOLUTION OF CROP PLANTS

Unit 1 Mechanism of Crop Evolution
Unit 2 Forces of Evolution
Unit 3 Role of Speciation in the Evolution of Crop Plants
Unit 4 Role of Hybridisation in Crop Evolution

UNIT 1 MECHANISM OF CROP EVOLUTION

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  3.1 Natural Selection
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    3.1.3 Types of Natural Selection.
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1.0 INTRODUCTION

Evolution is the force that shapes the living world. Countless different kind of plants and animals pack the earth and each species is itself composed of a wide range of morphologies and adaptations. These species are continually being modified as they face the realities of their particular environments. In its simplest sense, evolution can be defined as a change in gene frequency over time. Genetic variability is produced by mutation and then that variability is shuffled and sorted by the various evolutionary forces. The way organisms evolve is dependent on their genetic characteristics and the type of environment they must face.

The Variation that exists in a population is the resource on which Natural Selection works. Evolution from the origin of life to the level of modern diversity must have required more variation than existed in the original population. The extra or new variation is generated by Mutation and Recombination. Mutation introduces less variation in other life forms that have lower population sizes, lower reproductive rates, and lower mutation rates. But in all species, Mutation is an abundant source of New Variation, providing Raw Material for Evolutionary Change.

A broad spectrum of evolutionary forces, including migration, selection and random chance, interact to alter natural species. These same forces operated during the domestication of crops. The primary requirement for evolutionary change is genetic variability and mutation generates these building blocks. The mechanisms for crop evolution are natural selection, mutation and recombination.

2.0 OBJECTIVES

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

- define Natural selection
- explain the concept of evolution by natural selection
- describe the condition for natural selection
- explain mutation in the context evolution
- discuss the different types of recombination process

3.0 MAIN CONTENT

3.1 Natural Selection

3.1.1 Introduction

Evolution is the change in inheritable traits in a population over generations. Change in traits is caused by changes in the genes (in DNA) that code for those traits. Natural selection tends to increase favorable traits in a population and decrease unfavorable traits.

Evidence from the natural world showed that change happens to organisms over time. According to Darwin and Wallace Natural Selection provides a natural mechanism for change and the path for Crop Evolution. Natural selection occurs in a population because of the existence of the following forces:

1. Variation within any population:, Individuals differ from one another in many ways.

2. Inheritance: Some differences between individuals are inheritable, and can be passed from parent to offspring.
3. Differences in survival and reproduction: In most populations, more young are born than can survive. Many of the young will die. A few will live long enough to reproduce.
4. Success is not random: While random accidents do happen, an individual's survival depends mainly on the individual's traits. Those that live and reproduce may pass their traits to the next generation.
5. Selection favours organisms that are best adapted to the environment: Selection does not produce new traits, nor does it make organisms "perfect." Selection is all about survival, and those organisms with traits that help them survive are more likely to reproduce.

3.1.2 The Concept of Natural Selection

According to Darwin's theory of evolution plant species have evolved through the process of evolution and adaptation. While his theory of natural selection proposed that crop plants have develop through human breeding (artificial selection) and selecting power of nature. This selection of forms by human agency and active selection in the natural world have resulted in the creation of the varieties of domestic plants species. The process of natural selection separates out those features most beneficial to plants in relation to their environmental conditions in a similar action to the selection by man on cultivated crops in the production of different hybrid varieties.

Natural selection is a grand plan that allows the process of selection to go on adapting crop plants to diverse ends. A theory explaining the evolution and adaptation of cultivated plants relevant to the concept of natural selection is the "principle of divergence", which states that organism under the action of natural selection will tend to radiate and diversify within their "conditions of life". (i.e. the complex of environmental and species-interaction relationships). The principle of divergence forms an important link between natural variation and the conditions of existence under the action of the driving force of population increase.

3.1.3 Types of Natural Selection.

Natural Selection produces evolution when the environment changes; it will also produce evolutionary change in a constant environment if a new form arises that survives better than the current form of the species. Natural Selection can not only produce evolutionary change, it can also cause a population to stay constant. If the environment is constant and no superior form arises in the population, natural selection will keep the population the way it is. Natural selection can explain both evolutionary change and the absence of change.

Natural selection will operate among any entities that reproduce, show inheritance of their characteristics from one generation to the next, and vary in “fitness” (i.e., the relative number of offspring they produce) according to the characteristic they possess.

In evolutionary biology, it is often useful to think about evolution in Continuous Characters such as body size slightly differently from Evolution in Discrete Characters such as drug resistance and drug susceptibility. However, no deep difference exists between the two ways of thinking. Discrete Variation blurs into Continuous Variation, and evolution in all cases is due to changes in the frequency of alternative genetic types. Natural Selection can act in three main ways on a character, such as body size, that is Continuously Distributed. These are directional, stabilising, or disruptive**:**

<u>Directional</u>

Assume that smaller individuals have higher fitness (that is, produce more offspring) than larger individuals. Natural selection is then *directional*: it favours smaller individuals and will, if the character is inherited, produce a decrease in average body size. Directional selection could, of course, also produce an evolutionary increase in body size if larger individuals had higher fitness.

<u>Stabilising</u>

A second (and in nature, more common) possibility is for natural selection to be stabilising. The average members of the population, with intermediate body sizes, have higher fitness than the extremes. Natural selection now acts against changes in body size, and keeps the population constant through time, lighter than average did not survive as well as babies of average weight. Stabilising selection has probably operated on birth weight in human populations from the time of the evolutionary expansion of our brains about one to two million years ago until the 20th century.

<u>Disruptive</u>

The third type of natural selection occurs when both extremes are favored relative to the intermediate types. This is called *disruptive* selection. In an environment with a bimodal resource distribution, natural selection drives the finch population to have a bimodal distribution of beak sizes. Natural selection is then disruptive. Disruptive selection is of particular theoretical interest, both because it can increase the genetic diversity of a population (by frequency-dependent selection) and because it can promote speciation.

3.2 Mutation

3.2.1 Introduction

Mutation is an important source of genetic variability that is critical for evolution. Genes arise from genes through division. Heredity is maintained due to accurate gene reproduction. The primary requirement for evolutionary change is that genetic variability and mutation should generate these building blocks for evolution. A wide range of mutations can occur at all levels of genetic organisation from nucleotide sequence to chromosome structure.

Mutations can be classified as beneficial, harmful, or neutral. Harmful mutations are eliminated through selection if they reduce the fitness of an individual. Neutral alleles are neither beneficial nor detrimental to an individual. When the environment changes, a neutral allele or a new mutant allele may be favoured and eventually become the dominant allele in that population. If a mutation is beneficial to the species as a whole, migration must occur for it to spread to other populations of the species.

Mutations can occur by

1. Point mutation - changes in a single nucleotide
2. Small insertions or deletions of the nucleotide sequence
3. Whole genes or blocks of genes could be duplicated

A mutation may be transparent (resemble an allele already in the population). Alternatively, it could generate an entirely new allele. Most of these mutations will be detrimental and lost.

Gene duplication favours and facilitates mutational events. The duplicated gene can undergo mutations to generate a new gene that has a similar, but a slightly modified function for the organism. The original gene maintains the function that was adaptive in the initial environment. This type of evolution generates multigene families (Examples: gluten proteins and other seed storage genes, photosynthetic genes in plants).

3.2.2 Types of Mutation

Genes arise from genes through division. Heredity is maintained due to accurate gene reproduction. Occasionally gene reproduction goes wrong, and a different gene is produced from the parental one, which is gene mutation. Darwin’s theory of evolution, made the hereditary changes, very important for evolution. The sudden appearance of new hereditary types recorded by many plant and animal breeders is referred as mutation (or "sports").

The Shirley poppy, the dwarf "Cupid" sweet pea, and dwarf, cut-leaved, double-flowered, and white-flowered varieties of many plants have descended each from a single mutant individual that appeared under cultivation. Most of these mutations in plants arose from seed, but in some instances the mutant character was found to be confined to a single branch. Such a branch, when artificially propagated, remains true to its new type. Many horticultural varieties, especially those with variegated foliage, have arisen from such somatic mutations, or "bud sports".

There are four major types of mutation: (i) point mutation; (ii) chromosomal sequence alterations; (iii) chromosomal additions and deletions; and (iv) chromosomal number changes.

<u>Point mutation</u>
Point mutations arise when nucleotides are altered or substituted. Nucleotide changes occur spontaneously due to errors in replication and repair. Generally, mutations occur at rates of 1 x 10^{-6} to 10^{-7}. Mutation rates can be increased by numerous environmental agents such as ionizing radiation, chemical mutagens and thermal shock.

<u>Sequence alterations</u>
Chromosomal sequence alterations occur when the order of nucleotides is changed within a chromosome. Three types of DNA sequence alterations occur: translocation, inversions and transpositions. Small numbers of redundant nucleotide blocks may be involved or a whole groups of genes. Translocations occur when nucleotide sequences are transferred from one chromosome to another. Translocations are wide spread in a number of plant genera, including *Arachis, Brassica Capasicum, Gossypium, Triticum*etc

<u>Duplications and deficiences</u>
Chromosomal duplications and deletions are produced when portions of chromosomes are added or subtracted. Chromosomal deficiencies occur when nucleotide blocks are lost from within a chromosome, while duplications arise when nucleotide sequences are multiplied.

<u>Chromosomal number changes</u>
Chromosomal numerical changes arise when the number of chromosomes changes. There are three primary types of numerical changes: (i) aneeuploiddy; (ii) haploidy; and (iii) polyploidy.

3.3 Recombination

3.3.1 Introduction

Cultivated crops have evolved with the aid of recombination through the process of sexual, asexual and obligate meiotic sex that brings about the reshuffling of plant genums through a variety of mechanisms. Recombination is essential for the spread of favorable alleles in a population. Thus sex and recombination are adaptations whose purpose is to bring together new combinations of alleles.

Recombination involves the random shuffling of genes that break up well-adapted sets of alleles. Sex and recombination among plant species facilitate natural selection by generating useful variation. The adaptation and domestication of cultivated crops is facilitated by recombination as well as selection.

In addition, plant and animal breeders have long known the importance of outcrossing, and the extraordinary increases in crop yield that have been essential to feeding mankind have come from the efficient selection of large sexual populations.

3.3.2 Genetic Recombination

One of the ways that genetic variability is maintained within a population is through recombination, a process involving the exchange of genetic information among different DNA molecules that results in a reshuffling of genes. Recombination provides a mechanism for redistributing the informational changes that occur in DNA as a result of mutation and can produce numerous new combinations of genetic information. Regardless of the mechanism, recombination results new combinations of alleles (during meiosis).

Recombination provides a mechanism for generating diversity within the gene pool of a microbial population. The generation of heterogeneity, however, is restricted by the fact that the exchanges must be between alleles of the same gene or between genes that have large sequences of corresponding nucleotides. As a result, reciprocal (mutual) exchange occurs within species, but this process does not genetically permit genetic exchange between different species.

3.3.3 Types of Recombination Processes

There are two different types of recombination exchange processes:
Homologous or Reciprocal recombination

The classic type of exchange occurs between homologous region of DNA molecules, that is, between regions containing the same or nearly the same nucleotide sequences, as seen in the crossing over of chromosomes (during meiosis) where pairs of chromosomes containing the same gene loci pair and exchange allelic portions of the same chromosomes. The term homologous indicates that the exchange is between allele of the same gene and is not meant to imply that the exchange of DNA segments has exactly the same nucleotide sequence.

In homologous recombination, there is relatively good base pairing of corresponding regions of the DNA and the aligned chromosomes may establish duplex between homologous DNA regions. In eukaryotic microorganisms this often occurs during meiosis, the process whereby homologous chromosome pairs are separated and one member of each pair is distributed to each of the two daughter cells. Meiosis results in the conversion of a diploid cell into a haploid cell.
A similar homologous alignment of DNA molecules can occur when a bacterial chromosome or a portion, there of a transferred from a donor to a recipient bacterium.

Non- homologous or Non- reciprocal recombination
When the recombination takes place between non- homologous segments of DNA, is known as non- homologous recombination. Non-homologous recombination does not mean that there is no nucleotide homology in the segments of DNA that are exchanged, but it does imply that the extent of such homologous region is limited.

Non homologous recombination can be a site-specific exchange process, that is, a process in which DNA exchange occurs only at a given location within the genome. Non homologous recombination permits the joining together of DNA molecules from different sources. For example, Viral DNA may become incorporated into a bacterial chromosome, Plasmids, which may be transposed within chromosomes.

The difference between homologous and non- homologous recombination is a matter of degree, and the distinction is not always clear. Both general and site-specific recombination alters the arrangement of the genome and introduces variation into the gene pool of the population.

SELF-ASSESSMENT EXERCISE

Define natural selection explain the concept of evolution by natural selection
Discuss mutation in the context evolution
Explain the different processes of gene recombination

4.0 CONCLUSION

We learned in this unit that Darwin's theory of evolution states that plant species have evolved through the process of evolution and adaptation, while his theory of natural selection proposed that crop plants have develop through human breeding (artificial selection) and selecting power of nature. It was stated that the process of natural selection separates out those features most beneficial to plants in relation to their environmental conditions in a similar action to the selection by man on cultivated crops in the production of different hybrid varieties. The unit explained three types of natural selection as directional, stabilising, or disruptive**.**

The unit further explains that genes arise from genes through division with heredity maintained due to accurate gene reproduction. However, mutation occurs when gene reproduction goes wrong, and a different gene is produced from the parental one. It was explained that there are four major types of mutation:

(i) point mutation;
(ii) chromosomal sequence alterations;
(iii) chromosomal additions or deletions; and
(iv) chromosomal number changes.

In addition, the unit explained that recombination involves the random shuffling of genes that break up well-adapted sets of alleles. While sex and recombination among plant species facilitate natural selection by generating useful variation. We were also taught that the adaptation and domestication of cultivated crops is facilitated by recombination as well as selection. We now know that there are two different types of recombination exchange processes that include homologous or reciprocal recombination and non-homologous or non- reciprocal recombination.

5.0 SUMMARY

Darwin's theory of evolution states that plant species have evolved through evolution and adaptation, while his theory of natural selection proposed that crop plants have developed through human breeding (artificial selection) and natural selection. Natural selection process separates out those features most beneficial to plants in relation to their environmental conditions in a similar action to the selection by man on cultivated crops in the production of different hybrid varieties.

The Variation that exists in a population is the resource on which Natural Selection works. Evolution from the origin of life to the level of modern diversity must have required more variation than existed in the original population. The extra or new variation is generated by Mutation and Recombination. Mutation introduces less variation in other life forms that have lower population sizes, lower reproductive rates, and lower mutation rates. But in all species, mutation is an abundant source of New Variation, providing Raw Material for Evolutionary Change.

A broad spectrum of evolutionary forces, including migration, selection and random chance, interact to alter natural species. These same forces operated during the domestication of crops. The primary requirement for evolutionary change is genetic variability and mutation generates these building blocks. The mechanisms for crop evolution are natural selection, mutation and recombination.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define and explain the process of natural selection
2. Discuss the concept of evolution by natural selection
3. Highlight the necessary condition for natural selection
4. Explain mutation in the context evolution
5. Describe gene recombination and outline different types of recombination process.

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UNIT 2 FORCES OF EVOLUTION

CONTENTS

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1.0 INTRODUCTION

Evolution is the process by which the genetic constitution of populations is changed through time. Evolution change is a two-step process. First, mutation produces heredity variation and then that variability is shuffled and sorted from one generation to another. The major forces of evolution are migration, selection and genetic drift. Migration is a movement of genes within and between populations via pollen or seeds. Selection is a direct change in a population's gene frequency due to differential survival and reproduction. Genetic drift is a non-directional change in a population's gene frequency due to random events.

Migration is important in the development of plant species, and also played an important role in the spread of agriculture among human beings. Gene movement affects variation patterns not only between populations, but also within populations. Limited gene flow results in a highly sub structured population in which only adjacent plants have a high likelihood of mating referred to as intra-population migration.

While selection is very valuable in shaping natural populations, non-directional forces such as genetic drift can also make significant contribution to the process of crop plant evolution. The survival and proliferation of any genotype in any population is strongly dependent on adaptation to its environment and the survival of its progeny to maturity. While natural selection results from directional changes taking place over time in plant populations (or genotype/environmental correlations), drift is difficult to measure because it is non-directional and often masked by other forces. This unit defines and explains migration, selection, genetic drift and their interaction as driving forces behind the evolution and adaptation of plant species.

2.0 OBJECTIVES

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

- define migration and describe its mathematical representation.
- explain selection and discuss the different types of selection
- describe genetic drift and its role in the evolution of crop plants
- highlight the combine effect of migration, drift and selection in crop evolution.

3.0 MAIN CONTENT

3.1 Migration

The influx of genes from another population can increase variability in the recipient population if the immigrants are unique. The factors limiting the relative importance of gene flow are the difference in gene frequency between populations and the rate of migration.

The rate of migration (m) varies from 0 to 1: m = 0 signifies no immigrant alleles and m = 1 represents a complete replacement by immigrants. This can be mathematically represented as:

m = number of immigrants per generation/total
If the frequency of an allele among the natives is represented by q_o and among the immigrants by q_m then allele frequency in the mixed population will be:
$q = m\,(q_m – q_o) + q_o$
The change in gene frequency per generation (q) due to migration is:
$\Delta q = m(q_m – q_o)$
For example, if the native population originally contains qo = 0.3, and the immigrant group is qm = 0.1, and the migration rate is m = 0,001, then the change in gene frequency due to one generation of immigration is:
$\Delta q = 0.001(0.05 – 0.3) = 0.0002$

It is important to note that, two populations must have different gene frequencies to be greatly affected by gene flow, and the greater the input of novel genes, the greater the overall change.

Numerous methods of measuring migration of gene flow among plant populations have been developed. In some, pollen and seeds are simply captured in “traps” and identified, while in others the movement of pollinators and dispersers is closely monitored. Pollen and seeds have also been tagged with dyes and other chemical markers. The most popular method is to find unique alleles such as allozymes or molecular makers in parents, and trace their movement in to progeny.

3.1.1 Agents Responsible for Migration

Wind-carried pollen has been found hundreds of kilometers from its source and insects have been shown to carry viable pollen for several kilometers. Many seeds have long distance dispersal mechanisms such as wings to catch air patterns, stickers that attach to animal fur, or hard seed coats that a survive trips through the digestive tracts of migrating animals. All these mechanisms ensure at least some long-range dispersal of gene, although only a small percentage travels more than a few meters from a plant.

Human beings have played an important role in plant evolution by planting cultigens next to wild species, and by providing disrupted sites for population expansion. Numerous crop species such as barley, carrots, wheat, oats, sorghum and rye have been shown to hybridize with their wild progenitors. This sexual transfer of genes to weedy relatives has brought on concerns about the escape of engineered genes into the natural environment. This interspecies hybridization has a long-term effects.

Migration is important in the development of plant species, and also played an important role in the spread of agriculture among human beings. Gene movement affects variation patterns not only between populations, but also within populations. Limited gene flow results in a highly sub structured population in which only adjacent plants have a high likelihood of mating referred to as intra-populational migration.

3.2 Selection

Selection is defined as a change in a population’s gene frequency due to differential survival and reproduction. Many factors influence the persistence of gene, including germination rate, seedling survival, adult mortality, fertility and fecundity.

The “*fitness*” of a genotype is mathematically defined as the mean number of offspring left by the genotype relative to the mean number of progeny from other, competing genotypes. It is commonly designated by the letter W. Since it is a relative measure, the genotype with the highest fitness (most fit) is assigned a value of 1. Other fitness values are decimal fractions ranging between 1 and 0. The selection coefficient is the proportional reduction in each genotype’s fitness due to selection.

As an example, suppose we have the following genotype frequencies before and after selection:

	AA (genotype)	**Aa** (genotype)	**Aa** (genotype)
Gene frequency before selection	0.25	0.50	0.25
Gene frequency before selection	0.35	0.48	0.17

Then the relative reproductive contribution of each genotype would be:

Genotype	**Reproductive contribution**
AA	0.35/0.25 = 1.40
Aa	0.48/0.50 = 0.96
aa	0.17/0.25 = 0.68

To assign the most fit a value of 1, we must divide each genotype by the reproductive contribution of the most successful genotype:

Genotype	**Fitness (W)**
AA	1.4/1.4 = 1
Aa	0.96/1.4 = 0.7
aa	0.68/1.4 = 0.5

Since the selection coefficient is given by 1 – W; then for genotype:

AA 1.0- 1.0 = 0 ; Aa 1.0 – 0.7 = 0.3 ; aa 1.0 – 0.5 = 0.5

It has been reported that, Selection Coefficients in nature range from 0.001 to 0.5,. Humans probably used even more extreme values in the domestication of crop species.

3.2.1 Types of Selection

There are three primary types of selection: (i) directional; (ii) stabilising; and disruptive or diversifying. In directional selection, one side of a distribution is selected against, resulting, resulting in a directional change. Under stabilising selection, both extremes are selected against and the intermediate type becomes more prevalent. In disruptive selection, the intermediate types are selected against, resulting in the increase of divergent types. The amount of genetic variability present in a population and the strength of the selection coefficient determine how fast and much a population will change.

An example of directional selection is the domestication of maize, in which under human guidance the size of the ear was increased between

7000 and 3500 BP (before present) from less than 2.5 cm to well over 15 cm. The fact that most plant species are definable entities indicates that stabilising selection is common in nature, otherwise species lines would be much more blurred than they are. A typical example of stabilising selection is found in the plants *Linanthusandrosceus*that almost always have five lobes per flower even though their environments vary greatly and there is genetic variation for the trait at every site.

Many unique races of crops were developed by human beings through disruptive selection as they gathered and grew populations from distinct and habitats. Perhaps the most distinct alteration came in *Brassica oleracea*, where several distinct crops were developed including kale, broccoli, cabbage, kohlrabi and Brussels sprouts. Diverse races of rice, chickpea and chili peppers also emerged in response to isolation and differential selection pressure from humans.

Plant breeders have on numerous occasions employed diversifying selection to produce differences in harvest dates and quality factors. Example, the protein quality of maize was greatly improved by a repeated selection process for high and low values over 60 generations. In a long-term study selecting for high and low oil levels in kernel oil content, a 20-fold difference was obtained between high and low lines.

3.3 Genetic Drift

Random drift or genetic drift is a random change in gene frequency due to sampling error. Random drift occurs in small populations because sampling error is greater in a smaller population than in a larger one. Ultimately, the frequency of one of the alleles becomes zero and that of the other allele becomes one. The allele with the frequency of one is said to be fixed in the population because there would be no further change in its frequency, it may be expected that in a small population all the genes would become homozygous, or would be fixed in due course of time. Breeding populations are generally small; hence a certain amount of genetic drift is bound to occur in them.

While selection is very valuable in shaping natural populations, non-directional forces such as genetic drift can also make significant contribution to the process of crop plant evolution. The survival and proliferation of any genotype in any population is strongly dependent on adaptation to its environment and the survival of its progeny to maturity. While natural selection results from directional changes taking place over time in plant populations (or genotype/environmental correlations), drift is difficult to measure because it is non-directional and often masked by other forces.

Drift operates in a population by bringing about the fixation of one allele in a population similar to directional selection. Two primary factors influence the effect of drift in a population: allele frequency and population size. The more frequent an allele, the greater its chances of being fixed, and the smaller the population, the faster it will stumble towards fixation. The probability that an allele will be fixed is equal to its frequency in a population. Both the force of drift and selection are important in maintaining variability in natural population. However, the relative strengths of the two forces are dictated by each individual set of circumstances.

3.4 Interaction between Major Forces of Evolution

As mentioned previously the evolutionary forces of migration, drift and selection rarely act alone. The relative importance of these forces depends on the particular circumstances at hand.

Selection is directional, while drift is not. The relative influence of these two forces is tempered by the strength of the selective coefficient and the population size. Where drift is the predominant force, alleles will be fixed essentially at random: where selection is the predominant force, particular allele will be favored. All bets are off in the intermediate zone where neither drift nor selection strongly dominates.

Migration can act to supply variability to a population, but it can also act in opposition to drift and selection if the migrants are distinct as to the changes being imposed. In general, very small amount of migration can block the effects of genetic drift. Likewise, if the migration rate is greater than or equal to the selection coefficient, then the importance of selection of population differentiation becomes almost insignificant.

Mutation can act like migration in tempering the effects of selection and drift. However, its rate of occurrence is generally quite low ($<10^{-6}$) and therefore its greatest importance lies as a generator of new variability. Such rare variants can be established much faster in small populations than in large ones even if selective coefficients are quite high.

SELF-ASSESSMENT EXERCISE

Define migration, selection and genetic drift.
Highlight the combine effect of migration, drift and selection in crop evolution.

4.0 CONCLUSION

We learned from this unit that migration is the inflow of gene from one population to another and that the influx of genes from another population can increase variability in the recipient population if the immigrants are unique. We know that the factors limiting the relative importance of gene flow are the difference in gene frequency between populations and the rate of migration. It was explained that the agents responsible for migration are: Wind-carrying pollen hundreds of kilometers from its source, insects carrying viable pollen for several kilometers and human beings planting cultigens next to wild species.

The unit defines selection as a change in a population's gene frequency due to differential survival and reproduction with many factors influence the persistence of gene, including germination rate, seedling survival, adult mortality, fertility and fecundity. We learned that the there are three primary types of selection: (i) directional; (ii) stabilising; and disruptive or diversifying.

The unit further explains random drift or genetic drift as a random change in gene frequency due to sampling error with random drift occurring in small populations because sampling error is greater in a smaller population than in a larger one. It was also mentioned that the evolutionary forces of migration, drift and selection rarely act alone and that the relative importance of these forces depends on the particular circumstances at hand.

5.0 SUMMARY

Migration is the inflow of gene from one plant population to another. The influx of genes from another population can increase variability in the recipient population if the immigrants are unique. The factors limiting the relative importance of gene flow are the difference in gene frequency between populations and the rate of migration. The agents responsible for migration are wind-carrying pollen hundreds of kilometers from its source and insects carrying viable pollen for several kilometers. Human beings also play an important role in plant evolution by planting cultigens next to wild species.

Selection is defined as a change in a population's gene frequency due to differential survival and reproduction. Many factors influence the persistence of gene, including germination rate, seedling survival, adult mortality, fertility and fecundity. There are three primary types of selection: (i) directional; (ii) stabilising; and disruptive or diversifying. The amount of genetic variability present in a population and the strength of the selection coefficient determine how fast and much a population will change.

Random drift or genetic drift is a random change in gene frequency due to sampling error. Genetic drift occurs in small populations because sampling error is greater in a smaller population than in a larger one. Generally, the evolutionary forces of migration, drift and selection rarely act alone. The relative importance of these forces in the evolution of crop plants depends on the particular circumstances at hand.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define migration and describe the mathematical representation of the change in gene frequency per generation (q) due to migration
2. Explain selection and discuss the different types
3. Describe genetic drift and its role in the evolution of crop plants
4. Highlight the combine effect of migration, drift and selection in the evolution of crop species.

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UNIT 3 ROLE OF SPECIATION IN THE EVOLUTION OF CROP PLANTS

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1.0 INTRODUCTION

Species are populations that can be distinguished by prominent morphological differences. This definition implies that species may retain the ability to freely interbreed, and in reality behaving as one genetic entity. The biological species concept defines species in terms of interbreeding. Species are defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups." The expression "reproductively isolated" means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding.

The crucial event for the origin of a new species is reproductive isolation. Generally, the members of a species usually differ genetically, ecologically, and in their behaviour and morphology (that is, phenetically) from other species, as well as in who they will interbreed with. Some biologists prefer to define species not by reproductive isolation but by other properties, such as genetic or ecological differences. There are many different ways that plants can be reproductively isolated. These reproductive isolating barriers (RIBs) are generally broken into two classes: (i) pre-mating or prezygotic mechanisms and (ii) post-mating or postzygotic isolating mechanisms. Prezygotic barriers typically contribute more to total reproductive isolation in plants than do postzygotic barriers.

New species are thought to arise through a number of different pathways. One way the different modes are distinguished is by the degree of separation between the speciating populations. Based on this there are four types of speciation: 1) Geographic Speciation; 2) Peripatric Speciation 3) Parapatric Speciation and 4) Sympatric (instantaneous) speciation. This unit defines a species and explains the biological species concept, speciation, reproductive isolating barriers (RIBs) along with the various types of speciation in relation to their role in the evolution of crop plants.

2.0 OBJECTIVES

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

- define a species and explain the biological species concept
- discuss speciation and its role in the origin of a new species
- what do you understand by reproductive isolating barriers (RIBs)
- explains the various mode of speciation

3.0 MAIN CONTENT

3.1 What is a Species?

Species are populations that can be distinguished by prominent morphological differences. This definition implies that species may retain the ability to freely interbreed, and in reality behaving as one genetic entity.

Biological species are defined as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from each other. By this definition if taxa are reproductively isolated, they are evolving separately and therefore must have an identity of their own. However, some strongly divergent groups of plants often maintain some degree of inter-fertility even though they differ at numerous loci and are effectively evolving on their own. In addition, plants show great ranges in fertility from obligate outcrossing to complete selfing to apomixes (uniparental). Example many of grain and legume species are highly inbred, and most of the starchy staples like banana, cassava, potato, sugarcane, sweet potato, taro and yam are only propagated through asexual means.

In view of the above observations, scientists have developed the "Gene Pool System" to deal with the varying levels of inter-fertility between related taxa. This concept recognized three types of genic assemblages:

1. Primary Gene Pool (GP-1): hybridization easy; hybrids generally fertile.
2. Secondary Gene Pool (GP-2): hybridization possible, but difficult; hybrid week with low fertility.
3. Tertiary gene pool (GP-3): hybrids lethal or completely sterile.

The primary gene pool is directly equivalent to the biological species. The recognition of GP-2 and GP-3 allows other levels of inter-fertility to be incorporated into the overall concept of species. These are related taxa which share a considerable amount of genetic homology with GP-1, but are divergent enough to have greatly reduced infertility. Several agronomically important groups have been described using this system including legume, wheat and most of other cereals.

To minimize the problems associated with uniparental species the idea of an "Evolutionary Species" was developed, in which it was suggested that a species must meet four criteria: (i) is a lineage; (ii) evolved separately from other lineargs: (iii) has its own particular nitch or habitat; (iv) hasits own evolutionary tendencies.

3.2 The Biological Species Concept

The biological species concept defines species in terms of interbreeding. Species are defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups." The expression "reproductively isolated" means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding.

The biological species concept is important because it places the taxonomy of natural species within the conceptual scheme of population genetics. A community of interbreeding organisms make up in population genetic terms, a gene pool. In theory, the gene pool is the unit within which gene frequencies can change. In the biological species concept, gene pools become more or less identifiable as species. The identity is imperfect, because species and populations are often subdivided. The species, in this concept, is the unit of evolution. Organisms do not evolve but species do, and higher taxonomic groups such as phyla only evolve in so far as their constituent species are evolving.

The biological species concept explains why the members of a species resemble one another, and differ from other species. When two organisms breed within a species, their genes pass into their combined offspring; as the same process is repeated every generation, the genes of different organisms are constantly shuffled around the species gene pool. Different family lineages (of parent, offspring, grandchildren, and so on) soon become blurred by the transfer of genes between them. The shared gene pool gives the species its identity. By contrast, genes are not (by definition) transferred to other species, and different species therefore evolve a different appearance. The movement of genes through a species by migration and interbreeding is called gene flow. According to the biological species concept, gene flow explains why each species forms a phonetic cluster.

3.3 Speciation

Speciation means the evolution of reproductive isolation between two populations. Two main processes have been suggested by which reproductive isolation can evolve. Reproductive isolation may evolve as a by-product of evolutionary divergence between two populations. Or it may be directly favored, in a process called reinforcement.

The crucial event for the origin of a new species is reproductive isolation. Generally, the members of a species usually differ genetically, ecologically, and in their behaviour and morphology (that is, phenotically) from other species, as well as in who they will interbreed with. Some biologists prefer to define species not by reproductive isolation but by other properties, such as genetic or ecological differences.

Probably no single property can provide a universal species definition, applicable to all animals, plants, and microorganisms. However, many species do differ by being reproductively isolated, and even if the evolution of reproductive isolation is not always the crucial event in speciation, it is certainly the key event in research on speciation. The topic of this chapter is the evolution of reproductive isolation. The aim is to understand how barrier to interbreeding can evolve between two populations, such that one species evolves into two.

3.4 Reproductive Isolating Barriers (RIBs)

There are many different ways that plants can be reproductively isolated. These reproductive isolating barriers (RIBs) are generally broken into two classes: (i) pre-mating or prezygotic mechanisms that prevent the formation of hybrid zygotes; and (ii) post-mating or postzygotic isolating mechanisms that reduce the viability or fertility of hybrid zygotes. Prezygotic barriers typically contribute more to total reproductive isolation in plants than do postzygotic barriers.

In eco-geographic isolation, the habitats of two species are sufficiently different that they rarely have the opportunity to interbreed. The low bush-blueberry, *Vacciniumangustifolium,* is generally found on dry hillsides and gravelly barrens, while the high-bush blueberry Vacciniumcorymbosum is located in boggy wetlands. In this case the species remain distinct from each other as long as their habitats are not in close proximity. When they come in contact with each other, they can hybridize and form viable hybrids that survive when an intermediate habitat is present.
Species that are isolated temporally have distinct flowering times that do not have sufficient overlap to allow hybrid formation. The blueberry and *Tradescantia* species mentioned above are not only separated by habitat, but also by bloom date. This further reduces the production of hybrids. Floral isolation occurs when species have flowers that attract different types of pollinators. *Penstemon* spp. In California have flowers of different animals including hummingbird, wasps and two different-sized carpenter bees, species of columbines in western North America have distinct-looking flowers with nectar at the base of spurs that can only be reached by specific pollinators.

One of the strongest RIBs involves gametic incompatibility where foreign pollen grains cannot germinate in another species' stigmata, or they cannot successfully grow down the style to the ovaries. Species show a broad range of interaction from no hint of germination to successful pollen growth but failed fertilization. Fruit trees in the subgenus *Amygdalus of Prunus*freely cross, but gene transfer outside this section is generally obstructed by pollen and/or ovule sterility barriers.

Hybrid sterilties occur when hybrids do not produce functional gametes. The basis of these sterility barriers can be genic in nature or the result of meiotic irregularities due to chromosomal imbalances, crosses between the wild chickpea species *CicerEchinospermum* and

*Cicerreticulatum*yield very few hybrids and those that are produced are sterile due to poor chromosome pairing.

Inter-ploidy crosses generally result in hybrid sterility as unbalanced sets of chromosome are distributed to the different gametes. Most banana cultivars are triploid and produce no viable gametes. This trait is critical to edibility, as normally pollinated diploids have flinty, teeth breaking seeds. The final class of isolating mechanisms is hybrid breakdown, where the F_2 or backcross hybrids have reduced viability or fertility. Low vigor is found in many of the F_2 populations of interspecific bean crosses.
Any kind of RIB reduces the amount of gene flow between species, but combinations of mechanisms results in the tightest isolation. Most good species are separated by multiple combinations of RIBs. For example, the leafy-stemmed *Gilia* of central California, *G. millefoliata*and *G. capitata*, are isolated in five ways: 1) ecological isolation: *G. capitata*occures on sand-dunes and *G. millefoliata* on flats. 2) Floral: *G. capitata*is larger-flowered and bee pollinated, while *G. millefoliata*is small flowered and self-polinating. 3) Seasonal isolation: *G. millefoliata*blooms earlier than *G. capitata*. 4) Incompatibility: Hybrids are very difficult to produce by artificial crosses in the experimental gardens. 5) Hybrid sterility: The F_1 plants when they can be obtained are chromosomally sterile to a high degree, producing only about onepercent of good pollen grains and no F_2 seeds.

3.5 Mode of Speciation

New species are thought to arise through a number of different pathways. One way the different modes are distinguished is by the degree of separation between the speciating populations. The populations are geographically well isolated in *allopatric* speciation, there is no separation between populations in *sympatric* speciation, and the populations touch along one axis in *parapatric* speciation.

Other important criteria used to describe speciation pathways are: (1) how large the speciating groups are: and (ii) how much genetic differentiation precedes the formation of strong RIBs. Allopatric speciation is broken into two groups: *geographic* and *peripatric.* In geographic speciation, large populations are thought to gradually diverge and form RIBs, while in small populations without much differentiation. Sympatric speciation occurs when a single individual or small group arises that is reproductively isolated from the surrounding population. Parapatric speciation is closely related to sympatric speciation, except that the gradually diverging crowd of genotypes is on one side of the parent population rather than surrounded by it.

3.5.1 Geographic Speciation

The most widely recognised type of speciation is geographic speciation. In its first stage, there is a single population found in a large homogenous environment. The environment then becomes partly diversified due to physical or biotic factors and population becomes isolated. These populations begin to diverge genetically and eventually acquire sufficient variation to become reproductively isolated from each other. Further changes in the environment allow some of the newly evolved groups to come back in contact, but they do not produce successful hybrids because of past differentiation. Natural selection against the formation of weak or sterile hybrids promotes the reinforcement of RIBs through additional differentiation.

3.5.2 Peripatric Speciation

This type of speciation is very similar to the geographic mode, except the speciating population is much smaller. Other terms used for this type of speciation are quantum speciation by catastrophic selection and founder-induced speciation. Because of reduced population size, genetic drift becomes more important and the rate of speciation is accelerated. Peripatric speciation can result in reproductively isolated species that are otherwise quite similar to their progenitors or they may become morphologically quite distinct depending on how many genes are affected.

The dramatic reduction of a population due to an environmental catastrophe or the establishment of a founder population of a few individuals can also lead to a morphologically distinct species when the remaining sample of the gene pool is unbalances and undergoes a genetic revolution or genetic transilience. Genetic drift and changes in selection pressure can result in a shift of many genes into new coadapted complexes. A wide range of distinct plant species in the Hawaiian islands are thought to have arisen in this manner. Small founder populations do not always undergo dramatic alterations as most crop species are based on relatively few genotypes and still retain a strong resemblance and inter-fertility with their progenitors.

3.5.3 Parapatric Speciation

In this mode of speciation, RIBs evolve without geographical separation. The diversifying population is adjacent to the progenitor population (neighbouring sympatric). The process occurs when a subgroup diverges in response to environmental challenged and isolating barriers begin to form as a by-product of ecological differentiation.

It is not clear whether populations can diverge sufficiently without geographical separation as portions of populations are unlikely to differentiate enough to become genetically isolated in the face of strong gene flow. This is particularly true among sympatric subgroups where the diverging race is completely contained within the parent population and is bombarded on all sides by pollens and seeds. There are, however, numerous examples where paropatric populations have undergone substantial differentiation in the face of one-dimensional gene flow.

3.5.4 Sympatric (Instantaneous) Speciation

Occasionally, new species arise through spontaneous mutation without any ecological or geographical separation. A new isolated type appears in only a few generations without substantial genetic differentiation. Most of these types face a high likely hood of going rapidly extinct due to their low numbers, but even against these odds, many species are known to have gotten their start in this manner.

Examples of instantaneous speciation abound in plant species, like the case of polyploidy where a chromosomal duplication instantly isolates a progeny plant from its parents – at least half of all plant species are polyploid. Even the appearance and fixation of simple chromosomal rearrangements can result in a new species.

Factors distinguishing major modes of speciation in sexual plants

Mode of Speciation		Separation	Population Size	Differentiation Before RIBs
1.	Allopatric			
a.	Geographic (Type 1)	Wide	Large	Much
b.	Peripatric (Type 2)	Wide	Small	Little
2.	Parapatric	Douching	Large	Much
3.	Sympatric	None	One	Little

SELF-ASSESSMENT EXERCISE

Define speciation and its role in the origin of a new species
What do you understand by reproductive isolating barriers (RIBs)?

4.0 CONCLUSION

This unit defines species as populations that are distinguished by prominent morphological differences and retain the ability to freely interbreed, and in reality behaving as one genetic entity. It also defines biological species as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from each other. We were informed that the biological species concept defines species as "groups of interbreeding natural populations that are reproductively isolated from other such groups." The unit further highlights that the biological species concept is important because it places the taxonomy of natural species within the conceptual scheme of population genetics.
The unit also explains that speciation means the evolution of reproductive isolation between two populations. This highlights the fact that reproductive isolation is a crucial event for the origin of new species. The unit also stress that reproductive isolation may evolve as a by-product of evolutionary divergence between two populations. Or it may be directly favored, in a process called reinforcement. We were informed that members of a species usually differ genetically, ecologically, and in their behaviour and morphology from other species, as well as in who they will interbreed with. We also understand that new species arise through a number of different pathways that are distinguished by the degree of separation between the speciating populations.

5.0 SUMMARY

Species are populations that can be distinguished by prominent morphological differences. This definition implies that species may retain the ability to freely interbreed, and in reality behaving as one genetic entity. The biological species concept defines species as "groups of interbreeding natural populations that are reproductively isolated from other such groups." The expression "reproductively isolated" means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding. The biological species concept is important because it places the taxonomy of natural species within the conceptual scheme of population genetics.

Speciation means the evolution of reproductive isolation between two populations. Two main processes have been suggested by which reproductive isolation can evolve. Reproductive isolation may evolve as a by-product of evolutionary divergence between two populations. Or it may be directly favoured, in a process called reinforcement. New species develops through a number of different modes or pathways. One way the different modes are distinguished is by the degree of separation between the speciating populations. Based on this there are 4 types of speciation: 1) Geographic Speciation; 2) Peripatric Speciation 3) Parapatric Speciation and 4) Sympatric (instantaneous) speciation.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define a species and explain the biological species concept
2. Discuss speciation and its role in the origin of a new species
3. What do you understand by reproductive isolating barriers (RIBs)?
4. Explains the various mode of speciation

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UNIT 4 ROLE OF HYBRIDISATION IN CROP EVOLUTION

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1.0 INTRODUCTION

The mating or crossing of two plants or a line of dissimilar genotype is known as hybridisation. A significant proportion of plant and animal taxa have experienced hybridisation (natural hybridisation) and introgression. Genetic introgression, which is the movement of genetic material between parental types through the production of and mating with hybrids increases phenotypic variation in areas of contact between plant species. The widespread hybridisation and introgression existing among plant species have significant evolutionary consequences as they contribute to biological diversity.

Hybridisation has played an important role in the Evolution of many lineages through gene flow between Divergent Taxa. In addition, hybridisation has immediate phenotypic consequences through the expression of hybrid vigour and on a longer evolutionary time scales, hybridisation leads to: 1) local adaption; 2) Transgressive Segregation and 3) formation of new hybrid species. Hybridisation is purposefully employed in the breeding of domesticated plants (artificial hybridisation) to take advantage of transient hybrid vigor, move desirable variation among lineages, and generate novel phenotypes.

Hybridisation is the most important method of crop improvement. The process of hybridisation itself is fairly simple and easy. The chief objective of hybridisation is to create genetic variation. The plants or lines involved in hybridisation may belong to the same variety, different varieties of the same species, different species of the same genus or species from different genera. Based on the taxonomic relationships of the parents involved, hybridisation may be classified into two broad groups: (1) intervarietal and (2) distant hybridisation.

2.0 OBJECTIVES

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

- define hybridisation and explain its role in the evolution of crop plants
- differentiate between hybridisation and introgression
- discuss the objectives of hybridisation
- outline and describe different types of hybridisation

3.0 MAIN CONTENT

3.1 Definition and Concept of Hybridisation

Natural variability present in self- pollinated populations is exhausted quickly when they are subjected to selection. Individual plant selection or pure line selection is the most common procedure applied to genetically variable homozygous populations of self- pollinated crops. Consequently, the variability is soon exhausted as the land varieties are replaced by pure lines. For further improvement, therefore, new genetic variability has to be created by the plant breeder. This is easily and most commonly achieved by crossing two different pure lines.

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

The three corner-stones of hybridisation and the activities to achieve them

	Corner-stone	**Activity to achieve (the corner-stone)**
1	Prevention of self-pollination in flowers of female parents	Emasculation of the flowers
2	Prevention of pollination of the flowers of female parent by pollen from undefined sources	Bagging of the flowers
3	Ensuring pollination by the selected male parent (prevention of contamination of the pollen used for pollination- in a crop like maize)	Hand pollination- Bagging of the male inflorescence)

A significant proportion of plant and animal taxa have experienced hybridisation (natural hybridisation) and introgression. Genetic introgression, which is the movement of genetic material between parental types through the production of and mating with hybrids increases phenotypic variation in areas of contact between plant species.

The widespread hybridisation and introgression existing among plant species have significant evolutionary consequences as they contribute to biological diversity. Hybridisation has played an important role in the Evolution of many lineages through gene flow between Divergent Taxa that:

1. Generate new phenotypic diversity,
2. Allow for adaptation to novel environments, and
3. Contribute to speciation.

In addition, hybridisation has immediate phenotypic consequences through the expression of hybrid vigour and on a longer evolutionary time scales, hybridisation lead to:

1. Local adaption through the introgression of novel alleles and
2. Transgressive Segregation and,
3. In some cases, result in the formation of new hybrid species.

In natural populations, hybridisation can act in opposition to divergence, introduce adaptive variation into a population, drive the evolution of stronger reproductive barriers, or generate new lineages. Hybridisation is purposefully employed in the breeding of domesticated plants (artificial hybridisation) to take advantage of transient hybrid vigour, move desirable variation among lineages, and generate novel phenotypes. While Hybridisation between Species is increasingly appreciated to be a common occurrence, little is known about the forces that govern the subsequent Evolution of Hybrid Genomes.

3.2 Hybridisation and Introgression

Interspecific hybridisation contributes greatly to plant evolution. In the middle of the last century, the role of hybridisation was considered to be substantial, based on a number of morphological studies of native and crop species. Hybrid speciation in different floras is estimated to ranging from 25 to 80 per cent. It has also been reported that 16 to 34 per cent of the families in five biosystematics floras have at least one pair of species that hybridize locally and 6 to 16 per cent of the genera.

Hybridisation between native and introduced species has often led to the development of new taxa and has even been implicated in the evolution of a number of new invasive species. It has been estimated that 45 per cent of the British flora was alien, and sevenper cent of those introduced species are involved in the production of hybrids now prominent in the native flora. Highly invasive thistles from Europe have widely hybridised in Australia with about 28 examples where invasiveness was preceded by hybridisation and at least half of these hybrid lineages were the product of native x non-native hybridisations

Many plant species retain the ability to hybridise with their relatives, even when they are quite distinct and have relatively string RIBs. Numerous hybrid populations or “hybrid swarms” have been identified where closely related species come into contact. These hybrid zones are often narrow and stable when hybrid fitness is low or the species are adapted to very distinct habitat. However, interspecies hybridisation can act as the nucleus for evolution if hybrids are at least partially viable and suitable habitats exist to support them.

Hybridisation can stimulate evolutionary change in two ways: (i) the adaptive potential of one or both parents might be increased through backcrossing, or “introgressive hybridisation” and (ii) the hybrid population itself may evolve unique adaptations through genetic differentiation and genomic reorganisation or “recombinational speciation”. This process is generally thought to occur over a number of generations. The F_1 hybrids produced tend to have unique phenotypes that could be a nucleus for speciation, or they may be less fit than their progenitors but in some cases the hybrids could have higher fitness and unique adaptation. Many hybrid species are polyploid, but speciation via homoploid hybridisation is also found in several instances.

3.3 Objectives of Hybridisation

Hybridization is the most important method of crop improvement. The process of hybridisation itself is fairly simple and easy. The chief objective of hybridisation is to create genetic variation. When two genotypically different plants are crossed, the genes from both the parents are brought together in F_1. Segregation of and recombination among the genes that are heterozygous in F_1 would produce many new gene combinations in F_2 and the later generations, i.e., the segregating generations. The degree of genetic variation produced in the segregating generations would, therefore, depend on the number of the heterozygous genes in the F_1. This, in turn, will depend upon the number of the genes for which the two parents, used in hybridisation, were different.

If the two parents are closely related, they are likely to differ for few genes only. But if they are not related, or are distantly related, they may differ for several, even a few hundred, genes. However, it is not likely that the two parents will ever differ for all their genes. Therefore, when it is said that the F_1 is 100 percent heterozygous, it has reference only to those genes for which the two parents differ. The aim of hybridisation may be (1) the transfer of one or few qualitative characters, (2) the improvement in one or more quantitative characters, or (3) the use of F_1 as a hybrid variety. These objectives are briefly discussed below.

3.3.1 Combination Breeding (the Transfer of One or few Qualitative Characters,)

The main aim of combination breeding is the transfer of one or more characteristics into a single variety from another variety or other varieties. These characters may be governed by oligogenes or polygenes. The intensity of the character in the new variety is either compatible in or, more generally, lower than that in the parent variety from which it was transferred. In the approach, the increase in yield of the variety is obtained by correcting the weaknesses in the yield contributing traits, e.g., tiller number, grains per spike, test weight etc., of the concerned parent variety.

A familiar example of combination breeding is that for disease resistance. The backcross method of breeding was designed for combination breeding, and often pedigree method also fulfills the same purpose. In combination breeding, the genetic divergence between the parents is not the major consideration. What is important is that one of the parents must have in a sufficient intensity the character (s) under transfer, while the other parent is generally a popular variety.

3.3.2 Transgressive Breeding (the Improvement in One or more Quantitative Characters)

Transgressive breeding aims at improving yield or its contributing characters through transgressive segregation. Transgressive segregation refers to the appearance of such plants in an F_2 generation that are superior to both the parents for one or more characters. Such plants are produced by an accumulation of the plus or favorable genes from both the parents as a consequence of recombination.

Obviously, the parents involved in hybridisation must combine well with each other, and should preferably be genetically diverse, i.e., quite different. In such a situation, each parent is expected to contribute different plus genes, which when brought together by recombination, give rise to transgressive segregants. As a result, the intensity of character in the transgressive segregant, i.e., the new variety, is greater than that in either of the parents. The pedigree method of breeding and its modifications, particularly the population approach, are designed for the production of transgressive segregants.

3.3.3 Hybrid Varieties (the use of F_1 as a Hybrid Variety)

In most self-pollinated crops, F_1 is more vigorous and higher yielding than the parents. Wherever it is commercially feasible, F_1 may be used directly as a variety; such a variety is call hybrid variety. In such cases, it is important that the two parents should combine well to produce an outstanding F_1. Hybrid varieties are being cultivated on a commercial scale in rice and some other self-pollinated crops.

3.4 Types of Hybridisation

The plants or lines involved in hybridisation may belong to the same variety, different varieties of the same species, different species of the same genus or species from different genera. Based on the taxonomic relationships of the parents involved, hybridisation may be classified into two broad groups: (1) intervarietal and (2) distant hybridisation.

3.4.1 IntervarietalHybridisation

The parents involved in intervarietal hybridisation belong to the same species; they may be two strains, varieties or races of the same species. It is also known as intraspecific hybridisation. In crop improvement programmes intervarietal hybridisation is the most commonly used. In fact, it is so common that it may often appear, particularly to a casual observer, to be the only form of hybridisation used in crop improvement.

The intervarietal crosses may be simple or complex depending upon the number of parents involved.

3.4.2 Distant Hybridisation

Distant hybridisation includes crosses between different species of the same genus or of different genera. When two species of the same genus are crossed, it is known as interspecific hybridisation; but when the species belong to two different genera, it is termed as intergenric hybridisation. Generally, the objective of such crosses is to transfer one or few simply inherited characters like disease resistance to a crop species. Sometimes, interspecific hybridisation may be used for developing a new variety, e.g., Clinton oat variety was developed from a cross between *Avena sativa* x A. Byzantine (both hexaploidy oat species) and CO31 rice variety was developed from the cross *Oryza sativa* var. indica x O. perennis.

Almost all the present-day sugarcane varieties have been developed from complex crosses between *Saccharumofficinarum*(noble canes), *S. barberi* (Indian canes) and other Saccharum species, e.g., *S. spontaneum* (‘kans’). The improvement in fiber length of Indian cotton (*Gossypium arboretum*) has been brought about by crossing it with American cultivated cotton (*G. hirsutum*): many improved varieties have resulted from such crosses. Intergeneric hybridisation may also be used to develop a new crop species, e.g., *Triticale hexaploide* from a cross between *Triticumturgidum* and *Secale cereal* (rye). Wild species often provide genes, which are not present in the cultivated species. For example, many of the genes for rust resistance in wheat are derived from related wild species. Distant hybridisation is likely to become increasingly important in the correction of specific defects of crop species. In many cases, wild species may contribute valuable ‘yield genes’ as well to the cultivated species.

SELF-ASSESSMENT EXERCISE

Define hybridisation and explain its role in the evolution of crop plants
Differentiate between hybridisation and introgression
Explain the objectives of hybridisation

4.0 CONCLUSION

We were informed in this unit that the mating or crossing of two plants or a line of dissimilar genotype is known as hybridisation. We now know that a significant proportion of plant and animal taxa have experienced hybridisation (natural hybridisation) and introgression. The unit also describes genetic introgression as the movement of genetic material between parental types through the production of and mating with hybrids. It further explains that the widespread hybridisation and introgression existing among plant species have significant evolutionary consequences as they contribute to biological diversity.

The unit highlights that hybridisation plays an important role in the evolution of many lineages through gene flow between Divergent Taxa. We equally understand that hybridisation has immediate phenotypic consequences through the expression of hybrid vigour and on a longer evolutionary time scales, hybridisation can lead to: 1) local adaption; 2) transgressive segregation and 3) formation of new hybrid species. The unit also stress that hybridisation is purposefully employed in the breeding of domesticated plants (artificial hybridisation) to take advantage of transient hybrid vigour, move desirable variation among lineages, and generate novel phenotypes.

This unit explains that hybridisation is the most important method of crop improvement and its chief objective is to create genetic variation in a plant population. We now know that the plants involved in hybridisation may belong to the same variety, different varieties of the same species, different species of the same genus or species from different genera. We were further informed that based on the taxonomic relationships of the parents involved, hybridisation may be classified into two broad groups: (1) intervarietal and (2) distant hybridisation.

5.0 SUMMARY

Hybridisation is the mating or crossing of two plants or a line of dissimilar genotype. Many plant and animal taxa have experienced hybridisation (natural hybridisation) and introgression. Introgression is the movement of genetic material between parental types through the production of and mating with hybrids. The widespread hybridisation and introgression existing among plant species have significant evolutionary consequences as they contribute to biological diversity.

Hybridisation plays an important role in the evolution of many plants through gene flow between different taxa. Furthermore, hybridisation has immediate phenotypic consequences through the expression of hybrid vigour and on a longer evolutionary time scales, hybridisation lead to: 1) local adaption; 2) transgressive segregation and 3) formation of new hybrid species. Hybridisation is purposefully employed in the breeding of domesticated plants (artificial hybridisation) and is the most important method of crop improvement.

The principal aim of hybridisation is to create genetic variation in a population. The plants or lines involved in hybridisation may belong to the same variety, different varieties of the same species, different species of the same genus or species from different genera. Based on the taxonomic relationships of the parents involved, hybridisation may be classified into two broad groups: (1) intervarietal and (2) distant hybridisation.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define hybridisation and explain its role in the evolution of crop plants
2. Differentiate between hybridisation and introgression
3. Discuss the objectives of hybridisation
4. Outline and describe the types of hybridisation you know

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MODULE 3 ORIGIN OF CULTIVATED CROPS

Unit 1 Plant Genetic Variation in a Population
Unit 2 Origin of Commonly Cultivated Crops
Unit 3 Centers of Agriculture
Unit 4 Domestication of Plants

UNIT 1 PLANTS GENETIC VARIATION IN A POPULATION

CONTENTS

1.0 Introduction
2.0 Objectives
3.0 Main Content
 3.1 Key Terms and Concept of Genetic Variation
  3.1.1 Key Genetic Terms
  3.1.2 Concept of Genetic Variation
 3.2 Genetic Variation as Mechanism for Selection and Evolution
 3.3 Genetic variation, Evolution and Adaptation to Environment
  3.3.1 Geographic Variation
  3.3.2 Sources of Genetic Variation
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

Genetic variation is a measure of the genetic differences that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele. Genetic variation is caused either by: 1. Mutation, 2. Random mating between organisms 3. Random fertilisation or Crossing over (or recombination) between chromatids of homologous chromosomes during meiosis.

Despite the biochemical mechanisms that are designed to ensure the fidelity of DNA replication, alterations in genetic information can and do occur. Variability within the genomes of an organism provides a mechanism for selection and evolution. Genetic variability also provides the heterogeneity needed within a population to adapt to environmental variability. In addition, Variation allows some individuals within a population to adapt to the changing environment.

Furthermore, Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment. Gene duplication, mutation, or other processes can produce new genes and alleles and increase genetic variation. Overall, the main sources of genetic variation are the formation of new alleles, the altering of gene number or position, rapid reproduction, and sexual reproduction.

2.0 OBJECTIVES

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

- define genetic variation and explain its concept
- describe genetic variation as a mechanism for selection and evolution
- discuss genetic variation in relation to its role in evolution and adaptation
- highlight the sources of genetic variation

3.0 MAIN CONTENT

3.1 Key Terms and Concept of Genetic Variation

3.1.1 Key Genetic Terms

Allele:- one of the different forms of a gene that can exist at a single locus. The form of the gene is determined by its DNA sequence. When an individual has different forms of an allele at a locus, it is a heterozygote. When its alleles are the same, it is a homozygote.

Genetic diversity:-the level of biodiversity, refers to the total number of genetic characteristics in the genetic makeup of a species

Crossing over:- the exchange of genetic material between homologous chromosomes that results in recombinant chromosomes

Phenotypic variation:- variation (due to underlying heritable genetic variation); a fundamental prerequisite for evolution by natural selection

Genetic variation:- variation in alleles of genes that occurs both within and among populations

Genotype:- The sum total of all the alleles at all the loci in an organism, considered as a measure of 'breeding value' for evolution and crop improvement efforts.

Phenotype:- The external and observable expression of the genes, and the result of genes interacting with the environment the appearance of individuals.

Phenotype (P) = Genotype (G) + Environment (E) + (GXE)

An individual's phenotype can be viewed as the sum of the effects due to genes, the effects of the environment, and interactions between the genes and the environment (GXE).

Heritability:- The proportion of total phenotypic variance at the population level that is contributed by genetic variance. If a trait is largely determined by environmental factors, then the heritability will be low. Traits that are largely controlled by genes have a high heritability and consequently are more likely to change in response to selection.

Genome:- The entire complement of genetic material in a chromosome set. The number of chromosomes in one nuclear genome is designated 'n', which is equivalent to the haploid number.

Diploid:- species have one set of homologous chromosome pairs, so their total number of chromosomes is 2n. Some species are polyploid which means that they have multiple sets of n chromosomes (triploids are 3n, tetraploids are 4n, etc.).

Population:- is a community of individuals that share a common gene pool. It is 'a breeding group' of individuals that may intermate. The genetic constitution of a population is described by the array of gene frequencies and alleles that are present at each locus.

3.1.2 Concept of Genetic Variation

Genetic variation is a measure of the genetic differences that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele. For example, a population with many different alleles at a single chromosome locus has a high amount of genetic variation. Genetic variation is essential for natural selection because natural selection can only increase or decrease frequency of alleles that already exist in the population.

Genetic variation is caused either by: 1. Mutation, 2. Random mating between organisms 3. Random fertilisation or Crossing over (or recombination) between chromatids of homologous chromosomes during meiosis. Out of which, the last three of these factors reshuffle alleles within a population, giving offspring combinations which differ from their parents and from others.

3.2 Genetic Variation as Mechanism for Selection and Evolution

Despite the biochemical mechanisms that are designed to ensure the fidelity of DNA replication, alterations in genetic information can and do occur. The genomes of microorganisms are subject to change by a variety of mechanisms. Heritable changes in the sequence of nucleotide bases of an organism, known as mutations alter the genome of the organism and introduce variability into the gene pool of a population. Variability within the genomes of an organism provides a mechanism for selection and evolution. Genetic variability also provides the heterogeneity needed within a population to adapt to environmental variability.

Once variability is introduced into the gene pool of a population, there are several ways in which it is maintained. Genetic information can be transferred between organisms, with the exchange of such information ensuring the passage of genetic variation from one generation to another. Recombination of genetic information from two different organisms produces progeny that contain genetic information derived from two potentially different genomes.

In the case of eukaryotic organisms, genetic exchange during sexual reproduction affords a mechanism for gene re-assortment within the population and maintenance of genetic heterogeneity. Even in prokaryotic microorganisms, where reproduction is asexual or parasexual (not involving gamete formation or a long-lasting diploid state), there are genetic exchange processes that lead to the recombination of genetic information.

3.3 Genetic Variation, Evolution and Adaptation to Environment

Variation allows some individuals within a population to adapt to the changing environment. Because natural selection acts directly only on phenotypes, then more genetic variation within a population usually enables more phenotypic variation. Some new alleles increase an organism's ability to survive and reproduce, which then ensures the survival of the allele in the population. Other new alleles may be immediately detrimental (such as a malformed oxygen-carrying protein) and organisms carrying these new mutations will die out. Neutral alleles are neither selected for nor against and usually remain in the population. Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment. The natural evolution of organisms is based on the selection of the genetic variants best suited for survival, and artificial manipulation of genetic exchange between organisms can be used to create new organisms. The development of an understanding of the molecule basis of genetics has spawned the new and exciting field of genetic engineering and application of genetic engineering promise to revolutionise the industrial applications of molecular biology.

3.3.1 Geographic Variation

Some species display geographic variation as well as variation within a population. Geographic variation, or the distinctions in the genetic makeup of different populations, often occurs when populations are geographically separated by environmental barriers or when they are under selection pressures from a different environment. One example of geographic variation is clines: graded changes in a character down a geographic axis.

3.3.2 Sources of Genetic Variation

Gene duplication, mutation, or other processes can produce new genes and alleles and increase genetic variation. New genetic variation can be created within generations in a population, so a population with rapid reproduction rates will probably have high genetic variation. However, existing genes can be arranged in new ways from chromosomal crossing over and recombination in sexual reproduction. Overall, the main sources of genetic variation are the formation of new alleles, the altering of gene number or position, rapid reproduction, and sexual reproduction.

SELF-ASSESSMENT EXERCISE

Define genetic variation and explain its concept
Discuss genetic variation in relation to its role in evolution and Adaptation
Describe the various sources of genetic variation

4.0 CONCLUSION

In this unit, we explained the concept of genetic variation and how it affects the evolution of populations. You learnt that genetic variation is a measure of the genetic differences that exist within a population and that the genetic variation of an entire species is often called genetic diversity. It was also stated that genetic variation is essential for natural selection because natural selection can only increase or decrease frequency of alleles that already exist in the population. You have equally been informed that genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment while allowing them to adapt to it. We have seen that some species display geographic variation as well as variation within a population. Final, you have learnt that, the main sources of genetic variation are the formation of new alleles, the altering of gene number or position, rapid reproduction, and sexual reproduction.

5.0 SUMMARY

Genetic variation is an important force in evolution as it allows natural selection to increase or decrease frequency of alleles already in the population. Genetic variation can be caused by mutation (which can create entirely new alleles in a population), random mating, random fertilisation, and recombination between homologous chromosomes during meiosis (which reshuffles alleles within an organism's offspring). Genetic variation is advantageous to a population because it enables some individuals to adapt to the environment while maintaining the survival of the population.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define genetic variation and explain its concept
2. Describe genetic variation as a mechanism for selection and evolution
3. Discuss genetic variation in relation to its role in evolution and Adaptation
4. Highlight the sources of genetic variation

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UNIT 2 ORIGIN OF COMMONLY CULTIVATED CROPS

CONTENTS

1.0 Introduction
2.0 Objectives
3.0 Main Content
  3.1 Center of Origen of Cultivated Crops
  3.2 Vavilove’s Center of Origin/Spread of Crops
  3.3 Primary and Secondary Centers of Origin
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

The center of origin is a geographical area where the particular group of organisms (either domesticated or wild) first originated on earth. Many people believed that centers of origin are also centers of diversity. But, the centers of diversity may not represent the centers of origin of crop plants. The information on origin of crop plants is important in plant breeding to locate wild relatives, related species and new genes. Knowledge of the origins of crop plants is important to avoid genetic erosion, the loss of germplasm due to the loss of ecotypes and habitat.

The Russian scientist Nikolai Ivanovich Vavilov and his colleagues visited several countries and collected a large number of crop plants and their wild relatives. They used this collection in Russian breeding program of developing improved varieties. His deductions were based on evidences from morphology, anatomy, cytology, genetics, plant geography and distribution. He considered that great centers of origin were always located in lower mountains and hills of tropical, sub-tropical regions. He also recognises some secondary centers of origin where two or more species crossed together.

In 1926 Vavilov published "Studies on the Origin of Cultivated Plants" which described his theories on the origins of crops. He concluded that each crop has a characteristic primary center of diversity which is also its center of origin. Eight areas were recognised and suggested as centers from which all of our major crops were domesticated; these centers are: china, Hindustan, Central Asia, Asia Minor, Mediterranean, Abyssinia, Central and South America. Later, he modified his theory to include "secondary centers of diversity" for some crops.

2.0 OBJECTIVES

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

- explain the Center of Origen of cultivated Crops
- describe the contribution of Nikolai IvanovichVavilov to the origin of cultivated crops
- explain Vavilov, Centers of Origin/Spread of Crops
- discuss with examples primary and secondary centers of origin

3.0 MAIN CONTENT

3.1 Center of Origen of Cultivated Crops

The center of origin is a geographical area where the particular group of organisms (either domesticated or wild) first originated on earth. Many people believed that centers of origin are also centers of diversity. But, the centers of diversity may not represent the centers of origin of crop plants. Although a few species may have been originated separately at more than one place, but most species had their origin at a certain place and then spread elsewhere. In other words, in the center of origin a crop is generally confined to one place, whereas the center of diversity may be found at more than one place. The exact location of origin of species is only a matter of speculation based on indirect evidences.

The information on origin of crop plants is important in plant breeding to locate wild relatives, related species and new genes. Knowledge of the origins of crop plants is important to avoid genetic erosion, the loss of germplasm due to the loss of ecotypes and habitat. The Russian scientist Nikolai Ivanovich Vavilov and his colleagues visited several countries and collected a large number of crop plants and their wild relatives. They used this collection in Russian breeding program of developing improved varieties. His deductions were based on evidences from morphology, anatomy, cytology, genetics, plant geography and distribution.

He considered that great centers of origin were always located in lower mountains and hills of tropical, sub-tropical regions. He also recognises some secondary centers of origin where two or more species crossed together. Secondary centers of origin are the places where natural and artificial selection occurred on after another. He stated that plants were not domesticated at random but it was a continuous process.

3.2 Vavilov, Centers of Origin/Spread of Crops

Nicolai Vavilov (1887-1943) was a Russian scientist who headed the Lenin All-Union Academy of Agricultural Sciences (later named the Vavilov All-Union Institute of Plant Industry in his honour) in St. Petersburg (Leningrad) from 1920 to 1940. He established 400 research institutes that employed up to 20,000 people. He planned to collect all of the useful germplasm that had potential in the Soviet Union, to classify it, and to use it in a national plant breeding effort. He and his colleagues conducted extensive germplasm explorations and collections in many parts of the world. The Vavilov Institute remains an important resource for germplasm maintenance, access, and utilisation.

In 1926 he published "Studies on the Origin of Cultivated Plants" which described his theories on the origins of crops. Vavilov concluded that each crop has a characteristic primary center of diversity which is also its center of origin. Eight areas were recognised and suggested as centers from which all of our major crops were domesticated. Later, he modified his theory to include "secondary centers of diversity" for some crops.

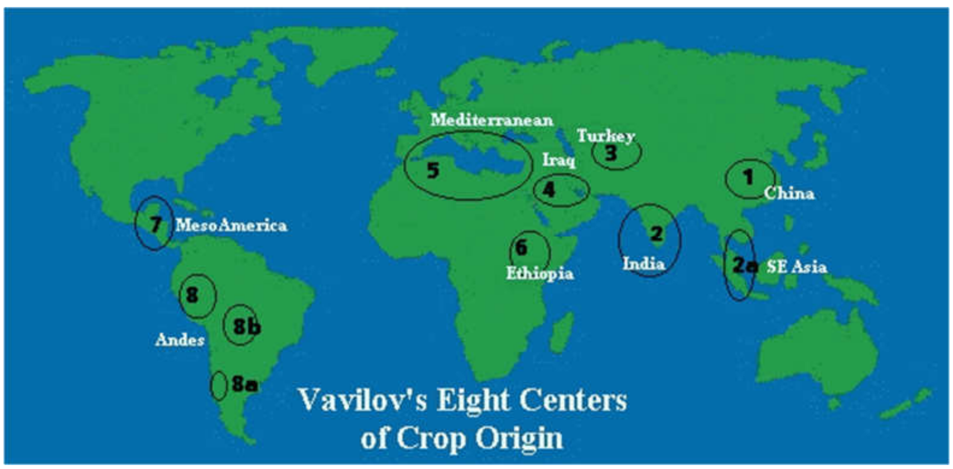
3.3 Primary and Secondary Centers of Origin

There is considerable evidence that the cultivated plants were not distributed uniformly throughout the world. Even today, certain areas show far greater diversity than others in the forms of certain cultivated crops and their wild relatives. In 1926, N.I. Vavilov proposed that crop plants evolved from wild species in the areas showing great diversity and termed them as primary centers of origin. Later, crops moved to other areas primarily due to the activities of man. These latter areas generally lack the richness in variation found in the primary centers of origin. But in some areas, certain crop species show considerable diversity of forms although they did not originate there; such areas are known as secondary centers of origin of these species.

The concept of centers of origin was given by Vavilov based on his studies of a vast collection of plants at the Institute of Plant Industry, Leningrad. He was director of this institute from 1916 till 1936. He also postulated the Law of Homologous Series in Variation; this law states that characters found in one species also occur in other related species. Thus diploid (2x), tetraploid (4x) and hexaploidy (6x) wheat show a series of identical contrasting characters. Similarly, genus

Secaleduplicates the variation found in genus Triticum. Thus, a character absents in a species, but found in a related species, is likely to be found in the collections of that species made from the center of its origin.

Eight main centres of origin were originally proposed by Vavilov in 1926; these centres are: china, Hindustan, Central Asia, Asia Minor, Mediterranean, Abyssinia, Central and South America (table Y). Later, in 1935, Vavilov divided the Hidustan Centre of Origin into two centres, viz, Indo-Burma and Siam-malaya-Java Centre of Origin. Similarly, the South American Centre was divided into three centres, namely, Peru, Chile and brazil-Paraguay Centre of Origin. Thus, the eight main centres were regrouped into 11 centres of origin. At the same time, he introduced a new centre of origin, the U.S.A. Centre of Origin. Two plant species, sunflower (Helianthus annuus) and Jerusalem artichoke (Helianthus tuberosus), are believed to have originated in the U.S.A. Centre of Origin.



The centres of origin as proposed by N.I. Vavilov (1926,1935)

Centre of origin	**Primary centre of origin**	**Secondary centre of origin**
Abyssinian Centre	Barley, *Triticum*spp., jowar, bajra, gram, lentil, sem (*Dolichos*sp), pea, khesari, linseed, safflower, sesame, castor, coffee, onion, okra, etc.	Broad bean (*Viciafaba*)
Asia Minor Centre (*Syn.*, Near East or Persian Centre)	*Triticum*spp., rye, alfalfa, carrot, cabbage, oat, lettuce, apple, *Pyrus*spp., *Prunus*spp., grape, almonds, chestnut, pistachio nut, Persian clover, etc.	*B. campestris, B. nigra*, turnip, apricot, etc.

Central American centre (*Syn.*, Mexican Centre)	Maize, rajma (*P. vulgaris*), lima beans, melons, pumpkin, sweet potato, arrowroot, chillies, *G. hirsutum*, papaya, guava, avocado, etc.	Rye (*Secale cereal*)
Central Asia Centre (*Syn.*, Afghanistan Centre)	*T. aestivum*, pea, mung, linseed, sesame, safflower, hemp, *G. herbaceum*, radish, musk melon, carrot, onion, garlic, spinach, pear, almond, grape, apple, etc.	Rye (*Sevalecereale*)
China Centre	Soybean, radish, bunda (*Colocasia*sp.), proso millet, buckwheat, opium poppy, brinjal, pear, peach, apricot, plum, orange, Chinese tea, etc.	Maize, rajma, cowpea, turnip, sesame (til)
Hindustan Centre [Divided into: 1. Indo-Burma, and 2. Siam-Malaya-Java Centres]	Rice, pigeon pea, chickpea, cowpea, mung, brinjal, cucumber, Indian radish, noble canes, *G. arboretum*, mango, orange, coconut, banana, etc.	
Mediterranean Centre	*Triticum*spp., barley, *Avena*spp., lentil, pea, broad bean, lupins, *Lathyrus*spp., chickpea, clovers, *Brassica* spp., onion, garlic, beets, lettuce, asparagus, lavender, peppermint, etc.	
South American Centre [Divided into: 1. Peru, 2. Chile, and 3. Brazil-Paraguay Centres]	potato, maize, limabean, peanut, pineapple, pumpkin, *G. barbadense*, tomato, tobacco, guava, quinine tree, cassava, rubber, etc.	
U.S.A. Centre	Sunflower, Jerusalem artichoke	

SELF-ASSESSMENT EXERCISE

What do you understand by primary and secondary centers of origin

Explain the contribution of Nikolai IvanovichVavilov to the origin of cultivated crops

Describe Vavilov, Centers of Origin/Spread of Crops

4.0 CONCLUSION

This unit described the center of origin as a geographical area where the particular group of organisms (either domesticated or wild) first originated on earth. It explains that the centers of diversity may not represent the centers of origin of crop plants. We were also informed that knowledge on the origin of crop plants is important in plant breeding to locate wild relatives, related species and new genes. In addition, the unit stress that the information of the origins of crop plants is also important to avoid genetic erosion, the loss of germplasm due to the loss of ecotypes and habitat.

The unit explains that a Russian scientist Nikolai IvanovichVavilov and his colleagues visited several countries and collected a large number of crop plants and their wild relatives. It was also reported that the scientist used this collection in Russian breeding program of developing improved varieties. We were made to understand that in 1926 Vavilov published "Studies on the Origin of Cultivated Plants" which described his theories on the origins of crops. It was further stated that the he concluded that each crop has a characteristic primary center of diversity which is also its center of origin.

The unit also informs us that Vavilov recognised and suggested Eight areas as centers from which all major crops were domesticated; these centers are: china, Hindustan, Central Asia, Asia Minor, Mediterranean, Abyssinia, Central and South America. We were made to understand that the scientist later modified his theory to include "secondary centers of diversity" for some crops.

5.0 SUMMARY

The center of origin is a geographical area where the particular group of organisms (either domesticated or wild) first originated on earth. It’s believed that centers of origin are also centers of diversity. However, the centers of diversity may not represent the centers of origin of crop plants. The information on origin of crop plants is important in plant breeding to locate wild relatives, related species and new genes. Knowledge of the origins of crop plants is important to avoid genetic erosion, the loss of germplasm due to the loss of ecotypes and habitat.

The Russian scientist Nikolai Ivanovich Vavilov and his colleagues visited several countries and collected a large number of crop plants and their wild relatives. They used this collection in Russian breeding program of developing improved varieties. In 1926 Vavilov published "Studies on the Origin of Cultivated Plants" which described his theories on the origins of crops. He concluded that each crop has a characteristic primary center of diversity which is also its center of origin. Eight areas were recognized and suggested as centers from which all of our major crops were domesticated; these centers are: china, Hindustan, Central Asia, Asia Minor, Mediterranean, Abyssinia, Central and South America. Later, he modified his theory to include "secondary centers of diversity" for some crops.

6.0 TUTOR-MARKED ASSIGNMENT

1. Explain the Center of Origen of cultivated Crops
2. Describe the contribution of Nikolai Ivanovich Vavilov to the origin of cultivated crops
3. Explain Vavilov, Centers of Origin/Spread of Crops
4. Discuss with examples Primary and Secondary Centers of Origin

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UNIT 3 CENTERS OF AGRICULTURE

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1.0 Introduction
2.0 Objectives
3.0 Main Content
3.1 Centers of Agricultural Origin
3.1.1 Introduction
3.1.2 Characteristics of Center for Agricultural Origin
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1.0 INTRODUCTION

Agriculture originated in at least six different areas of the world: Mesoamerica, the Andes of South America (including their piedmonts), South Asia (the Fertile Crescent), Africa (Ethiopia and the Sahel), Southern China, and Southeast Asia. Additional areas include North America, North China, and Europe. In each of these centers, similar types of crops were domesticated. For example, in each center one or more sources of carbohydrates (cereals or root or tuber crop) and of proteins (legumes) were domesticated. The commonalities between these geographically disparate regions are: 1) They are located in tropical or subtropical regions; 2) Their topography is generally mountainous and 3) Have abundance of resources.

Biome is a major regional terrestrial community, or grouping, with its own type of climate, vegetation, and animal life. Biomes are not sharply separated, but merge gradually into one another over what is called an ecotone. Climatic conditions, such as rainfall and temperature, are the major determinants of the type of biome that develops in an area. Altitude is another important factor determining the distribution of biomes. Most domesticated plants originated in one of two biomes, the Mediterranean and the Savannah.

2.0 OBJECTIVES

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

- describe the centers of agricultural origin

- explain the similarities between the centers of agricultural origin and their characteristics
- define a biome and discuss its distribution
- describe the two major biomes where domesticated plants originated

3.0 MAIN CONTENT

3.1 Centers of Agricultural Origins

3.1.1 Introduction

Among technological development and inventions, agriculture is perhaps one of the few, if not the only one, that originated independently in more than one location. Although the number and precise boundaries of the different centers of origin of agriculture remain to be determined, agriculture originated in at least six different areas of the world: Mesoamerica, the Andes of South America (including their piedmonts), South Asia (the Fertile Crescent), Africa (Ethiopia and the Sahel), Southern China, and Southeast Asia. Additional areas include North America, North China, and Europe, but their impact has been much less than that of the aforementioned centers. In each of these centers, similar types of crops were domesticated. For example, in each center one or more sources of carbohydrates (cereals or root or tuber crop) and of proteins (legumes) were domesticated.

The commonalities between these geographically disparate regions are:

1. They are located in tropical or subtropical regions generally between 35° N. and 35° S. Lat.
2. Their topography is generally mountainous or hilly containing a wider range of resources compared to the areas that are located at higher or lower altitudes.
3. This abundance of resources has allowed early famers to more easily identify plants or animals that were predisposed to domestication.

3.1.2 Characteristics of Center for Agricultural Origin

The prerequisite for a potential center of agricultural origin includes the following:

1. Presence of wide relatives
2. An alternation of rainy and dry seasons
3. Limits to migration as an alternative to agricultural intensification

4. Topography or territoriality that prevents populations from migrating to other areas to obtain supplementary or alternative source of food.
5. Absence of heavily forested areas, that makes the conversion to agricultural land difficult.
6. The existence of different groups with different traditions, cultures, and technology

3.2 Origin of Crops in Biomes

3.2.1 Introduction

Biome is a major regional terrestrial community, or grouping, with its own type of climate, vegetation, and animal life. Biomes are not sharply separated, but merge gradually into one another over what is called an ecotone. A biome embraces the idea of community, interactions among vegetation, animal populations, and soil types within a regional climate.

Climatic conditions, such as rainfall and temperature, are the major determinants of the type of biome that develops in an area. Deserts develop in areas with low annual precipitation. Slightly higher rainfall will favour grassland, and high yearly precipitation will favour the development of a forest.

Altitude is another important factor determining the distribution of biomes. Cool temperatures at high altitudes may favour a type of plant community normally encountered at higher latitudes. It is on record that certain biomes or vegetative types may have been more conducive to crop domestication than others. The Mediterranean woodlands and tropical savannas were ideal for domestication because they both have long dry seasons, which generate annuals.

3.2.2 Two Major Biomes

Most domesticated plants originated in one of two biomes, the Mediterranean and the Savannah.

The Mediterranean biome is distributed on the western or southern edge of some continents or land masses, including the area around the Mediterranean sea, southern Africa and Australia, Chile, and California. Its main vegetation type is shrubby or park-like grassland. Trees include conifers (ceder, pines) and evergreen broadleaf trees (such as oaks). Shrubs are often aromatic (such as rosemary, sage, and oregano). Many plants in this biome are adapted to fire.

The Savannah biome is also a lightly forested grass land that merges gradually into dry deciduous forests. It is found in Africa, South

America, India, and Australia. Trees include baobab and acacia. The vegetation is also adapted to fire. Both biomes are characterised by an alternation of humid and dry seasons. In the Mediterranean biomes, rains occur primarily during the colder season, whereas in the savannah biome rains occur mainly in the warmer season.

List examples of crops arranged by their biome of origin.

Crop	Biome
Date palm	Desert
Wheat, barley, rye, pea, lentil, chickpea, rapeseed	Mediterranean
Maize, rice, sorghum, cassava, sweet potatoe, bean, peanut, yams	Savannah (and tropical deciduous forest)
Coconut, cabbage, beet, cotton	Sea coasts
Sunflower	Temperate prairies
Proso and foxtail miller, and *Triticumtauschii* (donor of the D genome of bread wheat	Temperate steppes
Apple, pear, cherry, grape, walnut	Temperate forest
Potato (and other root crops from the Andes) and *arabica coffee*	Temperate highland
Sugarcane, banana and plantain, citrus, mango, cacao	Tropical rain forest

The existence of a marked dry season in the two biomes has constituted an impetus for the transition from hunting-gathering to agriculture. A rise in population and the pressure exerted on existing food made the hunter-gatherers to plant the seeds of the grain crops they were already harvesting and consuming to increase the size of the harvest. This explains why a majority of the basic food crops domesticated in these biomes are actually annual grains.

SELF-ASSESSMENT EXERCISE

Explain the centers of agricultural origin

Describe the similarities between the centers of agricultural origin and their characteristics

Define a biome and describe the two major biomes where domesticated plants originated

4.0 CONCLUSION

This unit explains that agriculture originated in at least six different areas of the world that include: Mesoamerica, the Andes of South America (including their piedmonts), South Asia (the Fertile Crescent), Africa (Ethiopia and the Sahel), Southern China, and Southeast Asia. We were told that additional areas include North America, North China, and Europe. The unit also informs us that in each of these centers, similar types of crops were domesticated. For example, in each center one or more sources of carbohydrates (cereals or root or tuber crop) and of proteins (legumes) were domesticated. It was further stated that the commonalities between these geographically disparate regions are that: 1) They are located in tropical or subtropical regions; 2) Their topography is generally mountainous and 3) Have abundance of resources.

The unit also defines a biome as a major regional terrestrial community, or grouping, with its own type of climate, vegetation, and animal life. It also explains that biomes are not sharply separated, but merge gradually into one another over what is called an ecotone. We were also informed that climatic conditions, such as rainfall and temperature, are the major determinants of the type of biome that develops in an area. In addition, the unit also describes altitude as another important factor determining the distribution of biomes. We equally got to know that most domesticated plants originated in one of two biomes, the Mediterranean and the Savannah.

5.0 SUMMARY

Among technological development and inventions, agriculture is perhaps one of the few, if not the only one, that originated independently in more than one location. The number and precise boundaries of the different centers of origin of agriculture is not determined yet. Agriculture originated in at least six different areas of the world: Mesoamerica, the Andes of South America (including their piedmonts), South Asia (the Fertile Crescent), Africa (Ethiopia and the Sahel), Southern China, and Southeast Asia. Additional areas include North America, North China, and Europe.

In each of these centers, similar types of crops were domesticated. For example, in each center one or more sources of carbohydrates (cereals or root or tuber crop) and of proteins (legumes) were domesticated. The commonalities between these geographical regions are: 1) They are located in tropical or subtropical regions; 2) Their topography is generally mountainous and 3) Have abundance of resources.

6.0 TUTOR-MARKED ASSIGNMENT

1. Describe the centers of agricultural origin
2. Explain the similarities between the centers of agricultural origin and their characteristics
3. Define a biome and discuss its distribution
4. Describe the two major biomes where domesticated plants originated

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UNIT 4 DOMESTICATION OF PLANTS

CONTENTS

1.0 Introduction
2.0 Objectives
3.0 Main Content
3.1 Domestication and the Origin of Agriculture
3.2 Domestication of Plants
3.3 Role of Natural and Artificial Selection in Domestication of Plants
3.4 Consequences of Domestication
3.5 Morphological and Genetic Changes During Domestication
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

Agriculture has so far been able to keep pace with human population growth and provides sufficient food and other needs so that humans can tend to other activities. There is a close relationship between humans and their domesticated plants and animals. Whereas humans have had a marked effect on domesticated plants and animals, domesticated (and, in some cases, undomesticated) plants and animals have had a significant effect on human history. For example, exotic plants (at least to the Europeans of the 15th and 16th centuries) were one of the driving forces behind the explorations of new continents.

Domestication is the outcome of a selection process that leads to increased adaptation of plant and animals to cultivation or rearing and utilisation by humans. Domestication is a continuing process. While in the strictest sense of the definition, domestication could refer only to the first stages of selection that coincided with the initiation of agriculture, selection by humans continues to this day. The advent of scientific plant and animal breeding has greatly accelerated the pace of change.

2.0 OBJECTIVES

Bythe end of this unit, you should be able to:

- discuss the origin of agriculture in relation to domestication
- describe the domestication process of crop plants
- explain the role of natural and artificial selection in domestication of plant

- highlight the consequences of domestication

3.0 MAIN CONTENT

3.1 Domestication and the Origin of Agriculture

Human beings are heterotrophs. They derive their nutrition from plants and animals. But man has evolved from herbivorous ancestors. About two million years ago, the early Paleolithic man started using weapons for hunting. Later he began eating fruits and roots of wild plants. Much later, man started cultivating plants and raising animals and started a settled life.

The earliest settlements have been found to be located in the river valleys and plains of northern Indian. In these areas, the soil was fertile, plenty of water was available so, it was easy to cultivate crops. As a result of successful and plentiful agriculture originated about 7000-13000 years ago, somewhere in the then well-watered highlands of the Indus, Euphrates and Nile and Tigris rivers. Some other prehistoric sites of ancient agricultural activity are Tehuacana valley in modern Mexico and banks of Yellow river in modern china.

South East Asia was ideal for agriculture beginning because of its diverse vegetation to support a stable human population. In these areas, planting of vegetative parts like rhizomes, tubers or bulbs which is simpler than ploughing of seeds formed the basis of agriculture. But it was seed-planting that led to more profound changes in the life of man. All early civilisations whose diets were known to us were based on seed reproducing plants such as wheat, maize or rice.

It was reported that agriculture originated independently in several parts of the world. The first conscious act of civilisation was based on finding seeds and twigs struck into the ground. When a plant is raised consciously it is called cultivation. First, those plants were brought into cultivation that grow rapidly and produce crop within a season which include the present-day cereals. Cereals were originally weeds, which grew in mountain areas of Asia, Europe and Africa (old world) and North and South America (New world).

3.2 Domestication of Plants

The domestication of plants is the starting step in the direction of a full-fledged agricultural economy. A plant is termed as domestic when its natural characteristics are so much improved that it cannot grow and reproduce without human involvement. Domestication is thought to be the result of the development of a symbiotic relationship between the plants and humans, called co-evolution, because plants and human behaviours evolve to suit one another. Humans harvest a plant selectively based on specific characteristics like taste of the fruits, size of the flowers and fruits and so on. Humans use the seeds of these specific plants for further growth.

List of commonly cultivated crops and the regions they were domesticated

Plants name	**Domesticated at**	**Plants name**	**Domesticated at**
Fig tree	Near East	Chili Peppers	South America
Rice	East Asia	Water melon	Near East
Barley	Near East	Olives	Near East
Einkorn wheat	Near East	Cotton	Peru
Emmer wheat	Near East	Pomegranate	Iran
Chick pea	Anatolia	Hemp	East Asia
Bottle gourd	Asia	Cotton	Meso America
Potato	Andes mountain	Cocoa	South America
Squash	Central America	Squash	North America
Maize	Central America	Sunflower	Central America
Broomcorn millet	East Asia	Sweet potato	Peru
Bread wheat	Near East	March Elder	North America
Cassava	South America	Sorghum	Africa
Avocado	Central America	Sunflower	North America
Cotton	Southwest Asia	Pearl millet	Africa
Chocolate	Mexico	Egg Plant	Asia
Chenopodium	North America	Vanilla	Central America

Majority of the plants were cultivated first during historical times and hence have very poor evidence. The paleontological data is usually entirely unavailable for cultivated plants and archaeological data is very poor and fragmented. In the beginning of 19th century the origin of most of the cultivated species was not known. No species was common to the tropical regions of the two hemispheres before cultivation.

Strawberry, chestnut and mushrooms were common to northern regions of the world. A great number of species originated in Europe, India, West Asia, Brazil, Colombia. In short, the original distribution of the cultivate species was very unequal. There was no proportion with the needs of the man and the number of plants cultivate.

3.3 Role of Natural and Artificial Selection in Domestication of Plants

With regard to domestication, Darwin made the following major observations:

1. Morphological modifications selected during domestication have been of such magnitudes that many crop plants usually cannot survive in the wild anymore without human assistance.
2. Selection by breeders could lead to a wide array of variation in domesticated plants and animals when compared with their wild progenitors.
3. Selection under human cultivation happened unconsciously or inadvertently, that is, without deliberate human action.

Domestication is a selection process that results in the adaptation of plant and animals to cultivation or rearing and utilisation by humans. However, the question arises whether this selection took place consciously by humans or if it was an inadvertent phenomenon as a by-product of human plant cultivation or animal rearing.

Proponents of unconscious selection argue that the first farmers could not have possibly foreseen or set out to specifically select for the marked phenotypic changes that eventually arose during domestication. Proponents of conscious selection argue that the first farmers were actually quite knowledgeable about their environment. They were well aware of the life cycle and some of the biological characteristics of plants and animals surrounding them well before the advent of agriculture. A comparison of the morphological and physiological differences among domesticated plants has shown that a similar set of traits has been selected during domestication. This set has been called "the domestication syndrome". Traits included in this syndrome include those increasing adaptation to cultivation and desirability of human consumption and use.

The degree of domestication in cultivated plants has been observed to vary widely. Highly domesticated plants, typified by plants such as maize, rice, common bean, and peanut, have a broad range of domestication traits and express these traits at a high level. Other crops, encompassing a wide range of domestication phenotypes, can be considered to be only partially domesticated. Crops such as soybean and sesame also suffer from excessive shattering at maturity. On the other hand, the African oil palm has only been subjected to limited changes during domestication. In general, tree and forage crops are considered to be only partially domesticated.

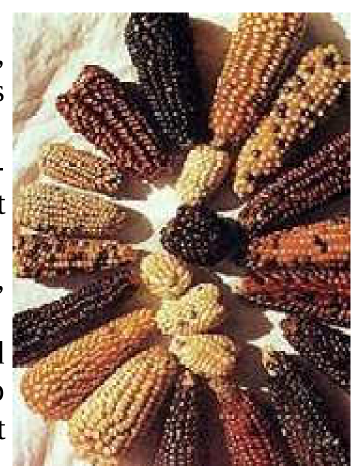
3.4 Consequences of Domestication

There are important corollaries to the phenomenon of domestication these are:

1. Plant cultivation or animal rearing is a necessary but insufficient condition for domestication. Thus, each crop or animal breed will have been grown or reared for a generally undefined period (predomestication cultivation or rearing) during which selection operated.
2. Certainly for plants, complete domestication leads to a lack of fitness in natural environments. Fully domesticated plants cannot survive on their own in the wild. One of the best examples of this situation is maize, where the husks surrounding the ear and the tight attachment of kernels to the cob prevent natural dispersal.
3. A mutualistic relationship exists between humans and their crop plants or animal breeds. The transition from hunting-gathering to agriculture was an experiment in cultural evolution that represented a drastic change in human societies and their environment. In turn, agriculture became a necessary condition for the development of civilisations because it provided a surplus of food, which allowed specialisation and diversification of crafts, trades, and other occupations.
4. While fully domesticated plants and animal breeds (the latter to a lesser extent) cannot survive on their own, it can also be argued that humans would not be able to survive without domestication.

3.5 Morphological and Genetic Changes during Domestication

In the "Origin of Species", Darwin used domesticated plants and animals as evidence to support his theory of evolution:



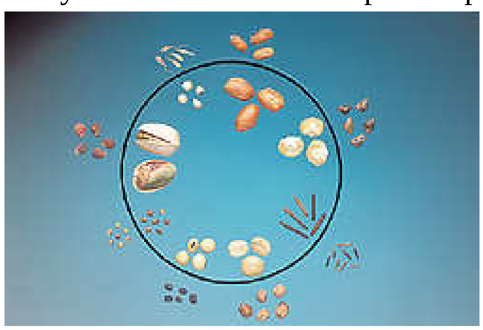
- "Domesticated races show adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy."
- "Very many of the most strongly-marked domestic varieties could not possibly live in a wild state."
- Gigantism of harvested organs: e.g., seeds of domesticated plants.
- Artificial selection has created tremendous diversity within crop species for the parts of the plant that have economic value (flowers, leaves, pods, or tubers). In comparison, there is little variation within species for parts of the plant that are not of interest

to man.

The process of plant domestication occurs as early wild-type crops are sown from seed gathered from wild stands. The key to domestication is the selective advantage of rare mutant alleles, which are necessary for survival in cultivation, but unnecessary for survival in the wild. The process of selection continues until the mutant phenotype dominates the population.

Cultivation also creates selection pressure, resulting in allele frequency changes, gradations within and between species, fixation of major genes, and improvement of quantitative traits.

Early domestication and important plant traits



Seeds from domestic crops (inner circle) are usually larger, lighter in color, and more uniform than their wild relatives. Clockwise from top: Peanuts, corn, rice, coffee, soybean, hops, pistachio, and sorghum.

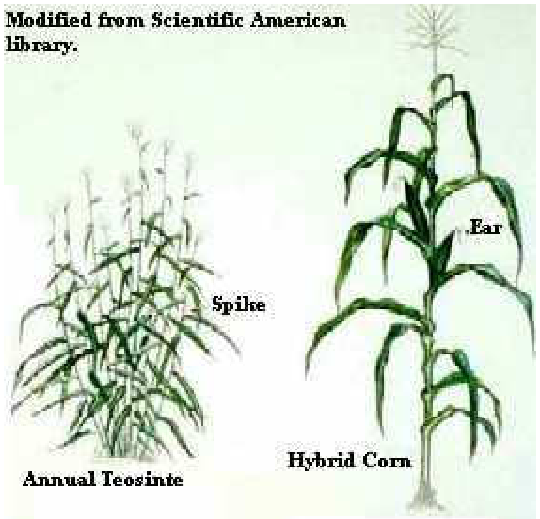
Photo by Stephen Ausmus, USDA

Selection associated with cultivation, harvesting, and food uses

Loss of seed dispersal mechanisms and seed dormancy traits are most important in the domestication process.

- Non-shattering - crop seeds remain attached to the plant until harvest
- Non-brittle rachis - the rachis (central axis of the inflorescence) remains intact in crop species
- Non-dehiscence - fruits do not split open to release contents at maturity
- Free threshing

- the seed is easily removed from other parts of the plant



Changes in growth habit

- Compact growth habit
- Reduction in branching
- Synchronous tillering
- Synchronous flowering

Example: climbing to bush habit in beans

In the wild, a climbing habit allows plants to access limited light. More compact plants are often favored by domestication.

- Reduction in internode length
- Reduction in number of nodes, branches
- Suppression of twining reponse
- Determinacy (simultaneous

flowering)

Harvesting: Increases in seed yield

- Reduction in daylength sensitivity - provides broader adaptation (plants will flower at wider latitudes); there is an adaptive value for daylength sensitivity in wild plants (ensures that they germinate at the right time of the year)
- Increased number of seeds
- Reduced sterility
- Larger inflorescence size
- Increased number of inflorescences
- Increased harvest index (weight of harvested portion of the plant to the weight of the whole plant)


Seed heads of foxtail millet (right) and its likely wild ancestor, green bristle grass (left), show the increase in size of the seed head that took place with domestication

Planting: increased seedling vigour

- Larger seeds
  - o More carbohydrates; increased reserves
  - o Fewer number, larger seeds
- Non-dormant seeds
  - o Dormancy has an adaptive value for the wild type, ensuring that it germinates when environmental conditions are most favourable (e.g. there is enough water or temperatures are stable.) However, it is not a desirable character for a crop. A farmer wants the seeds that he plants to germinate quickly and uniformly throughout the field.
  - o Conflict – lack of dormancy may cause premature germination (e.g. sprouting of a cereal head before harvest)
  - o Correlated response: reduced chaff

Reproductive system

- Shift from out crossing to predominantly self-pollination for many crops
- Reduced or absence of sexual reproduction in some crops - banana, plantain, navel orange
- Vegetatively propagated crops - instant domestication, because the selected plants can be reproduced without further changes occuring through meiosis

SELF-ASSESSMENT EXERCISE

Describe the domestication process of crop plants
Explain the origin of agriculture in relation to domestication of crop plants
Discuss the role of natural and artificial selection in domestication of plant

4.0 CONCLUSION

We learn from this unit that domestication is the outcome of a selection process that leads to increased adaptation of plant and animals to cultivation or rearing and utilisation by humans. We have also learned that a plant is considered to be domestic when its natural characteristics are so much improved that it cannot grow and reproduce without human involvement. It was also demonstrated that while domestication could refer only to the first stages of selection that coincided with the initiation of agriculture, artificial selection by humans still continues today.

This unit also thought us that the act of domestication could be the result of the development of a symbiotic relationship between the plants and humans (referred to as co-evolution) because plants and human behaviours evolve to suit one another. We also understand that humans harvest a plant selectively based on specific characteristics like taste of the fruits, size of the flowers and fruits and so on. Consequently, humans use the seeds of these specific plants for further growth.

We now know that the degree of domestication in cultivated plants has been observed to vary widely. The unit also explains that highly domesticated plants, typified by plants such as maize, rice, common bean, and peanut, have a broad range of domestication traits and express these traits at a high level. It further stress that other crops, encompassing a wide range of domestication phenotypes, are considered to be only partially domesticated.

5.0 SUMMARY

Domestication is the outcome of a selection process that leads to increased adaptation of plant and animals to cultivation or rearing and utilisation by humans. A plant is termed as domestic when its natural characteristics are so much improved that it cannot grow and reproduce without human involvement. While domestication could refer only to the first stages of selection that coincided with the initiation of agriculture, selection by humans continues to this day. However, the advent of scientific plant and animal breeding has greatly accelerated the pace of change. Thus the domestication of plants is the starting step in the direction of a full-fledged agricultural economy.

Domestication is thought to be the result of the development of a symbiotic relationship between the plants and humans, called co-evolution, because plants and human behaviours evolve to suit one another. Humans harvest a plant selectively based on specific characteristics like taste of the fruits, size of the flowers and fruits and so on. Humans use the seeds of these specific plants for further growth.

The degree of domestication in cultivated plants has been observed to vary widely. Highly domesticated plants, typified by plants such as maize, rice, common bean, and peanut, have a broad range of domestication traits and express these traits at a high level. Other crops, encompassing a wide range of domestication phenotypes, can be considered to be only partially domesticated. Crops such as soybean and sesame also suffer from excessive shattering at maturity. On the other hand, the African oil palm has only been subjected to limited changes during domestication. In general, tree and forage crops are considered to be only partially domesticated.

6.0 TUTOR-MARKED ASSIGNMENT

1. Discuss the origin of agriculture in relation to domestication
2. Describe the domestication process of crop plants
3. Explain the role of natural and artificial selection in domestication of plant
4. Highlight the consequences of domestication

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MODULE 4 CROP ADAPTATION

Unit 1 Evolutionary Adaptation
Unit 2 Adaptation of Crops to Environment
Unit 3 External Factors Regulating Crop Adaptation
Unit 4 Adaptive Response of Crop to Environment

UNIT 1 EVOLUTIONARY ADAPTATION

CONTENTS

1.0 Introduction
2.0 Learning Objectives
3.0 Main Content
3.1 Definition and Key Terms
3.2 Adaptation: a Process and a Trait
3.3 Adaptation, Flexibility, Acclimatisation and Learning
3.4 Adaptedness and Fitness
4.0 Conclusion
5.0 Summary
6.0 Tutor-Marked Assignment
7.0 References/Further Reading

1.0 INTRODUCTION

Adaptation is defined as a dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also defined as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection.
Adaptation is primarily a process rather than a physical form or part of a body. However, as a practical term, "adaptation" often refers to a *product*: those features of a species which result from the process. The two can be distinguished by using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product).

Adaptation is one of the two main processes that explain the observed diversity of species. The other process is speciation, in which new species arise, typically through reproductive isolation. Thus the interplay of adaptation and speciation is very important in the evolution of crop plant. All adaptations help organisms survive in their ecological niches. The adaptive traits may be structural, behavioural or physiological. Adaptation affects all aspects of the life of an organism.

2.0 OBJECTIVES

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

- give different definitions of adaption with brief explanations
- discuss adaptation as process and a trait
- explain adaptation, flexibility, acclimatisation and learning
- define and describe the concept of adaptedness and fitness

3.0 MAIN CONTENT

3.1 Definition and Key Terms

Adaptation is defined as a dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also defined as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection.

Adaptation is related to biological fitness, which governs the rate of evolution as measured by change in gene frequencies. Often, two or more species co-adapt and co-evolve as they develop adaptations that interlock with those of the other species, such as with flowering plants and pollinating insects. In mimicry, species evolve to resemble other species.

Adaptation:-is the evolutionary process whereby an organism becomes better able to live in its habitat or habitats.

Adaptedness:- is the state of being adapted, that is the degree to which an organism is able to live and reproduce in a given set of habitats.

Adaptive trait:- is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing.

3.2 Adaptation; a Process and a Trait

Adaptation is primarily a process rather than a physical form or part of a body. Example, an internal parasite (such as a liver fluke) has a very simple bodily structure, but the organism is highly adapted to its specific environment. However, as a practical term, "adaptation" often refers to a *product*: those features of a species which result from the process. Many aspects of an animal or plant can be correctly called adaptations, though there are always some features whose function remains in doubt. The two can be distinguished by using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product).

Adaptation is one of the two main processes that explain the observed diversity of species. The other process is speciation, in which new species arise, typically through reproductive isolation. Thus the interplay of adaptation and speciation is very important in the evolution of crop plant. Adaptation is not always a simple matter where the ideal phenotype evolves for a given environment. An organism must be viable at all stages of its development and at all stages of its evolution. This places *constraints* on the evolution of development, behavior, and structure of organisms.

All adaptations help organisms survive in their ecological niches. The adaptive traits may be structural, behavioral or physiological. Structural adaptations are physical features of an organism, such as shape, body covering, armament, and internal organisation. Behavioral adaptations are inherited systems of behaviour, whether inherited in detail as instincts, or as a neuropsychological capacity for learning. Examples include searching for food, mating, and vocalisations. Physiological adaptations permit the organism to perform special functions such as making venom, secreting slime, and phototropism, but also involve more general functions such as growth and development, temperature regulation, ionic balance and other aspects of homeostasis. Adaptation affects all aspects of the life of an organism.

3.3 Adaptation, Flexibility, Acclimatisation and Learning

Adaptation differs from flexibility, acclimatisation, and learning, all of which are changes during life which are not inherited. Flexibility deals with the relative capacity of an organism to maintain itself in different habitats: its degree of specialisation. Acclimatisation describes automatic physiological adjustments during life; learning means improvement in behavioural performance during life.

Flexibility stems from phenotypic plasticity, the ability of an organism with a given genotype (genetic type) to change its phenotype (observable characteristics) in response to changes in its habitat, or to move to a different habitat. The degree of flexibility is inherited, and varies between individuals. A highly specialised animal or plant lives only in a well-defined habitat, eats a specific type of food, and cannot survive if its needs are not met. Many herbivores are like this; extreme examples are koalas which depend on *Eucalyptus*, and giant pandas which require bamboo.

A generalist, on the other hand, eats a range of food, and can survive in many different conditions. Examples are humans, rats, crabs and many carnivores. The *tendency* to behave in a specialised or exploratory manner is inherited—it is an adaptation. Rather different is developmental flexibility: An animal or plant is developmentally flexible if when it is raised in or transferred to a new condition, it changes in structure so that it is better fitted to survive in the new environment.

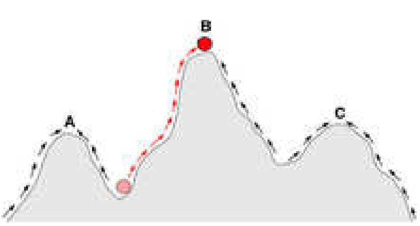
3.4 Adaptedness and Fitness

There is a relationship between adaptedness and the concept of fitness used in population genetics. Differences in fitness between genotypes predict the rate of evolution by natural selection. Natural selection changes the relative frequencies of alternative phenotypes, insofar as they are heritable. However, a phenotype with high adaptedness may not have high fitness. While adaptation was a retrospective concept referring to the history of a trait, fitness predicts a trait's future and it can be absolute or relative.

Relative fitness:- The average contribution to the next generation by a genotype or a class of genotypes, relative to the contributions of other genotypes in the population. This is also known as Darwinian fitness or selection coefficient.

Absolute fitness:- The absolute contribution to the next generation by a genotype or a class of genotypes. It is also known as the Malthusian parameter when applied to the population as a whole.

Adaptedness:- The extent to which a phenotype fits its local ecological niche. Researchers can sometimes test this through a reciprocal transplant.



The Fitness Landscape

In this sketch of a fitness landscape, a population can evolve by following the arrows to the adaptive peak at point B, and the points A and C are local optima where a population could become trapped. Sewall Wright proposed that populations occupy *adaptive peaks* on a fitness landscape. To evolve to another, higher peak, a population would first have to pass through a valley of maladaptive intermediate stages, and might be "trapped" on a peak that is not optimally adapted.

SELF-ASSESSMENT EXERCISE

Define adaption and brief explanations the process of adaptation
Differentiate between adaptation, flexibility, acclimatisation and learning
Discuss the concept of adaptedness and fitness

4.0 CONCLUSION

We learn from this unit that adaptation is defined as a dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It further defines adaptation as a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection.

We also learnt from this unit that adaptation is primarily a process rather than a physical form or part of a body. We have equally been informed that as a practical term, "adaptation" often refers to a *product*: that is those features of a species which result from the process. It was also demonstrated that the two can be distinguished by using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product).

This unit also thought us that adaptation is one of the two main processes that explain the observed diversity of species. It went on to explain that the other process is speciation, in which new species arise, typically through reproductive isolation. The unit further highlights that the interplay of adaptation and speciation is very important in the evolution of crop plant. We were made to understand that all adaptations help organisms survive in their ecological niches. We were also informed that the adaptive traits may be structural, behavioural or physiological with adaptation affecting all aspects of the life of an organism.

5.0 SUMMARY

Adaptation is a dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness until the population reached a stable state during the process. It is also a phenotypic trait or adaptive trait, with a functional role in an organism, which is maintained and has evolved through natural selection.

Primarily, adaptation is a process rather than a physical form or part of a body. In practice however, the term, "adaptation" often refers to a *product*: those features of a species which result from the process. The two can be distinguished by using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product).

In the context of evolution, adaptation is one of the two main processes that explain the observed diversity of species. The other process is speciation, in which new species arise, typically through reproductive isolation. Thus the interplay of adaptation and speciation is very important in the evolution of crop plant. All adaptations help organisms survive in their ecological niches. The adaptive traits may be structural, behavioural or physiological. Adaptation affects all aspects of the life of an organism.

6.0 TUTOR-MARKED ASSIGNMENT

1. Give different definition of adaption with brief explanations.
2. Discuss adaptation as a process and a trait.
3. Explain what you understand by adaptation, flexibility, acclimatisation and learning
4. Define and explain the concept of adaptedness and fitness

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UNIT 2 ADAPTATION OF CROPS TO ENVIRONMENT

CONTENTS

1.0 Introduction
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 3.1.1 Definition and Concept of Adaptation
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1.0 INTRODUCTION

The pattern in which the production of crop is distributed throughout the world is governed by many factors, with the main ones being climate, soils, topography, insect pressure, plant disease and economic conditions. In most developed countries, segregation of crop types into particular production areas is largely governed by profit motives. The profitability of any crop is determined by its adaptation to the environment and its ability to grow and produce moderate to high yields of acceptable quality in the area it is cultivated.

Crop adaptation is determined primarily by genotype-environment interaction with the suitability of the crop to a particular region depending largely on the climatic features of the region in relation to the requirements of the crops normal growth and development. Hence, climatic variables and physiological factors are the principal elements governing the adaptation, distribution and confinement of the major crop species to current production areas of the world.

2.0 OBJECTIVES

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

- define adaptation and explain its concept
- distinguish between adaptation and acclimation

- discuss plant growth and development in Relation to Adaptation
- define growth and describe its stages
- define development and describe its stages

3.0 MAIN CONTENT

3.1 Adaptation to External Environment

3.1.1 Definition and Concept of Adaptation

Adaptation may be defined as any feature of an organism which has survival value under the existing conditions of its habitat. Such a feature or features may allow the plant to make fuller use of the nutrients, water, and temperature or light, available, or may give protection against adverse factors such as temperature extremes, water stress, disease or insect pressures. The concept of adaptation can be difficult to define, as it is used in respect to both the evolutionary origins of a character and its contribution to the fitness of the plant to survive in its present environment.

The external adaptation of crop plants depends on many factors that includes environmental conditions, edaphic (soil) and biotic. When one factor (e.g. water availability) dominates the prevailing conditions the plant's responds by adapting to the existing level of that factor. More typically, adaptation is expressed as a response to a combination of factors (e.g. temperature and day length) and the nature of the response then reflects the plant's adaptation to the factors in combination. Success of a plant in a particular environment rarely depends on possession of a single adaptive character. Rather, fitness or adaptation to an environment depends on possession of an optimum combination of characters that minimizes the deleterious effects and maximises the advantageous effects.

Consequent on above, plant breeders are engaged in a difficult and complex task of generally developing genotypes with an optimum combination of adaptive characters, rather than ones with a single adaptive character. Whatever the growing conditions, the important consideration is the nature of the adaptive plant response itself and, for commercial purposes, the consequences of that response in terms of the economic output of the crop. For example, a plant that grows well under a given set of conditions, but fails to flower and set seed, is of little value as a grain crop in that situation. It may, however, be an excellent forage crop under those conditions, as the economic product (leaves and stems) is not dependent on flowering and seed set.

3.1.2 Adaptation and Acclimation

Adaptation is also heritable, i.e. it is determined by the genotype of the plant. Hence the definition of adaptation above can be refined to 'the heritable modifications to a plant which enable it to survive, reproduce, or both, in a given environment'. Reproduction, as well as survival, is a critical consideration in the commercial production of seed (grain) crops, as their economic product results from successful completion of the reproductive phase of their life cycles. In these crops, completion of all phases of development is fundamental to economic performance. In other crops such as sugar cane or forages, where the economic product is biomass (plant dry matter) that results from vegetative growth, development is a less important consideration than growth.

In contrast to adaptation, acclimation (or hardening) is the non-heritable modification of plant characters caused by exposure to new environmental conditions such as warmer or drier weather. It results from temporary modifications to the plant phenotype caused by the changing environment. Generally, plants subjected to several cycles of mild water or low temperature stress suffer less injury from subsequent drought or very low temperature exposure than plants which have not been previously stressed.

3.2 Concepts of Growth and Development in Relation to Adaptation

In order to discuss the ways that plants have evolved to be better adapted to their environments, it is necessary to have a basic understanding of plant growth requirements. Therefore, the concepts of growth and development are important to an understanding of plant adaptation to its environment.

3.2.1 Growth

Growth is the increase in plant biomass (dry matter) over time. About 95 per centof biomass is the net result of photosynthetic gains and respiratory losses, with the remaining five per cent derived from nutrient uptake. Growth is affected by the supply and level of availability of all factors that are essential to normal plant metabolism and function. The major factors are:

- Water
- Nutrient elements
- Light (the visible component of incoming solar radiation – it includes the red and blue wavelengths which provide energy for photosynthesis)

- Gases, particularly carbon dioxide (CO_2) for photosynthesis and oxygen (O_2) for respiration.

All of these are usually in finite supply and are frequently the subject of competition between plants or species in a community. Temperature is an important factor affecting, and in many cases controlling, plant growth. While the concept of a limited supply does not apply to temperature (i.e. plants do not compete for it), the thermal environment in which a plant is grown has significant effects on growth rate and dry matter yield. Adaptation to temperature is a major factor governing the natural distribution of plants, and is a principal determinant in the selection of crop species for commercial production throughout the world.

Plant adaptation and response to temperature is usually described in terms of so-called Cardinal Temperatures for growth. The Cardinal temperatures for any species are:

1. A Minimum, below which growth will not occur and above which growth rate will rise with temperature, to
2. An Optimum, at which growth rate is maximal, and above which growth rate will decline with increasing temperature, to
3. A Maximum, at which growth will cease.

Cardinal temperature ranges for the major plant groups are outlined in the Table below.

Cardinal temperature ranges (oC) for temperate species, tropical legumes, and tropical grasses (adapted from Crofts et al., (1963) and Fitzpatrick and Nix, (1975)).

Adaptation	**Minimum Temperature (°C)**	**Optimum Temperature (°C)**	**Maximum Temperature (°C)**
Temperate Species	1-3	18-22	32-35
Tropical Legumes	10-12	27-32	36-41
Tropical Grasses	12-15	37-43	50-55

3.2.2 Development

Development is the progression of a plant through the successive stages of its normal life cycle. The life cycle is best considered in two main phases, Vegetative and Reproductive, each of which includes one or more stages:

Vegetative

1. Establishment – seed germination, emergence and, ultimately, independence of seed reserves.
2. Vegetative growth – initiation, development and expansion of leaves, stems and roots.

Reproductive

1. Floral initiation – the transition of stem apices (growing points) from vegetative (producing leaf and stem primordia [buds]) to reproductive (producing inflorescence structures and floral primordia).
2. Flowering and pollination (anthesis), resulting in fertilised ovules which will develop into seeds (grains).
3. Seed growth (grain filling) to a maximum wet weight at physiological maturity.
4. Seed (grain) maturation – grain dries naturally to a moisture content suitable for harvesting and storage.
5. Harvest ripeness – dry (12-14% moisture) grain ready for harvest.

Reproductive development in plants is controlled more by regulatory than by assimilatory processes. The consequences of this are that reproductive development can proceed relatively independently of growth, and can be modified by selection more readily than growth. In many cases, the adaptation of crops to harsher environments has depended more on changes in the length and timing of their life cycles - allowing them to escape the most adverse conditions - than on changes in their ability to tolerate such environments.

In contrast to those for growth, the external governing factors for development are principally environmental, with day length and temperature the most important. As the most regular and predictable component of climate, day length is the most potent and universal controlling element in the timing of life cycles of both wild and cultivated plants, and the modification of their responses to day length has been a major factor in the spread and adaptation of many crop plants.

SELF-ASSESSMENT EXERCISE

Define adaptation and differentiate between adaptation and acclimation

Explain the concept of plant growth and development in Relation to Adaptation

Discuss the process of growth and describe its stages

4.0 CONCLUSION

This unit defines adaptation as any feature of an organism which has survival value under the existing conditions of its habitat. It further explains that such a feature or features may allow the plant to make fuller use of the nutrients, water, and temperature or light, available, or may give protection against adverse factors such as temperature extremes, water stress, disease or insect pressures. We also understand that the concept of adaptation can be difficult to define, as it is used in respect to both the evolutionary origins of a character and its contribution to the fitness of the plant to survive in its present environment.

The unit further highlights that adaptation is also heritable, i.e. it is determined by the genotype of the plant. Base on which the previous definition of adaptation was refined to 'the heritable modifications to a plant which enable it to survive, reproduce, or both, in a given environment'. We also learnt that in contrast to adaptation, acclimation (or hardening) is the non-heritable modification of plant characters caused by exposure to new environmental conditions such as warmer or drier weather. The unit further states that acclimation results from temporary modifications to the plant phenotype caused by the changing environment.

This unit also thought us that growth is the increase in plant biomass (dry matter) over time with about 95per cent of biomass as the net result of photosynthetic gains and respiratory losses, and the remaining five per cent derived from nutrient uptake. It equally informed us that growth is affected by the supply and level of availability of all factors that are essential to normal plant metabolism and function. We also understand that the necessary factors are: water, nutrient elements, light, and gases. Similarly, we learned the fact that development is the progression of a plant through the successive stages of its normal life cycle. The unit then informs us that the life cycle is best considered in two main phases, vegetative phase and reproductive phase.

5.0 SUMMARY

Adaptation may be defined as any feature of an organism which has survival value under the existing conditions of its habitat. Such a feature or features may allow the plant to make fuller use of the nutrients, water, and temperature or light, available, or may give protection against adverse factors such as temperature extremes, water stress, disease or insect pressures. The concept of adaptation can be difficult to define, as it is used in respect to both the evolutionary origins of a character and its contribution to the fitness of the plant to survive in its present environment.

Adaptation is also heritable, i.e. it is determined by the genotype of the plant. Hence the definition of adaptation above can be refined to 'the heritable modifications to a plant which enable it to survive, reproduce, or both, in a given environment'. In contrast to adaptation, acclimation (or hardening) is the non-heritable modification of plant characters caused by exposure to new environmental conditions such as warmer or drier weather. It results from temporary modifications to the plant phenotype caused by the changing environment.

Growth is the increase in plant biomass (dry matter) over time. About 95per cent of biomass is the net result of photosynthetic gains and respiratory losses, with the remaining five per cent derived from nutrient uptake. Growth is affected by the supply and level of availability of all factors that are essential to normal plant metabolism and function. The major factors are: water, nutrient elements, Light, and gases. Development is the progression of a plant through the successive stages of its normal life cycle. The life cycle is best considered in two main phases, vegetative and reproductive.

6.0 TUTOR-MARKED ASSIGNMENT

1. Define adaptation and explain its concept
2. Distinguish between adaptation and acclimation
3. Discuss plant growth and development in relation to adaptation
4. Define growth and describe its stages
5. Define development and describe its stages

7.0 REFERENCES/FURTHER READING

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UNIT 3 EXTERNAL FACTORS REGULATING CROP ADAPTATION

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1.0 INTRODUCTION

Adaptation of cultivated plant species is a factor of genotype-environment interaction with the performance of the crop in a particular region determined by the climatic elements of the environment in relation to the requirements of the crops growth and development. Climatic variables and physiological factors are the principal elements governing the adaptation, distribution and confinement of the major crop species to current production areas globally. The external factors regulating the adaptation of crops to their environment include: 1) day length, 2) temperature and, 3) competition

Competition arises in plant communities ‘when the supply of a single necessary factor for plant growth falls below the combined needs of the plant and its neighbours (competitors)’. It does not occur when the available pool of each factor exceeds the total needs of the plant community. Plants compete only for factors that are necessary for growth – not development - and that are available to the plant community. The essential growth factors for which crop plants compete in the environment are: 1) water, 2) nutrients, 3) light (solar radiation) and 4) gases (carbon dioxide and oxygen).

Adaptation to water limited conditions reflects the ability of the plant to either access and use limited available water at the expense of its competitors, or to limit transpiration water loss better than its competitors, or both. Adaptations which enable successful competition for nutrients include: extensive root growth, rapid uptake and utilisation of nutrients, meeting owns nutrient requirements, tolerance to low nutrient levels and tolerance to low pH or high salinity. Competition for light arises where one leaf shades another or as the result of superior growth of one plant or species relative to another. Competition for CO_2 may arise where a crop, well supplied with water and nutrients and under high light intensity is photosynthesising at a high rate. Competition may also occur for oxygen (O_2), typically in waterlogged soils.

2.0 OBJECTIVES

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

- outline the external factors regulating the adaptation of crops to their environment.
- discuss the response of crop plants to the effect of:
  1. Day length
  2. Temperature
  3. Competition
- explain the competition for water among crop plants
- highlight the adaptations which enable crop plants to succeed in competition for nutrients

3.0 MAIN CONTENT

3.1 Environmental Factors Regulating Crop Adaptation

It was previously stated that the adaptation of cultivated plant species is a factor of genotype-environment interaction with the performance of the crop in a particular region determined by the climatic elements of the environment in relation to the requirements of the crops growth and development. Hence, climatic variables and physiological factors are the principal elements governing the adaptation, distribution and confinement of the major crop species to current production areas globally. Consequent on the above, the external factors regulating the adaptation of crops to their environment include the following:

3.1.1 Day length

The physiological response of plants to the relative lengths of the diurnal cycles of light (day length) and dark periods is called Photoperiodism.

The most fundamental aspect of this response is the transition from vegetative to reproductive phase in photoperiod sensitive plants, which includes most modern day crop species. Depending on their adaptation, photoperiod sensitive species are induced to progress from vegetative to reproductive phase when subjected to certain critical day lengths. Most species of tropical or subtropical adaptation are classed as Short Day (SD) plants – they grow vegetatively through the long days of late-spring/summer/early-autumn, and undergo floral initiation when autumn day length declines to a certain critical value.

In contrast, most species of temperate adaptation are described as Long Day (LD) plants. Their vegetative phase occurs during the short-day late-autumn/winter/early-spring period, floral initiation occurring when spring day length increases to a certain critical value. In a third major group, floral initiation occurs after a certain period of vegetative growth has been completed, regardless of day length. Plants in this photoperiod-insensitive group are described as Day Neutral (DN).

Over the last 50 years, plant breeders have consistently strived to develop improved cultivars of the major crop species by reducing their dependence on day length to initiate the reproductive phase. Their aim has been to increase flexibility in the length of the crop life cycle and thus extend the optional range for sowing time. This has been an important strategy in the development of better adapted cultivars for rain fed crop production, where unreliable rainfall, (either too low or too high), often delays sowing. Development of modern crop plants has seen the manipulation of the processes regulating reproductive development by selection and breeding, with sensitivity to day length being considerably reduced or muted in some, and even enhanced in others.

Duration of day length (length of astronomical day in hours [h] and minutes[m]) at selected latitudes in Australia.

	Season (Southern Hemisphere)							
	Autum		**Winter**		**Spring**		**Summer**	
	March		**June**		**September**		**December**	
Latitude (^{O}S)	**h**	**m**	**h**	**m**	**h**	**m**	**h**	**m**
10	12	08	11	33	12	07	12	42
20	12	08	10	55	12	07	13	20
30	12	10	10	13	12	08	14	04
40	12	12	09	20	12	09	15	01

(Adapted from Gentilli, 1971, based on data from Astronomical Ephemeris, HMSO, London).

3.1.2 Temperature

Some temperate crop species, particularly the cereals (wheat, oats, barley, rye and triticale) and brassicas (canola, rape) have both 'winter' and 'spring' types. Winter types require a period of exposure to very low temperatures (0-2oC) before they can respond to increasing spring day length. In Europe, Canada and the USA they are planted in autumn, remain dormant through an intensely cold winter, often under snow, then undergo floral initiation as days lengthen in spring. True winter types will not respond to day length until the cold requirement has been met. It can also be met by subjecting pre-soaked, germinating seeds to an intense cold period (e.g. 21 days at 1oC), a process known as vernalisation. Spring types, in contrast, exhibit no cold requirement and varying degrees of LD requirement for floral initiation. Modified winter wheats have found a place as grazing and grain crops in southern Australia, but apart from those, practically all Australian temperate crops are spring types that are shorter season and lower yielding than their winter counterparts.

The lengths of the vegetative and reproductive phases in DN species are temperature dependent, being shorter when conditions are warm to hot and longer when it is cold. To complete each phase or stage of development of the crop requires the accumulation of a certain total number of 'heat units' – the warmer the environment, the more rapidly the units are accumulated and the plant progresses to the next developmental phase or stage. The standard heat unit expression is degree days (oD), which are calculated for each day as the average temperature minus the base temperature for the species or cultivar.

A variation on this approach has been used successfully for winter crop management in southern Australia using oD summations based on daily maximum, rather than average, temperature. For these crops, once floral initiation has occurred, plants in all groups will then progress through the successive stages of the reproductive phase to maturity, provided they are not disrupted by adverse weather, pest and disease conditions. The rate of progress from floral initiation to maturity depends on subsequent temperature and day length conditions. At high temperatures, individual stages will progress rapidly and be of short duration, leading to early maturity and usually lower grain yield, because the grain filling period has been shortened. In some crop plants, such as soybeans and many of the grain legumes, development after floral initiation is particularly sensitive to day length as well as to temperature.

3.1.3 Competition

The concept of competition is fundamental to an understanding of adaptation, particularly with crop plants that are grown in moderate to high density monocultures. Here, competition for one or more factors almost always limits growth and yield in rain fed (dry land) production systems. The outcomes of competition illustrate the relative adaptation of competing plants in optimising their capture or use of essential factors for growth that are in limited supply. Plants compete only for factors that are necessary for growth – not development - and that are available to the plant community from a finite pool or supply. The occurrence and intensity of competition for any factor is determined by the amount of the factor available and the number of plants competing for it.

At community level, competition may be interspecific (between plants of different species, for example weeds in a crop) or intraspecific (between plants of the same species, for example neighbouring crop plants). The outcomes of interspecific competition reflect the differences in relative competitive ability between the species present for the factor in limited supply, and one species will eventually dominate the other(s). In contrast, where intraspecific competition occurs, all plants are of similar competitive ability and are affected equally, and at about the same time. At individual plant level, competition may be interplant (between different, neighboring plants) or intraplant(between different parts of the same plant).

3.2 Competition for External Factors Necessary for Crop Growth

Competition arises in plant communities 'when the supply of a single necessary factor for plant growth falls below the combined needs of the plant and its neighbours (competitors)'. It does not occur when the available pool of each factor exceeds the total needs of the plant community. Plants compete only for factors that are necessary for growth – not development - and that are available to the plant community. The essential growth factors for which crop plants compete in the environment are: water, nutrients, light (solar radiation) and gases (carbon dioxide and oxygen).

3.2.1 Competition for Water

Adaptation to water limited conditions reflects the ability of the plant to either access and use limited available water at the expense of its competitors, or to limit transpiration water loss better than its competitors, or both. Superior access to and use of water usually results from more rapid and extensive root growth, enabling the limited pool of available soil water to be exploited before the roots of less well adapted competitors can reach it. Limiting water loss under stress conditions may result from adaptive characteristics such as rough leaf surfaces that shield stomatas, and from leaf rolling. Both limit direct stomatal exposure to solar radiation and wind, thereby reducing transpiration. While sunken stomates and rough leaf surfaces are typical of arid zone plants (xerophytes), some commercial crop species (e.g. sorghum, millets and maize) exhibit leaf rolling under water stress.

Millets and sorghum also exhibit rapid stomatal closure when stress develops, which reflects their adaptation to the hot and often arid environments of their African centres of origin. When the stress is relieved, these species are able to rapidly resume active growth. In contrast, crop species such as sunflower and soybeans exhibit rather lax stomatal control, resulting in slow stomatal closure, such that transpiration water loss may continue for some time after stress is imposed and root water uptake has ceased. As a result, water loss temporarily exceeds uptake and the plant loses turgor (wilts), closing its stomates to prevent further water loss. Recovery from water stress with these species is slower, and the yield penalty usually greater, than in sorghum or millet. As will be outlined later, these adaptive characteristics are reflected in the geographic distribution of rainfed commercial production of these species in Australia.

3.2.2 Competition for Autrients

Adaptations which enable successful competition for nutrients include:

1. more rapid and extensive root growth, which enables one competitor to access and exploit available nutrients at the expense of its neighbours;
2. the capability to take up and use a nutrient which may be present in the soil in a chemical form which their competitors are not able to utilise;
3. the ability to meet its own requirements for an essential nutrient independently of soil supply (e.g. a legume growing in a nitrogen deficient soil);
4. tolerance of low levels of essential nutrients in the soil which enables normal growth at levels too low for other species to grow, or even survive;
5. tolerance of soil conditions such as low pH or high salinity which enables uptake of essential nutrient elements under conditions where other species are unable to grow, or even survive.

3.2.3 Competition for Light

Competition for light arises where one leaf shades another, regardless of whether the competing leaves are on the same or on different plants. In contrast to water and nutrients, light energy cannot be redistributed internally in the plant unless it has been captured by chlorophyll in the photosynthetic tissue of the leaves or stems. It is instantaneously available, and must be instantaneously intercepted and absorbed by chlorophyll, or it is lost.

Competition for light usually arises as the result of superior growth of one plant or species relative to another, which frequently reflects the outcomes of earlier competition for water and/or nutrients. The greater growth of the successful competitor results in shading of its neighbours, exacerbating the effects of existing competition for water and/or nutrients. Successful competition for light may also result directly from adaptive characteristics that enable a more rapid and/or extensive development of the leaf canopy, resulting in an early onset of shading of less well adapted competitors. This situation is usually exacerbated with time, resulting in increasing shading and suppression of the inferior plant or species. Where competition for nutrients or water also exists, the inferior plant or species may be completely suppressed.

Leaf display and canopy structure are also significant factors, particularly in the high density monocultures typical of commercial crops. The vertical leaf display of grass species enables more efficient capture of incoming light than the more horizontally disposed canopies of broadleaf species, particularly at high light intensities, which are typical of some croplands during the summer months.

3.2.4 Competition for Gases

Competition for carbon dioxide may arise where a crop, well supplied with water and nutrients, and under high light intensity conditions around midday, is photosynthesising at a high rate. Under these conditions, rapid uptake of CO_2 depletes its concentration in the air within the canopy, causing a decline in photosynthetic rate. This happens only under still conditions, where the absence of air mixing by wind prevents CO_2 being replenished from outside the canopy. It occurs mainly in intensive production systems, where irrigated and well fertilised crops are grown in typically high density monocultures.

Most modern crop species show a positive growth response to higher air CO_2 levels than those in normal air, which reflects their ancient origins when air levels of CO_2 were much higher (~0.10%) than those of today (0.034 – 0.036%). The C4 photosynthetic pathway is a successful adaptation which enables C4 species such as maize, sugar cane and sorghum to maintain high photosynthetic rates even at the comparatively low air CO_2 levels of modern times.

Competition may also occur for oxygen (O_2), typically in waterlogged soils. With the exception of rice, no commercial crop species are able to survive continuous root inundation, although many can tolerate periodic inundation in waterlogged soils. Water logging severely reduces O_2 supply to root cells, inhibiting their respiration and hence normal nutrient uptake. Crop yellowing in waterlogged, low lying areas of paddocks during wet periods is a common occurrence and usually reflects an induced nitrogen deficiency, as uptake is severely limited or even prevented.

SELF-ASSESSMENT EXERCISE

Explain the external factors regulating the adaptation of crops to their environment.
Describe the response of crop plants to the effect of: Day length, Temperature and Competition
Discuss the processes by which crop plants succeed in their competition for nutrients

4.0 CONCLUSION

This unit describes the adaptation of cultivated plant species as a factor of genotype-environment interaction with the performance of the crop determined by climatic elements in relation to the requirements of the crops growth and development. The unit also explains that climatic variables and physiological factors are the principal elements governing the adaptation, distribution and confinement of the major crop species to current production areas globally. It further highlights that the external factors regulating the adaptation of crops to their environment include: 1) day length, 2) temperature and, 3) competition

The unit thought us that competition arises in plant communities 'when the supply of a single necessary factor for plant growth falls below the combined needs of the plant and its neighbours (competitors)'. It also informed us that competition does not occur when the available pool of each factor exceeds the total needs of the plant community. In addition, the unit stated that plants compete only for factors that are necessary for growth – not development - and that are available to the plant community. We also know that the essential growth factors for which crop plants compete in the environment are: 1) water, 2) nutrients, 3) light (solar radiation) and 4) gases (carbon dioxide and oxygen).

We learn from this unit that adaptation to water limited conditions reflects the ability of the plant to either access and use limited available water at the expense of its competitors, or to limit transpiration water loss better than its competitors, or both. The unit highlighted that adaptations which enable successful competition for nutrients include: extensive root growth, rapid uptake and utilisation of nutrients, meeting owns nutrient requirements, tolerance to low nutrient levels and tolerance to low pH or high salinity. We were also informed that competition for light arises where one leaf shades another or as the result of superior growth of one plant or species relative to another. We also know that the competition for CO_2 may arise where a crop, well supplied with water and nutrients and under high light intensity is photosynthesising at a high rate. The unit equally states that competition may also occur for oxygen (O_2), typically in waterlogged soils.

5.0 SUMMARY

Adaptation of cultivated plant species is a factor of genotype-environment interaction with the performance of the crop in a particular region determined by the climatic elements of the environment in relation to the requirements of the crops growth and development. Climatic variables and physiological factors are the principal elements governing the adaptation, distribution and confinement of the major crop species to current production areas globally. The external factors regulating the adaptation of crops to their environment include: 1) day length, 2) temperature and, 3) competition

Competition arises in plant communities 'when the supply of a single necessary factor for plant growth falls below the combined needs of the plant and its neighbours (competitors)'. Plants compete only for factors that are necessary for growth – not development - and that are available to the plant community. The essential growth factors for which crop plants compete in the environment are: 1) water, 2) nutrients, 3) light (solar radiation) and 4) gases (carbon dioxide and oxygen).

Adaptation to water limited conditions reflects the ability of the plant to either access or use limited available water, or to limit transpiration water loss, or both. Adaptations which enable successful competition for nutrients include: extensive root growth, rapid uptake and utilisation of nutrients, meeting owns nutrient requirements, tolerance to low nutrient levels and tolerance to low pH or high salinity. Competition for light arises where one leaf shades another or as the result of superior growth of one plant or species relative to another. Competition for CO_2 may arise where a crop, well supplied with water and nutrients and under high light intensity is photosynthesising at a high rate. Competition may also occur for oxygen (O_2), typically in waterlogged soils.

6.0 TUTOR-MARKED ASSIGNMENT

1. Outline the external factors regulating the adaptation of crops to their environment.
2. Discuss the response of crop plants to the effect of day length
3. Describe the response of crop plants to the effect of temperature
4. Explain the competition for water among crop plants
5. Highlight the adaptations which enable crop plants to succeed in competition for nutrients

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UNIT 4 ADAPTIVE RESPONSE OF CROPS TO ENVIRONMENT

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1.0 INTRODUCTION

Plants have evolved to be better adapted to their environment in order to thrive and ensure the long term survival of their species, The important factors required for plant growth are CO_2, O_2, light (quality, intensity and duration), adequate water, nutrients (16 essential nutrients), proper temperature and proper pH. The three important processes in plants that are essential for plant growth and development are: photosynthesis, respiration and transpiration. Generally, plants have developed physiological mechanisms that make them adapted to their environments.

Plant species capable of maximizing photosynthesis, within the constraints of the available resources in its physical environment, will have a significant competitive advantage over other species present in the community. The process of photosynthesis depends on the intake of CO_2 through open stomates in the leaves. This intake is, however, inextricably linked with the parallel process of water loss when the stomates are open, and photosynthetic rates may be severely limited by partial or complete stomatal closure under water stress conditions.

2.0 OBJECTIVES

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

- discuss the physiological responses adapting crops to the environment
- describe the following physiological processes:
  a. Photosynthesis
  b. Photoperiod
  c. Vernalization
- explain plant photosynthetic pathway as an adaptive mechanism
- describe the following photosynthetic pathways:
  a. C3 Photosynthesis
  b. C4 Photosynthesis
  c. CAM photosynthesis

3.0 MAIN CONTENT

3.1 Physiological Responses Adapting Crops to the Environment

To thrive and ensure the long term survival of their species, plants have evolved to be better adapted to their environment. As stated previously the important factors required for plant growth are CO_2, O_2, light (quality, intensity and duration), adequate water, nutrients (16 essential nutrients), proper temperature and proper pH. While, the three important processes in plants that are essential for plant growth and development are: photosynthesis, respiration and transpiration. However, the physiological mechanisms plants have developed that make them adapted to particular environments are:

3.1.1 Photosynthesis (and Related Processes)

<u>Photosynthesis</u>
Photosynthesis is the joining together of CO_2 (carbon dioxide) with H_2O (water) to make CH_2O (sugar) and O_2 (oxygen), using the sun's energy. The sugar contains the stored energy and serves as the raw material from which other compounds are made. Basic photosynthetic pathway is:

$$6CO_2 + 12\ H_2O \dashrightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$$

Energy to carry out the reaction comes from light absorbed by chlorophyll, stored as ATP and NADH. There are three types of photosynthesis: C3, C4, and CAM. The type of photosynthesis utilised by a species influences its adaptation to different environments.

<u>Respiration</u>

Respiration is the opposite of photosynthesis -- the stored energy in the sugar is released in the presence of oxygen, and this reaction releases the CO_2 and H_2O originally joined together by the sun's energy.

Photorespiration

Photorespiration is what happens under high light and high heat, where the enzyme (RUBISCO) that grabs carbon dioxide for photosynthesis may grab oxygen instead, causing respiration to occur instead of photosynthesis, thus reducing the production of sugars from photosynthesis.

During photorespiration, O_2 + Rubp (ribulosebisphosphate, a 5-carbon compound) are catalyzed by RUBISCO to produce one molecule of 3-PGA (3-phosphoglycerate, a 3-carbon organic acid) and one molecule of phosphoglycolate.

$$O_2 + \text{Rubp} \xrightarrow{\text{RUBISCO}} \text{3-PGA} + \text{phosphoglycolate}$$

Photorespiration can reduce photosynthetic efficiency by 30%. Furthermore, the phosphoglycolate is toxic and must be broken down by the plant. Higher levels of CO_2, or lower levels of O_2, will increase photosynthesis by decreasing photorespiration.

3.1.2 Photoperiod

Many angiosperms will flower at about the same time every year, regardless of when they are planted. This is a response to daylength that promotes cross-pollination and ensures that plant development is well synchronised with the length of the growing season. Short-day plants flower only after exposure to short days, long-day plants flower only after exposure to long days, and day-neutral plants show no response to daylength.

Some plants can only be grown at certain latitudes due to photoperiodism. Spinach is a long-day plant, and will never flower if it is grown in the tropics. Maize is a short-day plant - if a tropical variety is grown at northern latitudes it will grow very tall and may never flower. Selection for the day-neutral characteristic has permitted many crops, such as maize and soybeans, to be grown over much wider geographic areas.

Phytochrome is the plant compound that is responsible for the photoperiod response. The P_R form absorbs red light during the day and is converted to P_{FR} . The P_{FR} form can absorb far red light, and will spontaneously convert back to the P_R form in the night. Consequently, it is the length of the night period that is really important in determining photoperiod response. Short-day plants should really be called long-night plants and long-day plants should be called short-night plants.

3.1.3 Vernalization

Vernalization in crops is the acceleration of flowering in response to a long period of cold temperature. Winter crops require a period of exposure to temperatures between 0 to 12 °C for a period of time from 10 to 60 days from germination to proceed into the reproductive phase. Vernalization requirements vary greatly among species and cultivars. Vernalization ensures that plants overwinter vegetatively and flower in the favourable conditions of spring. The majority of crops grown in northern Europe and Canada (wheat, barley, oilseed rape and sugarbeet) have been bred with a strong vernalization requirement to extend geographical range or prevent bolting.

3.2 Photosynthetic Pathway as an Adaptive Mechanism

A plant species that is capable of maximising photosynthesis, within the constraints of the available resources in its physical environment, will have a significant competitive advantage over other species present in the community. The process of photosynthesis depends on the intake of CO_2 through open stomates in the leaves. This intake is, however, inextricably linked with the parallel process of water loss when the stomates are open, and photosynthetic rates may be severely limited by partial or complete stomatal closure under water stress conditions. The photosynthetic pathway and capacity utilised by plants as an adaptive mechanism to thrive and perform well in the environment are:

3.2.1 C3 Photosynthesis

Most plants use C3 photosynthesis. It is called the C3 pathway because CO_2 is first incorporated into a 3-carbon compound. CO_2 and ribulosebisphosphate are combined by RUBISCO, resulting in the production of two molecules of the 3-carbon organic acid 3-PGA.

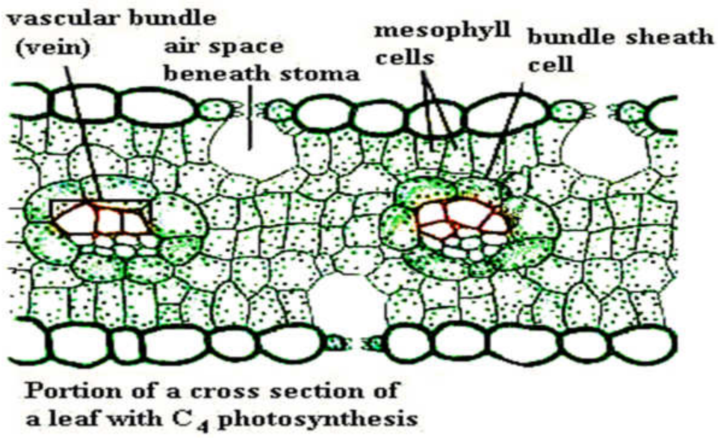
$$CO_2 + \text{Rubp} \xrightarrow{\text{RUBISCO}} 2\ \text{3-PGA}$$

Photosynthesis takes place throughout the leaf. Stomata are open during the day. Photorespiration may occur in C3 plants during light fixation of CO_2.

Adaptive Value: C3 plants are more efficient than C4 and CAM plants under cool and moist conditions and under normal light because they have less machinery (fewer enzymes and no specialized anatomy).

3.2.2 C4 Photosynthesis

C4 plants can photosynthesize faster under high heat and light conditions than C3 plants because they use an extra biochemical pathway and special leaf anatomy to reduce photorespiration. The leaves of C4 plants have Kranz anatomy. The xylem and phloem of these leaves are surrounded by thick walled parenchyma cells called bundle sheath cells where most of the photosynthesis takes place.



Source: http://www2.mcdaniel.edu/Biology/botf99/photodark/c4.htm

Stomata open in the morning. CO_2 is first combined with phosphoenolpyruvic acid (PEP) in mesophyll cells by phosphoenolpyruvate carboxylase (PEPCase). This allows CO_2 to be taken into the plant very quickly. The 4-carbon compound oxaloacetic acid is produced, and then converted to malic or aspartic acid. These are also 4-carbon compounds, hence the name C4 photosynthesis. The malic or aspartic acid is then moved through plasmodesmata (at the expense of ATP) into the bundle sheath cells.

In the bundle sheath cells, the malic or aspartic acid is broken into CO_2 and PEP. The CO_2 is "delivered" to the RUBISCO enzyme for photosynthesis. This system allows the plant to maintain a high concentration of CO_2 in the bundle sheath cells for photosynthesis. The higher concentration of CO_2 prevents photorespiration and allows the plant to close its stomata during the hot hours of the day.

RUBISCO

CO_2 + --------> oxaloacetic ----- malic or -----> CO_2 + PEP

PEP	acid	>	aspartic acid	
mesophyll cells				bundle sheath cells

Adaptive Value: C4 plants photosynthesise faster than C3 plants under high light intensity and high temperatures. C4 plants do not have a photorespiration pathway, increasing photosynthetic efficiency. Water use efficiency of C4 plants is high because PEP Carboxylase brings in CO_2 faster, so the plant does not need to keep stomata open as much (less water lost by transpiration) to have sufficient CO_2 for photosynthesis. The C4 pathway is more expensive energetically than normal photosynthesis, but not as expensive as photorespiration.

C4 plants include several thousand species in at least 19 plant families. Examples include corn, sorghum, and many of our summer annual plants.

3.2.3 CAM Photosynthesis

CAM stands for Crassulacean Acid Metabolism. Stomata open at night (when evaporation rates are usually lower) and are usually closed during the day. The CO_2 is converted to an acid and stored during the night. During the day, the acid is broken down and the CO_2 is released to RUBISCO for photosynthesis.

Adaptive Value: Better water use efficiency than C3 plants under arid conditions because stomata are open at night when transpiration rates are lower (no sunlight, lower temperatures, lower wind speeds, etc.).

When conditions are extremely arid, CAM plants can CAM-idle. They leave their stomata closed night and day. Oxygen given off in photosynthesis is used for respiration and CO_2 given off in respiration is used for photosynthesis.

CAM-idling allows the plant to survive dry spells, and to recover very quickly when water is available again. CAM plants include many succulents such as cactuses and agaves and also some orchids and bromeliads.

The Table below summarises the features and effects of photosynthetic pathway on plant adaptation to different environments, growth and productivity.

Characteristic	**C3 Species**	**C4 Species**	**CAM Species**
Leaf anatomy	No distinct bundle	Bundle	No distinct

	sheath cell	sheath cells	bundle sheath cells
Stomata	Open during the day	Open during the day	Usually open at night and closed during the day
Transpiration ratio*	350 - 1000	150 - 300	50 - 100
Optimum temp, ^{o}C	15 to 25	25 - 35	25 - 35
First products	3-phosphoglyceric acid	Oxaloacetic acid (converted to malic or aspartic acid)	Oxaloacetic acid (converted to malic or aspartic acid)
Location of photosynthesis	Entire leaf	Bundle sheath cells	Entire leaf
Light response**	Saturated at half of full sunlight	Not Saturated at half of full sunlight	Saturated at one fourth of full sunlight
Photorespiration & CO_2compensation point	Yes, 50 ppm	No, 10ppm or less	Yes, 50 ppm in light
Photosynthesis rate, umoles m^{-2}	6 to 40	14 - 64	1.5 to 6
Maximum growth rate, g d^{-1}	34 - 39	50 - 54	15, up to
Climatic adaptation	Temperate to tropical	tropical	Arig tropical to Mediterranean
Crops	Rice, wheat, barley, soybean, peanut, potato, sweet potato, bean, most vegetables, beet, cabbage, sunflower, all fruit trees studied, etc	Corn, sugarcane, sorghum, millets, tropical grasses, Chinese spinach	Pineapple, prickly pear cactus, many orchids, sisal and other cactus, etc

*The ratio kg water transpired per kg dry weight produced (low values indicate high water use efficiency)

**Light saturation of a single leaf is indicated by failure of the CO_2 assimilation rate to increase with an increase on light intensity

Adapted from Sherman. 2002. Lecture notes for Agron./Hort 200. University of Hawaii.
See also http://eee.uci.edu/99w/07350/Doc/C3C4CAM.html

SELF-ASSESSMENT EXERCISE

Explain the plant physiological responses that enable crops to adapt to their environment
Discuss the following physiological processes: Photosynthesis, Photoperiod and Vernalization
Describe the plant photosynthetic pathway as an adaptive mechanism to the environment

4.0 CONCLUSION

We learn from this unit that plants have evolved to be better adapted to their environment in order to thrive and ensure the long term survival of their species, We were also informed that the important factors required for plant growth are CO_2, O_2, light (quality, intensity and duration), adequate water, nutrients (16 essential nutrients), proper temperature and proper pH. We have understood that the three important processes in plants that are essential for plant growth and development are: photosynthesis, respiration and transpiration. We now know that generally plants have developed physiological mechanisms that make them adapted to their environments.

This unit explains that plant species capable of maximizing photosynthesis, within the constraints of the available resources in its physical environment, will have a significant competitive advantage over other species present in the community. The unit also highlighted that the process of photosynthesis depends on the intake of CO2 through open stomata in the leaves. The unit further stated that this intake is, however, inextricably linked with the parallel process of water loss when the stomata are open, and photosynthetic rates may be severely limited by partial or complete stomatal closure under water stress conditions.

5.0 SUMMARY

Plants have evolved to be better adapted to their environment in order to thrive and ensure the long term survival of their species, The important factors required for plant growth are CO_2, O_2, light (quality, intensity and duration), adequate water, nutrients (16 essential nutrients), proper temperature and proper pH. The three important processes in plants that are essential for plant growth and development are: photosynthesis, respiration and transpiration. Generally, plants have developed physiological mechanisms that make them adapted to their environments.

Plant species capable of maximising photosynthesis, within the constraints of the available resources in its physical environment, will have a significant competitive advantage over other species present in the community. The process of photosynthesis depends on the intake of CO_2 through open stomata in the leaves. This intake is inextricably linked with the parallel process of water loss when the stomataare open, and photosynthetic rates may be severely limited by partial or complete stomatal closure under water stress conditions.

6.0 TUTOR-MARKED ASSIGNMENT

1. Discuss the physiological responses adapting crops to the environment
2. Describe the following physiological processes:
   - Photosynthesis
   - Photoperiod
   - Vernalization
3. Explain plant photosynthetic pathway as an adaptive mechanism
4. Describe the following photosynthetic pathways:
   - C3 Photosynthesis
   - C4 Photosynthesis
   - CAM photosynthesis

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