Uttar Pradesh Rajarshi Tandon Open University

Bachelor of Science

DCEBY-105

Plant embryology and morphogenesis

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Block

1 plant embryology - I

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DCEBY – 105 : Plant embryology and morphogenesis
ISBN-

Printed By: Chandrakala Universal Pvt. 42/7 Jawahar Lal Nehru Road, Prayagraj.

Block I

Plant Embryology I

Plant embryology deals with sexual cycle of the plant. This block of plant embryology explains sexual cycle of plant partially. This block is divided into four Units viz. I, II, III and IV. The details of Units is as follows:

Unit I- is the introduction to embryology which touches all the units of embryology (Unit 1 to 8) like life cycle of angiosperms, microsporogenesis, megasporogenesis, polination, fertilization, post fertilization development, polyembryony and apomixis.

Unit II- is the life cycle of angiosperm in which you will study structure of flower and process of reproduction.

Unit III- is the microsporgenesis which deals with structure of anther, development of pollengrains (Microsporogenesis) as well as structures of pollengrains and post-pollination development.

Unit IV- is the megasporogenesis which will tell you about structure of ovule, it's various types, development of megaspore within the ovule (megasporogenesis) and development of female gametophyte or embryosac.

Objective:

After studying this block you will be able to:

- Known about embryology
- Understand life cycle of angiosperms
- Have knowledge of microsporogenesis and megasporogenesis.

Unit-I

Introduction to Embryology

Structure

1.1 Introduction

Objectives

1.2Introduction to Embryology

- **Life Cycle of angiosperms:**
- **Microsporogensis:**
- **Megosporogenesis**:
- **Pollination:**
- **Fertilization**
- **Post fertilization Development:**

1.3 Summary

1.4Terminal Questions

1.5 Answers

1.1 Introduction

The embryology of angiosperms, a research area encompassing investigations on virtually all the events relevant to sexual reproduction, has contributed much over the last century to an understanding of the structural diversity in micro- and megasporogenesis, the development of micro- and megagametophytes, the fertilization, and the development of embryo, endosperm and seed coat. At various times in the past, an attempt has been made to compile accumulated data and to clarify embryological attributes for each family. Thus the embryology is at present incorporated in most general publications on angiosperm systematics as one of the major sources of systematic characters. The systematic value of embryological characters has often been persuasively argued. In so doing, authors have usually demonstrated the utility of embryological information in clarifying the position of certain problematic families.

Davis (1966) and Philipson (1974) have taken a broader view on assessing the systematic value of embryological characters; in particular, they have attempted to show a restricted occurrence of character states in angiosperms. The most illustrative evidence for consistent occurrence of certain character states was presented by Dahlgren (1975) in his two-dimensional map, the "Dahlgrenogram", a construct further refined by Gertrud Dahlgren in the XIV International Botanical Congress at Berlin in 1987. Despite the increasing value of embryological characters in angiosperm systematics, however, studies on embryology have apparently become progressively inactive over the last 20 years. Early in 1960s more than 150 articles on plant embryology were published a year, while early in 1980s only 20-30 papers were published a year. This may have occurred in part because most of the major easily accessible groups have already been studied, and in part because the time-consuming and difficult tasks of embryology, largely based on microtome sections and optical microscopy, are no longer fashionable and have been increasingly replaced by studies using new technologies (e.g., electron microscopy and molecular techniques). However, the information obtained by such new technologies is still extremely limited, and our knowledge is still much far from sufficient to allow overall comparisons of any higher rank taxa. Further, even where other evidence is not yet fully available or has failed to resolve disputed systematic problems, embryological characters alone can often provide a sound basis for the resolution of such problems.

Objectives

After studying this unit, you will be able to:

- To define the term embryology.
- To know the developmental process in embryology.
- To know fertilization and post fertilization changes.

1.2 Introduction to Embryology

- **Life Cycle of angiosperms:**
  Angiosperms, have two phases in their life cycle a diploid sporophytic phase and a haploid gametophytic phase. The sporophytic phase is the main phase of angiosperm’s life cycle. At maturily the sporophyte products flowers which bears fertile appendages stamens (microsporphylls) and carples (megasporophylls).
  The stamen has a proximal sterilepart the flament, and a distal fertile part, the anther. Microsporangia present in anther contains numerous pollen grains (microspores). The carpel has a proximal overy which bears ovual, a distal stigma to receice pollen grains and a sterite region style between stigma and overy.
  Pollination is the transfer of pollengrains from anther to the stigma of flower. It is occurs in angiosperms either by self-pollination or by cross pollination. It result in

fertilination u.e. fusion of egg (female gamete) present in embryosac with male gametes presentment in pollen tube. In angiosperm **double fertilization** and **triple fusion** is an unique phenomenon. Double fertilization is funsion of one male gamete with egg cell and other male gamete with polar nuclei is triple fusion because here three nuclei fuse together (one nucleus of male gamete and two polar nuclei).

Double fertilization results in formation of zygate which develops into embryo. The embryo may be dicotyledonous in dicot and monocotyledonous in monocots.

The product of triple fusion is primary endosperm cell which give rise endosperm (cellular, nuclear or helobial type.). The endosperm is nutritive tissue and provides nutrition to the developing embroyo.

The embryo develops into seed and Overy into fruits. The seed may be endospermic it may be non-endospermic or ex-albuminous when endosperm is absent in it.

- **Microsporogensis:** Typically each anther has two lobes and each labe has a pair of pollen sac or microsporangia. Microspores or pollen grains are produced in microsporangia after microsporogenesis. During microsporogenesis the nucleus of each microspore mother cell or pollen mother cell (2n) undergo meiosis or reduction division, giving rise to four haploid ('n' number of chromosomes) microspores. Aggregates of four microspors are called as microspores tetrad.

On the basis of arrangement of spores, tetrad are classified as:

Tetrahedral: Four microspores are arranged in tetrahedral manner.

Isobilateral: The four microspores are arranged in one plane.

T-Shaped: Out of the four microspore, two lies perpendicular to the others, so that tetrad has the shape of "T".

Decussate: Microspores may be arranged in decussate manner.

Sometimes microspores do not separate from each other and remain stuck together in groups. Such groups are called compound pollen grains e.g. Pollinium. In this all microspores (pollens) in a pollen sac remain together to form a single mass called pollinium.

Each pollen grain has an outer thick exine and inner then intine. The germination of pollen grain begins before pollination and pollen grains have a gernerative cell and a tube cell. The generative cell further divides mitotically to form two non-motile male gamees where as tube cell forms pollen tube. The pollen grain having male gametes with pollen tube represents the mature male gametophyte.

- **Megosporogenesis**:

  The ovule or megasporangiem consists of nucellus and its protective coats the integument. It remains attached to the placenta, on the inner wall of the ovary by a stalk called funicle. The body of ouval attaches to the funcicle at a point known as hilum.

  An ouval has various parts like junicle nucellus integument, micorpyle, Chalaza, hilum and embryosac. All parts of an ovuale are sporphyte (2n) located in the nucellus, developed from megaspore.

  There are six main types of ouvals e.g. **orthotropous, Anatropous, Campylotropous, Amphitropous, Hemainatropou** and **Circinotropous**.

  "The development of the megaspore within the ouule (megasporangium) is known as megasporgensis".

  During megasporogenesis the primary sporogenous cell differentiated into nucellus functions as megaspore mother cell. It is the last cell of the sporphytic generation and undergoes a reduction division (meiosis) to form four haploid megaspores. Out of four megaspores, three towards micropylar end dygenerates and one lowest remain functional. It represents first cell of female gametophyte and give rise embryosac.

  The mature embryosac has an egg (n) and two synergids (N) towards micropylar end, three antipodal cells (N), towards chalazal end and one secondary mucleus (2N) in the centre.

- **Pollination:**

  The pollination is the transfer of pollen grains from anthers to the stigma of a flower.

  The transfer of pollen grains from an anther to the stigma of the same flower or to a flower on the same plant is known as **self-pollination.** For self pollination flower and anther and stigma of a flower ripe almost simultaneously must be bisexnal. The pollination of a flower by its own pollens is known as **outogamy.** The self-pollination occurring between two different flower present on the same plant is known as **geitonogamy.**

  The self pollinated flower have homogamy and cleistogamy as an adaptation. In homogamy anther and stigma of a flower matures at the same time. In cleistogamy bisexual flower newer open.

Self pollination is almost certain in a bisexual flower where stamens and carpels mature at the same time. But the continued self pollination generation after generation results in weaker progeny.

The transfer of pollen grains from anther to the stigma of another flower is called cross-pollination. For cross-pollination, flower are mostly unisexual. Self-sterility, unisexuality, dichogamy, hterostyly and herkogamy are various adaptation for cross-pollination. Better seeds and healthier offspring are produced by cross-pollination.

The process of cross- pollination depends on various external agencies which may be abiotic or biotic. The abiotic agents are nonliving agents such as air water. The biotic agents includes living organisms such as insect birds.

- Pollination by wind is called
- Pollination through water is called **hydrophily.**
- Pollination by insect is called **entomophily**
- Pollination by bird is called **orinthophily**
- Pollination by bat is called **cheiropteriphily**

Cross-pollination results in healthier offspring, viable seeds and new varities of crops.

SAQ.-1

a. The …………………….. phase is the main phase of angiosperm's life cycle.
b. ………………………. are produced after microsporogenesis.
c. Pollination by bird is called ……………………………..

- **Fertilization**

In an embryo two sexual fusion occurs; one is syngamy (i.e. fusion of one male gamete with the egg) and another is triple fusion (i.e. fusion of other male gamete with the polar nuclei or secondary nucleus) and therefore, the phenomenon is known as double fertilization. This is a very unique phenomenon in angiosperms and was discovered by S.G. Nawaschin (1898).

Once the pollen grain reaches the receptive stigma, as a result of pollination, it germinates producing a long slender pollen tube. Two male gametes and the tube nucleus migrate into the pollen tube which now represents the mature male gametophyte. Pollen tube penetrates the stigmatic tissue and pushes its way through the style and then down the wall of the ovary. After arriving in the ovary, the pollen tube may enter into the ovule through micropyle (porogamy), through chalazal end (chalazogamy) or thrugh integuments (mesogamy). Irrespective of the route of the entry of the pollen tube into the ovule, it always enters the embryo sac from the micropylar end. After entering into the embryo sac, the tip of the pollen tube bursts and the two male gametes are released. Out of the two male gametes one male gamete fuses with the egg nucleus and result in the formation of zygote or oospore (2n). Second male gamete fuses with two polar nuclei, resulting into primary endosperm nucleus (3n). This phenomenon is termed as double fertilization.

- **Post fertilization Development:**

  Post fertilization development means development of the embryo and the endosperm within the ovule. Both the development goes side by side in the ovule.

  The endosperm (3N) develops from primary endosperm nucleus. This undergoes a series of divisions and ultimately forms endosperm. Depending upon mode of development three types of endosperm has been recognized: (1) Nuclear type (2) Cellular type (3) Helobial type. The endosperm is nutritive tissue. It provides nutrition to the developing embryo.

  With the development of endosperm, the oospore develops in the embryo side by side. The development of embryo from diploid oospore is called embryogenesis.

  Development of dicot embryo (crucifer type):

  1. Zygote (oospore) divides transversely. As a result of this a two-celled proembryo is formed.

  2. The larger basal cell at the micropylar end is called suspensor cell. The smaller one, away from it termed as terminal cell or embryo cell.

  3. The suspensor cell divides transversely a few times to produce a filamentous suspensor of 6 to 10 cells. The suspensor helps in pushing the embryo in the endosperm.

  4. The first cell of the suspensor (towards micropyle) becomes swollen and called haustorium or vesicular cell.

  5. The last cell of suspensor (towards embryo cell) is known as hypophysis. It forms radicle and root cap.

  6. The embryo cell undergoes two vertical divisions and one transverse division to form quadrant and then octant stage. In octant, eight cells arranged in two tiers-epibasal (terminal) and hypobasal (near the suspensor).

Development of monocatembryo:

The early development of dicot and monocot embryos are similar uptooctant stage. Later on differentiation starts.

1. The zygote or oospore elongates and then divides transversely to form basal and terminal cells.

2. The basal cell (towards micropylar end) produces a large swollen, vesicular suspensor cell. It may function as haustorium.

3. The terminal cell divides by another transverse wall to form two cells.

4. The top cell after a series of divisions forms plumule and a single cotyledon.

5. Cotyledon called scutellum, grows rapidly and pushes the terminal plumule to one side. The plumule comes to lie in a depression.

6. The middle cell, after many divisions forms hypocotyl and radicle. It also adds a few cells to the suspensor.

7. In some cereals both plumule and radicle get covered by sheaths developed from scutellum called coleoptile and coleorhiza respectively.

- **Polyembryony and Apomixis:**

  Polyembryony is defined as "The development of several embryos within the same ovule". It is common in gymnosperms but very rare in angiosperms. In angiosperms polyembrony may be due to:

  1. Clevage of the proembryo.
  2. Embryos developing from cells of the embryosac other than the egg.
  3. More than one embryosac in the same ovule.
  4. Activation of some sporphytic cell of the ovule.

Apomixis is defined as "Phenomenon of substitution of sexual process by asexual methods is known as apomixes". The plants which show spomixis are called **apomictic plants.**

SAQ.-2

a. The phenomenon of double fertilization was discovered by ……………………...
b. Post fertilization development means development of ………….. and ………… within the ovule.
c. In polyembryony ………………….. embryos develop with in the same ovule.

1.3 Summary

In this unit you have learnt that:

- Embryology is at present incorporated in most general publications on angiosperm systematics as one of the major sources of systematic characters.
- The most illustrative evidence for consistent occurrence of certain character states was presented by Dahlgren (1975) in his two-dimensional map, the "Dahlgrenogram", a construct further refined by Gertrud Dahlgren in the XIV International Botanical Congress at Berlin in 1987.

1.4 Terminal Question

Q.1 What is embryology?

Answer:---

Q.2 Give a detail account of developmental process in embryology.

Answer:---

Q.3 Describe the life cycle of angiosperms?

Answer:---

1.5 Answers

SAQ 1.

a. Sporophytic b. Microspores c. Orinthophily

SAQ 2.

a. G.S. Nawaschin b. embryo and endosperm c. Several

Unit- II

Life cycle of Angiosperm

Structure

2.1 Introduction

Angiosperms are seed producing plants that generate male and female gametophytes, which allow them to carry out double fertilization.

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle**(Figure 2.1)**. As with gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will produce pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes meiosis, generating four megaspores: three small and one large. Only the large megaspore survives; it produces the female gametophyte referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator and will eventually fuse to form a 2n polar nucleus. The three cells away from the egg form antipodals while the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids (“helper” cells), three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle, an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote, the future embryo. The other sperm fuses with the 2n polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called cotyledons. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the dicots. Seed food reserves are stored outside the embryo in the form of complex carbohydrates, lipids, or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and the well-protected embryo at the center.

Some species of angiosperms are hermaphroditic (stamens and pistils are contained on a single flower), some species are monoecious (stamens and pistils occur on separate flowers, but the same plant), and some are dioecious (staminate and pistillate flowers occur on separate plants). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water) or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

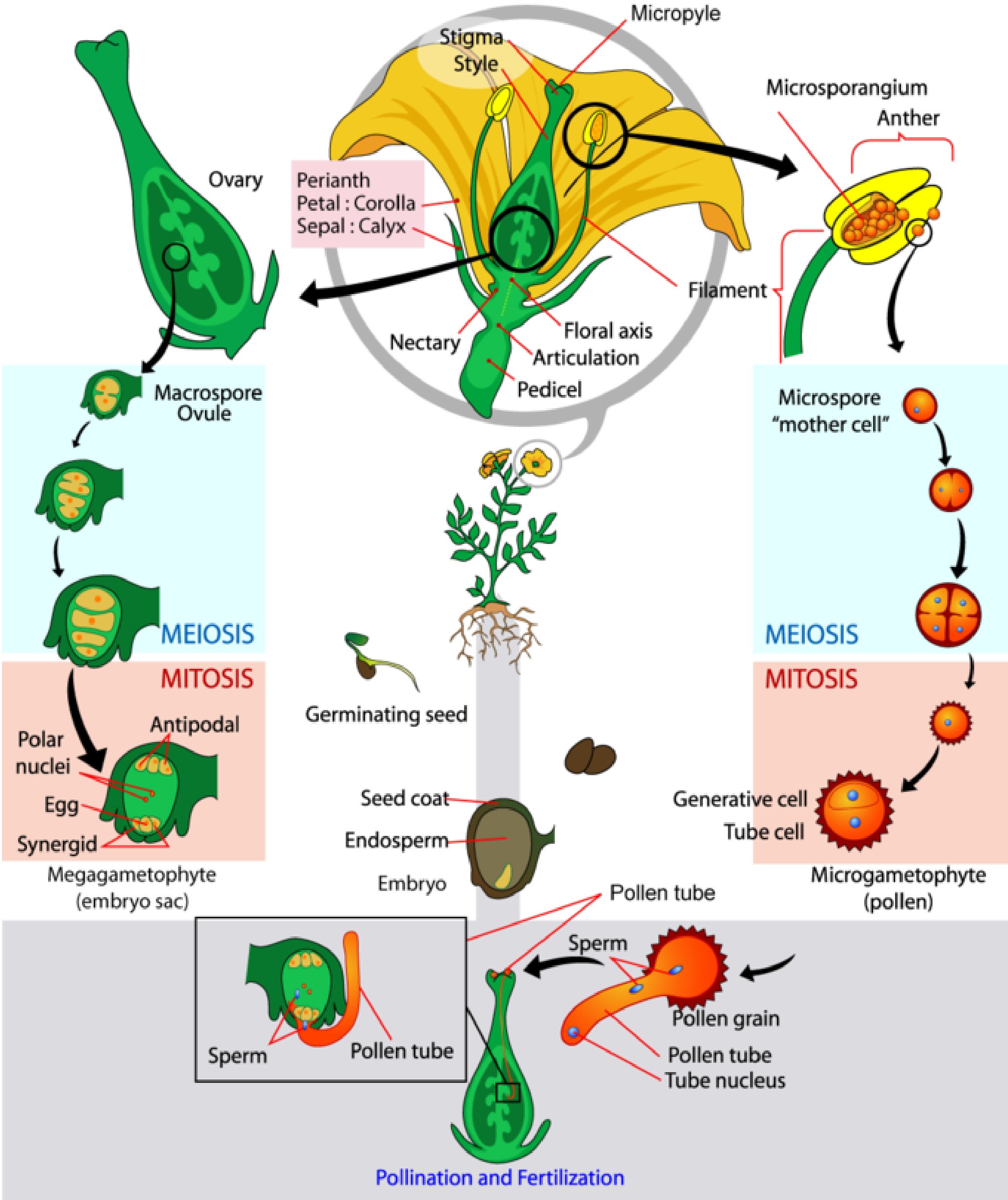


Figure 2.1Life cycle of angiosperms: The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms.

Objectives

After studying this unit, you will be able to:

- To explain the life cycle of angiosperm, including cross-pollination and the ways in which it takes place.
- To knowthe structure of flower.
- To study the process of reproduction.

2.2 Structure of flower

Flowers are the site of sexual reproduction in flowering plants.

A typical angiospermic flower has following parts arranged in four whorls. They are Calyx, Corolla, Androecium and Gynoecium**(Figure 2.2)**.

1. Calyx: It is the outer most whorl of the flower. It is composed of leaf like green sepals.

2. Corolla: It is the second whorl of flower and consists of number of petals.

3. Androecium: It is the third whorl of flower consisting of stamens. Stamen is the male reproductive organ of flower. Each stamen is made up of filament and anther.

4. Gynoecium: This is the last and fourth whorl of the flower consisting of pistil or carpel. Pistil is the female reproductive organ of the flower. Each pistil is composed of ovary, style and stigma.

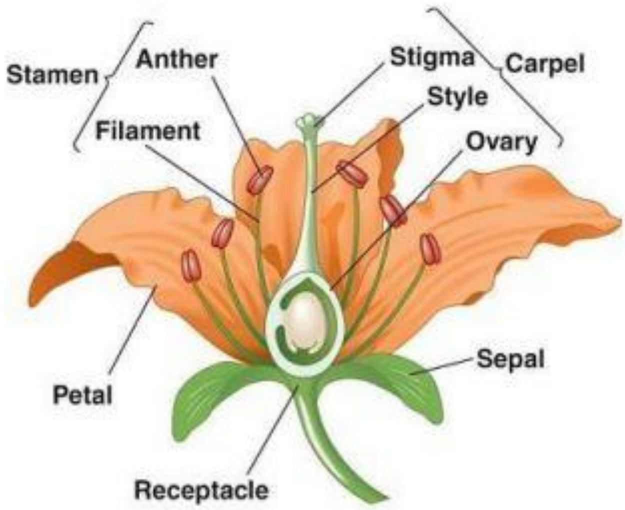


Figure 2.2 Structure of flower

SAQ.1

a. Angiosperm are________producing plants.
b. Pollen grain consist two cells, one_________cell and second tube cell.
c. The megaspore divides three times to form an__________celled stage.
d. Flowers are the site of_____________reproduction in flowering plants.
e. ______________is the female reproductive organ of the flower.

2.3 Process of reproduction

Angiosperms reproduce both by vegetative as well as by sexual methods. In this section we will study the sexual reproduction in angiosperms. As you know sexual reproduction occurs by fusion of male and female gametes produced in the flower. Thus, flower represents the reproductive unit of a flowering plant. How frequently do plants flower? There is great variation shown by the angiospermic plants in this respect.

Angiosperms can be classified as annuals, biennials and perennials depending upon the time they take to complete the life cycle including flowering, fruiting, and death.

(a) Annuals: The plants which complete their life cycle including flowering to seed formation within one season are called annuals eg. pea

(b) Biennials: Plants which complete their life cycle in two seasons are called biennials. In the first season these plants remain in the vegetative state, and in the second season, they produce flowers, fruits, and seeds and then die e.g. radish.

(c) Perennials: Plants which live for several years are termed perennials. Their vegetative stage may last from one to a few years after which they produce flowers, fruits, and seeds every year e.g. mango, peepal, and neem.

(d) Monocarpic: All the annuals, all the biennials and, some perennial plants that reproduce only once in their life-time and then die, are called Monocarpic e.g. bamboo, agave, all the annuals and all the biennials.

(e) Polycarpic: Plants which flower and fruit many times in their life cycle and live for several years, are called Polycarpic e.g. many perennial fruit bearing trees e.g. mango, guava, apple and pear.

Sexual reproduction in plants occurs when the pollen from an anther is transferred to the stigma. Plants can fertilize themselves. This is called self-fertilization. Self-fertilization occurs when the pollen from an anther fertilizes the eggs on the same flower. Cross-fertilization occurs when the pollen is transferred to the stigma of an entirely different plant.

When the ovules are fertilized, they will develop into seeds. The petals of the flower fall off leaving only the ovary behind, which will develop into a fruit. There are many different kinds of fruits, including apples, oranges, and peaches. A fruit is any structure that encloses and protects a seed, so fruits are also “helicopters”, acorns, and bean pods. When you eat a fruit, you are actually eating the ovary of the flower.

SAQ.2

a. The plants which complete their life cycle including flowering to seed formation within_______season are called annuals.

b. All the annuals, all the biennials and, some perennial plants that reproduce only once in their life-time and then die, are called____________.

c. Self-fertilization occurs when the pollen from an anther fertilizes the eggs on the __________flower.

d. __________fertilization occurs when the pollen is transferred to the stigma of an entirely different plant.

e. Plants which live for several years are termed______________.

2.4 Summary

In this unit you have learnt that:

- Alternation of generation is a remarkable aspect of the life cycle of all higher plants. Angiosperm plants are diploid sporophytes i.e. spore bearing plants and the haploid spores are developed by meiosis.
- In this unit we have discussed the meaning of various terms i.e. gametophyte, male gametophyte, microsporogenesis, etc. and about the structure of anther.
- We also learnt about the process of microsporogenesis, and various steps of gametophyte development.
- Gametophyte is the haploid generation producing gametes in plants.
- When we are talking about male then it is said to be male gametophyte.
- Male and female reproductive organs in plants are stamen and carpel, the necessary parts of flower.

2.5 Terminal Question

Q.1 Name the first cell of male gametophyte and explain it.

Answer:---

Q.2 Name the last cell of male sporophyte and explain it.

Answer:---

Q.3 Describe the structure of flower.

Answer:---

Q.4 Discuss the process of reproduction.

Answer:---

Q.5 Give detail account of life cycle of angiosperm.

Answer:---

Short Questions

Q.6 Write short notes on:

1. Parts of the flower
2. Annuals, Biennials and perennials
3. Monocarpic and polycarpic

Q.7 Multiple choice questions:

1. Which one of the following is mismatched?

(a) Gynoecium - female reproductive organ

(b) Tapetum - one of the layer of anther wall

(c) Anther- fertile part of stamen

(d) Pollen grain-diploid

2. A heterosporous plant:

(a) Produces microspores and megaspores

(b) Produces only microspores

(c) Produces only megaspores

(d) None

3. Sporophyte is:

(a) Haploid

(b) Diploid

(c) May be haploid

(d) May be diploid

4. Last cell of sporophytic generation or sporophyte:
   (a) Embryo
   (b) Zygote
   (c) Spore
   (d) Spore mother cell

2.6 Answers

1. (d) 2. (a) 3. (b) 4. (d)

Self-assessment questions

SAQ.1

a. Seed**b.** Generative**c.** Eight**d.**Sexual**e.**Pistil

SAQ.2

a. One**b.** Monocarpic **c.** Same**d.**Cross**e.**Perennials

Unit- III	Microsporogenesis

Structure

3.1 Introduction

A living organism cannot survive forever. For existence each species has to continue and for it, each member must reproduce its own kind. Dear students you all know that plants reproduce by asexual, vegetative and sexual means.

Asexual reproduction is the formation of new individuals from the cells of single parent. The offspring will be exact genetic copies of the parent except in specific cases of 'automixis'. Asexual reproduction is of various types (fission, sporulation, budding, fragmentation, parthenogenesis) and vegetative propagation is one of asexual reproduction types. Regeneration of plant from any vegetative part of it i.e. stem cutting, rhizome, tuber, bulb, leaves etc. is known as vegetative reproduction or vegetative propagation. Asexual reproduction including vegetative one is an accessory mean of propagation and do not involve genes from different cell lineages whereas in sexual reproduction, fusion of two dissimilar gametes from two different parents leads to formation of new combination of genes.

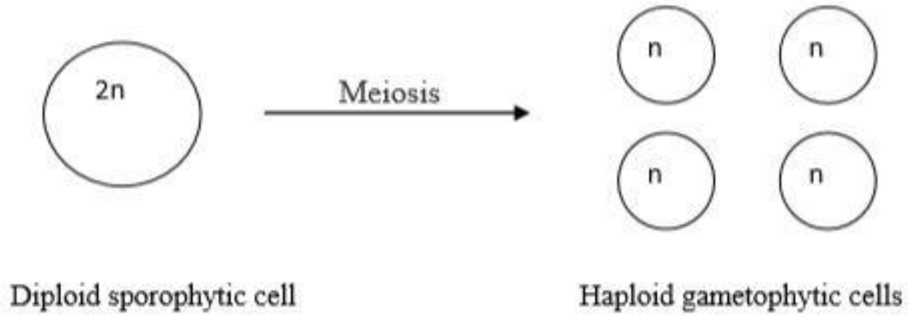
If we are talking about the life cycle of flowering plants, it is characterized by an alternation between a dominant sporophytic generation and a highly reduced gametophytic generation. Dominant sporophytic generation is diploid and reduced gametophytic generation is haploid.

The normal sexual cycle (amphimixing) involves two important processes:

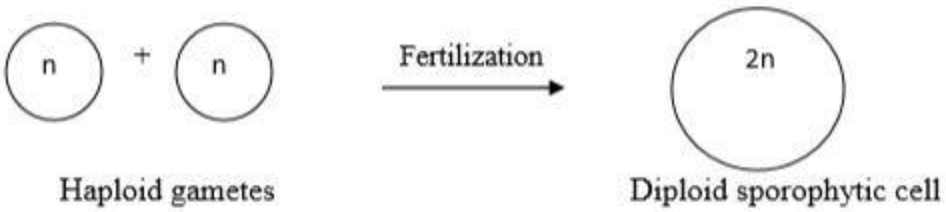
(i) Meiosis and

(ii) Fertilization

In meiosis also known as reduction division, a diploid sporophytic cell (SMC; spore mother cell) gets converted into four haploid gametophytic cells. ("2n" number of chromosomes becomes half i.e. "n" number of chromosome)



In fertilization, two haploid gametes of opposite sex fuse to form diploid sporophytic generation.



So we can say, in a sexual cycle a diploid generation (sporophytic) alternates with a haploid generation (gametophytic).

The major function of diploid sporophytic generation is to produce haploid spores, which are the products of meiosis. Spores undergo cell proliferation and differentiation to develop into gametophytes. The major function of gametophytic generation is to produce haploid gametes. The fusion of egg and sperm gives rise to the zygote, which is the beginning of diploid sporophyte generation, thereby completing the life cycle.

During the Angiosperm life cycle, the sporophyte produces two types of spores, microspores and megaspores. These spores give rise to male gametophytes and female gametophyte, respectively. The Angiosperm gametophyte develops within sporophytic tissues that constitute the sexual organs of the flower.

The male gametophyte, also referred to as the pollen grain or microgametophyte, develops within the stamen's anther and is composed of two sperm cells encased within a vegetative cell.

The female gametophyte, also referred to as the embryo sac or megagametophyte, develops within the ovule, which is found within the carpel's ovary**(Figure 3.1)**.

The sporophyte eventually produces flowers.

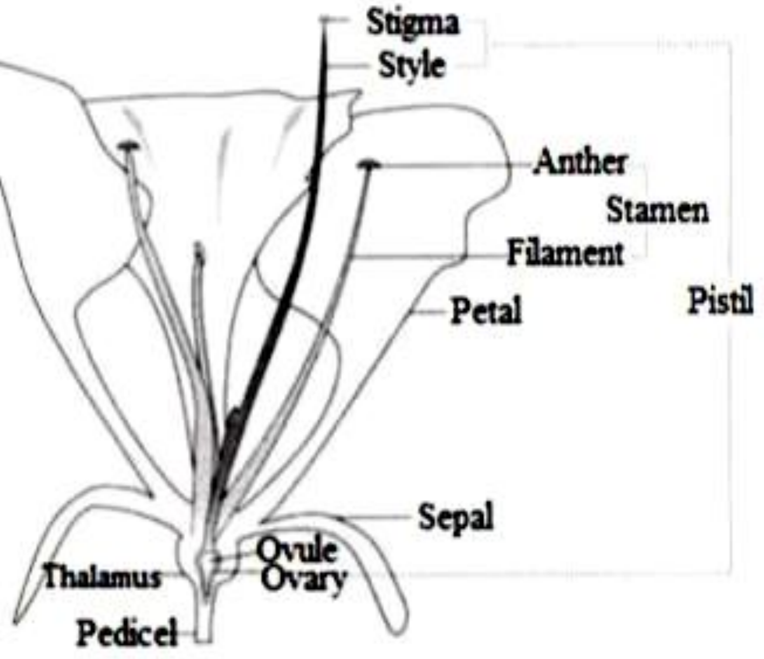


Figure 3.1 Flower showing reproductive organs

Production of spores and formation of gametes are important events in the sexual reproductive cycle that take place in the flower.

The floral organ concerned with male sexual reproduction is the stamen, and the part of the stamen where events of male sexual reproduction occur is the anther. Similarly the floral organ concerned with female sexual reproduction is the pistil (carpel), and the part of the pistil where events of female sexual reproduction occur is the ovule inside the ovary.

Now it is clear to you that Angiosperm plants are diploid sporophytes i.e. spore bearing plants and haploid spores are developed by meiosis or reduction division. The male spores or microspores are developed by meiosis within the microsporangium (pollen sac) while the female spores or megaspores are developed by meiosis within the megasporangium (ovule). These, in their turns, develop the male and the female gametophytes which are endosporous (developing inside the spores **Figure 3.2)**.

The process of development of the spore is termed as sporogenesis. When it is microspore (pollen), it is termed as microsporogenesis. When it is megaspore, it is termed as megasporogenesis.

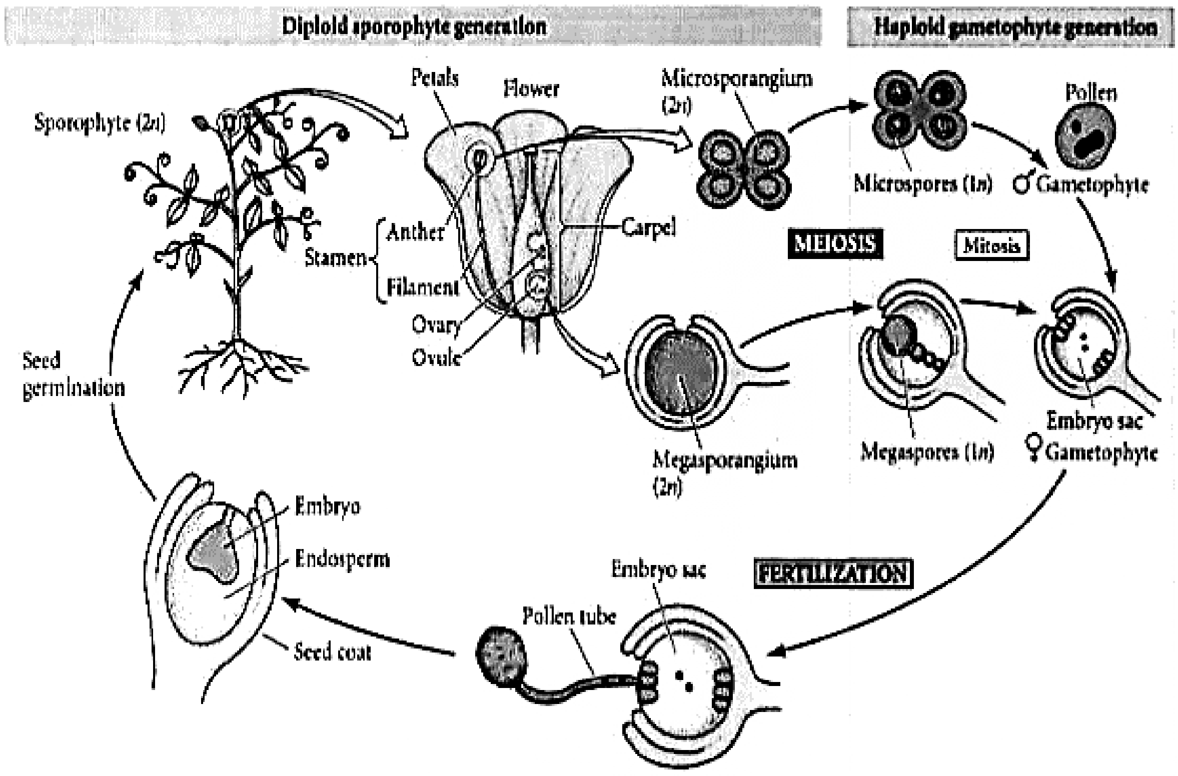


Figure 3.2Life cycle of a typical Angiosperm (example - a pea plant).

The sporophyte is the dominant generation, but multicellular male and female gametophytes are produced within the flowers of the sporophyte. Cells of the microsporangium within the anther undergo meiosis to produce microspores. Subsequent mitotic divisions are limited, but the end result is a pollen grain. The megasporangium is protected by two layers of integuments and the ovary wall. Within the megasporangium, meiosis yields four megaspores-three small and one large. Only the large megaspore survives to produce the embryo sac. Fertilization occurs when the pollen germinates and the pollen tube grows toward the embryo sac. The sporophytic generation may be maintained in a dormant state, protected by the seed coat.

Objectives

After studying this unit, you will be able:

- To know about male gametophyte.
- To study the structure of anther.
- To understand the term microsporogenesis.
- To differentiate the sporogenesis and microsporogenesis.
- To study the process of development of male gametophyte in Angiosperms.

3.2 Structure of anther

The fertile portion of stamen is called anther. Actually the stamen is a slender organ and consists of the proximal sterile part, the filament (stalk) bearing at its distal end a fertile part, the anther.

A typical anther has two anther lobes connected by a connective and each anther lobe has two pollen chambers (microsporangia or pollen sacs). Pollen grains (microspores), which contribute the male gametes, are present in each microsporangium or we can say are formed within an anther.

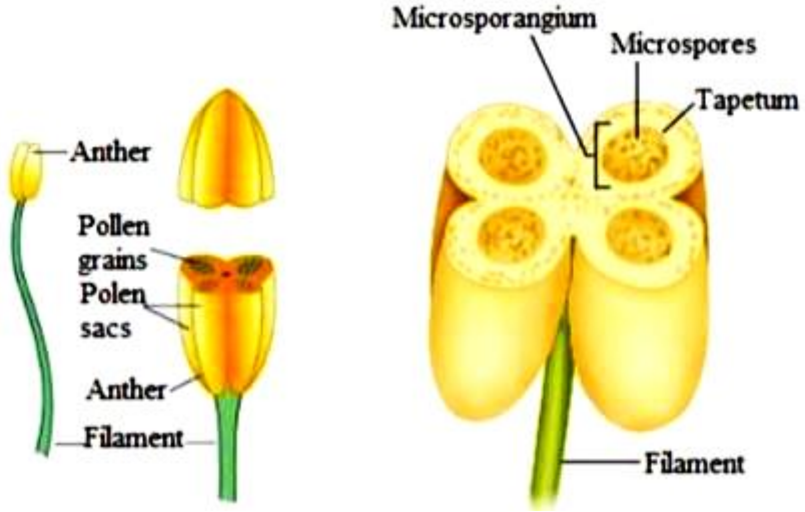


Figure 3.3 Stamen showing dithecous anther

When the anther has two lobes then it is termed as dithecous as in *Citrus* having four microsporangia **(Figure 3.3)**. Sometimes anther may have single lobe instead of two, at this condition anther is termed as monothecous as in *Hibiscus rosa-sinensis* having two microsporangia. A young anther comprises a mass of undifferentiated thin walled cells bounded by epidermis.

Flowers are structures of sexual reproduction. The essential organs of flower are stamens (microsporophylls) - which make the androecium, and carpels (megasporophylls) - which together form the gynoecium

or

The androecium represents the male reproductive elements of the flower and gynoecium, the female reproductive elements of the flower.

Few terms to remember:

Microsporophyll = Stamen

Megasporophyll = Carpel = Pistil

Microsporangium = Pollen sac = Pollen chamber

Male gametophyte = Germinating pollen grain = Pollens = Microgametophyte

Male gametes = Sperms

Megasporangium = Ovule

Megaspore mother cell = Megasporocyte

Female gametophyte = Embryo sac = Megagametophyte

Female gamete = Egg

SAQ.1

---

a. Asexual reproduction is the formation of new individuals from the cells of_______parent.
b. Dominant sporophytic generation is________ and reduced gametophytic generation is__________.
c. The major function of diploid sporophytic generation is to produce____________, which are the products of meiosis.
d. The female gametophyte, also referred to as the__________ or megagametophyte, develops within the ovule.
e. When the anther has two lobes then it is termed as__________ (two lobed) as in *Citrus* having four microsporangia.

Microsporangium (pollen sac or pollen chamber)

The microsporangium is a structure in an anther which produces the microspores and eventually the male gametophyte. A microsporangium or future pollen sac is a cylindrical sac which appears circular in transverse section**(Figure 3.4)**. It consists of two parts, outer wall and central homogeneous mass of sporogenous tissue. Microsporangial wall has four types of layers:

1. Epidermis (common anther covering)

2. Endothecium

3. 2-3 middle layers and

4.Tapetum

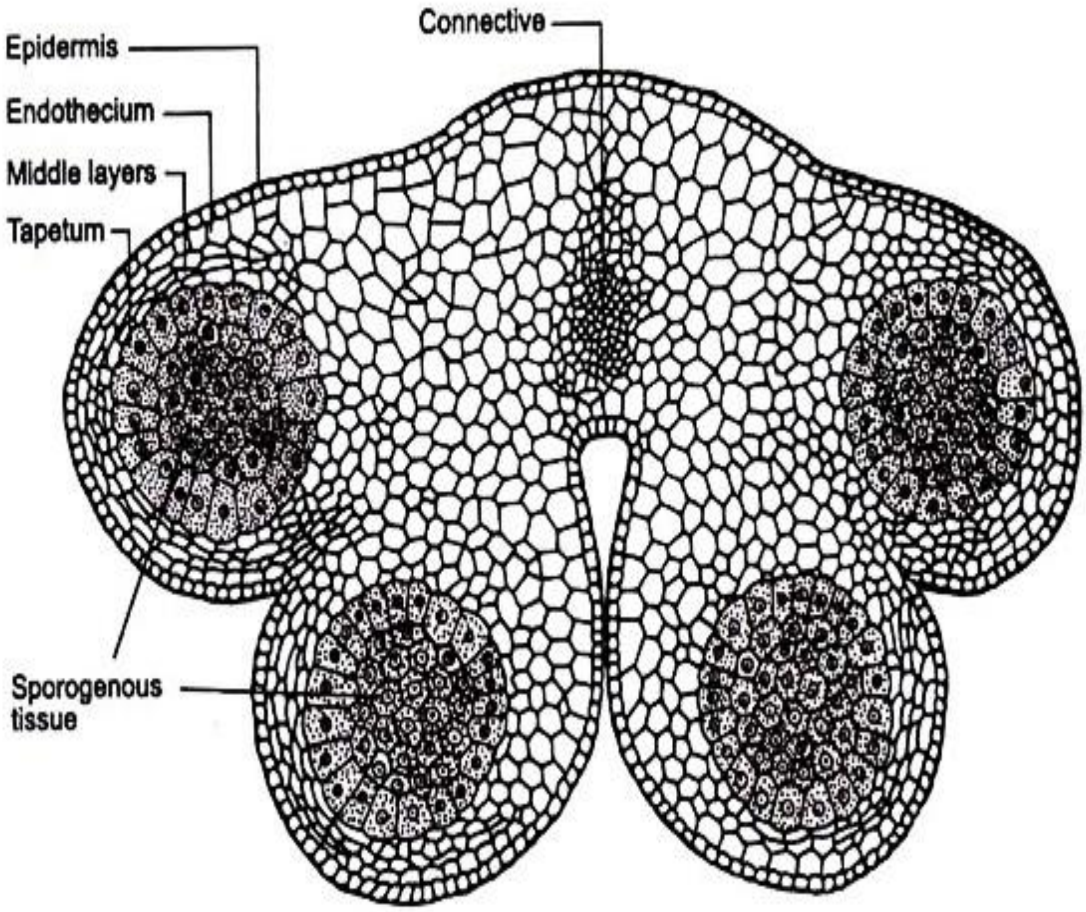


Figure 3.4 Transverse section of a tetrasporangiate anther showing various tissues

Development of Microsporangium

During the development of microsporangium, the anther is seen initially as a homogeneous mass of meristematic cells, oblong in cross section and surrounded by a well defined epidermis **(Figure 3.5 A)**. It then becomes more or less four lobed and in each lobe some hypodermal cells become more prominent than the others because of their larger size, more deeply staining cytoplasm and conspicuous nuclei. These cells constitute the archesporial initials (archesporium) **(Figure 3.5 B)**. There may be only one archesporial cell in each of the four lobes as in *Boerhaavia*. The archesporial cells divide by periclinal division (in a plane parallel to the outer wall of the anther lobe), cutting off primary parietal cells toward the epidermis and primary sporogenous cells toward the interior of the anther. Then the cells of parietal layer forms 2-5 layers of anther wall by undergoing a series of divisions, both periclinalas well as anticlinal. The primary sporogenous cells either directly or after few mitotic divisions functions as microspore mother cells or pollen mother cells (MMCs or PMCs).

Anther wall

The mature anther wall as described above, comprises an epidermis followed by a layer of endothecium, 2 or 3 middle layers and a single-layered tapetum.

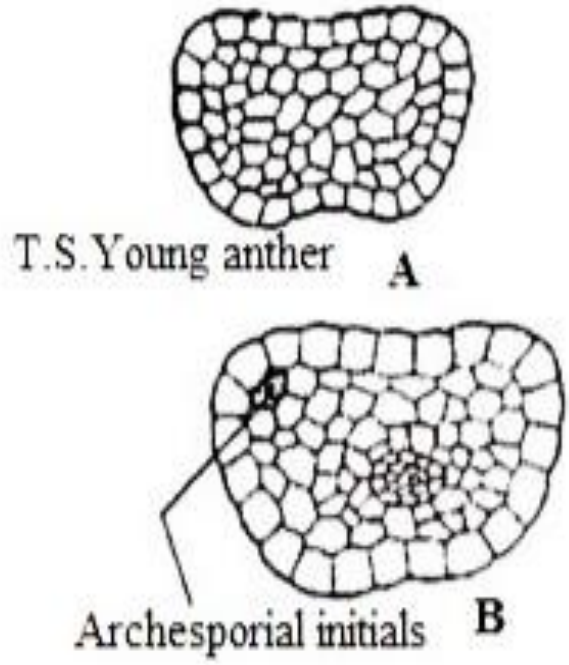


Figure 3.5: In cross section anther is showing - A: Homogenous mass of meristematic cells surrounded by epidermis; B: Archesporial initials

The outermost layer, epidermis undergoes only anticlinal divisions. Its cells are flattened and become greatly stretched so that they keep pace with the enlargement of the anther. The epidermis performs its usual protective function.

Beneath the epidermis endothecium or fibrous layer is present. The cells of endothecium are radially elongated which later loses the cell contents, usually becomes fibrous and forms the dry coat of the mature anther. This layer attains its maximum development when anther is ready to dehisce for the discharge of pollen. The presence of fibrous bands, differential expansion of the outer and inner tangential walls and hygroscopic nature of the endothecial cells help in dehiscence of anthers at maturity. The cells of endothecium are thin walled along the line of dehiscence of each anther lobe. The opening through which the pollen grains are discharged from the pollen sac is called stomium. On maturity of the anther, a strain is exerted on the stomium due to the loss of water by the cells of endothecium, with the result the stomium ruptures and the anther dehisces. Mature anther, generally dehisces by means of slit or apical pores. Next to endothecium, 2 or 3 middle layers are present. The middle layers are usually crushed by the time actual meiosis occurs in the sporogenous cells. In many species the cells of the middle layers are storage centers for starch and other reserves which get mobilized during later development of pollen.

Tapetum is the innermost layer of the anther wall characterized by the presence of dense cytoplasm and prominent nuclei. Tapetum is of considerable physiological significance. It attains its maximum development at the tetrad stage of microsporogenesis. It is a nutritive tissue nourishing the developing microspores, all the food material to the sporogenous tissue must pass through it **(Figure 3.6)**.

Sporogenous tissue

The sporogenous cells may directly functions as microspore mother cells (MMCs) or pollen mother cells or they may undergo few mitotic divisions to add up to their number before entering meiosis. Although all the sporogenous cells in the anther are potentially capable of giving rise to microspores, some of them frequently degenerate and absorbed by other cells**(Figure 3.6)**.

From the above discussion it is clear that the process of development of anther till the MMCs formation is as follows-

Archesporial cell ----------- Primary parietal cells and Primary sporogenous cells

Primary parietal cells--------------Parietal cells and Endothecium

Parietal cells -------------Tapetum and Middle cell layer

Primary sporogenous cells------------Pollen mother cells/Microspore mother cells

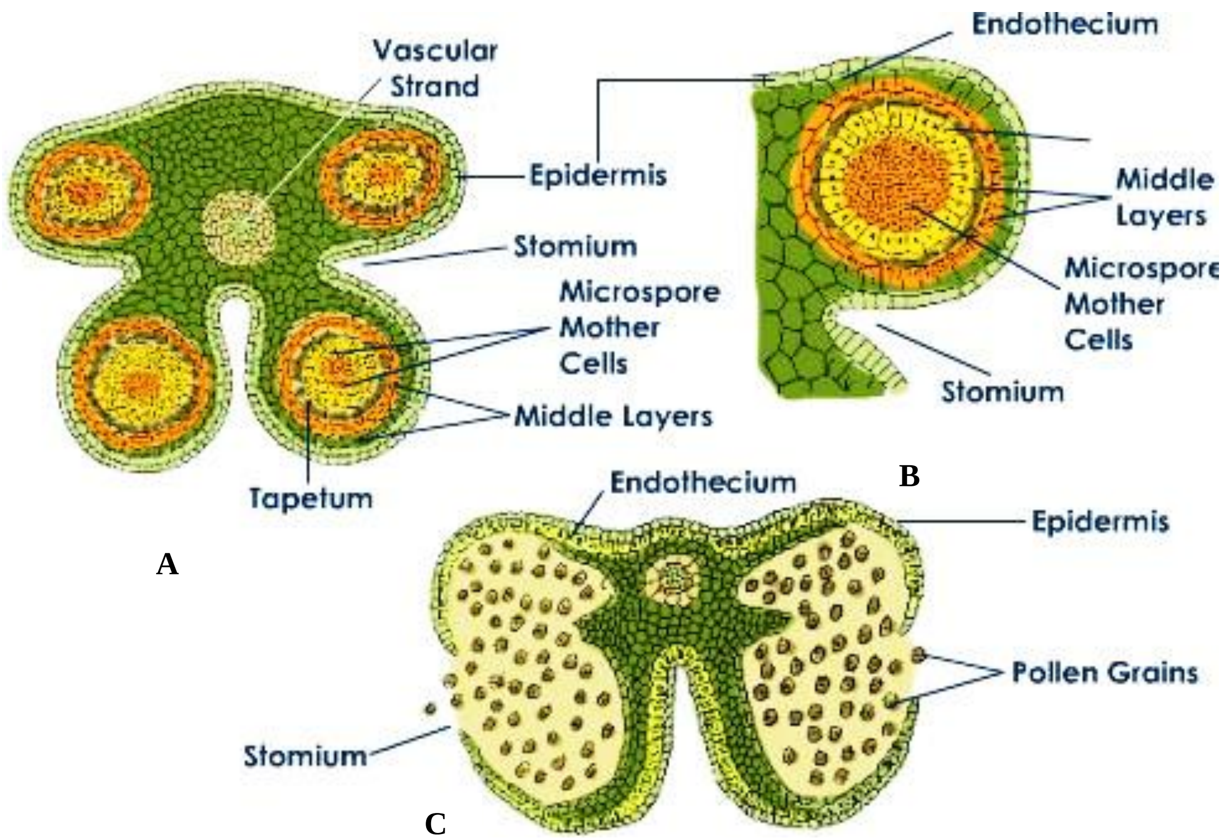


Figure 3.6 A. T.S. of tetrasporangiate anther; B. Enlarged view of one microsporangium showing four wall layers; C. T.S. of a mature dehisced anther

SAQ.2

a. The opening through which the pollen grains are discharged from the pollen sac is called____________.

b. ___________is the innermost layer of the anther wall characterized by the presence of dense cytoplasm and prominent nuclei.

c. The microsporangium is a structure in an anther which produces the microspores and eventually the___________.

d. Microsporangial wall has______types of layers.

e. The sporogenous cells may directly functions as____________.

3.3 Microsporogenesis

"Microsporogenesis means development of microspores/pollen grains".

The process of development of the microspore (pollen) is termed as microsporogenesis. During microsporogenesis the nucleus of each microspore mother cell or pollen mother cell (2n) undergo meiosis or reduction division, giving rise to four haploid (possessing ‘n’ number of chromosomes) microspores. At the end of meiosis four haploid microspores are enclosed in a common callose wall. The individual spore lacks a wall of its own and it is a callose partition which separates spores from each other. Aggregates of four microspores are called as microspore tetrads. Later on each spore forms its own wall **(Figure 3.7)**.

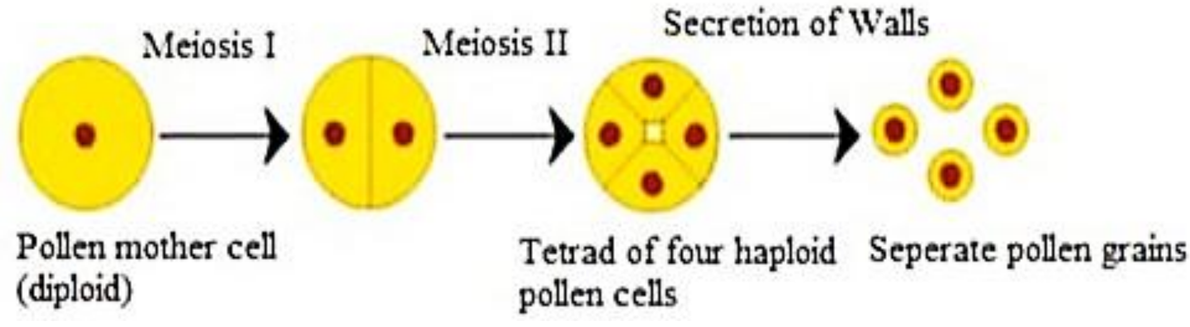


Figure 3.7 Microsporogenesis

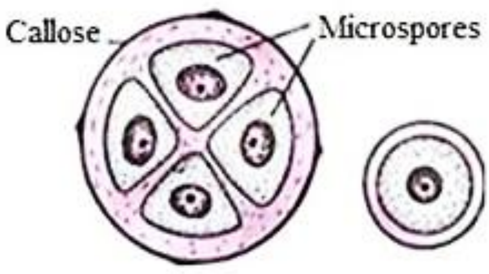


Figure 3.8: Microspores showing callose wall

Microspore tetrad

All the four spores within a tetrad are completely isolated from one another and from the spores in other tetrads of the locule by means of callose wall **(Figure 3.8)**.

On the basis of arrangement of spores, tetrads are classified into various types**(Figure 3.9)**. Usually the arrangement of microspores in a tetrad is tetrahedral or isobilateral. However, other arrangements i.e. decussate, linear and T-shaped tetrads are also found.

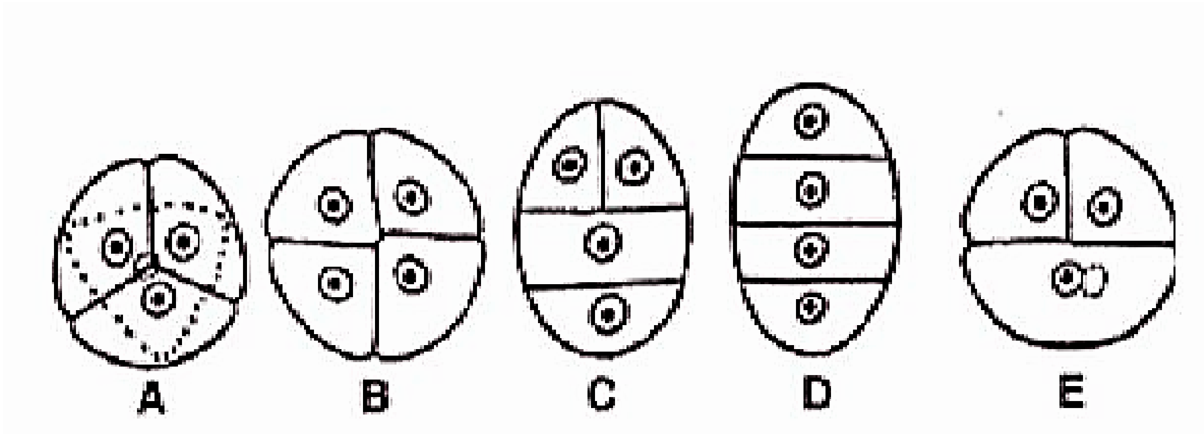


Figure 3.9: Arrangement of microspores/pollen grains, A. Tetrahedral; B. Isobilateral; C. T-shaped; D. Linear; E. Decussate

Tetrahedral: This type of tetrad is very common among dicots. The four microspores are arranged like a quadrant of a sphere so when see from an angle, only three microspores are visible and fourth lies at the back.

Isobilateral: This type of tetrad is very common among monocots. The four microspores are arranged at four corners of a square in one plane.

T-shaped: Out of the four microspores, two lies perpendicular to the others, so that the tetrad has the shape of “T”. Example: as in *Aristolochia* and *Butomopsis*.

Linear: The four microspores aligned linearly as a result of transverse division in mother cell. Example: In some genera of the Asclepiadaceae and in the genus *Halophila* of the Hydrocharitaceae.

Decussate: A decussate arrangement of the cells has been recorded in *Magnolia*, *Atriplex* and many other plants.

In *Aristolochiaelegans* all the five types of tetrad have been reported. The microspores of a tetrad usually separate from each other shortly after meiosis as the anther matures. Now they are called pollens. Pollen grains are uninucleate when they separate from the tetrad and they have their own wall. However, in some plants it has been reported that the microspores of a tetrad tend to remain together in a tetrad and develop into compound structures i.e. Compound pollen grains and pollinium etc.

Compound pollen grains

Sometimes microspores do not separate from each other and remain stuck together in groups. Such groups are called compound pollen grains. Example- *Drosera, Annona, Elodea, Typha* (several members of the Ericaceae, Apocynaceae, Asclepiadaceae, Juncaceae, and Orchidaceae).

Pollinium

All microspores (pollens) in a pollen sac remain together to form a single mass called pollinium. Example - *Calotropis*, *Orchids* (members of the family Asclepiadaceae and Orchidaceae respectively). Each pollinium is provided with a stalk called caudicle and a sticky base called disc or corpusculum**(Figure 3.10)**.

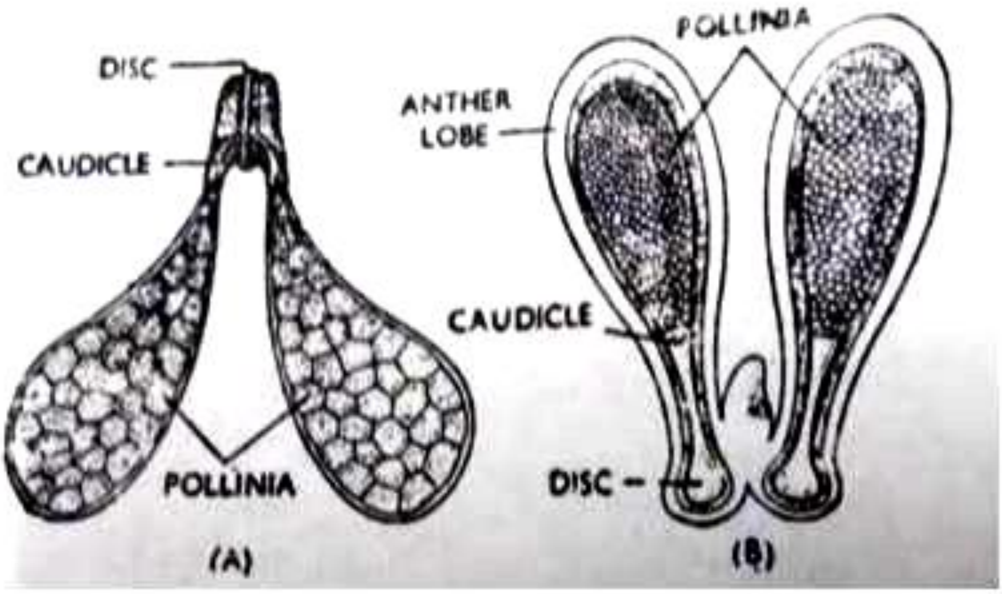


Figure 3.10: Pollinia (A). of Calotropis; (B). of orchid

Polyspory

Occurrence of more than four spores in a tetrad is called polyspory. The phenomenon of polyspory has been reported in a number of plants as an abnormality. Polyspory has been noted in *Hyphaene* by Mahabale and Chennaveeraiah (1957). *Cuscutareflexa* is a plant where tetrad with as many as eleven microspores have been observed.

Microspores soon dry up and become powdery while the tapetum becomes absorbed. The anther now becomes a dry structure, the partition walls between the sporangia (i.e. loculi) are usually destroyed and the microspores are soon liberated by dehiscence of the anther.

Haploid microspores or pollens are the first cell of male gametophyte.

SAQ.3

a. The process of development of the microspore (pollen) is termed as____________.

b. Aggregates of_____________microspores are called as microspore tetrads.

c. The four microspores are arranged at four corners of a square in one plane known as_____________.

d. In *Aristolochiaelegans* all the____________types of tetrad have been reported.

e. All microspores (pollens) in a pollen sac remain together to form a single mass called__________.

3.4 Development of male gametophyte

Gametogenesis

Process of development of male gametophyte is known as gametogenesis and haploid microspores or pollens formed from diploid Microspore Mother Cell (MMC) as a result of meiosis are the first cell (mother cell) of male gametophyte. Therefore, MMC could be called as **last cell of sporophytic generation or sporophyte**. Soon microspores released from the tetrad and are referred to as pollen grains.

Microspore/Pollen grain

Pollen grains are contained in the microsporangia (pollen chamber). They are very minute in size (approximately 0.025 to 0.125 mm) and are like particles of dust. A freshly formed pollen grain is richly cytoplasmic with a prominent, centrally located nucleus. The wall of the mature pollen grain is stratified. It comprises of two layers. The outer layer is called exine and inner layer is termed as intine. The term exine and intine were proposed by Fritsch (1837).

Exine: Thick, tough cutinized layer which is often provided with spinous outgrowths or sometimes smooth. The exine is composed of a complex substance, called sporopollenin.

Intine: It is thin, smooth, delicate pecto-cellulosic layer lying internal to the exine.

Waxy coating (cutinization of exine) makes the pollen more or less water proof. Sporopollenin is resistant to physical and biological decomposition and due to this property the pollen grain walls are often preserved for long periods in fossil deposits. The pollen wall also protects pollen during its journey from anther to the stigma. At one or more places exine is lacking. These areas are known as germ pores/slits. If they are round in appearance then we call them germ pores, if they seems elongated then termed as germinal furrows. Pollen grains are generally tricolpate (with three germ pores) in dicots and monocolpate (with single germinal furrow) in monocots. Germ pore facilitate the emergence of pollen tube through it at the time of male gametophyte development **(Figure 3.11)**.

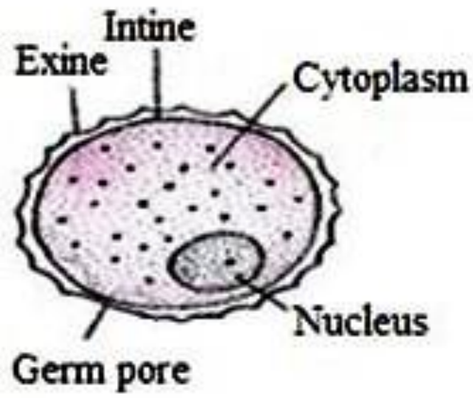


Figure 3.11: Uninucleate pollen grain

Pollenkitt

It is an oily layer forming a thick viscous coating over the pollen grain surface of many insect pollinated species. The stickiness, odour and colour of the grains are because of the pollenkitt. It comprises mainly of carotenoid or flavonoid pigments which impart the characteristic yellow or orange colour to the pollen. The pollenkitt or the surface pollen cement also contains glycoproteins, lipids, glycolipids and monosaccharides which are responsible for sticky nature of the pollen. Pollenkitt is believed that it may be contributing in the following ways:

- Acting as insect-attractant.
- Protecting the pollen against the damaging effect of ultraviolet radiation.
- Acting as an adherent to the insect body because of the sticky nature.
- Being hydrophobic, it might even be associated with the dispersal of pollen.
- Functioning as the pollen-borne substances involved in sporophytic incompatibility.

The development of the male gametophyte is remarkably uniform in angiosperms. Microspore is the first cell of a male gametophyte. This cell undergoes only two divisions. The second division is concerned with generative cell only and this division may take place either in the pollen grain or in the pollen tube. The life of the male gametophyte is very short as compared to that of the sporophyte.

Pre-pollination development

Pollen grains begin to germinate before pollination.

A pollen grain divides mitotically (first division) to form two unequal cells, a smaller generative cell and a larger vegetative cell (also known as tube cell) **(Figure 3.12)**.

Pollen grain

1st mitotic division

Larger vegetative cell (tube cell) Smaller generative cell

The nuclei of both the cells differ in size and structure. The vegetative cell has a prominent nucleus, cytoplasm is rich in RNA whereas generative cell nucleus is small, cytoplasm is almost without RNA.

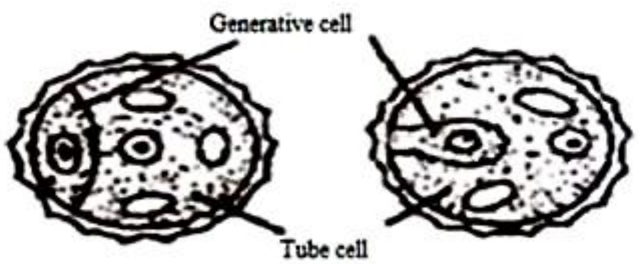


Figure 3.12: Pollen grain at 2-celled stage having generative cell and tube cell

Larger vegetative cell is central and the generative cell is peripheral in position, initially attached to the intine but later gets detached from it and lies free in the cytoplasm of the vegetative cell (tube cell). At this stage the pollen grain become two celled.

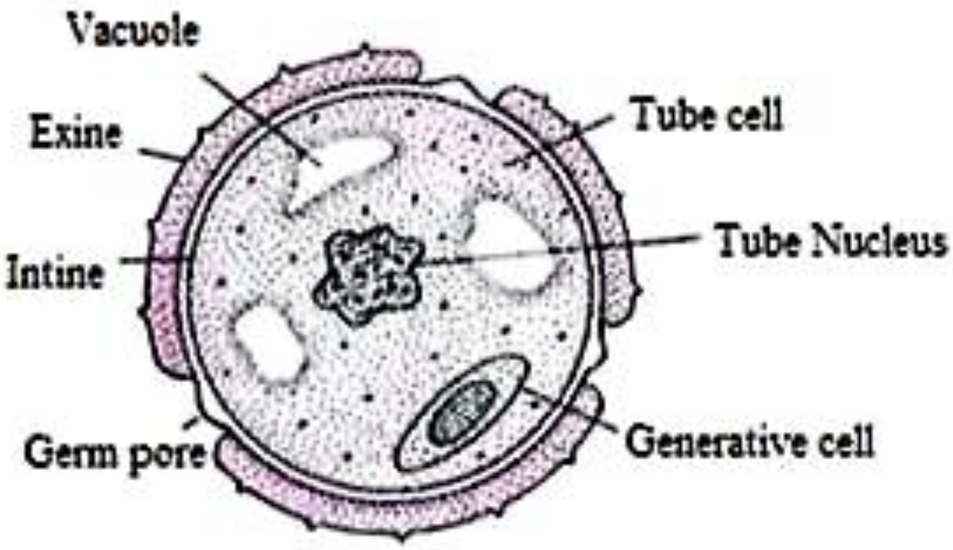


Figure 3.13: Mature 2-celled pollen grain showing generative cell lies free in the cytoplasm of the vegetative cell (tube cell)

In over 60% of flowering plants, mostly dicots, pollen grains are shed from the microsporangium at 2-celled stage (tube cell + generative cell) for pollination. Generative cell divides after pollination and in the remaining species, pollen grains are shed at 3-celled stage (tube cell + two male gametes). Generative cell divides before pollination **(Figure 3.13)**.

- When the sperm (gamete) formation takes place after the release of pollen from the anther, it is called 'the pollens are shed at the 2-celled stage' and
- When the sperm (gamete) formation takes place while the pollens are still confined to the anther, it is called 'the pollens are shed at the 3-celled stage'.

Post-Pollination development

Once the pollen grain reaches the receptive stigma by means of pollination, it germinates. On the stigma the compatible pollen grain absorbs water and nutrients from the stigmatic secretion through its germ pores. The tube or vegetative cell enlarges and forms a long slender pollen tube by coming out of the pollen grain through one of the germ pores. It secretes pectinase and other hydrolytic enzymes to create a passage for it in the style if the latter is solid. The pollen tube absorbs nourishment from the cells of the style for its growth.

As the pollen germinates and the pollen tube comes out through the germ pore, the generative cell soon divides mitotically for the second time to form two non-motile sperms (male gametes). This act is known as spermatogenesis. The generative cell or its products, i.e. two male gametes and the tube nucleus migrate into the pollen tube which now represents the mature male gametophyte **(Figure 3.14)**.

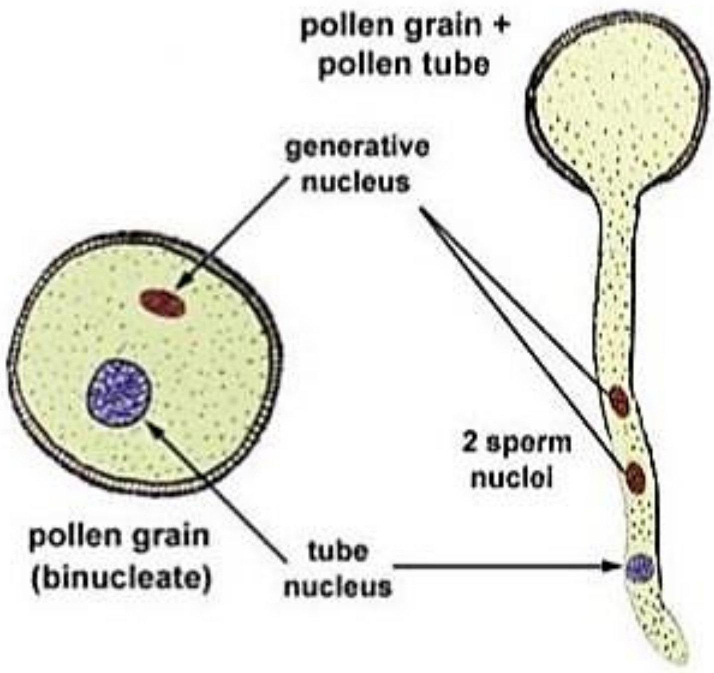


Figure 3.14: Formation of pollen tube and two male gametes

The generative cell or its products i.e. two male gametes and the tube nucleus migrate into the pollen tube which now represents the mature male gametophyte. Each male gamete has a large nucleus which is surrounded by a thin sheath of cytoplasm. The tube nucleus may degenerate completely. Pollen tube not only carries male gametes but also secretes hormones and absorbs food from style **(Figure 3.15)**.

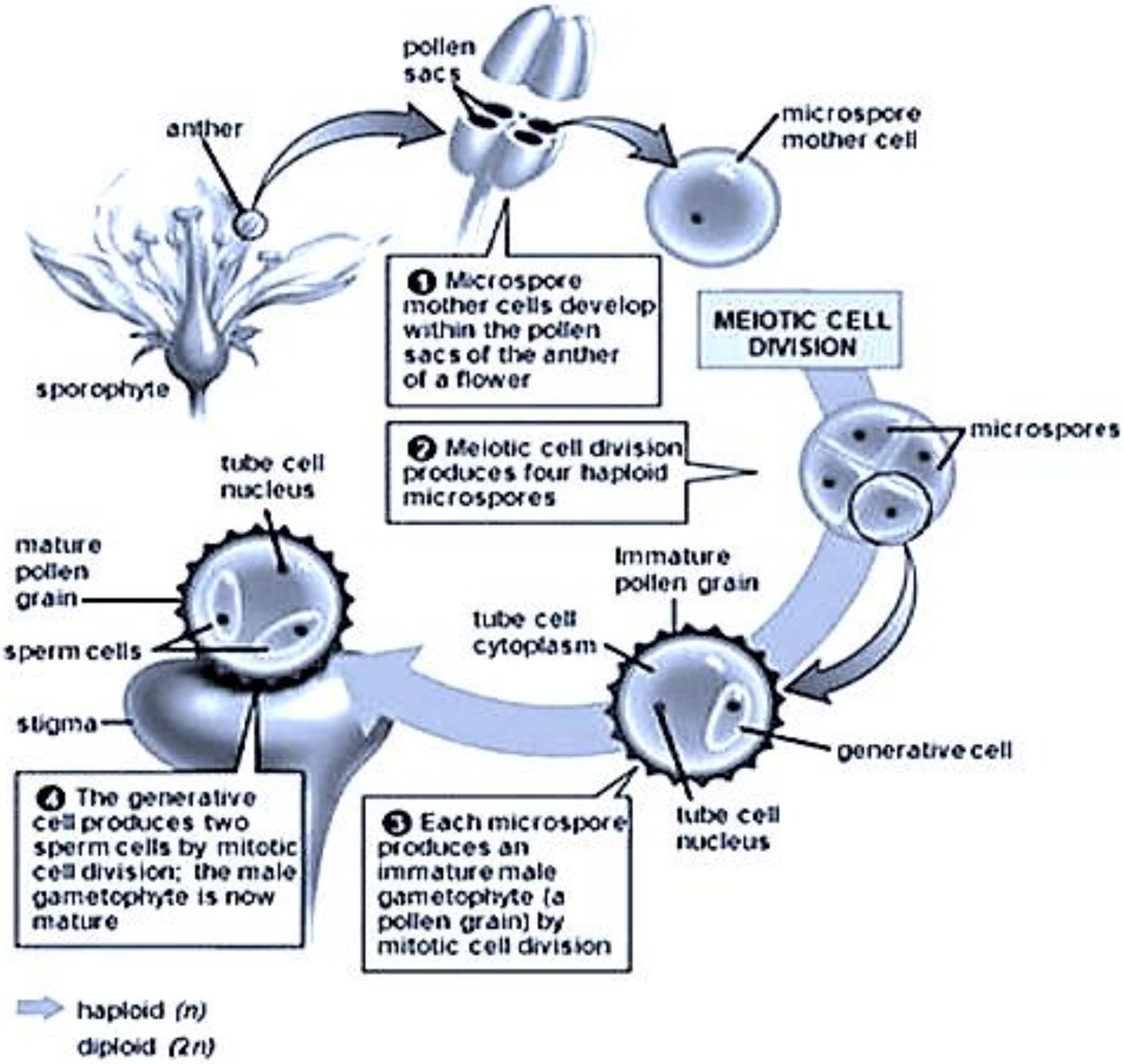


Figure 3.15: showing male gametophyte development

Palynology

The study of external morphological features of mature pollen grain is known as palynology.

Pollination

It is the process of pollen transfer from anther to stigma of a flower. Therefore, for pollination the first and very important requirement is the release of pollen grains from the pollen chamber and for releasing pollens anther must dehisce.

SAQ.4

a. Process of development of male gametophyte is known as______________.

b. The term exine and intine were proposed by_____________.

c. The exine is composed of a complex substance, called____________.

d. _________is the first cell of a male gametophyte.

e. The process of pollen transfer from anther to stigma of a flower is known as____________.

Anther dehiscence

For dehiscence of anther three types of specialized cells are required- stomium, septum and endothecium. The opening through which the pollen grains are discharged from the pollen sac is called stomium. The septum, that separates the two lobes of an anther, breaks down at a later stage. The cells of endothecium are thin walled along the line of dehiscence of each anther lobe. On maturity of the anther, a strain is exerted on the stomium due to the loss of water by the cells of endothecium, with the result the stomium ruptures and the anther dehisces. Mature anther, generally dehisces by means of slit or apical pores.

3.5 Summary

After studying this unit, you have learnt that:

- Gametophyte is the haploid generation producing gametes in plants.
- When we are talking about male then it is said to be male gametophyte.
- Male and female reproductive organs in plants are stamen and carpel, the necessary parts of flower.
- The male spores or microspores (pollens) are developed by reduction division or meiosis within the microsporangium (pollen sac).
- Numerous microspore mother cells are formed in the anther lobe.
- Each mother cell undergoes meiosis or reduction division to form four microspores (pollen grains).
- Microspores thus formed are held together in tetrad.

- The process of development of the microspore (pollen) is termed microsporogenesis.
- On the basis of arrangement of four microspores in a tetrad, there are mainly five types of tetrad. They are: tetrahedral, isobilateral, T-shaped, linear and decussate.
- Each pollen grain has two layers, outer thick, rough exine and inner thin intine having germ pores.
- The pollen grain or microspore is the first cell (mother cell) of the male gametophyte.
- It divides to form two unequal cells, a smaller generative cell and a larger vegetative cell ((tube cell).
- The generative cell further divides mitotically to form two non-motile male gametes whereas tube cell forms pollen tube.
- The pollen grain having male gametes with pollen tube represents the mature male gametophyte.
- Male gametophyte is endosporous i.e. developing inside the spores.
- In some plants gamete formation takes place after the release of pollen from the anther, it is called "the pollens are shed at the 2-celled stage".
- In some plants gamete formation takes place while the pollen are still confined to the anther, it is called "the pollens are shed at the 3-celled stage".
- At maturity, pollen grains released and through various agents i.e. wind, water, animal etc. reach the compatible stigma (either of the same flower or another). This is known as pollination.

3.6 Terminal Question

Q.1 What is the region behind this statement that "Pollen grain walls are often preserved for long periods in fossil deposits".

Answer:---

Q.2 What do you understand by the term Pollinium?.

Answer:---

Q.3 What is the main function of germ pores in pollen grains.

Answer:--

Q.4 What kind of enzyme, pollen tube secretes?

Answer:--

Q.5 What do you mean by pollen grains are shed at 2-celled stage or 3-celled stage?

Answer:--

Short Questions

Q.6 Write short notes on:

1. Gametogenesis.
2. Endothecium
3. Difference between microspore and pollen
4. Different types of tetrad.
5. Chemical nature of two layers of microspore

Q.7 Multiple choice questions:

1. Microspore develops into a:
   (a) Polar nuclei
   (b) Female gametophyte
   (c) Male gametophyte
   (d) Embryo
2. The site of formation of pollen grains is in the:
   (a) Pistil
   (b) Petal
   (c) Stamen

(d) Stigma

3. A microspore mother cell is located in the:

   (a) Anther

   (b) Filament

   (c) Style

   (d) Stigma

4. Pollen grains are tricolpate, if they have:

   (a) Three germ pores

   (b) Two germ pores

   (c) One germ pore

   (d) Many germ pores

5. Pollen grains are shed at 2-celled stage, represented by:

   (a) Tube cell + vegetative cell

   (b) Tube cell + generative cell

   (c) Tube cell + male gamete

   (d) None

3.7Answers

Q. No. 7 1. (c)2. (c) 3. (a) 4. (a) 5. (b)

SAQ.1

a. Single**b.** Diploid, haploid**c.** Haploid spores**d.**Embryosac**e.**Dithecous

SAQ.2

a. Stomium**b.** Tapetum**c.** Male gametophyte **d.**Four**e.**Microspore mother cell

SAQ.3

a. Microsporogenesis**b.** Four **c.** Isobilateral **d.** Five **e.**Pollinium

SAQ.4

a. Gametogenesis **b.** Fritsch (1837) **c.** Sporopollenin**d.** Microspore **e.** Pollination

Unit- IV

Megasporogenesis

Structure

4.1 Introduction

Life cycle of plants alternate between multicellular haploid gametophyte and multicellular diploid sporophyte and both differ morphologically as well as functionally. According to Gifford and Foster (1989), in a life cycle of a plant:

- Diploid sporophyte produces haploid spores as a result of reduction division (meiosis).
- Spores develop into gametophytes.
- Gametophytes produce haploid gametes.
- The fusion of female gamete (egg) and male gamete gives rise to the zygote.
- Zygote is the beginning of diploid sporophyte.

When we are talking about the life cycle of Angiosperms:

- Diploid sporophyte produces two types of spores- microspores and megaspores.
- Microspore develops into male gametophyte as discussed in previous unit and megaspore produces female gametophyte which we will study in this unit. In the previous unit you have studied about the structure of anther, microsporogenesis as well as the development of male gametophyte in Angiosperms. By going through that unit it must be clear to you that the pollens or microspores are developed by reduction division or meiosis in microspore mother cell within the microsporangium and they represent the first cell of male gametophyte.

The gametophyte in angiosperms develops within sporophytic tissue –the sexual organs of the flower. The male gametophyte (developing pollen grain composed of two sperm cells encased within a vegetative cell) develops within the anther, fertile part of the stamen. The female gametophyte (embryo sac) develops within the ovule which is found within the ovary.

In this unit we describe structure and types of ovule, megasporogenesis, megagametogenesis and different types of female gametophytes.

Gynoecium or pistil represents the female reproductive organ in a flower and carpel is a unit of it. A carpel consists of a basal swollen ovary bearing one or more ovules, a receptive stigma, and often a stalk-like style between them**(Figure 4.1)**.

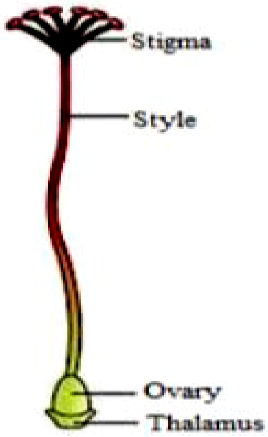


Figure 4.1 Gynoecium

Ovules as you have read, are enclosed by the ovary wall. The part of the carpellary tissue to which the ovules are attached is called placenta and the distribution of ovules in the ovary is described as placentation.

Ovule also known as megasporangium is the place of formation of the megaspores and the female gametophyte. The latter, after fertilization produces the embryo and endosperm, while the entire megasporangium with its enclosed structure becomes the seed and the progenitor of the next generation.

Objectives

After studying this unit, you will be able:

- To study the structure and types of ovule.
- To know about megasporogenesis.
- To understand female gametophyte formation.
- To classify as monosporic, bisporic or tetrasporic.

- To explain Polygonum type of embryo sac.

4.2 Structure of ovule

The **megasporangium** or **ovule** consists of nucellus and its protective coats, the integuments. It is attached to the placenta, on the inner wall of ovary by a stalk called funiculus (funicle) and the point of attachment of the body of the ovule to the funiculus is called hilum.

A mature ovule, ready for fertilization, consists of nucellus enveloped almost completely by one or two sheaths, known as integuments, leaving a small opening at the apical end. This opening is known as micropyle. The basal region of the ovule where it is attached to the placenta by funicle, is called chalaza and so this side is known as chalazal end. Its opposite end is termed as micropylar end, the main passage for the entry of the pollen tube into the ovule. In the nucellus, female gametophyte is present, also known as embryo sac.

Nucellar tissue is parenchymatous and represents the wall of the megasporangium. The nucellus is mostly consumed by the developing embryo sac or endosperm. Each ovule has only one nucellus. However, two nuclei may occur as abnormality within a common fold of integuments as has been observed in *Aegle marmelos* **(Figure 4.2)**.

The ovule with a single integument is called unitegmic, with two integuments is called bitegmic and without integument is called ategmic.

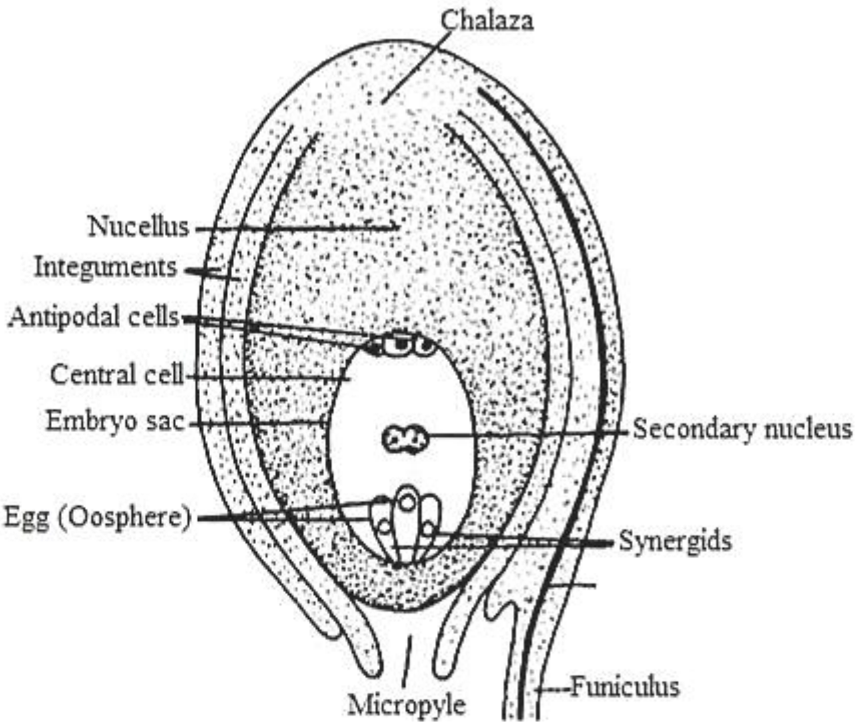


Figure 4.2 Structure of ovule

<u>Parts of the ovule</u>

1. Funiculus or Funicle: A stalk by which ovule is attached to the placenta.

2. Nucellus: the body of ovule.

3. Integument: the protective covering of nucellus.

4. Micropyle: small opening formed by two integuments over nucellus.

5. Chalaza: basal part of the ovule.

6. Hilum: region where ovule fuses with funiculus.

7. Embryo sac: female gametophyte located in the nucellus, developed from megaspore.

<u>Types of ovule</u>

On the basis of the position of the micropyle with respect to the funiculus, mature ovule can be classified into six main types. These are:

1. Orthotropous
2. Anatropous
3. Campylotropous
4. Amphitropous
5. Hemianatropous
6. Circinotropous

1. Orthotropous ovule: Orthotropous ovule is also known as atropous. It is upright. In this type the micropyle, chalaza and the funiculus lie in one straight line as in Polygonaceae and Piperaceae **(Figure 4.3)**.

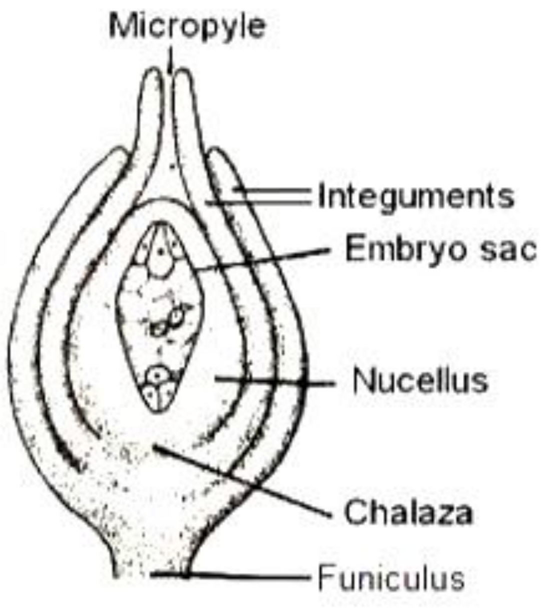


Figure 4.3 Orthotropous ovule

2. Anatropous ovule: In this type, the funiculus is long; the body of the ovule becomes completely inverted so that micropyle comes to lie close to the base of the funiculus. This happens due to unilateral growth of the ovule. The nucellus remains straight so micropyle and chalaza lie in one line and funiculus lie parallel to it. It is the most common type of ovule in Angiosperms **(Figure 4.4)**.

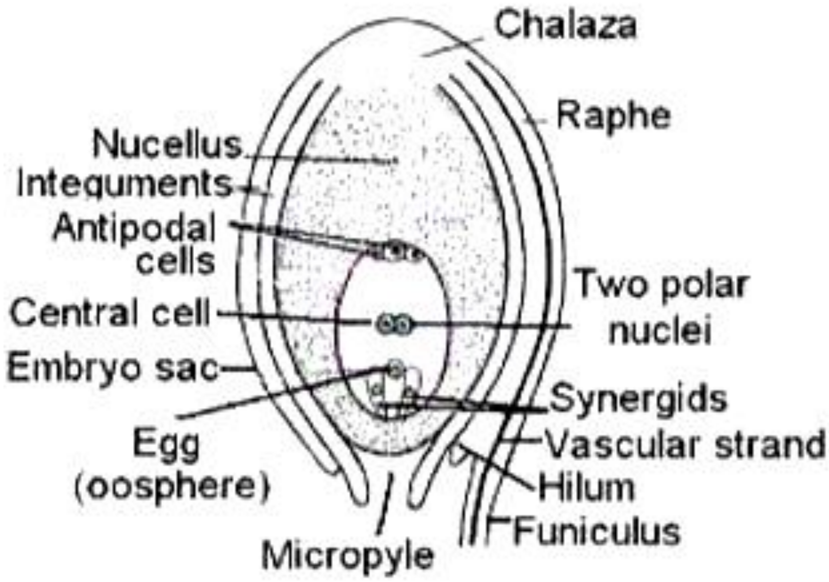


Figure 4.4 Anatropous ovule

3. Campylotropous ovule: In campylotropous ovules body of the ovule is not completely inverted, the curvature is less than that in anatropous ovules. The micropyle and chalaza do not lie in the straight line and the funiculus lies at right angle to the chalaza as in Chenopodiaceae and Capparaceae**(Figure 4.5)**.

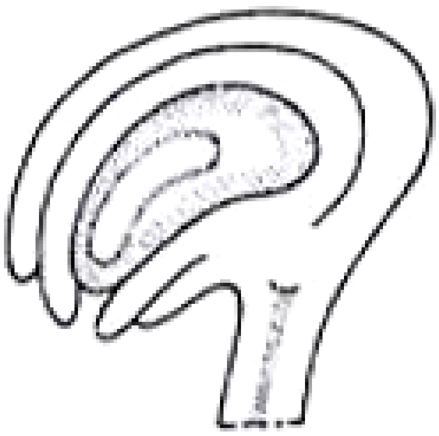


Figure 4.5 Campylotropous ovule

4. Amphitropous ovule: It is similar to campylotropous, but in this case the curvature of the ovule also affects the nucellus/embryo-sac so that it bent like 'horse shoe' as in Alismaceae and Butomaceae**(Figure 4.6)**.

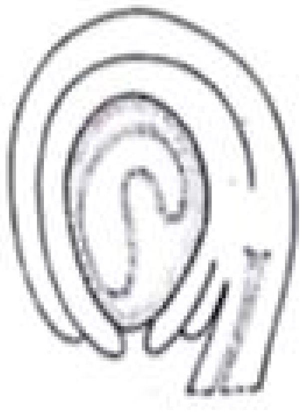


Figure 4.6 Amphitropous ovule

5. Hemianatropous ovule: Also known as hemitropous. In this type of ovule the funiculus is at right angle to the nucellus and the integuments. Micropyle and chalaza, lie in the same plane as in *Ranunculus, Nothoscordum,* and *Tulbaghia***(Figure 4.7)**.

Figure 4.7 Hemianatropous ovule

6. Circinotropous ovule: A very peculiar type of ovule is seen in some members of the Plumbaginaceae. Here the nucellar protuberance is at first in the same line as the axis, but the rapid growth on one side causes it to become anatropous. The curvature does not stop but continues until the ovule has turned over completely so that the micropylar end again points upwards. It has been suggested that this kind of ovule, also seen in *Opuntia*, is distinctive enough to merit a separate name, Circinotropous**(Figure 4.8)**.

Figure 4.8 Circinotropous ovule

Depending on the extent of development of the nucellus and on the basis of position of sporogenous cell, ovule can also be categorized as:

1. Tenuinucellate type **2.** Crassinucellate type

1. Tenuinucellate type: The archesporial cell directly functions as the megaspore mother cell so that the sporogenous cell is also hypodermal. Such ovules, where the sporogenous cell is hypodermal and the nucellar tissue around it remains single-layered, are called tenuinucellate.

2. Crassinucellate type: The hypodermal archesporial cell divides transversely, forming outer parietal cell and an inner sporogenous cell. The parietal cell may either remain undivided or undergo a few divisions (both periclinal as well as anticlinal) so that the sporogenous cell becomes embedded in the massive nucellus. The sporogenous cell may be embedded in the massive nucellus by divisions in the nucellar epidermis. All such ovules where the sporogenous cell becomes subhypodermal, by either above two means, are called crassinucellate.

> **Tenuinucellate ovule:** where the sporogenous cell is hypodermal and the nucellar tissue around it remains single layered
> **Crassinucellate ovule:** where the sporogenous cell becomes subhypodermal, either due to formation of parietal cells, or due to divisions in the nucellar epidermis, or both

Development of ovule

The ovule at first arises as a primordium on the placenta in the cavity of the ovary. Later due to meristematic activity of the cells of ovular primordia, the protuberance become prominent and grows into a mass of tissue, the nucellus. The initials of two integuments arise at the base of the nucellus. The inner integument which is usually formed first, initiates from the epidermal layer and the outer integument is initiated either dermally or sub-epidermally.

With the differentiation of integuments, the ovule begins to curve and by the megaspore tetrad stage it assumes its final shape. Although the integuments initiate later they grow faster than the nucellus. The integuments soon cover the nucellus, leaving a small opening at the tip, the micropyle.

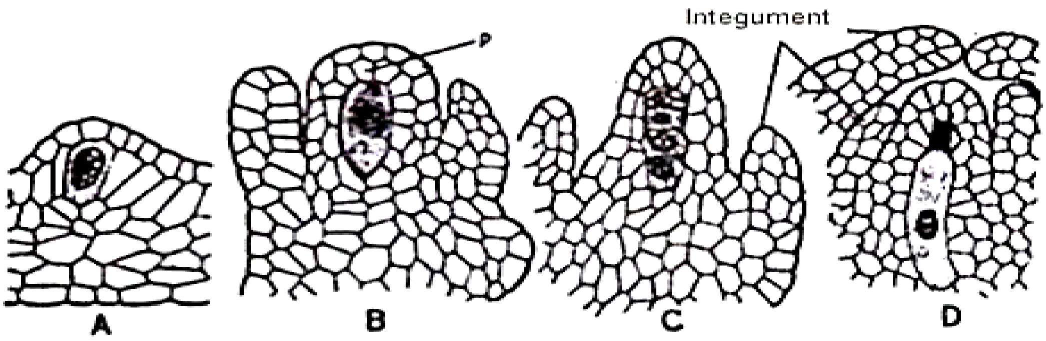


Figure 4.9 Stages of ovule development and megasporogenesis.A. Protuberance of placental tissue and differentiation of archesporium (shaded); **B.** Parietal cells and megaspore mother cell (shaded). One integument is developing; **C.** Linear tetrad of megaspores (shaded); **D.** Disintegration of the three upper megaspores and enlargement of the functional megaspore. Both integuments have developed.

Female gametophyte development occurs in two phases:

1.Megasporogenesis

2.Megagametogenesis

The developmental pattern exhibited by most species is referred to as the *Polygonum* type because it was first described in *Polygonumdivaricatum*

SAQ.1

---

a. The part of the carpellary tissue to which the ovules are attached is called_____________ and the distribution of ovules in the ovary is described as_________.

b. Nucellar tissue is parenchymatous and represents the wall of the________________.

c. A stalk by which ovule is attached to the placenta called as___________.

d. In hemianatropous ovule, the funiculus is at___________to the nucellus and the integuments.

e. In___________ovule, the sporogenous cell is hypodermal and the nucellar tissue around it remains single layered.

4.3 Megasporogenesis

"Development of the megaspore within the ovule (megasporangium) is known as megasporogenesis."

A hypodermal cell in the nucellus (at the micropylar end) differentiates and functions as the archesporium (archesporial cell). It is distinguishable from the other cells as it becomes more prominent than its surrounding cells due to its large size, dense cytoplasm and large nucleus.

As it is now clear to you from the previous section that ovule can be categorized into two types (tenuinucellate and crassinucellate), on the basis of position of sporogenous cell. So here in tenuinucellate type of ovule, the archesporial cell directly functions as megaspore mother cell (MMC) and in crassinucellate type of ovule the archesporial cell do not directly behave as MMC and instead of that it divides periclinally into two cells. An outer primary parietal cell (towards epidermis) and an inner primary sporogenous cell. Now this primary sporogenous cell functions as the megaspore mother cell.

Megaspore mother cell is also known as megasporocyte having diploid (2n) chromosome number. It undergoes meiosis i.e. reduction division. As a result of this four haploid megaspores are formed. After first meiotic division, the wall is laid down transversely, forming a dyad. The second meiotic division in the two dyad cells is also transverse. In this way a row of four haploid megaspore cells (linear tetrad) is formed. Meanwhile, two integuments develop from the base of the ovule. In the linear tetrad the lowermost megaspore (the chalazal megaspore) enlarges and becomes functional. Rest three megaspores of tetrad do not participate in the formation of female gametophyte and degenerate. **(Figure 4.9, 4.10)**.

The functional megaspore now forms the female gametophyte (embryo sac). Haploid tetrad of megaspores may be T-shaped, isobilateral or tetrahedral, T-shaped tetrad arises due to vertical division in the micropylar dyad cell and transverse division in the chalazal dyad cell.

Functioning megaspore

During megasporogenesis, the diploid megaspore mother cell undergoes meiosis and gives rise to four haploid nuclei. Angiosperms exhibit three main patterns of megasporogenesis, referred to as monosporic, bisporic, and tetrasporic. The three types differ mainly in whether wall (cell plate) formation occurs after these divisions, thus determining the number of meiotic products that contribute to the formation of the mature female gametophyte. In the monosporic pattern, both meiotic divisions are accompanied by wall formation, resulting in four one-nucleate megaspores (linear tetrad). Only one becomes functional and forms the female gametophyte, Subsequently, three megaspores, generally the micropylar-most megaspores degenerates. It is the chalazal megaspore of the tetrad that is functional. Sometimes the female gametophyte (embryo sac) is formed by the micropylar megaspore as observed in Onagraceae.

In the bisporic pattern, wall forms after meiosis I but not after meiosis II. The result is two bi-nucleate megaspores (dyad cells). One of the dyad cells with two haploid megaspore nuclei contributes towards the formation of female gametophyte (embryo sac) and other dyad cell degenerates.

In the tetrasporic pattern, wall formation fails to form after both meiotic divisions, resulting in one four-nucleate megaspore. All four megaspore nuclei participate in the formation of female gametophyte (embryo sac).

Thus, these three patterns give rise to a single functional megaspore that contains one (monosporic), two (bisporic), or four (tetrasporic) meiotic nuclei.

If you remember the microsporogenesis where a haploid microspore was said to be the first cell (mother cell) of male gametophyte, similarly here a haploid megaspore is known as the first cell (mother cell) of female gametophyte.

In Angiosperms the development of the female gametophyte is completely endosporous means within the megaspore.

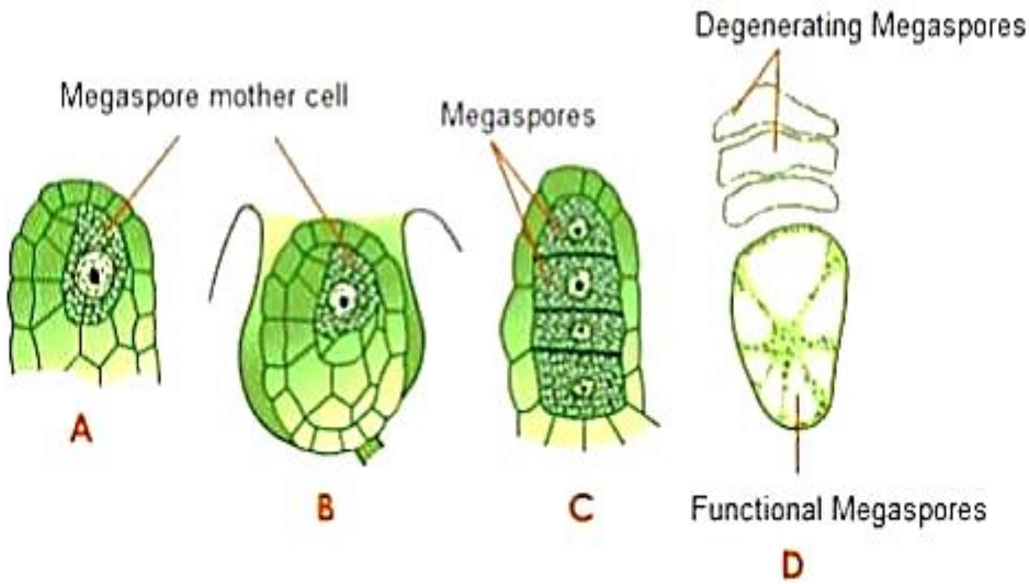


Figure 4.10: Formation of 4 haploid megaspores from diploid megaspore mother cell

4.4 Development of the female gametophyte or embryo sac with particular reference to *Polygonum*type

Megagametogenesis

During megagametogenesis, the functional megaspore gives rise to the mature female gametophyte. We have already discussed the functional megaspore is the first cell of the female gametophyte or you can also call it as the mother cell of the female gametophyte. It grows in size and forms an embryo sac.

The haploid nucleus of the megaspore divides mitotically (non-reductional division) which organize in a definite manner within the embryo sac. Three nuclei at the micropylar end, three at the chalazal end and the remaining two migrate to the centre of the embryo sac. Three nuclei at the micropylar end organize into an egg apparatus. The central large cell of the egg apparatus is called egg cell (female gamete) which is partially surrounded by two lateral synergid cells. Three nuclei of the chalazal end form antipodal cells. The two nuclei which migrates to the centre, called polar nuclei. These polar nuclei later fuse to form a single diploid secondary nucleus (a central cell).

These events result in a mature seven celled structure called female gametophyte or embryo sac consisting of three antipodal cells, one central cell having two polar nuclei, two synergid cells, and one egg cell. Since, this type of embryo sac develops from a single megaspore and has eight nuclei, it is said to be monosporic eight nucleate embryo sac or Polygonum type of embryo sac. Throughout the development, the female gametophyte exhibits a polarity along its chalazal-micropylar axis.

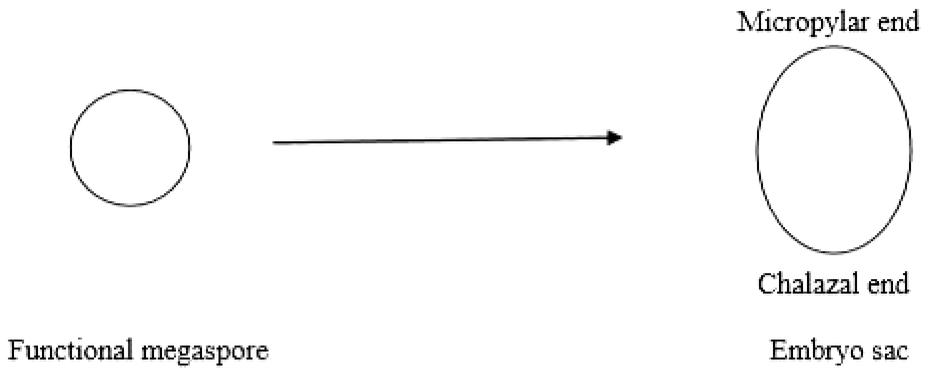
So in a nutshell:

- *Polygonum* type is a monosporic eight nucleate, 7-celled embryo sac formed as a result of three divisions in functional megaspore.
- Cells of the egg apparatus and the antipodal cells are uninucleate and haploids whereas the central cell is binucleate or diploid.

It is the most common type of embryo sac and is found in about 81% flowering plants.

Steps of development of the female gametophyte or embryo sac with particular reference to *Polygonum* type:

The development of embryo sac begins as the functional megaspore elongates. You know that in most cases the lowermost megaspore (chalazal) of the linear tetrad becomes functional and rest three degenerates. The elongation is largely along the micropylar-chalazal axis.



The first nuclear division (post- meiotic mitosis) in the megaspore is not followed by wall formation. A large central vacuole appears between the two daughter nuclei. Initially there is no vacuole in the cytoplasm of the megaspore but later small vacuoles appear which may fuse to form large vacuole. As the vacuole expands, the nuclei pushed toward opposite poles of the cell. In this way each pole has one nucleus. Now both the nuclei divide twice, forming four nuclei at each pole. All the divisions are mitotic and without wall formation.

At this stage all the eight nuclei are present in the common cytoplasm because after haploid megaspore formation all the nuclear divisions are not followed by cell wall formation. After the last nuclear division (when there are eight nuclei) the cell undergoes appreciable elongation, so that it looks like sac. The picture must be clear in your mind that out of these eight nuclei, four are at the micropylar end and four at the chalazal end **(Figure 4.11)**.

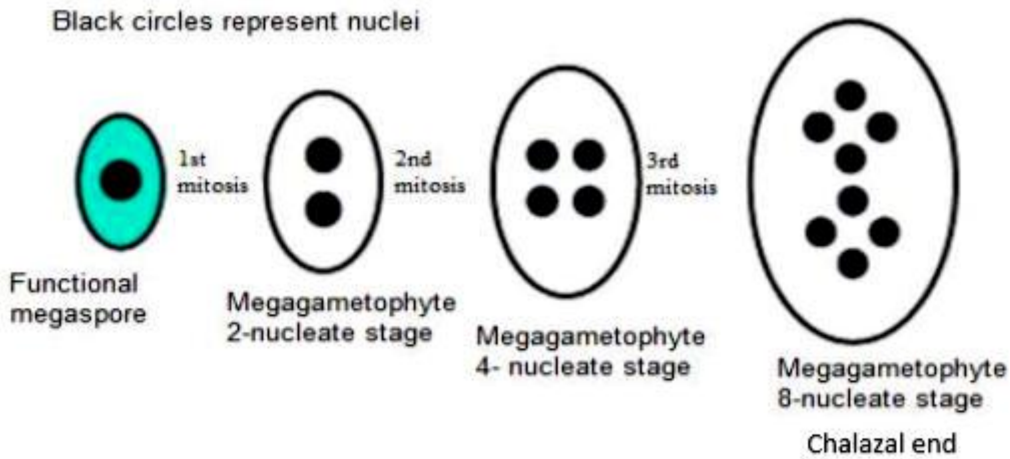


Figure 4.11: Development of embryo sac up to 8-nucleate stage

Finally, the embryo sac becomes organized. Three nuclei at the micropylar end of the embryo sac organize into egg apparatus and the fourth one is left free in the cytoplasm of the central cell and moves toward the centre as the upper polar nucleus. The egg apparatus (only upper portion) is attached to the wall of the embryo sac at the micropylar end, its major portion is surrounded by the central cell. In the egg apparatus the centre cell is egg cell (round, also known as ovum or oosphere) and the rest two side cells are synergids which are flask shaped. Only the synergid cells are in direct contact with the wall of the embryo sac. The centre egg cell is situated in such a way so that its upper portion is slightly below the apices of the synergids seems hanging between and below them. All the three cells are of same length therefore the egg cell extends a little more towards the centre cell in comparison to the synergids. Out of the four nuclei at the chalazal end of the embryo sac, three nuclei forms three antipodal cells and the fourth one moves toward the centre as the lower polar nucleus.

One nucleus from each pole moves to the center of the embryo sac, here they may fuse forming the fusion or secondary nucleus. The secondary nucleus (if fusion occurred between two polar nuclei) or two polar nuclei (if there is no fusion) remains at the center. **(Figure 4.12, 4.13)**.

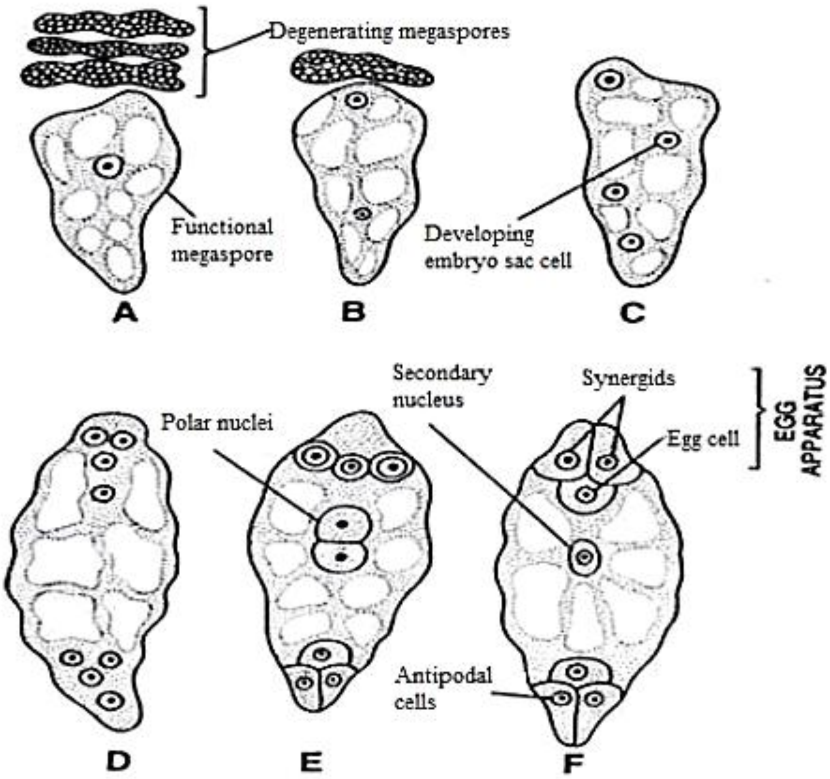


Figure 4.12: Female gametophyte.A-F: development of the embryo sac (Female gametophyte) of normal type (*Polygonum* type)

The female gametophyte (embryo sac) is 7-celled (mostly), 8-nucleate structure having three cells of egg apparatus (two synergid cells and one egg cell) at the micropylar end, three cells (antipodal cells) at the chalazal end and one cell (centre cell) in the centre having two polar nuclei.

- This type of embryo sac is designated as the *Polygonum* type.
- This mode of embryo sac development occurs in the majority of flowering plants. According to Davis (1966), about 81 per cent of the families show *Polygonum* type of embryo sac development.
- Two polar nuclei later fuse to form the secondary nucleus so you can also say that the central cell is binucleate or diploid and the antipodal cells and cells of the egg apparatus are uninucleate and haploid.

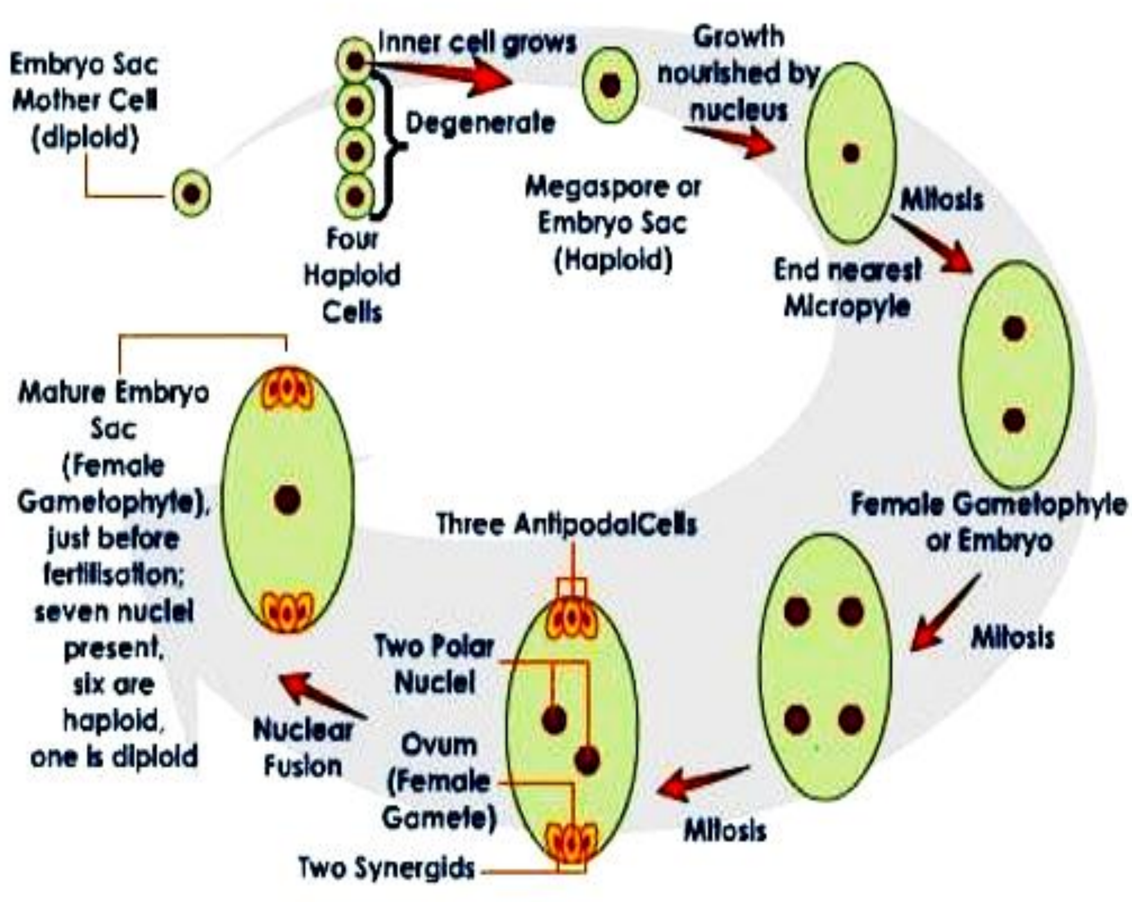


Figure 4.13: Diagrammatic representation of embryo sac development in Angiosperms

SAQ.2

a. Megaspore mother cell is also known as____________having diploid (2n) chromosome number.

b. In the____________pattern, wall forms after meiosis I but not after meiosis II.

c. In Angiosperms the development of the female gametophyte is completely_________.

d. _____________type is a monosporic eight nucleate, 7-celled embryo sac.

e. Cells of the egg apparatus and the antipodal cells are___________and haploids whereas the central cell is___________.

Types of embryo sac

The *Polygonum* type of embryo sac as described above is formed from one of the four haploid megaspore nuclei which in turn formed from diploid megaspore mother cell as a result of meiosis. Although it is the most common type of mode of embryo sac development in angiosperms, even there is a substantial number of plants where more than one megaspore nuclei take part in the process.

Therefore, depending on the basis of involvement of number of megaspore nuclei in its formation, the embryo sac can be of different types:

1.Monosporic

2.Bisporic

3.Tetrasporic

1. Monosporic Embryo sac:

Monosporic embryo sac is the one where only one of the four megaspores take part in its formation as in the *Polygonum* type. Three of the megaspores, usually those which are at micropylar end, degenerate, leaving only one functional megaspore. In this type of embryo sac all the nuclei are genetically identical because they are formed through mitosis of a single nucleus. Monosporic embryo sacs are further divided into two types.

1.*Polygonum* type (8 -nucleate)

2.*Oenothera* type (4- nucleate)

1. *Polygonum* type (8-nucleate): As described earlier, it is formed by the chalazal megaspore of the tetrad and is eight nucleate. A mature *Polygonum* type of embryo sac comprises a 3-celled egg apparatus, three antipodal cells and a binucleate central cell **(Figure 4.14)**.

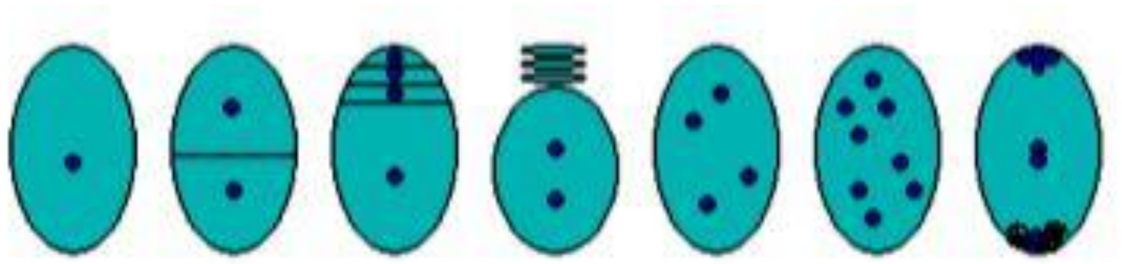


Figure 4.14: Polygonum type embryo sac

This type of embryo sac is the most common and is, therefore, commonly designated as the "Normal type." However, it is also designated as the Polygonum type because it was reported for the first time in *Polygonumdivaricatum* by Strasburger (1879).

2. *Oenothera* type (4-nucleate):*Oenothera* type of embryo sac is derived from the micropylar megaspore of the tetrad and is four nucleate. The mature embryo sac consists of an egg apparatus and a uninucleate central cell. *Oenothera* type of embryo sac is found in Onagraceae family **(Figure 4.15)**.

Geert (1908) found that in *Oenotheralamarckiana* the embryo sac is usually formed by the micropylar megaspore of the tetrad, which undergoes only two nuclear divisions instead of the usual three occurring in the *Polygonum*type of embryo sac. In this way, 4 nuclei are produced which organize into the two synergids, the egg and a single polar nucleus. Since the third division is omitted and all the nuclei are situated in the micropylar part of the developing embryo sac, there is neither a lower polar nucleus nor any antipodal cells.

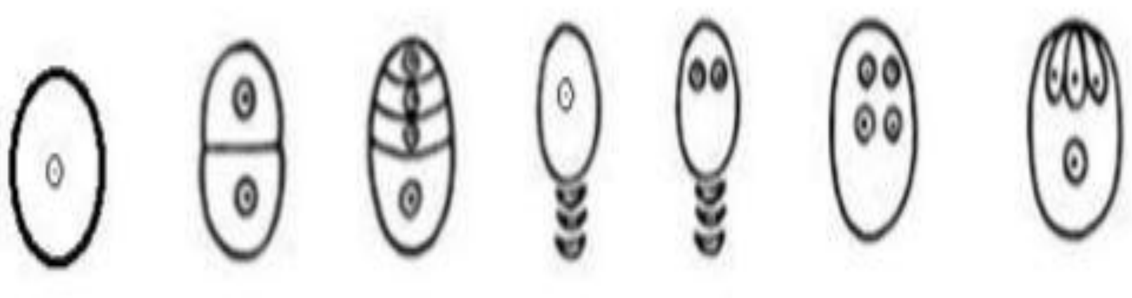


Figure 4.15: Oenothera type

4.5 Comparison with bisporic and tetrasporic types

Bisporic embryo sac

In this type of embryo sac as the name indicates two megaspore nuclei participate in its formation. After first meiotic division a dyad is formed by wall formation. Only one of the dyad cells undergoes the second meiotic division and the other one, near to micropyle, degenerates. In the functional dyad cell division is not followed by wall formation and so both the megaspore nuclei participate in the formation of the embryo sac. Each megaspore nucleus undergoes two mitotic divisions forming eight nuclei and mature embryo sac has the same organization like that of the *Polygonum* type.

So you can say the bisporic embryo sacs are 8- nucleate and arise from one of the two dyad cells formed after meiosis I.

Tetrad formed as a result of meiosis in MMC, has four genetically different nuclei. Being a derivative of two meiotic products, nuclei of a bisporic embryo sac are genetically different (four nuclei are of one type and other four of a different type).

A bisporic embryo sac was first described in *Allium fistulosum* (Strasburger, 1879) and has since been confirmed in several species of this genus.

Bisporic embryo sacs are also of two types:

1. Allium type

2. Endymion type

1. Allium type (8-nucleate): In this type chalazal dyad cell participates in the formation of the embryo sac **(Figure 4.16)**.

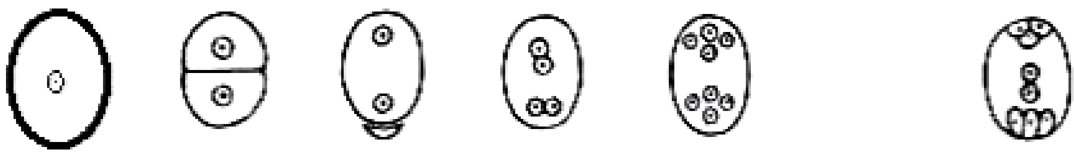


Figure 4.16: Allium type

2. Endymion type: In this type micropylar dyad cell participates in the formation of the embryo sac **(Figure 4.17)**.

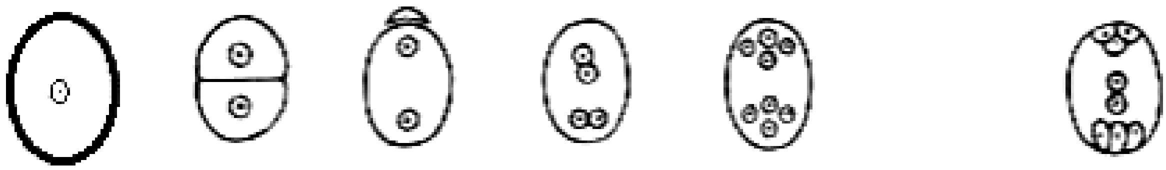


Figure 4.17: Endymion type

Tetrasporic embryo sac

When four megaspores take part in the formation of the embryo sac, it is called tetrasporic embryo sac. In this type neither of the meiotic division (first as well as second) is accompanied by wall formation so that at the end of meiosis all the four haploid nuclei remain in a common cytoplasm forming a coenomegaspore (four nuclei inside a cell) and all the four nuclei of the coenomegaspore take part in the formation of embryo sac. This type of embryo sac is more heterogenous than a bisporic one because all the four nuclei of the coenomegaspore, products of meiosis are genetically different.

Peperomia type: Campbell and Johnson reported that in *Peperomiapellucida* each of the 4 megaspore nuclei divides twice, resulting in a total of 16 nuclei which become more or less uniformly distributed in the rather thick layer of cytoplasm lying at the periphery of the embryo sac **(Figure 4.18)**.

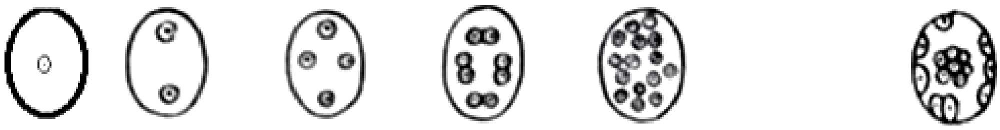


Figure 4.18: Peperomia type

According to P. Maheshwari, they are of 7 types, which are as follows:

1.Adoxa type

2.Penaea type

3.Plumbago type

4.Peperomia type

5.Drusa type

6.Fritillaria type

7.Plumbagella type

- Monosporic embryo sac: embryo sac developed from one functional megaspore.
- Bisporic embryo sac: embryo sac developed from two functional megaspore nuclei.
- Tetrasporic embryo sac: MMC by meiosis forms four haploid daughter nuclei. No wall formation is there between these four nuclei and all four nuclei participate in the formation of embryo sac.
- All three patterns give rise to a single functional megaspore that contains either one (monosporic), two (bisporic), or four (tetrasporic) haploid nuclei.
- The nuclei of the bisporic and tetrasporic embryo sacs are not genetically identical as they are in monosporic embryo sacs, because they arise from two or four different meiotic products.

SAQ.3

a. A mature *Polygonum* type of embryo sac comprises a____________egg apparatus.

b. *Oenothera* type of embryo sac is found in_____________family.

c. A_________embryo sac was first described in *Allium fistulosum.*

d. When four megaspores take part in the formation of the embryo sac, it is called___________embryo sac.

e. The nuclei of the bisporic and tetrasporic embryo sacs are not____________identical.

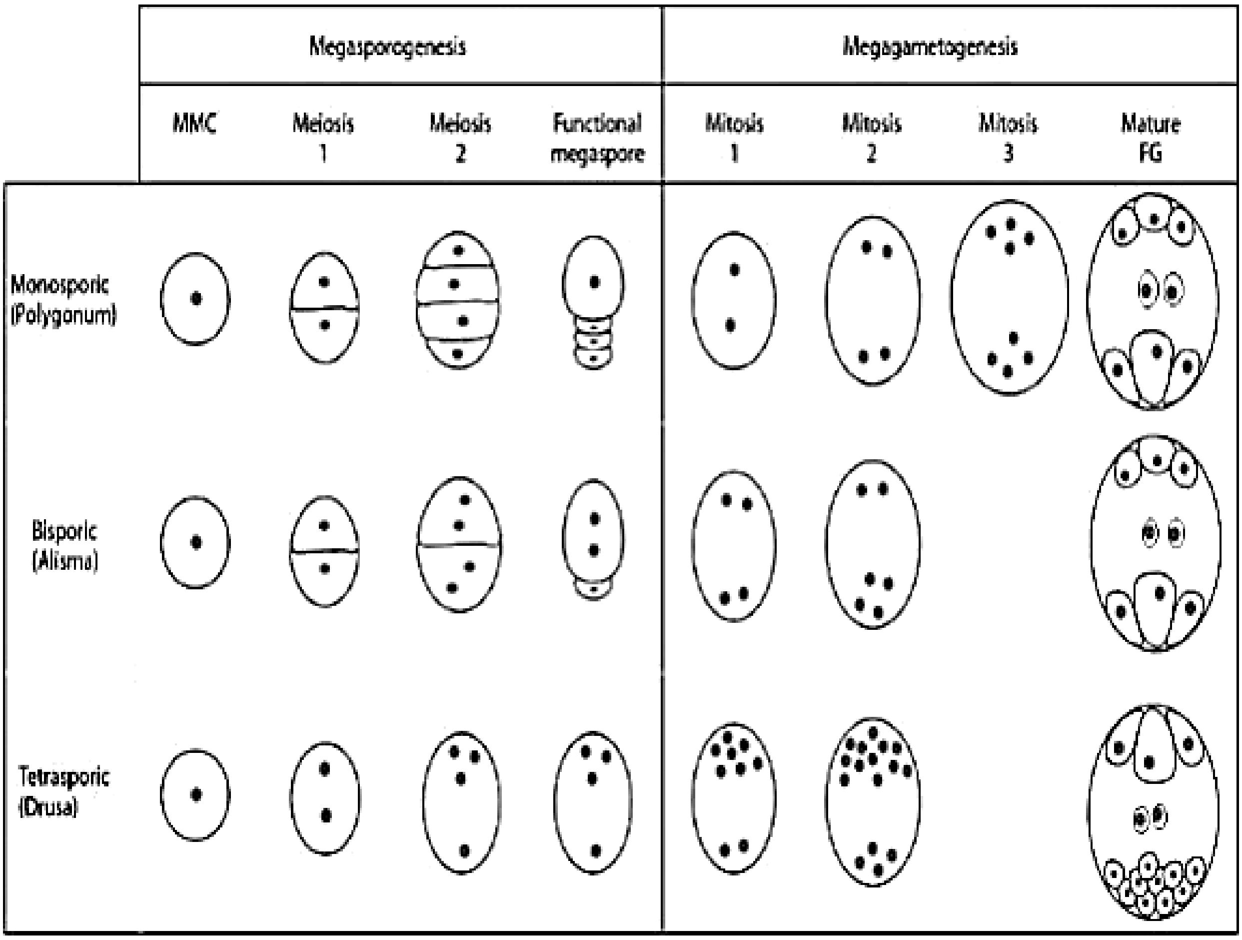


Figure 4.19: Diagrammatic representation of three main types of embryo sac development: monosporic, bisporic, tetrasporic

Organisation of mature embryo sac

The egg apparatus:

It is composed of an egg and two synergids. Usually the synergids are ephemeral structures which degenerate and disappear soon after fertilization or even before it.

The Antipodals: There are three antipodal cells.

Polar nuclei: The central portion of the embryo sac containing the polar nuclei eventually gives rise to the endosperm, called the "endosperm mother cell." The fusion of the polar nuclei may occur either before, or during, or sometimes after, the entry of the pollen tube in the embryo sac. The secondary nucleus formed after fusion usually lies just below the egg and is separated from the antipodal cells by a large vacuole.

4.6 Summary

In this unit we have discussed the structure of ovule, types of ovule on the basis of the position of the micropyle with respect to the funiculus, as well as on the basis of dependency on the extent of development of the nucellus and on the basis of position of sporogenous cell. Further development of ovule along with megasporogenesis, female gametophyte development with particular reference to Polygonum type was described. In addition to this monosporic embryo sac we have also discussed about bisporic and tetrasporic embryo sacs. Pollination and its agents were also discussed in short. Therefore, the whole unit is summarized in the following key points:

- Gametophyte is the haploid generation producing gametes in plants.
- When we are talking about female then it is said to be female gametophyte.
- The female gametophyte (embryo sac) develops within the ovule which is found within the ovary.
- A carpel consisting of a basal swollen ovary bearing one or more ovules, a receptive stigma, and often a stalk-like style between them.
- Ovule consists of nucellus surrounded by integuments.
- Ovule, on the basis of the position of the micropyle with respect to the funiculus, is of 5 types - Orthotropous, Anatropous, Campylotropous, Amphitropous, Hemianatropous.
- Ovule depending on the extent of development of the nucellus and on the basis of position of sporogenous cell, is of 2 types - tenuinucellate and crassinucellate.
- Female gametophyte (embryo sac) located in the nucellus, developed from megaspore.

- Female gametophyte development occurs in two phases - megasporogenesis and megagametogenesis
- The process of development of the megaspore is termed megasporogenesis.
- The female spores or megaspores are developed from MMC by reduction division or meiosis within the megasporangium (ovule).
- Each mother cell undergoes meiosis or reduction division to form four megaspores.
- Out of four megaspores, only one becomes functional.
- The functional megaspore now forms the female gametophyte (embryo sac).
- So megaspore is the first cell (mother cell) of the female gametophyte.
- On the basis of wall formation after meiotic divisions, Angiosperms exhibit three main patterns of megasporogenesis, referred to as monosporic, bisporic, and tetrasporic.
- Development of the female gametophyte is completely endosporous means within the megaspore.
- During megagametogenesis, the functional megaspore gives rise to the mature female gametophyte.
- Female gametophyte or embryo sac develops from a single megaspore and has eight nuclei, it is said to be monosporic-8-nucleate embryo sac or *Polygonum* type of embryo sac.
- Normal type (*Polygonum* type) of mature embryo sac has 3 antipodal cells at chalazal end, an egg apparatus (one egg cell and two synergids) at micropylar end and two polar nuclei in the centre (total 8 nuclei).
- Two polar nuclei later fuse to form secondary nucleus.
- The central cell is binucleate or diploid and the antipodal cells and cells of the egg apparatus are uninucleate and haploid.
- Depending on the basis of involvement of number of megaspore nuclei in its formation, the embryo sac can be of 3 types- monosporic, bisporic and tetrasporic.
- The nuclei of the bisporic and tetrasporic embryo sacs are not genetically identical as they are in monosporic embryo sacs, because they arise from two or four different meiotic products.

4.7 Terminal question

Q.1 What type of female gametophyte development is reported in Angiosperms?

Answer:---

Q.2 What do you understand by tenuinucellate type and crassinucellate type of ovule?

Answer:---

Q.3 What is megasporocyte?

Answer:---

Q.4 How many types of ovule are there? On what basis they are classified?

Answer:---

Q.5 What is the main criteria for classifying embryo sac?

Answer:---

Short Questions

Q.6 Write short notes on:

1. Polygonum type of embryo sac
2. Megasporogenesis in Angiosperms
3. Orthotropous ovule
4. Circinotropous ovule

Q.7 Multiple choice questions:

1. Ovule is also known as:

    (a) Megasporangium

(b) Microsporangium

(c) Embryo sac

(d) Endosperm

2. Stalk by which ovule is attached to the placenta is:

(a) Hilum

(b) Funiculus

(c) Style

(d) None

3. Linear tetrad is formed by two meiotic divisions in MMC. Both the divisions are:

(a) First division is transverse, second is vertical

(b) First division is vertical, second is transverse

(c) First division is transverse, second is also transverse

(d) May be any type.

4. Which cell in the embryo sac represent the female gamete:

(a) Egg cell

(b) Egg apparatus

(c) Synergids

(d) Polar nuclei

5. Which one of the following is the example of monosporic type of embryo sac:

(a) Polygonum type

(b) Allium type

(c) Endymion type

(d) Peperomia type

4.8 Answers

Q. No. 7 1. (a) 2. (b) 3. (c) 4. (a) 5. (a)

SAQ.1

a. Placenta, placentation**b.** Megasporangium**c.** Funicle**d.**Right angle **e.**Tenuninucellate

SAQ.2

a. Megasporocyte**b.** Bisporic**c.** Endosporous**d.**Polygonum**e.**Uninucleate, binucleate

SAQ.3

a. 3 celled **b.** Onagraceae**c.** Bisporic**d.**Tetrasporic**e.** Genetically

DCEBY-105

Plant embryology and morphogenesis

Uttar Pradesh Rajarshi Tandon Open University

Bachelor of Science

Block

2 Plant Embryology - II

UNIT - V	**Pollination**
UNIT - VI	**Fertilization**
UNIT - VII	**Post fertilization development**
UNIT - VIII	**Polyembryony and apomixis**

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DCEBY – 105 : Plant embryology and morphogenesis
ISBN-

Printed By: Chandrakala Universal Pvt. 42/7 Jawahar Lal Nehru Road, Prayagraj.

Block II

Plant Embryology II

This block explains remaining part of sexual cycle of plant (Plant embryology). The block has four units viz. V, VI, VII and VIII. The details of units is as follows:

Unit V- is pollination which will tell you about pollination, types of pollination, various adaptation for pollination in flower as well as agents of pollination.

Unit VI- is fertilization which defines fertilization process in angiosperms, different ways of entery of pollen tube into the ovule, double fertilization and triple fusion.

Unit VII- Deals with post fertilization development in angiosperms. In this you will study about the development of endosperms, dicotylednous embryo and monocotylednous embryo.

Unit VIII- is Polyembryony and apomixis in which you will study phenomenon of polyembryony, it's various types and apomixis in angiosperms.

Objectives: After studying this unit you will be able to:

- Know about pollination.
- Understand process of double fertilization and triple fusion.
- Know about post fertilization development i.e. the development of endosperm and embryo.
- Explain phenomenon of polyembryony and apomixis occuring in angiosperms.

Unit- V

Pollination

Structure

5.1 Introduction

Pollination means the transfer of the pollen from the anther to the receptive stigma whether of the same flower or of a different flower. Male gamete is contained within the microspore which develops as male gametophyte while the female gamete (egg) is contained within the female gametophyte which is the embryo sac develops within the megaspore and is located within the megasporangium or ovule. So the next biological phase is pollination.

The goal of every living organism, including plants is to create offspring for the next generation. One of the ways that plants can produce off springs is by making seeds. Seeds contain the genetic information to produce a new plant.

Flowers are the tools that plants use to make their seeds. Seeds can be produced when pollen is transferred between flowers of the same species. The importance of pollination in fruit and seed production is known from very early times. The Arab and Assyrian Kings used to performs a special religious ceremony in which the female inflorescence of date palm was touched by the female inflorescence to ensure good fruiting. The scientific basis to this process, however, was given by Thomas Millington towards the end of the 17th century.

Dehiscence of anthers is the prerequisite for pollination. Once the anther is dehisced, the pollination can occur through the agencies of air, water, insects, animals, etc.

Pollination leads to fertilization and production of seeds and fruits which ensure continuity of plant life.

Objectives

After studying this unit you will be able :

- To study the pollination and its types.
- To explain the agents for pollination.

5.2 Types of pollnation

Based on the destination of pollen grains, two types of pollinations are there:

(1) Self-pollination: If the pollen is transferred from anther to the stigma of the same flower, it is called self pollination or **autogamy** as in pea, wheat and rice. When the pollen of one flower pollinates the stigma of different flower, but on the same plant, it is called **geitonogamy**. For self pollination flower must be bisexual (hermaphrodite) and only those bisexual flower which achieve anther dehiscence and receptivity of stigma simultaneously means when anther releases pollen grains then stigma should be ready to receive them.

Autogamy: Autogamy means pollination of flower by its own pollens. It is possible only in a bisexual flower where stigma and another of flower ripe almost simultaneously. This facilitates self-pollination. The floral part of autogamous flower are also positioned in such a way that pollen grains can be easily transferred to the stigma.

Geitonogamy: In this pollengrains of a flower pollinate any other flower present on the same plant.

Adaptations for self pollination: Self pollinated flowers have following adaptations;

(a) **Homogamy**: In homogamy anthers and stigma of a flower nature at the same time. The stigma can receive the pollen shed by anther and self pollination occurs under natural conditions e.g. *Mirabilis, Catharanthus roseus* etc.

(b) **Cleistogamy:** In many cases bisexual flowers never open and remain closed. Such flowers are known as cleistogamous and condition as cleistogamy. In these flowers, self pollination in carried out within closed buds. *Oxalis, Saxifragfa, Draosera, Ajuga, Commelina* are some common examples of cleistogamous flowers.

Merits and Demerits of Self-pollination:

Merit: Pollination is almost certain in bisexual flower in which both stamens and carpels matured at the same time.

Demerit : Continued self-pollination generation after generation results in weaker progeny.

(2) Cross-pollination: If the pollen is transferred from anther to the stigma of the another flower, it is called cross pollination or allogamy as in hemp and willow. Cross pollination within a species (may be inter-varietal) is termed as xenogamy. For cross pollination, flowers are mostly unisexual.

Adaptation for Cross-Pollination: Better seeds and healthier offspring are produced by cross-pollination. Therefore, nature favours cross pollination by certain adaptations in flowers. These adaptations are as followers:

(a) **Self-sterility:** In this pollen of a flower donot grow or grow very slowly if they fall on the stigma of the same flower. Thus there in specific inhibition of pollen growth on the stigma. The pollen applied from another plant of the same or allied species in effective in pollinating. Therefore, cross pollination in the only method in them for the setting of seeds.

(b) **Unisexuality or Dicliny:** Unisexual or diclinous flower has either male reproductive organ or female reproductive organ. Such flowers are produced either on monoecious plants or on dioecious plant. In monoecious plant male and female flowers are born on the same plant but in dioecious plant male and female flowers are born on separate plant. In the flowers of dioecious plant only cross-pollination occurs but the flowers of monoecious plants may be self pollinated or cross pollinated.

(c) **Dichogamy:** This is a condition in which anther and stigma of a bisexual flower matures at different times. There are two conditions of dichogamy: (a) **Protoandry** in this anthers mature before the stigma becomes receptive. Here the pollengrains are carried over to the stigma of another flower e.g. cotton, lady's finger. (b) **Protogyny** in this gynoecium matures earlier than the anthers of the same flower. Therefore, the stigma receives pollin brought from another flower e.g. *Ficus, Magnolia* etc.

(d) **Heterostyly:** It is a special adaptation in which dimorphic flowers bear style of different lengths (heterostylous) one form bears long stamens and a short style, and the other form bears short stamens and a long style (dimorphic heterostyly). There are cases of stamens and styles of three different lengths (trimorphic heterostyly). In these cases cross-pollination is effective when it takes place between stamens and styles of the same length borne by different flower. Primrose, buch wheat, linseed etc. are example of dimorphic heterostyly (Fig. 5.1.) and *Oxalis* and *hinum* are example of trimorphic heterostyly.

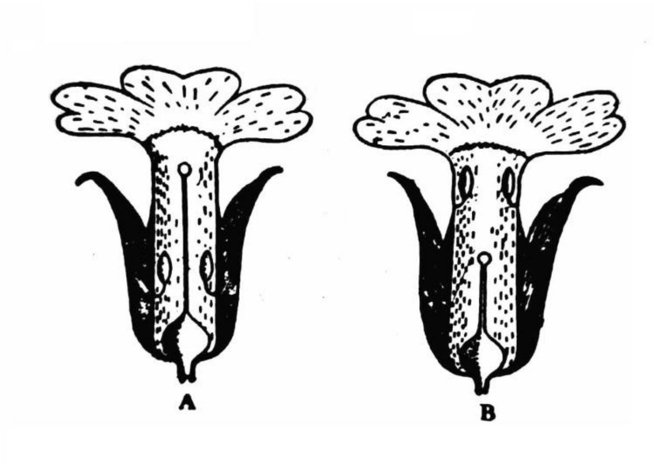

Fig.5.1. Primrose showing heterostyly**.** A. a flower with long style; B. a flower with Short style

Herkogamy: It is a condition in which autogamy is mechanically impossible in a bisexual flower due to some barrier between stamen and pistil. For example a hood covering stigma form a barriers in *Iris.* In Orchidaceae and Asclepiadaceae, the pollens are united into a single compact pollinium remain fixed to their position by adhesive disc. They can be carried to another flower by insects. (Fig. 5.2.)

Fig.5.2. Pollination in madar; A. a pair of pollinia; B. Flower of madar.

SAQ.1

---

a. Pollination means the transfer of the pollen from the anther to the_____________whether of the same flower or of a different flower.

b. If the pollen is transferred from anther to the stigma of the same flower, it is called____________.

c. If the pollen is transferred from anther to the stigma of the another flower, it is called______________.

5.3 Agents of Cross- pollination

The process of pollination depends on various external agencies. The various agencies which help in cross- pollination are classified into two categories:-

(i) **Abiotic:** The abiotic agents are nonliving agents such as air, water.

(ii) **Biotic:** The biotic agents includes living organisms such as insects, birds.

Types of Cross-pollination:

Cross-pollination is of following types:

(i) **Anemophily:** In anemophily pollination is brought about by the wind. The pollengrains are easily carried by wind and distributed over a wide area, evidently helping cross pollination. Anemophilous flowers have following characteristics:

- Flowers are small inconspicuous and not showy.
- They do not emit any smell.
- They do not secrete any nectar.
- Pollengrains are produced in large quality.
- Pollengrains are minute, light dry and sometimes have wings(*Pinus*).

Anemophily can be well explained in case of maize (Fig.5.3.). Here as the anther burst a large quantity of pollen grains are set adrift by air currents. They are caught by the long hanging styles of female flower of the sapdix lower down.

Fig.5.3. Anemophily in maize plant

(2) Hydrophily: Hydrophily means pollination is brought through the medium of water. Hydrophily is of two types: (a) Epi-hydrophily (b) hypo-hydrophily.

Epi-hydrophily is more common in nature. In this flower are pollinated at the surface of water. Epi-hydorphily is illustrated by *Vallisneria*. The plant is dioecious and submerged. The minute male flowers get detached from the small spadix of the male plant and float on water. Each female flower borne on a long stalk by the female plant is brought to the level of water. Then the free-floating male flowers are so adrift by currents, and some of them come in contact with the female flower. The anthers burst and the pollen grains are distributed on the stigma of the female flower. Thus pollination is brought about. The stalk of the female flower then becomes closely coiled and the fruit develops under water. (Fig.5.4.)

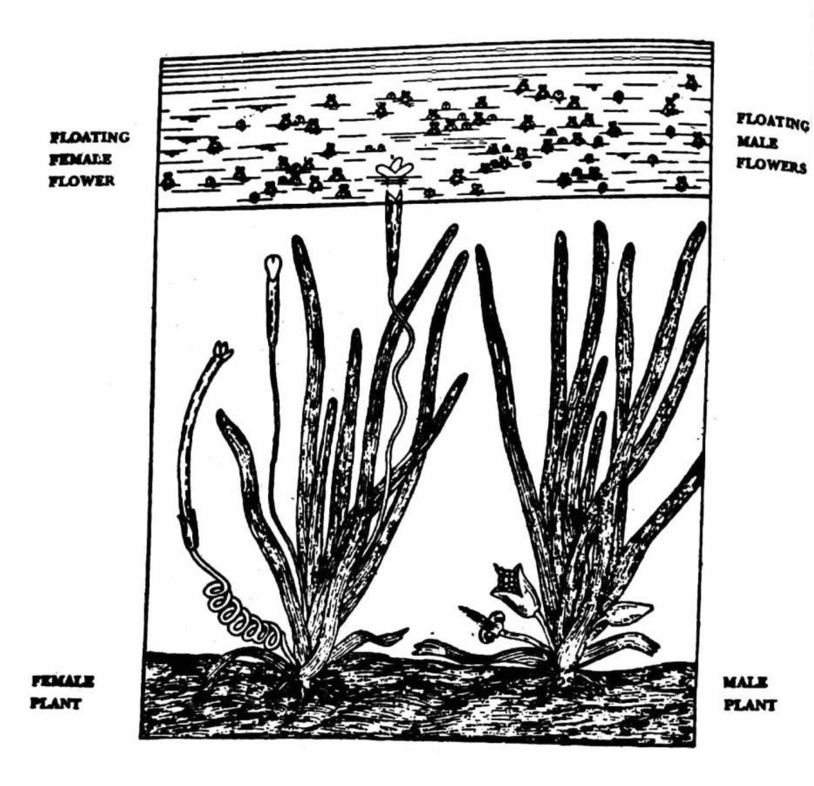

Fig.5.4. *Vallisneria* showing epi-hydorphily.

Hypo-hydrophily is the pollination of flower below water level. It can be illustrated in *Ceratophyllum.* The male flower of *Ceratophyllum* has 12-16 stamens and there is a prolonged double horned process of arenchyma in each anther which helps in floating. The anther ruptures during their upward caurse. As a result pollengrains are liberated and freely distributed in water. These pollens are trapped by the lower surface of the sticky style which serves as stigma.

(3) Entomophily: Pollination by insect is known as entomophily. Angiosperms are more dependent on insect than any other agency for pollination. Entomophilous flower have many adaptations by which they attract insects for pollination. These adaptations are as follows:

- They have bright coloured petal and irregular shape of flower.
- Flowers have scent and nectar to attract insect. Most of the nocturnal flowers are insect loving and they emit at night a sweet scent which attracts insects from a distance.
- If flowers are very small then other parts of flower becomes large, e.g. in *Baugainvillea* the bracts become large and brightly coloured.
- The pollen grains are either sticky or provided with spinous out growth. The stigma is also sticky.

- *Salvia* has lever mechanism as an adaptation for insect pollination and flowers of *Aristolochia* have a special trap mechanism to ensure cross pollination.

(4) **Orinthophily:** Pollination by bird is known as orinthophily. Orinthophilous flowers have a number of structural peculiarities to attract birds for pollination. These are as follows:

- Flowers are tubular, cup-shaped on Urn-shaped and scarlet coloured.
- To attract birds they secrete large quantities of nectar.
- Flowers have a tough texture so that they may withstand the onslanghts of little birds.

(5) Cheiropteriphily: Pollination by bats is known as cheiropteriphily. The bats visit flower to eat floral part or in search of moths. In their frequent visit from one flower to another, they help in pollination. The flowers of *Anthocephalus cadamba* and *Bauhinia megalander* are example of cheiropteriphily.

Merits and Demerits of Cross-pollination:

Merits:

- Cross-pollination results in healthier offspring which are better adapted to the struggle for existence.
- More abundant and viable seeds are produced whose germinating capacity is much better.
- New varities are produced.

Demerits:

- The plants have to depend on external agencies for pollination.
- In wind pollination a large number of pollens are wasted.

SAQ 2.

a. Pollination leads to fertilization and production of ……………. and ……………

b. Pollination by wind is known as……………………………

c. Pollination by water is known as…………………………….……….

d. Pollination by insect is known as……………………………………..

5.4 Summary

- After development of male and female gametophyte, the next biological phase is pollination, which is must for fertilization.

- Pollination means the transfer of the pollen from the anther to the receptive stigma whether of the same flower (self-pollination) or of a different flower (cross pollination).
- Abiotic (wind and water) and biotic (insects, birds and bats) agents are responsible for pollination.
- On the basis of these agents pollination may be anemophilous (by wind), hydrophilous (by water), entomophilous (by insects), ornithophilous (by birds) and chiropteriphilous (by bats).
- Pollination ends in a copious dusting of the stigma surface with pollen grains.

5.5 Terminal question

Q.1 What is pollination?

Answer:---

Q.2 What do you understand by cross and self pollination?

Answer:---

Q.3 Give a detail account of agent for pollination?

Answer:---

Short Questions

Q.4 Write short notes on:

1. Self -pollination
2. Hydrophily
3. Ornithophily
4. Homogamy and cleistogamy
5. Dichogamy

6. Heterostyly
7. Herkogamy

Q.5 Multiple choice questions:

1. If the pollen is transferred from anther to the stigma of the same flower, it is called:
   (a) Self pollination
   (b) Cross pollination
   (c) both of the above
   (d) None of the above

2. Abiotic (wind and water) and biotic (insects, birds and bats) agents are responsible for:
   (a) dissemination
   (b) dispersal
   (c) Pollination
   (d) None of the above

3. Entomophily refers to:
(a) Pollination by insect
   (b) Pollination by wind
   (c) Pollination by water
   (d) All of the above

5.6 Answers

Questiong No. 5. 1. (a) 2. (c) 3. (a)

SAQ.1

a. Receptive stigma**b.** Self pollination**c.** Cross pollination**d.**Seeds, fruits

SAQ.2

a. Ornithophily b. hydrophily c. anemophily d. entomophily

Unit- VI

Fertilization

Structure

6.1 Introduction

Objectives

6.2 Fertilization

6.3 Summary

6.4 Terminal Questions

6.5 Answers

6.1 Introduction

By going through the male gametophyte and female gametophyte units, it is now clear that gametophytic generation is haploid. The first male gametophytic cell is microspore or pollen grain. The first female gametophytic cell is functional megaspore. The pollen grains are liberated at the 2-celled or 3-celled stage. Female gametophyte is also known as embryo sac and in most of the species it is of *Polygonum* type. After development of male and female gametophyte, the next biological phase is pollination, which is must for fertilization. Pollination ends in a copious dusting of the stigma surface with pollen grains **(Figure 6.1)**.

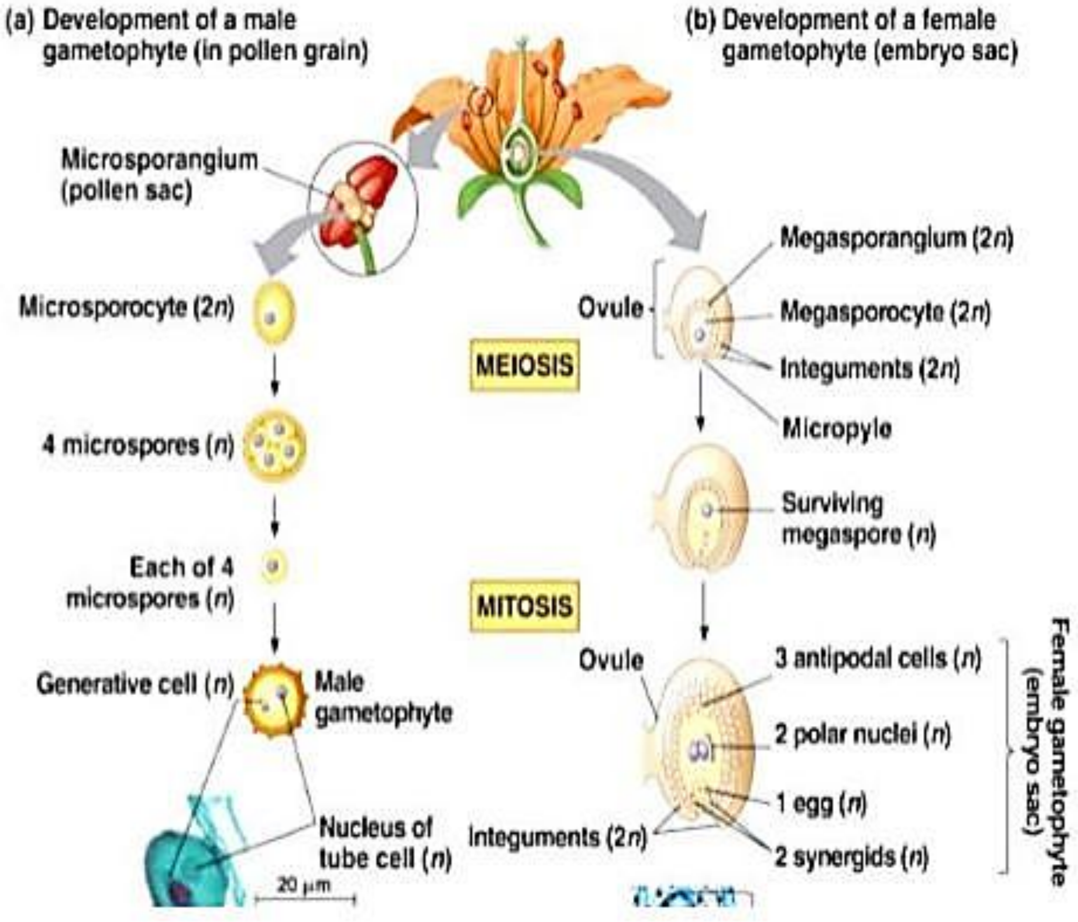

Figure 6.1: Showing development of male and female gametophyte

In this unit we will discuss about fertilization and post fertilization developments along with some very important phenomena occurring in the life cycle of Angiosperm plants i.e. apomixis, adventive embryony, polyembryony and parthenocarpy.

The capacity to reproduce is one of the most important characteristics of life and is aimed to sustain the individual species. Reproduction methods are mainly of two types- asexual and sexual. In flowering plants sexual method of reproduction requires fusion of two gametes, one from male organ and other from female organ of the plant. The product of the fusion of two different gametes is zygote and this fusion process is known as fertilization.

In angiosperms fertilization initiate with the compatible type pollen (male gametophyte) reaching the stigma and ends with the fusion of male and female gametes in the embryo sac (female gametophyte). The pollens received by the female reproductive organ i.e. gynoecium are held at the stigma.

There is no such way by which the pollen (male gamete) can reach to the egg (female gamete) in the embryo sac. So to overcome this difficulty pollen germinate on the stigma and forms pollen tube which penetrate the stigmatic tissue, grows down the style, enters the ovary and finally finds its way into the embryo sac (female gametophyte) through ovule. Here it releases two sperms (male gametes) in the vicinity of the female gametes. Out of the two sperms, one fuses with the egg (syngamy) and forms zygote. The other one fuses with the polar nuclei or the secondary nucleus (triple fusion) and forms primary endosperm nucleus. This phenomenon is known as double fertilization and is a characteristic unique feature of the Angiosperms.

After series of divisions primary endosperm nucleus forms endosperm. Endosperm is very nutritive tissue that nourishes the developing embryo. Zygote or oospore forms embryo, either dicotyledonous or monocotyledonous embryo, as the case may be.

Terms to remember:
Apical cell = terminal cell = (also known as embryo cell)
Basal cell = also known as suspensor cell
Meiosis = reduction division
Syngamy = fertilization
Sexual cycle = amphimixis
Asexual cycle = apomixis
Sperms = male gamete
Egg = female gamete
Vegetative cell = tube cell
Embryo sac = female gametophyte
Zygote = oospore = fertilized egg
Gynoecium = pistil

Objectives

After studying this unit, you will be able :

- To define fertilization.
- To know about the different ways of entry of pollen tube into the ovule.
- To understand syngamy.
- To know about triple fusion.
- To explain the unique phenomenon of double fertilization.
- To explain the post fertilization developments.

6.2 Fertilization

"Fertilization is the process of fusion of two dissimilar reproductive units, called gametes."

In flowering plants, the process of fertilization was first discovered by Strasburger in 1884. The female gametophyte (embryo sac) of angiosperm is situated in the ovule, at a distance from the stigma. There is no such device developed in the gynoecium (pistil) which facilitates transfer of pollen from stigma to embryo sac. Therefore, the pollen after reaching to the stigma produces a pollen tube which facilitates transport of male gametes deep into the embryo sac from stigma.

In Angiosperms, the fertilization is being completed as follows:

Germination of pollen grains and growth of pollen tube

When the pollen is shed from anther it has usually two cells:

1. A generative cell

2. A vegetative cell (tube cell).

The generative cell forms two male gametes. Once the pollen has landed on compatible receptive stigma as a result of pollination, its germination starts. On the surface of stigma, the pollen hydrates. This means pollen absorbs water from the surrounding and swells. After that the vegetative cell forms a pollen tube. The stigmatic fluid secreted by the stigma contains sugars, lipids and resins, etc. which provides suitable medium for the germination of pollen grains. Pollen grain as well as pollen tube contain an enzyme cutinase which helps in the penetration of pollen tube into the stigmatic tissue. Cutinase as the name indicates degrades the cutin of the stigma at the point of contact with the pollen tube. The entire content of the pollen including two male gametes of generative cell move into the pollen tube **(Figure 6.2)**. The growing pollen tube penetrates the stigmatic tissue and pushes its way through the style and then down the wall of the ovary. The style may be hollow or solid. If it is hollow, then the pollen tube grows along the epidermal surface but in case of solid style, the pollen tube travels through intercellular spaces between the cells which lie in its path.

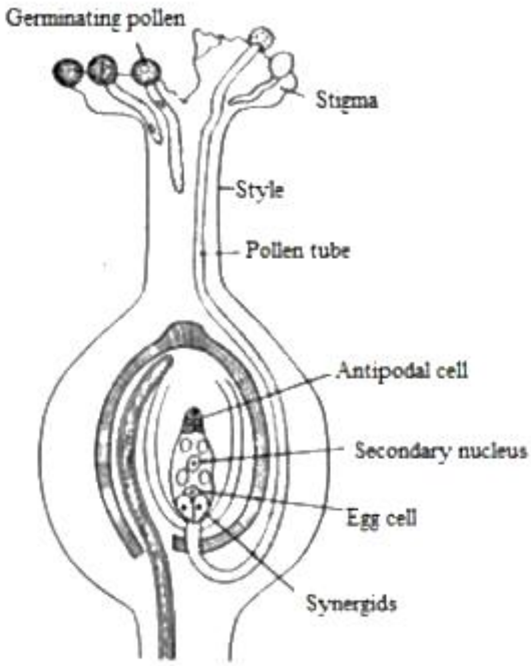

Figure 6.2: Longitudinal section of a flower showing growth of pollen tube

Entry of pollen tube into ovule

After arriving in the ovary, the pollen tube finds its way into the ovule. The pollen tube may enter into the ovule via three routes.

1. through the micropyle

2. through the chalazal end

3. through the integument

On that basis of modes of entry of pollen tube into the ovule, three terms are given as follows: **1. Porogamy:** When the pollen tube enters the ovule through the micropyle, the condition is known as porogamy. This is the most common mode of pollen tube entry into the ovule and so the most common type of fertilization.

2. Chalazogamy: When the pollen tube enters the ovule through the chalazal end, the condition is known as chalazogamy. This type of pollen tube entry into the ovule and so the type of fertilization is observed in *Casuarina*, *Betula* and *Juglansregia*. The chalazogamy was first reported by Treub (1891) in *Casuarina*.

3. Mesogamy: When the pollen tube enters the ovule through the integument or through the funiculus, the condition is known as mesogamy. This type of pollen tube entry into the ovule and so the type of fertilization is observed in *Cucurbita* (through the integument), and *Pistacia* (through the funiculus).

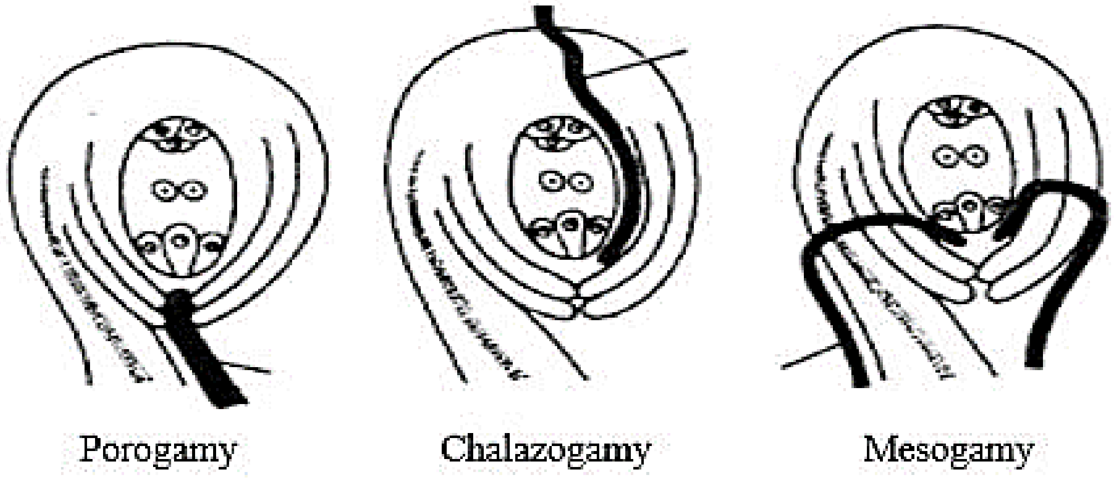

Figure 6.3: Modes of entry of pollen tube into the ovule

SAQ.1

a. Fertilization is the process of fusion of two dissimilar reproductive units, called______.

b. The generative cell forms_________male gametes.

c. When the pollen tube enters the ovule through the___________, the condition is known as porogamy.

d. When the pollen tube enters the ovule through the chalazal end, the condition is known as_____________.

e. When the pollen tube enters the ovule through the integument or through the funiculus, the condition is known as_________.

Therefore, depending on the place of pollen tube entry into the ovule, fertilization may also be called of three types:

1. Porogamous
2. Chalazogamous
3. Mesogamous

It does not matter through which way pollen tube enters into the ovule; it always enters in the embryo sac from the micropylar end means entry of pollen tube in the embryo sac is irrespective of pollen tube entry into the ovule **(Figure 6.3)**.

Again the entry of pollen tube into the embryo sac after passing micropyle may be via different passages. It may be:

(i) between the egg cell and one of the synergids e.g. *Fagopyrum*

(ii) between the wall of the embryo sac and one or other synergids.e.g. *Cardiospermum*

(iii) directly penetrates one of the synergids e.g. *Oxalis*

So we can say that synergids not only play an important role in determining the entry of pollen tube in the embryo sac but they also affect dissemination of male gametes in the embryo sac.

Discharge of male gametes from pollen tube

After reaching the embryo sac the pollen tube burst at its tip and deliver the (two) male gametes. Just prior to bursting of pollen tube the tube nucleus disorganizes. Immediately after releasing, the male gametes show amoeboid movement and one male gamete moves toward the egg and other one move to the polar nuclei **(Figure 6.4)**.

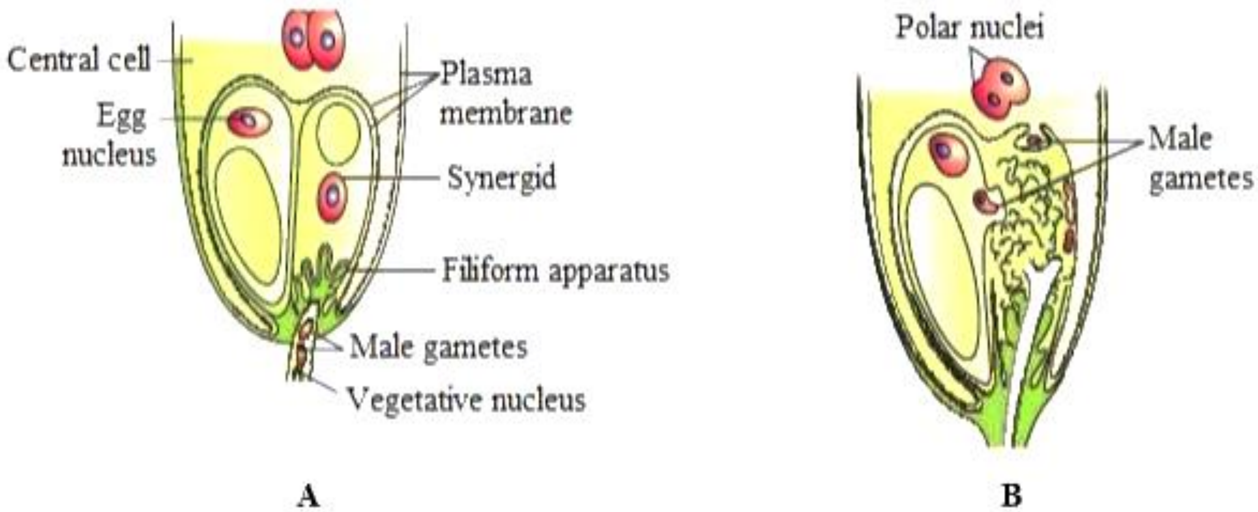

Figure 6.4:A: Enlarge view of an egg apparatus showing path of pollen tube growth; **B:** discharge of male gametes into a synergid and the movement of the male gametes, one into the egg and the other into the central cell.

Syngamy- fusion of gametes

As the one of the male gametes reached the egg, it fuses with it. As a result of this fusion diploid zygote/oospore (2n) forms (because you know the egg and the male gamete, both are haploid). The fusion of male and female gametes is known as fertilization. This is also known as syngamy.

One of the most significant discoveries was made by Strasburger in 1884, as mentioned above. He observed the actual fusion of the male gamete with the female gamete (egg) in *Monotropa*.

Since two male gametes are released by the pollen tube, what happened to the second male gamete? The answer was provided by S. G. Nawaschin (1898). He showed that the one male gamete fused with the egg (syngamy) and the other male gamete with the polar nuclei (triple fusion) while working with *Fritillaria* and *Lilium*. So this was the discovery of double fertilization.

Triple fusion The other male gamete fuses with the two polar nuclei (or secondary nucleus, if the two have already fused) and so forms triple fusion nucleus (3n), called primary endosperm nucleus **(Figure 6.5)**.

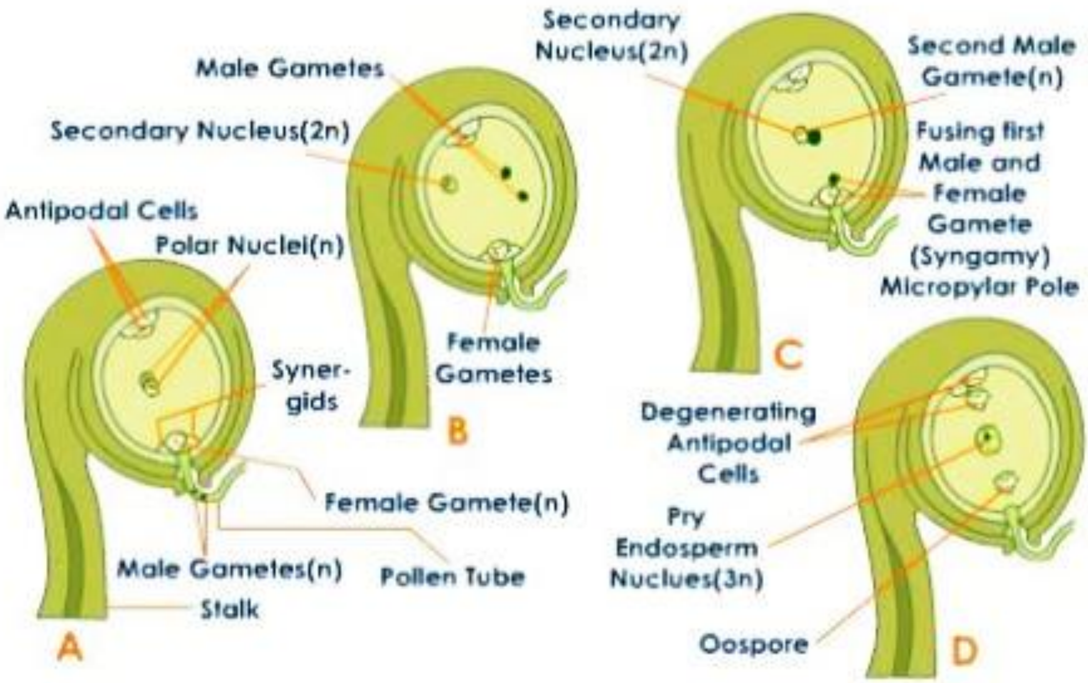

Figure 6.5: Showing syngamy and triple fusion

Double fertilization

Thus in an embryo sac two sexual fusions occur; one is syngamy (i.e. fusion of one male gamete with the egg) and another is triple fusion (i.e. fusion of other male gamete with the polar nuclei or secondary nucleus), and therefore, the phenomenon is known as double fertilization **(Figure 6.6)**.

As a result of first fertilization the zygote or oospore cell is formed which is the mother cell of the embryo and is a diploid cell containing 2n complement of the chromosomes. The nucleus of the triple fusion product (primary endosperm nucleus) is triploid or 3n. This is the first nucleus of the endosperm.

Double fertilization is a very unique phenomenon in angiosperms and discovered for the first time by S.G. Nawaschin (1898) in *Lilium* and *Fritillaria* species as described above.

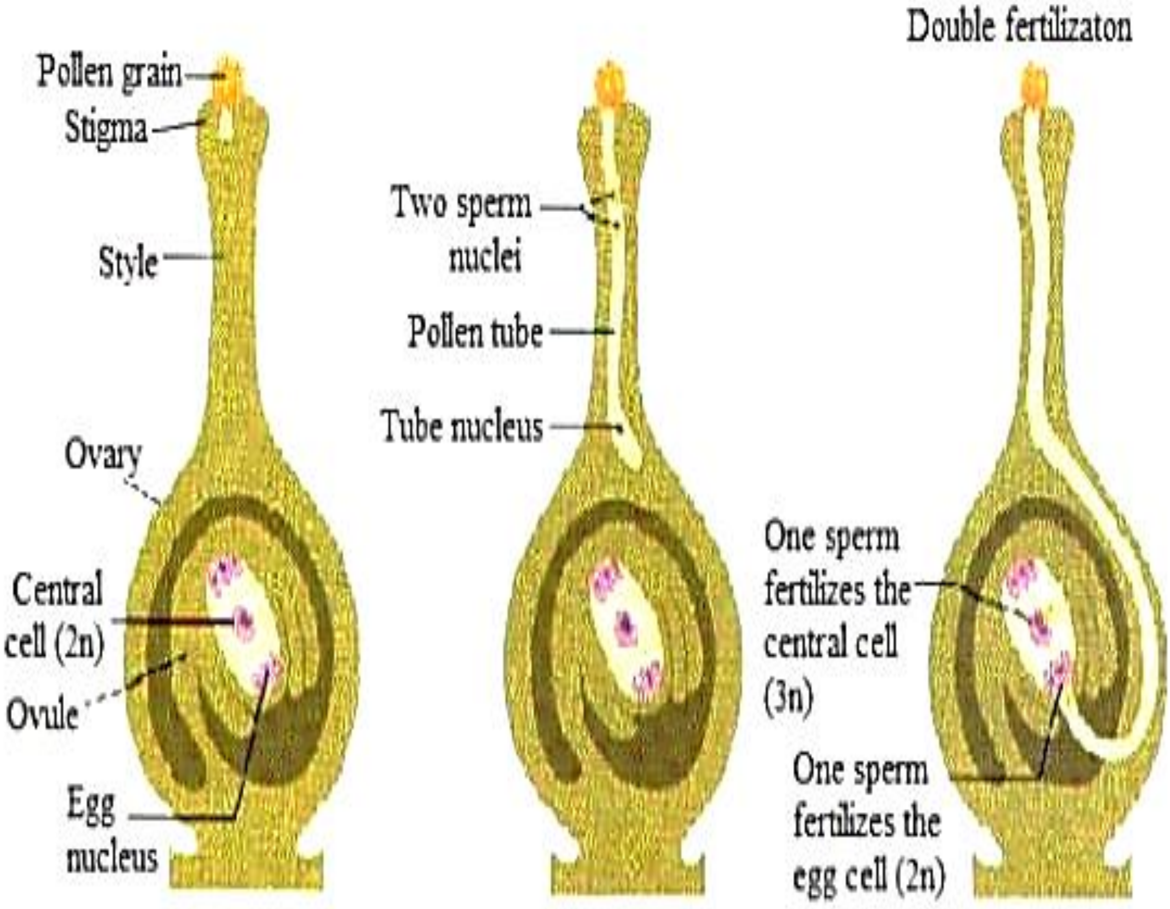

Figure 6.6: Process of double fertilization

SAQ.2

a. One male gamete moves toward the egg and other one move to the___________.

b. The fusion of male and female gametes is known as__________.

c. The nucleus of the triple fusion product (primary endosperm nucleus) is_________.

d. _________fertilization is a very unique phenomenon in Angiosperms.

e. Double fertilization is discovered for the first time by____________in*Lilium* and *Fritillaria* species.

6.3 Summary

In this unit we have discussed about fertilization, pathway of pollens to their destination for fertilization. After that we have also learnt post fertilization development process. Along with these topics light has been thrown on apomixis, adventives embryony, polyembryony as well as on parthenocarpy. Therefore, summary of all the topics covered in this unit is given in the following key points:

- Once the pollen grain reaches the receptive stigma, as a result of pollination, it germinates producing a long slender pollen tube. Two male gametes and the tube nucleus migrate into the pollen tube which now represents the mature male gametophyte.
- Pollen tube penetrates the stigmatic tissue and pushes its way through the style and then down the wall of the ovary.
- After arriving in the ovary, the pollen tube may enter into the ovule through micropyle (porogamy), through chalazal end (chalazogamy) or thrugh integuments (mesogamy).
- Irrespective of the route of the entry of the pollen tube into the ovule, it always enters the embryo sac from the micropylar end.
- After entering into the embryo sac, the tip of the pollen tube bursts and the two male gametes are released.
- Out of the two male gametes one male gamete fuses with the egg nucleus and result in the formation of zygote or oospore (2n). Second male gamete fuses with two polar nuclei, resulting into primary endosperm nucleus (3n). This phenomenon is termed as double fertilization.

6.4 Terminal question

Q.1 What is the role of enzyme cutinase in pollen tube?

Answer:---

Q.2 Is the way of entry of pollen tube to ovule and embryo sac same?

Answer:---

Q.3 What is the difference between syngamy and triple fusion?

Answer:---

Q.4 On the surface of stigma the pollen hydrates. What does this reflect?

Answer:---

Short Questions

Q.5 Write short notes on:

1. Porogamy
2. Chalazogamy
3. Mesogamy
4. Double fertilization

Q.6 Multiple choice questions:

1. Entry of pollen tube into the ovule through the funiculus or integuments is called:

    (a) Chalazogamy

    (b) Porogamy

    (c) Mesogamy

    (d) None

2. Product of syngamy is:

    (a) Zygote

    (b) Oosphere

    (c) Primary endosperm nucleus

    (d) Embryo

3. Product of triple fusion is:

    (a) Zygote

    (b) Oosphere

    (c) Primary endosperm nucleus

    (d) Embryo

4. Entry of pollen tube into the ovule through micropyle is called:

    (a) Chalazogamy

(b) Porogamy

(c) Mesogamy

(d) None

5. Entry of pollen tube into the ovule through the chalazal end is called:

(a) Chalazogamy

(b) Porogamy

(c) Mesogamy

(d) None

6.5 Answers

Q. No. 7 1. (c) 2. (a) 3. (c) 4. (b) 5. (a)

SAQ.1

a. Gametes**b.** Two**c.** Micropyle**d.**Chalazogamy**e.**Mesogamy

SAQ.2

a. Polar nuclei**b.** Fertilization**c.** Triploid **d.** Double**e.** S. G. Nawaschin (1898)

Unit- VII

Post fertilization developments

Structure

7.1 Introduction

After fertilization, development of the embryo and the endosperm within the ovule goes side by side. The oospore (zygote), formed as a result of fusion of one male gamete with the egg, develops into the embryo while the primary endosperm nucleus- product of triple fusion, develops the endosperm. The other nuclei or cells within the embryo sac (synergids, antipodal cells) disorganize sooner or later.

Objectives

After studying this unit you will be able:

- To know about post fertilization developments.
- To explain endosperm and it forms.
- To discuss the different types of endosperm.
- To know about endospermic seeds and non-endospermic seeds.
- To define embryo.
- To study the development of dicotyledonous and monocotyledonous embryo.

7.2 Development of endosperm

The primary endosperm nucleus is a product of triple fusion. This undergoes a series of divisions and ultimately forms endosperm. The angiospermic endosperm is a triploid (3n) tissue as it is a product of triple fusion. It is formed either by the fusion of one haploid male gamete and one diploid secondary nucleus (fusion product of two haploid polar nuclei) or by the fusion of three haploid nuclei (one male gamete belongs to male gametophyte and two polar nuclei belongs to the female gametophyte). It is therefore distinct from the endosperm of heterosporouspteridophytes and gymnosperms where the endosperm is a simple haploid (n) tissue of the gametophyte not involving any triple fusion like in angiosperms. Endosperm is a highly nutritive tissue which provides nourishment to the developing embryo.

In Orchidaceae and Podostemonaceae, the product of double fertilization soon disintegrates and endosperm development is completely suppressed.

Depending upon mode of development three types of endosperm has been recognized:

1. Nuclear endosperm

2. Cellular endosperm

3.Helobial endosperm

Of these nuclear endosperm is the most common type which occurs in about 56% families of angiosperms. It is followed by cellular endosperm (reported in 25% families of angiosperms) and then by helobial endosperm (reported in 19% families of angiosperms).

1. Nuclear endosperm

In this type of endosperm, the division of primary endosperm nucleus and number of subsequent nuclear divisions are not accompanied by wall formation and the nuclei thus produced remain free in the cytoplasm of the embryo sac. They remain in the peripheral layer of the cytoplasm surrounding a large central vacuole. Wall formation occurs at later stage around nuclei. The wall formation is mostly centripetal i.e. from the periphery towards the centre and usually begins from the basal periphery e.g. *Arachis hypogea*.

In some cases, the central vacuole may not be filled up even in the mature seed. This is seen in the palms. *Cocusnucifera* is the classical example of this type of nuclear endosperm. Development of endosperm in it deserves special mention. The primary endosperm nucleus undergoes a number of free nuclear divisions. Then the embryo sac gets filled with a clear fluid (watery liquid endosperm) in which numerous nuclei float. It is known as liquid syncytium. Gradually nuclei start settling at the periphery with the beginning of peripheral cell wall formation. This forms the coconut meat. In mature coconuts the liquid endosperm becomes milky. The watery endosperm of coconut contains growth promoting ‘coconut milk factor’ and that is why it is used as a nutrient medium in plant tissue culture experiments. Nuclear endosperm is commonly found in polypetalous dicotyledons **(Figure 7.1)**.

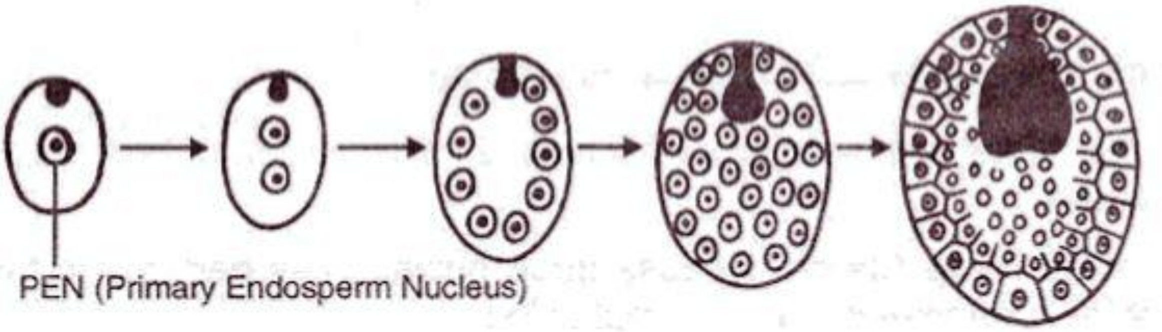

Figure7.1: Nuclear endosperm formation

2. Cellular endosperm

In this type of endosperm, division of the primary endosperm nucleus is immediately followed by wall formation so that the endosperm is cellular from the beginning. The first wall is laid down transversely but the subsequent divisions are irregular. *Adoxa*, *Peperomia*, *Villarsia* etc. are some common examples**(Figure7.2)**.

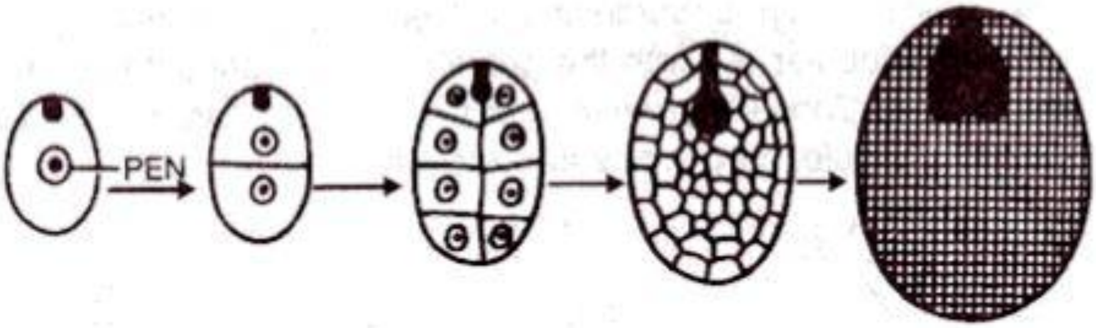

Figure 7.2: Cellular endosperm formation

3. Helobial endosperm

Among members of Helobiales (e.g. *Vallisneria*, *Eremurus*, *Limnophyton* etc.) there is helobial type of endosperm. The development of which is intermediate between the nuclear and the cellular type. Here the first division of the primary endosperm nucleus is accompanied by the formation of transverse wall. This divides the embryo sac unequally into two compartments - a small chalazal chamber and a large micropylar chamber. This step is followed by free nuclear division in both the chambers but there are relatively more free nuclear divisions in micropylar chamber in comparison to chalazal one. The chalazal chamber often degenerates. The free nuclear divisions in the micropylar chamber are followed by wall formation and thus a cellular endosperm tissue is formed and usually found in the members of the order Helobiales **(Figure 7.3)**.

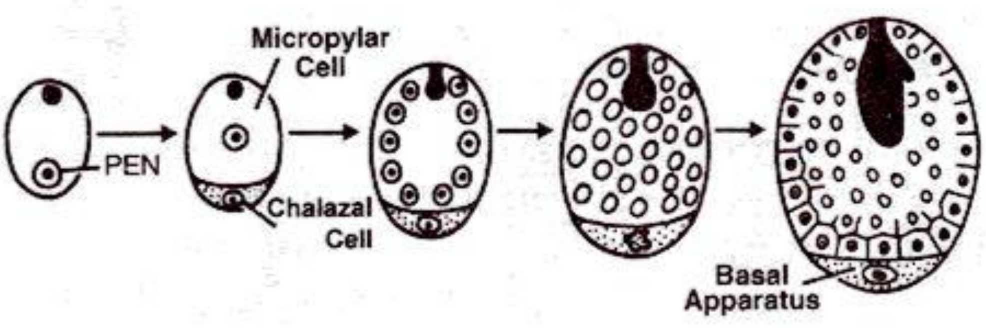

Figure 7.3: Helobial endosperm formation

It is the endosperm, on the basis of which seeds can also be categorized into two categories.

1. Non-endospermic seeds

2. Endospermic seeds

1. Non- endospermic seeds (ex-albuminous seeds)

In plants where the entire endosperm consumed or utilized in the nutrition of the developing embryo, the mature seeds thus formed are without endosperm. Such seeds are termed as non-endospermic seeds. Example are seeds of beans, peas etc. The non-endospermic seeds store their food material in cotyledons.

2. Endospermic seeds (albuminous seeds)

In plants where the seeds retain endosperm even at maturity and do not consumed or utilized the endosperm completely in the nutrition of the developing embryo. Such seeds are said to be endospermic seeds. Example are seeds of coconut, castor etc. The endosperm present in the seed is utilized after germination in the establishment of young seedlings.

SAQ.1

a. The primary endosperm nucleus is a product of__________fusion.

b. *Cocusnucifera* is the classical example of this type of_________endosperm.

c. The________endosperm of coconut contains growth promoting 'coconut milk factor'

d. ____________type of endosperm the development which is intermediate between the nuclear and the cellular type.

e. The non-endospermic seeds store their food material in___________.

7.3 Development of the embryo

After fertilization, a series of changes occurs in the ovule and finally seed is formed. Side by side with the development of the endosperm, the oospore (zygote, the fertilized egg) is developing the embryo after a period of rest.

The process of development of mature embryo from diploid oospore is called embryogenesis. Both dicotyledons and monocotyledons begin embryo development in the same way but there is considerable difference in later differentiation. Before proceeding let us discuss about the dicotyledonous and monocotyledonous embryo.

The dicotyledonous embryo as the name reflects, has two cotyledons attached laterally to an embryonical axis, whereas in the monocotyledonous embryo, the embryonical axis has a single cotyledon at its apex. Due to this organographic difference, it is very easy to distinguish the two types of embryo but there is no fundamental difference in their early stage of development. The development is very similar till the globular stage.

In all angiosperms the embryogenesis starts with the division in oospore and it divides to develop a two-celled proembryo by forming a transverse wall. The cell near the micropyle is termed the basal cell and the cell facing towards the centre of the embryo sac is called the terminal cell. The basal cell forms the suspensor and may or may not contribute in rest activities so sometimes called as suspensor cell, whereas terminal cell is responsible for further development of embryo so called embryo cell.

Types of embryo development

On the basis of plane of division of the terminal cell (also known as apical or embryo cell) in the 2-celled proembryo and the contribution of the basal cell and terminal cells in the formation of embryo proper, **six types of embryogeny** (embryo development) have been reported by Johansen (1950) among the Angiosperms.

1. Onagrad or Crucifer type (e.g. Annonaceae, Brassicaceae, Onagraceae, Pedaliaceae, Ranunculaceae, Scrophulariaceae).

2. Asterad type (e.g. Asteraceae, Balsamianceae, Violaceae, Vitaceae).

3. Solanad type (e.g. Campanulaceae, Linaceae, Solanaceae, Theaceae).

4. Caryophyllad type (e.g. Caryophyllaceae, Crassulaceae,Haloragaceae).

5. Chenopodiad type (e.g. Boraginaceae, Chenopodiaceae).

6. Piperad type (e.g. Loranthaceae, Piperaceae).

A. The terminal cell of 2-celled proembryo divides longitudinally:

(1). The basal cell plays only a minor role or none in the subsequent development of the embryo proper………………………………………………………………**Onagrad or Crucifer type**

(2). The basal cell and terminal cell both contribute to the development of embryo proper……………………………………………………….…………………...**Asterad type**

B. The terminal cell of 2-celled proembryo divides transversely. The basal cell plays only a minor role or none in the subsequent development of the embryo proper

(3) The basal cell usually forms suspensor…………………………………...…**Solanad type**

(4) The basal cell undergoes no further division and the suspensor, if present, is always derived from the terminal cell…………………………………………….**Caryophyllad type**

II. (5) The basal cell and terminal cell both contribute to the development of embryo proper…………………………………………………………………...**Chenopodiad type**

These five types of embryogeny are reported in those plants where first division of the oospore (zygote) is transverse forming terminal and basal cell.

Johansen (1950) has also reported a sixth type of embryogeny called **Piperad type**. In this type the first division of the oospore (zygote) is vertical.

- The process of development of mature embryo from diploid oospore is called embryogenesis.
- In majority of angiosperm plants, the first division of the zygote is transverse. Rarely it is vertical.
- Six types of embryogeny was reported among angiosperms by Johansen (1950) - Onagrad or Crucifer type, Asterad type, Solanad type, Caryophyllad type, Chenopodiad type and Piperad type.

7.4 Development of dicotyledonous embryo

The classical example is *Capsella bursa-pastoris* (shepherd's purse) of Brassicaceae. The ovule is campylotropous so that the embryo sac and the later developed endosperm as well as embryo are horseshoe-shaped. Here the development of embryo is Onagrad or Crucifer type. **1.** Zygote (oospore) divides transversely. As a result of this a two-celled proembryo is formed.

2. The larger basal cell at the micropylar end is called suspensor cell. The smaller one, away from it termed as terminal cell or embryo cell.

3. The suspensor cell divides transversely a few times to produce a filamentous suspensor of 6 to 10 cells. The suspensor helps in pushing the embryo in the endosperm.

4. The first cell of the suspensor (towards micropyle) becomes swollen and called haustorium or vesicular cell.

5. The last cell of suspensor (towards embryo cell) is known as hypophysis. It forms radicle and root cap.

6. The embryo cell undergoes two vertical divisions and one transverse division to form quadrant and then octant stage. In octant, eight cells arranged in two tiers- epibasal (terminal) and hypobasal (near the suspensor).

The epibasal cells eventually form the two cotyledons and the plumule. The hypobasal cells produce the hypocotyl. For this the octant embryo undergoes periclinal divisions producing outer layer of protoderm, procambium and ground meristem.

Protoderm forms epidermis, procambium gives rise to steal or vascular strand and ground meristem produces cortex and pith. It is initially globular but with the growth of cotyledons it becomes heart-shaped and then assumes the typical shape, e.g., *Capsella bursa-pastoris*.

Structure of Dicot Embryo

The mature embryo consists of an embryonal axis having two cotyledons. Embryonal axis above the level of cotyledons forms the plumule (epicotyl) and below the cotyledons, the radical (hypocotyl). Upon germination the plumule forms the shoot and the radical gives rise the root system. The reserve food material in the cotyledons is used in the establishment of

Dicot embryo

1. A typical dicotyledonous embryo consists of an embryonal axis and two cotyledons.
2. Above cotyledons level, embryonal axis is called epicotyl which forms shoot.
3. Below cotyledons level, embryonal axis is called hypocotyl which forms radicle.
4. The root tip is covered with a root cap (calyptra).

young seedlings **(Figure 7.4)**.

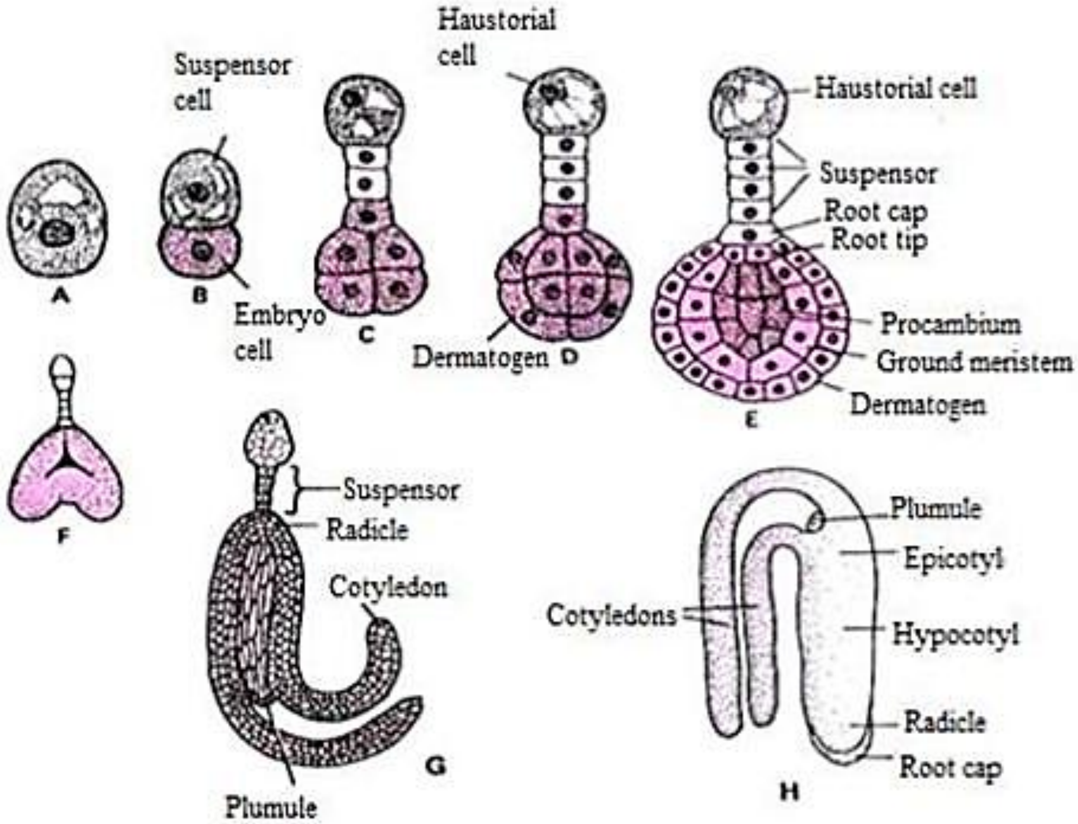

Figure7.4: Stages in the development of a dicot embryo;A. Zygote or oospore; **B.** Division of zygote into suspensor and embryo cells; **C.** Formation of suspensor and embryo octant; **D.**Periclinal divisions of embryo octants to form outer dermatogens; **E.** Globular embryo showing regions of radical, procambium, ground meristem and dermatogens; **F.** Heart-shaped embryo;

SAQ.2

---

a. The process of development of mature embryo from diploid oospore is called____________.

b. In majority of angiosperm plants, the first division of the zygote is______________.

c. . The suspensor cell divides transversely a few times to produce a filamentous suspensor of_____________cells.

d. The first cell of the suspensor (towards micropyle) becomes swollen and called___________.

---

e. _____________forms epidermis, procambium gives rise to steal or vascular strand and ground meristem produces cortex and pith.

7.5 Development of monocotyledonous embryo

There is no essential difference between the embryogeny of monocotyledons and that of dicotyledons but as a single cotyledon develops instead of two from the embryo in monocotyledons, there is some difference in later stages. We are taking an example of *Luzulaforsteri*of Juncaceae for describing the development of monocotyledonous embryo. Here the development of embryo is also Onagrad or Crucifer type.

The early development of dicot and monocot embryos are similar uptooctant stage. Later on differentiation starts.

1. The zygote or oospore elongates and then divides transversely to form basal and terminal cells.

2. The basal cell (towards micropylar end) produces a large swollen, vesicular suspensor cell. It may function as haustorium.

3. The terminal cell divides by another transverse wall to form two cells.

4. The top cell after a series of divisions forms plumule and a single cotyledon.

5. Cotyledon called scutellum, grows rapidly and pushes the terminal plumule to one side. The plumule comes to lie in a depression.

6. The middle cell, after many divisions forms hypocotyl and radicle. It also adds a few cells to the suspensor.

7. In some cereals both plumule and radicle get covered by sheaths developed from scutellum called coleoptile and coleorhiza respectively.

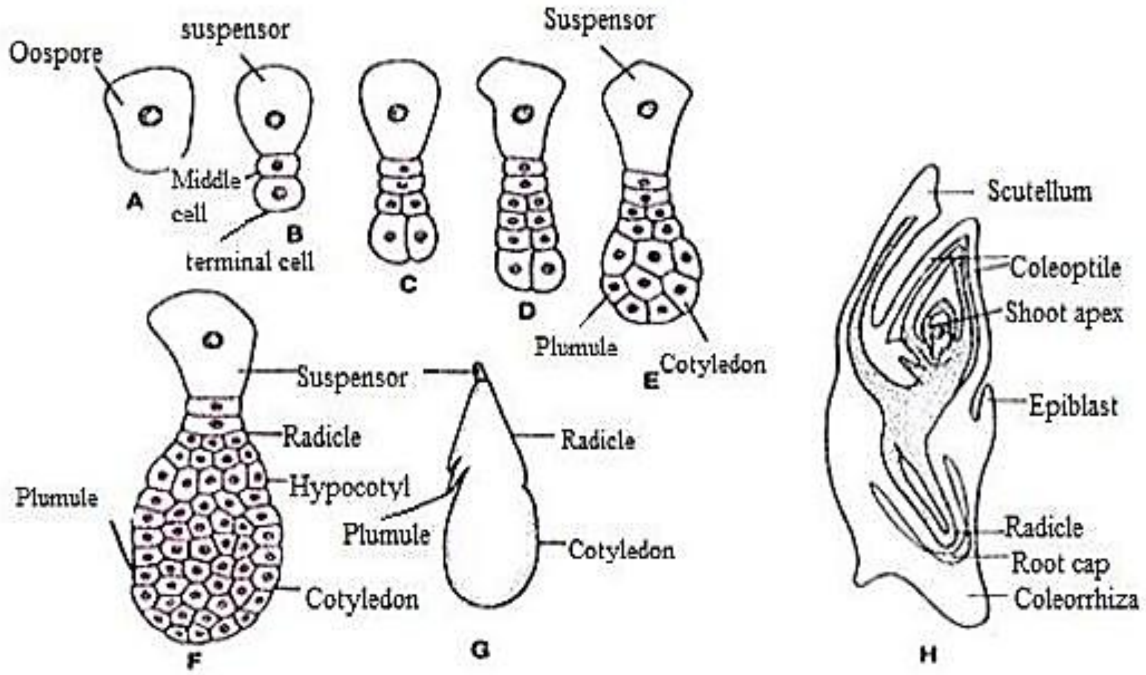

Figure7.5 A-G: Stages in development of a monocot embryo; **H.** A monocot embryo of a grass

Structure of Monocot Embryo

The embryos of monocotyledons have only one cotyledon. In grass family (Poaceae), this cotyledon is called scutellum. It is situated towards lateral side of embryonal axis. This axis at its lower end has radicle and root cap enclosed in a sheath called coleorhiza **(Figure 7.5)**. The part of axis above the level of attachment of scutellum is called epicotyl. It has shoot apex and few leaf primordia enclosed in a hollow foliar structure called coleoptile. Epiblast represents rudiments of second cotyledon.

Monocot embryo

1. A typical monocot embryo consists of an embryonal axis and one cotyledon.
2. In grasses, this cotyledon is called scutellum.
3. Embryonal axis at its upper end is called epicotyl which forms shoot.
4. Embryonal axis at its lower end is called hypocotyl which forms radicle.
5. The root tip is covered with a sheath (coleorhiza).

SAQ.3

a. The early development of dicot and monocot embryos are similar upto__________stage.

b. The top cell after a series of divisions forms_______________and a single cotyledon

c. Embryonal axis at its lower end is called_________which forms radicle.

d. In grasses, this cotyledon is called__________.

e. The root tip is covered with a sheath called as_______________.

7.6 Summary

- Zygote or oospore forms embryo.
- On the basis of plane of division of the terminal cell in the 2-celled proembryo and the contribution of the basal cell and terminal cells in the formation of embryo proper, six types of embryogeny (embryo development) have been reported by Johansen (1950) among the Angiosperms i.e. Onagrad or Crucifer, Asterad, Solanad, Caryophyllad, Chenopodiad and peperad types.
- A typical dicotyledonous embryo consists of an embryonal axis and two cotyledons.
- A typical monocotyledonous embryo consists of an embryonal axis and one cotyledon.

7.7 Terminal question

Q.1 Define endosperm.

Answer:---

Q.2 What is the main role of endosperm?

Answer:---

Q.3 Differentiate dicot and monocot embryo.

Answer:---

Q.4 Are Angiospermic and Gymnospermic endosperms same?

A**nswer:**--

Short Questions

Q.5 Write short notes on:

1. Types of endosperm
2. Embryogenesis
3. Types of embryo developments
4. Process of fertilization in flowering plants

Q.6 Multiple choice questions:

1. Endosperm is formed from:

   (a) Primary endosperm nucleus

   (b) Secondary nucleus

   (c) Egg

   (d) Embryo

2. Two- celled proembryo has:

   (a) Apical cell and terminal cell

   (b) Suspensor cells only

   (c) Spore cells

   (d) Basal cell and terminal cell

3. In dicots embryo development, the hypophysis is formed from:

   (a) Terminal cell

   (b) Embryo cell

   (c) Suspensor cell

   (d) None

3 The development of several embryos within the same ovule is known as:

   (a) Embryony

   (b) Polyembryony

   (c) Both

   (d) None

5. Endosperm:
(a) Provide nutrient to the embryo
(b) First cell of male gametophyte
(c) Produced by syngamy
(d) Product of meiosis in microspore mother cell

7.8 Answers

Q. No. 6 1. (a) 2. (d) 3. (c) 4. (b) 5. (a)

SAQ.1

a. Triple**b.** Nuclear**c.** Watery**d.**Helobial**e.**Cotyledons

SAQ.2

a. Embryogenesis **b.** Transverse **c.** 610 **d.**Haustorium**e.**Protoderm

SAQ.3

a. Octant **b.** Plumule**c.** Hypocotyl **d.** Scutellum **e.** Coleorhiza

Unit- VIII

Polyembryony and Apomixis

Structure

8.1 Introduction

After the study of post fertilization development process, some topics has been thrown light on apomixis, adventives embryony, polyembryony as well as on parthenocarpy.

Objectives

After studying this unit you will be able:

- To study the polyembryony and its types.
- To familiar with terms like apomixis, apogamy, apospory, parthenogenesis etc.
- To define parthenocarpy.

8.2 Polyembryony

After fertilization, ovules mature into seeds. In normal case, a single embryo is present in each seed but sometimes more than one embryo may present in a seed. When a seed contain more than one embryo, this condition is termed as polyembryony. Therefore, polyembryony has been defined by many workers as the occurrence of more than one embryo in a seed or "The development of several embryos within the same ovule."

Polyembryony is very common among gymnosperms but when we are talking about angiosperms, it is very rare. You can find it in *Citrus* species like lemons, oranges **(Figure 8.1)** and also in few *Quercus* species. Additional embryos do not always mature. They may degenerate during the course of development. The mature seed thus has only one embryo. The first case of polyembryony was reported by **Antoni van Leeuwenhoek in 1719** in certain **orange seeds**. Since then it has been observed in large number of plants.

Figure 8.1 Multiple seedlings grow from a single mandarin orange seed as the result of polyembryony

Classification of Polyembryony

In broad sense it is of two types:

1. Spontaneous- includes instances of naturally occurring polyembryony.

2. Induced- includes instances of experimentally induced polyembryony.

Ernst (1901, 1910) divides spontaneous polyembrony into two categories:

1. True polyembryony- development of two or more embryos in same embryo sac

2. False polyembryony - development of embryos in more than one embryo sac within the same ovule

Yakovlev (1967) divides spontaneous polyembrony into two categories on genetic basis-

1. Gametophytic: arising from any gametic cell of the embryo sac after or without fertilization.

2. Sporophytic: arising from the zygote, proembryo or the initial sporophytic cells of the ovule (nucellus, integuments).

There are number of factors responsible for polyembryony in angiosperms and on the basis of these factors the following four types of polyembryony have been recognized in angiosperms.

1. Cleavage polyembryony resulted due to cleavage or splitting of the proembryo.

2. Embryos from cells of the embryo sac other than the egg.

3. More than one embryo sac in the same ovule.

4. Activation of some sporophytic cells of the ovule.

1. Cleavage Polyembryony

Splitting of zygote or proembryo occurs and each split part develops into an individual embryo. This kind of polyembryony is called as cleavage polyembryony. It is very common phenomenon among gymnosperms and also reported in angiosperm plants e.g. *Erythronium*,**(Figure 8.2)**, *Nicotianarustica.*

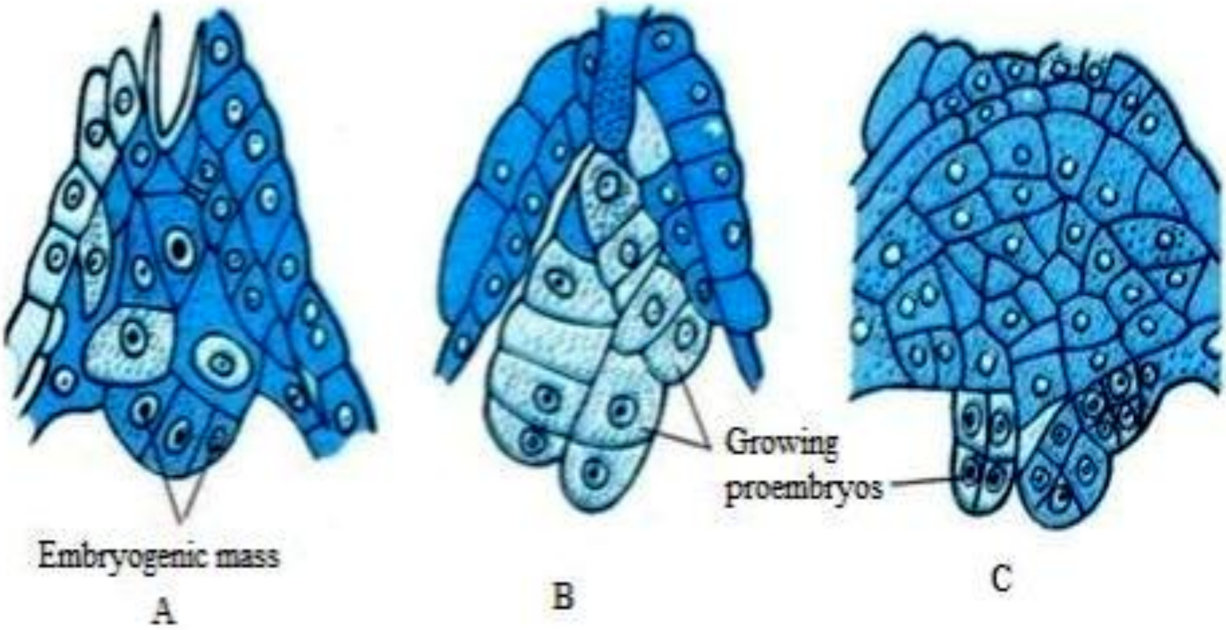

Figure 8.2:A-C showing cleavage polyembryony: **A.** Embryonic mass formed by the basal cell of the zygote in *Erythroniumamericanum*; **B-C.** Differentiation of embryos from the cells of the embryonic mass.

2. Embryos from cells of the embryo sac other than the egg

In this, the additional embryo forms mostly from synergids e.g. *Argemonemexicana, Phaseolus vulgaris*. Synergid embryo thus formed is haploid which can easily be distinguished from diploid zygotic embryo. Embryos can also be formed from antipodal cells e.g. *Ulnus* species **(Figure 8.3)**.

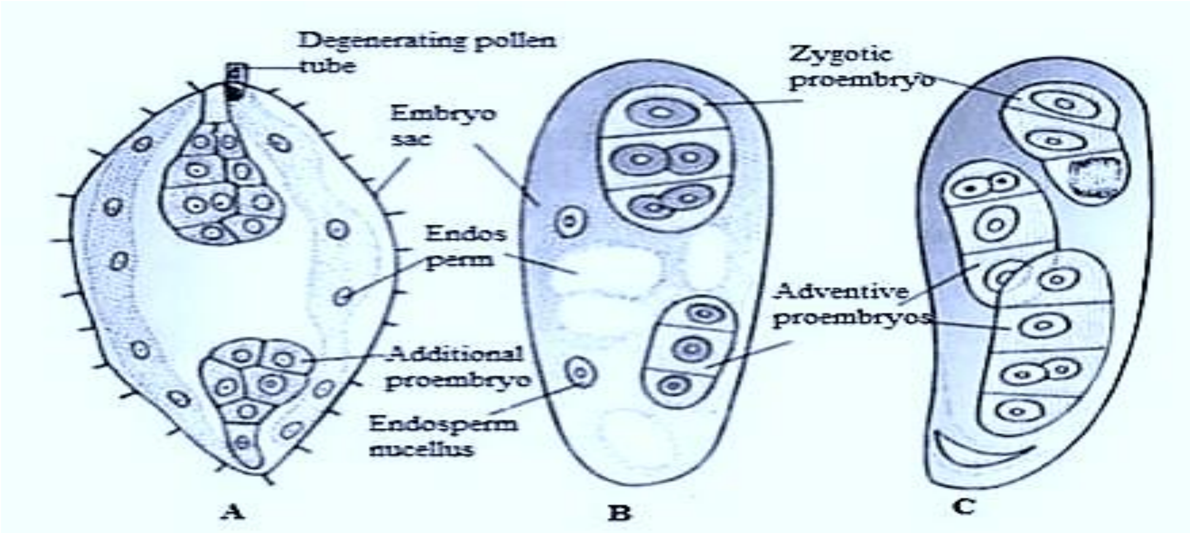

Figure 8.3: Polyembryony:A. Development of embryo from antipodal cells; **B-C.** Adventive proembryos developed from the cells of nucellus (they grow along with the zygotic embryos)

3. More than one embryo sac in the same ovule

Occurrence of multiple embryo sacs in an ovule may be from derivatives of the same megaspore mother cell or from derivatives of two or more megaspore mother cells or from nucellar cells e.g. twin embryo sacs within an ovule in *Casuarina, Citrus*.

4. Activation of some sporophytic cells of the ovule

We know that the embryos arising from the maternal sporophytic tissues (outside the embryo sac for example- nucellus and integuments) are called adventive embryos. Polyembryony because of adventives embryos is the most common type of polyembryony and known as adventive polyembryony or nucellar polyembryony e.g. *Citrus, Mangifera, Opuntia*.

SAQ.1

a. _______________polyembryony is development of two or more embryos in same embryo sac.

b. _____________polyembryony resulted due to cleavage or splitting of the proembryo.

c. When a seed contains more than one embryo, this condition is termed as_______________.

d. Embryos can also be formed from____________cells in *Ulnus* species

e. In *Citrus*, ___________polyembryony is found.

8.3 Apomixis

"Reproduction without fertilization"

Apomixis in flowering plants is defined as the asexual formation of a seed from the maternal tissues of the ovule, avoiding the processes of meiosis and fertilization, leading to embryo development.

The term Apomixis was first coined by Hackel in 1893. Apomixis, derived from two Greek word "Apo" (away from) and "mixis" (act of mixing or mingling). Winkler (1908) explained the term apomixis as the **substitution of sexual reproduction (amphimixis) by any such method which does not involve meiosis and syngamy.**

or we can say that Winkler used the term apomixis to signify any asexual method of propagation not involving the normal production of embryo by fertilization. It includes even propagation by bulbils.

The first discovery of this phenomenon is credited to **Leeuwenhoek** as early as 1719 in *Citrus* seeds.

When we are talking about asexual formation of seed, in this sense apomixis is synonymous with **agamospermy: seed formation without fertilization of the egg cell.** In some plants meiosis [which converts a diploid sporophytic cell into four haploid gametophytic cells] and **fertilization** [where two haploid gametes of opposite sex fuse to re-establish the diploid sporophytic generation], the two very important necessary processes of sexual cycle (amphimixis) are interrupted. Even then a viable embryo if formed resulting into asexual seeds. When these asexual seeds produce plants identical to the female parent are called apomictic seeds and the phenomenon is known as apomixis.

The plants showing apomixis are known as apomictic plants. It is most common in Poaceae, Asteraceae, Rosaceae and Rutaceae.

When apomixis is the only method of reproduction in a plant species, it is known as obligate apomixis. When gametic and apomictic reproduction occurs in the same plant, it is known as facultative apomixis.

Apomixis is of the following types as suggested by Maheshwari (1954):

i. Non-recurrent apomixis
ii. Recurrent apomixis
iii. Adventive apomixis

iv. Vegetative apomixis

(i) Non-recurrent apomixis:

Non-recurrent means which cannot be repeated. In this type of apomixis, the megaspore mother cell undergoes normal meiotic division and one of the four megaspores thus formed develops into haploid female gametophyte (i.e. embryo sac). However, there is no fertilization and the embryo arises directly from normal egg-cell (n). Since an egg cell is haploid, the resulting embryo will also be haploid and so sterile, therefore the process cannot be repeated in the next generation.

Haploid parthenogenesis (the embryo develops from the unfertilized egg) and haploid apogamy (the embryo develops from some other cell of the embryo sac like antipodal cell or synergid cell) are non- recurrent apomixis. Such types of apomixis are of rare occurrence.

(ii) Recurrent apomixis:

Recurrent means which can be repeated. In recurrent apomixis, the nuclei of the embryo sac are usually diploid. Such embryo sac may arise either from a cell of the archesporium due to disturbance in meiosis (generative apospory) or from some other cell of the nucellus due to disintegration of megaspore mother cell (somatic apospory).

The embryo subsequently develops directly from the diploid egg-cell without fertilization. Somatic apospory, diploid parthenogenesis and diploid apogamy are recurrent apomixis. However, diploid parthenogenesis or apogamy occurs only in aposporic (somatic) embryo-sacs. Therefore, it is the somatic or diploid apospory that constitutes the recurrent apomixis. Such apomixis occurs in some species of *Crepis, Taraxacum*, *Paa* (blue grass), and *Allium* (onion) without the stimulus of pollination.

(iii) Adventive apomixis:

In it, the development of embryo takes place from any diploid cell of the ovule lying outside the embryo sac. Since it takes place outside the embryo sac, it is not grouped with recurrent apomixis, though this is regenerated with the accuracy. In addition to such embryos, regular embryo within the embryo sac may also develop simultaneously, thus giving rise to polyembryony condition as in *Citrus, Opuntia*.

(iv) Vegetative apomixis:

In some cases, like *Poabulbosa* and some *Allium*, Agave and grass species, vegetative buds or bulbils, instead of flowers are produced in the inflorescence. They can also be reproduced without difficulty. However, Russian workers do not group this type of vegetative reproduction with apomixis.

Apomixis does not involve meiosis, so there is no segregation and recombination of chromosomes. Therefore, it could be useful in preserving desirable characters for indefinite period.

SAQ.2

a. The term Apomixis was first coined by Hackel____________in 1893.

b. When apomixis is the only method of reproduction in a plant species, it is known as _______apomixis.

c. In recurrent apomixis, the nuclei of the embryo sac are usually____________.

d. Apomixis does not involve meiosis, so there is no__________and recombination of chromosomes.

e. When gametic and apomictic reproduction occurs in the same plant, it is known as _________apomixis.

8.4 Some important terms

Parthenogenesis

Parthenogenesis means development of an embryo directly from an egg cell or a male gamete or it may be defined as - the development of female gamete into a new individual without fertilization. Parthenogenesis may be haploid or diploid as the case may be.

(i) Haploid parthenogenesis: Generally, normal haploid egg develops into an embryo, so the embryo and resultant plant are haploid. This type of parthenogenesis is termed as haploid parthenogenesis e.g. *Oenothera, Datura*. Plants thus produces are sterile.

(ii) Diploid parthenogenesis: When the cells of embryo sac including egg cell are already diploid as a result of apospory. This diploid egg when develops parthenogenetically into diploid embryo, termed as diploid parthenogenesis e.g. *Taraxacum.*

Apogamy

Apogamy is the development of a sporophyte (i.e. embryo) out of any gametophytic cell without fertilization i.e. the union of gametes. Plants formed in this way are sterile because they are haploid. Example - *Lilium, Nicotiana*. One of the two synergids develops into embryo in *Lilium* while male gamete forms embryo in *Nicotiana* by apogamy**(Figure 8.4)**.

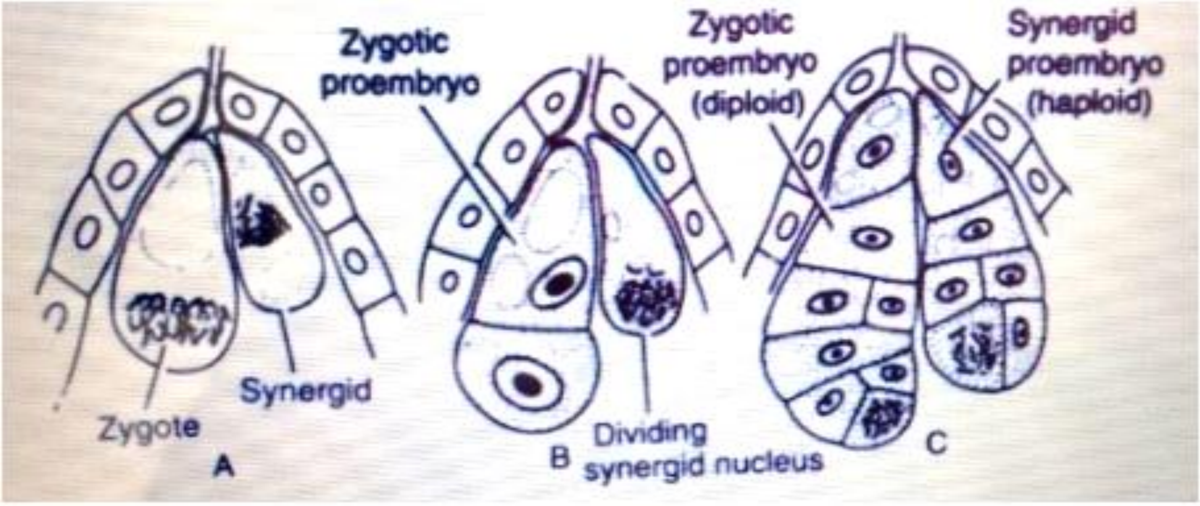

Figure 8.4: Haploid apogamy in *Lilium*A-B: dividing zygote and synergid; **C:** haploid (synergid proembryo) and diploid (zygotic proembryo) proembryos

Apospory

Apospory was discovered by Rosenberg (1907) in *Hieracium* species. In this type, megaspores are formed by usual process but all the four megaspores degenerate gradually. At the same time, somatic cells, usually nucellar cells enlarge and functions as initials of embryo sac. These initials enlarge, undergo mitotic divisions and develop embryo sacs. This type of apospory is also called as somatic apospory. Aposporic embryo sacs are diploid. It means the formation of gametophyte (i.e. embryo sac or pollen) on a sporophyte without any reduction division.

- **Apomixis:** reproduction without fertilization
- **Haploid parthenogenesis:** the embryo develops from the unfertilized egg
- **Diploid parthenogenesis:** the embryo develops from diploid egg formed as a result of aposopry
- **Haploid apogamy:** the embryo develops from some other cell of the embryo sac like antipodal cell or synergid cell
- **Apospory:** embryo sac arises from somatic cells like nucellus. Product is diploid. Therefore, apogamy is the development of a sporophyte (i.e. embryo) out of any gametophytic cell without fertilization i.e. the union of gametes while apospory is formation of gametophyte (i.e. embryo sac) out of sporophytic cell i.e. nucellar cell without reduction division.

Diagrammatic representation of embryo formation in different ways is given below **(Figure 8.5)**.

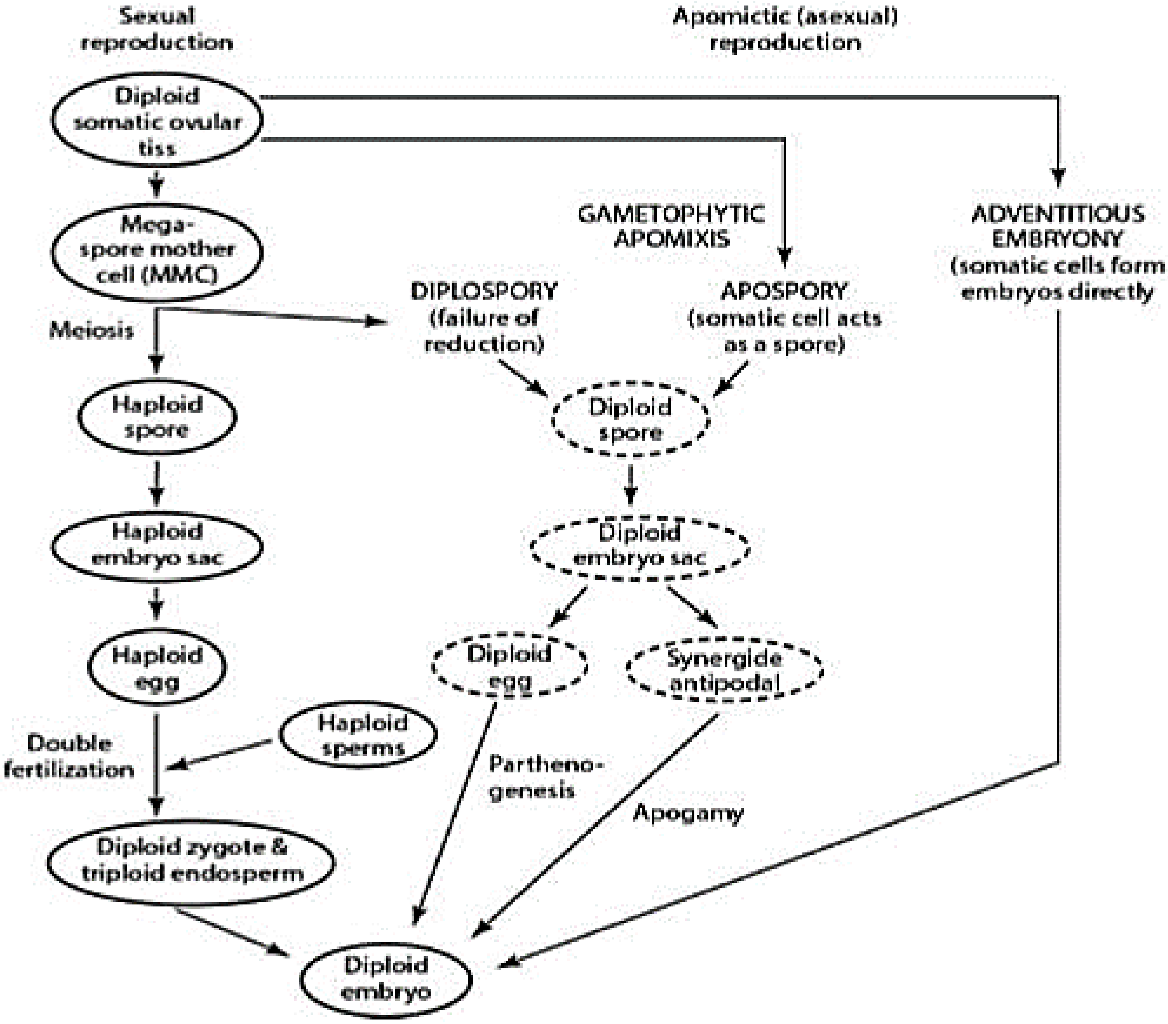

Figure 8.5: Diagrammatic representation of embryo formation through different ways

Adventive embryony

Adventive embryony is an embryony where an embryo develops directly from any diploid sporophytic cell for example- cells of nucellus, integument etc., without formation of gametophyte. This is also known as adventitious embryony or nucellarembryony. This may be considered as vegetative growth of the category of bulbils. Sometimes this is called sporophytic budding.

Or in simple way we can describe it as - cells outside the embryo sac also develop into embryos. These embryos are known as adventive embryos and the process as adventive embryony. Adventive embryony has great significance in horticulture and plant breeding. It provides uniform seedlings of the parental line as obtained through vegetative propagation by cuttings.

Parthe nocarpy

The term was introduced by Noll (1902). According to him, parthenocarpy means the development of fruits without pollination or any other stimulus. According to present concept- “Parthenocarpy is the formation of fruits without fertilization” (Nitsch, 1965).

Therefore, the fruits which develop without fertilization are called parthenocarpic fruits and the phenomenon is described as Parthenocarpy.

On the basis of requirement of pollination stimulus, it can be categorized into two categories:

(i) Stimulative parthenocarpy: In this type the parthenocarpic development of fruit may require the pollination stimulus.

(ii) Vegetative parthenocarpy: In this type the parthenocarpic development of fruit may occur in unpollinated flowers.

Nitsch (1963) had recognized three types of parthenocarpy:

1. Genetic

2. Environmental

3. Chemically induced

1-Genetic parthenocarpy

When many of the plants cultivated for their fruits show seeded as well as parthenocarpicvarities. This type of parthenocarpy is known to arise due to either mutations or hybridization. Example- Seedless navel oranges, *Citrus*, *Cucurbita*, *Musa*, *Punica* and *Vitis*.

2-Environmental parthenocarpy

Variations in environmental conditions such as frost, fog, temperature interfere with the normal functioning of sexual organs and causes parthenocarpy. Example- Seedless olives due to heavy fog, pears due to freezing temperature for 3-19 hours.

3-Chemically induced parthenocarpy

Plant growth regulators like auxins and gibberellins have been successfully use to induce parthenocarpy in a number of plants which normally bear seeded fruits e.g. parthenocarpic tomato, blackberry, strawberry, figs, *Citrus* etc.

8.5 Summary

- Development of several embryos within the same ovule is known as polyembryony.

- Reproduction without fertilization is referred as apomixis.
- Apogamy is the development of a sporophyte (i.e. embryo) out of any gametophytic cell without fertilization i.e. the union of gametes.
- Apospory is the formation of gametophyte (i.e. embryo sac) out of sporophytic cell i.e. nucellar cell without reduction division.
- When diploid embryo develops from any diploid cell of the ovule lying outside the embryo sac, this phenomenon is known as adventive embryony.
- Parthenocarpy is the formation of fruits without fertilization.

8.6 Terminal question

Q.1 What does the polyembryony means?

Answer:---

Q.2 What do you understand by parthenogenesis?

Answer:---

Q.3 Why apomixis is important?

Answer:---

Q.4 What do you understand by apomictic seeds?

A**nswer:**---

Short Questions

Q.5 Write short notes on:

1. Apogamy

2. Apospory

3. Parthenocarpy

4. Agamospermy

Q.6 Multiple choice questions:

1. The development of several embryos within the same ovule is known as:

(a) Embryony

(b) Polyembryony

(c) Both

(d) None

2. A special type of sexual reproduction in which egg develops without entrance of a sperm:

(a) Apospory

(b) Parthenogenesis

(c) Agamospermy

(d) Apogamy

3.Seed formation without fertilization of the egg cell called:

(a) Agamospermy

(b) Embryony

(c) Apogamy

(d) None of the above

8.7Answers

Q. No. 6 1. (b) 2. (b) 3. (a)

SAQ.1

a. True**b.** Cleavage**c.** Polyembryony**d.**antipodal **e.**adventive

SAQ.1

a. Hackel**b.** Obligate **c.** Diploid **d.** Segregation **e.** Facultative

Uttar Pradesh Rajarshi Tandon Open University

Bachelor of Science

DCEBY-105

Plant embryology and morphogenesis

Block

3 Plant Morphogenesis and Polarity

UNIT - IX	**Morphogenesis**
UNIT - X	**Polarity**

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DCEBY – 105 : Plant embryology and morphogenesis
ISBN-

Printed By: Chandrakala Universal Pvt. 42/7 Jawahar Lal Nehru Road, Prayagraj.

Block III

Plant Morphogenesis and Polarity

Morphogenesis means the origin of form, its controlled development and the effect of various external and internal factors which control the development of form. The study of this block tells you about morphogenesis, various factors of morphogenesis, polarity and symmetry in two units viz. IX and X which is as follows:

Unit IX- is morphogenesis which throws light on basic idea of morphogenesis and concept of differentiation in plants. Its also gives information about various morphogenetic factors that can affect phenomenon of morphogenesis.

Unit X- Deals with term polarity and how it affects morphogenesis. It also gives information about totipotency which is the basis of plant tissue culture.

Objectives:

After studying this unit you will be able to:

- Understand concept of morphogenesis and how process of differentiation plays a role in morphogenesis.
- Know about various morphogenetic factors which affects phenomenon of morphogenesis in plant.
- Know how polarity is developed which affects morphogenesis.
- Explain role to totipotency in growth and tissue culture of plant.

<u>**Unit- IX**</u>

Morphogenesis

Structure

9.1 Introduction

Morphogenesis is defined as a process concerned with formation and development of whole plant, a part of plant or a specific structure. During very early developmental stages polarity is established at the zygote stage due to which a polar difference is developed at both the ends of zygote. Cytological differences at the two ends determines the position of first cell division and also the fate of the structure which will be produced by the two cells (cells formed by division of zygote). Polarity is not limited to initial developmental stages but polarity is maintained throughout the growth. Plant axis (shoot and root tips) also exhibits polarity. If a portion of shoot is excised (cut) and allowed to regenerate the end toward shoot tips will always form shoot whereas end towards root will regenerate roots.

As in stem polarity is also exhibited in other organs like upper and lower surface of leaf, petals, sepals etc. Different parts of plant have different type of morphology. This diversity in different parts of plant is produced due to variation in growth rate of different parts and also because different parts show growth in different dimension. Rate of cell division, cell elongation along with orientation of plane of division and axis of cell elongation altogether establish the form of structure of plant.

Different factors (called as morphogenetic factors) affect growth and development of plants. These factors can be environmental such as light, temperature, water or nutritional factor, physical factors such as gravity, pressure and genetic factor. Genes are considered to be the ultimate factor which growth but they do not regulate growth independently. Instead genes interact with existing environmental conditions to control plant development.

During their growth and development plant cells exhibits a specific phenomenon called as totipotency. It is the ability of a cell two give rise to different types of cells and eventually lead to regeneration of a complete plant. Meristematic cells get differentiated to attain specific functions once the cell gets differentiated. They lose their ability to divide. However, differentiated plant cells can undergo a process of dedifferentiation (specially during plant tissue culture) and can again become meristematic. Now, such dedifferentiated cells can again redifferentiate (by a process known as redifferentiation) to form cells and tissues with specific structure and function.

Objectives

After studying this unit, you will be able:

- To understand concept of morphogenesis and how process of differentiation plays a role in morphogenesis.
- To study about different morphogenetic factors and how they affect morphogenesis of plants.

9.2 Basic idea of morphogenesis and concept of differentiation

The word morphogenesis comes from Greek words morphe (which means shape) and genesis (which means creation) to indicate a process of formation of a particular structure with a specific shape and size. Morphogenesis is considered to be a biological process which causes an organism to develop its shape. Morphogenesis is concerned with development of particular part or structure. Plants possess a longer period of morphogenesis. During development plants (unlike animals) do not exhibit a distinct body plan. Plants may grow and develop on and on till they die. This is because plants have meristematic tissue composed of actively dividing cells which result in formation of more and more new tissues, organs and structures throughout the life of plant.

The term differentiation was first of all used by Karl Willhelm. Differentiation refers to a process in which distinct (different) types of cells are formed from a precursor cell. Differentiation is a permanent localized qualitative change in size, biochemistry, structure and function of cells, tissues or organs. A cell which has ability to get differentiated into different cell types of an adult organism is called pluripotent. In plants such cells are also called as meristematic cells.

Different type of structural changes occurs inside a cell during the process of differentiation. These changes may occur in cell wall, protoplasm or both. For example when a cell gets differentiated into tracheary elements it loses its cytoplasm and the cells develop an elastic, strong, lingo cellulosic secondary cell wall to carry out transport of water.

Hence, meristematic cells are group of unspecialized (undifferentiated) cells which are capable of dividing throughout the life of plant and can get differentiated into different types of cells. When a cell gets differentiated it acquires specific morphological, physiological as well as biochemical properties. During growth and development of plant meristematic tissue give rise differentiated tissue where each cell has specified structure and function. Differentiation cells do not have ability to divide. In an another process known as dedifferentiation, differentiated tissue losses its differentiated state and becomes undifferentiated.

Such undifferentiated tissue can again undergo the process of differentiation known as redifferentiation and again become differentiated with specific structure and function. A dedifferentiated cell can divide and produce new cells **(Figure 9.1)**. Dedifferentiation is a commonly observed phenomenon during secondary growth in plants and also during the process of healing of wounds.

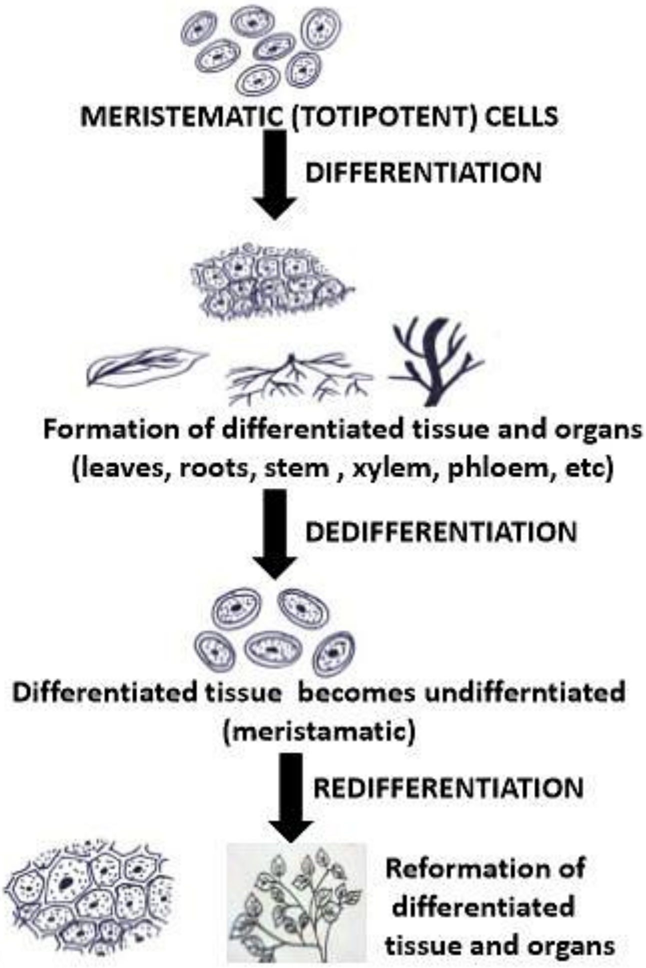


Figure 9.1: Diagrammatic representation of differentiation, dedifferentiation and redifferentiation

Plant cells are totipotent and possesses an inherent ability to undergo process of differentiation to give rise to different types of cells, which ultimately form different organs in plant system.

SAQ.1

a. During their growth and development plant, cells exhibits a specific phenomenon called as_____________.

b. The term differentiation was first of all used by_________.

c. Plants possess a_____________period of morphogenesis.

d. Dedifferentiation is a commonly observed phenomenon during______________in plants

9.3 Morphogenetic factors

1. Basic concept and effect of morphogenetic factors

Morphogenetic factors are physiological factors which induce regulate and coordinate morphogenetic events in plants. These factors can be a part of inner or outer environment of the plants. Morphogenetic factor can be divided into two groups:

(a) Environmental factors

(b) Genetic factors

Plants are multicellular organisms which survive in an environment which is complex and keeps on changing. Genetic makeup (genome / total genes present in nucleus) remains unchanged except for rarely occurring somoclonal variation. Now, even since there is no change in genetic constitution of plant but plants do exhibit phenotypic changes i.e. their appearance changes or gets modified with changes in their environment. Such phenotypic changes which occur in plants are considered to have occurred due to environmental factors. However, it is quite difficult to judge whether the morphogenetic change occurring in plant is due to genetic factor or environmental factor since both environmental as well as genetic factors are operating simultaneously. Responses such as flowering, thickness of cuticle, height of plant are greatly influenced by environment and gets altered according to the changing environment (change in temperature, pH, light, moisture etc).

Whereas characters such as formation of pits on side walls of vessels, arrangement of leaves etc. do not change with the change in environmental conditions. The degree of lobbing in leaves is greatly influenced by changes in temperature.

Another class of factors which influence plant growth or morphogenesis are nutrients. They act as chemical factors, come into plant body from outside and participate in biochemical processoccurring inside the plant. There are several growth substances which significantly influence morphogenesis in plants.

There are three possible attributes of action of morphogenetic factors.

(1) It is not necessary that a morphogenetic factor may directly result in a response but it may act as a stimuli to trigger other biochemical reaction in an organism.

(2) One morphogenetic factor can significantly influence or modify the action of another factor. No factor can act independently; response mediated by each factor is dependent upon the environment as well as on the status of plant.

(3) A plant is not a constant system i.e. character of plant changes from one phase of life cycle to another and also from one part of plant to other part of the plant.

Hence, plants may exhibit different response to same morphogenetic factor in different phases of life cycle. And also different part of plant may respond differently to same morphogenetic factor.

2. Morphogenetic effect of light

As we all know that light is one of the most crucial factors for growth, development and survival of plants. Light is required by the plants for vital processes such as photosynthesis, photo morphogenesis etc. Beside these processes, light also influences several other physiological processes. One of the most prominent effect of light as morphogenetic factor is that any plant reaches its maximum height with optimum growth only when the plant is exposed to sufficient amount of light. If insufficient light is provided the plants exhibited retarded growth even if supplied with sufficient water, nutrients and temperature.

There are three aspects of light which influence growth of plants:

(a) Intensity: It is the measure of brightness of light or other illumination i.e. actual energy of the radiation.

(b) Quality: It refers to wavelength of the light perceived by plants.

(c) Duration: By duration it means the length of lightness (day) and darkness (night) to which a plant is exposed.

The effect of light can have different effect on different parts of plant. Some of the effect of light on plants are:

- Rate of photosynthesis generally increases with increase in intensity of light to a certain extent.
- Intensity of light also affects qualitative traits such as strength of stem, development of xylem and phloem etc.
- Plants grown in shade have comparatively small root system.
- Light intensity is directly proportional to width of stem.
- Some herbaceous plants show zig-zag growth pattern in light but grow straight if same plants are grown in darkness.
- Whenever we think of light and plants. We get an image that light is required for photosynthesis by plants. But light is also needed by plants which lack chlorophyll.
- Etiolation is an important effect of light intensity. Plant grown in darkness are somewhat with pale leaves, weak roots and poorly developed xylem and phloem.
- Longer wavelength of light (red light) enhance elongation cells and tissues whereas blue light tends to present elongation.
- Quality of light also effects flowering in plants.
- Beside quality duration of light (photoperiodism) also effects flowering in plants.
- The length of photoperiod may also effect differentiation of sex e.g. in Cannabis sativa, when 16 hours photoperiod is given flowering occurs within 4-6 week. About half plants are male and half females. However, same plants when provided with 8 hours photoperiod, enhanced and fast development occurs with flowering occurring within 3-4 weeks and about half the plants are hermaphrodites and half females.

3. Morphogenetic effect of water

Water is another important morphogenetic factor which influences growth, development and morphogenesis in plants. Water is one of the key requires for photosynthesis to occur. Deficiency of water results in phenomenon known as xeromorphy. On the contrary presence of excess amount of water results in small roots. Poor development of mechanical and vascular tissue, leaves become thin, stomata are reduced or absent. These traits are generally regarded as adaptation to survive in aquatic environment. It has been found through several studies conducted by different scientist that there exists a definite correlation between the amount of water passing through the vascular tissue and the amount of vascular tissue developed.

Water also exerts other morphogenetic effects. Development of positive hydrostatic pressure generally occurs at early and rapid leaf growth and leads to formation of larger leaves. When the hydrostatic pressure is low at later stage smaller leaves are developed.

4. Mor phogenetic effect of temperature

For all living organisms including plants temperature is a crucial factor which influences morphogenesis as well as metabolic processes occurring inside the organism. A peculiar feature about temperature is that most of the response mediated by temperature are equally affected by light. The most important effect of temperature is on the growth of plant. Like any other living organisms plants also need an optimum temperature for growth and development. However, the optimum temperature may vary from one plant species to another, same plant may require different temperature during different phase of life cycle and moreover optimum temperature may be different for different region of plant.

As we study the concept of photoperiodism similarly there exists thermoperiodism. It refers to daily rhythm in reaction to temperature. If plant is provided with constant temperature throughout 24 hours, many plant show slow growth as compared to the growth obtained when the same plants are grown in comparatively warmer days and cooler nights.

A plant usually contains many buds out of which several buds do not develop. Significant amount of study has been conducted to find out which factors or growth substances decide that which bud will develop and which will not. Temperature is one of crucial factors which influences breaking of bud dormancy. Low temperature is considered to be an effective treatment for breaking dormancy.

Another morphogenetic effect of temperature is observed in form of vernalization. Vernalization is a process of providing low temperature for induction or acceleration of flowering. For some plants vernalization is a must for flower to occur. In Horticulture practice, seeds and seedlings are intentionally given treatment of low temperature to induce early flowering. In a study conducted by Burstrom (1956) it was found that exposure to high temperature results in reduction in length of root cells. This is due to shorter period of cell elongation.

5. Morphogenetic effect of mechanical factors

Physical factors such as compression, tension, bending and swaying, gravity also effect growth and development of plants. These factors are also referred to as mechanical factors. These factors may be called as mechanical but they are quite simple in character as compared to temperature and light.

Mechanical factors influence morphogenesis indirectly by affecting the physiological process occurring in plants. There are plants which display thigmotropism (response to contact). This type of response also involves morphogenetic changes. For example, when a tip of a tendril is touched by another branch or wire any other material tendril tends to coil around the wire or branch to provide support to the plant. This response involves enhanced growth of tendril in the direction of the support. When the stem of herbaceous plant bents, smaller cells are formed on convex side where as thick walled cells are formed on concave side. This difference is due to mechanical strain. Cells on convex side are under tension and cells on the concave side are under compression.

Gravity is another factor which influences growth of plants. Unlike other morphogenetic factors gravity is continuous, unchanging in intensity and also constant in direction. Downward growth of primary root, upward growth of main stem, etc are considered to be manifestations of geotropic growth reaction. Effect of gravity and light appears to be indistinguishable from one another. A change in relation to one generally produces a change in relation to the other. However unlike light (which directly affects morphogenesis) gravity exerts an indirect effect (by influencing other factors) on plant. Gravity is also known to play an important role in distribution of growth substances.

6. Morphogenetic effect of chemical factors

Chemical factors also affect morphogenesis in plants. Normally chemical factor are known to execute their effect on physiological processes occurring inside an organism but beside this they do affect form and structure of plant. Till now we have studied about factors such as light, temperature, water, gravity which execute their effect on plant through external environment. But chemical factors influence morphogenesis through external as well as internal environment. There is another peculiar feature of chemical factors that their effect can be localized to a particular part of plant instead of affecting the whole plant. Effect of chemical substance varies from time to time and from one phase of plant life cycle to another. Different elements are required by living organisms for several physiological functions. Elements such as O, N, K, Mg, C, Ca are considered to be macro elements. Since they are needed in larger amounts on the other hand elements such as B, Cu, Zn, Co, Mn are known as microelements (trace elements) as they are required in micro quantities by living organisms.

Nitrogen is essential constituent of all the proteins. Nitrogen is also reported to enhance growth of plants. In a study conducted by Burkholder and Mc Veigh in maize plant displayed better meristematic growth and enhanced length and diameter of stem when cultivated in presence sufficient quality of nitrogen. Nitrogen is also known to enhance differentiation in phloem with increased growth of sieve tube and vessels.

The ratio of C/N is also known to affect morphogenesis. Nitrogen is known to support vegetative growth hence plants having low C/N ratio tends to possess few flowers or fruits. Whereas when the ratio of C/N is high abundant flowering and fruiting occurs. Studies conducted have also related C/N ratio to the ratio of shoot length and root length.

Phosphorus is another element which is a prime constituent of nucleic acid (DNA and RNA). Besides being an important part of DNA and RNA, phosphorus also promotes cell division in roots but has little effect on elongation of stem. If we compare effect of phosphorus to that of nitrogen, elongation of stem is promoted by nitrogen but nitrogen does not directly affect cell division.

Calcium is known to support formation of cell wall. However, calcium is not directly a part of composition of cell wall but it produces its effect by bringing changes in cytoplasm. Zn is a trace element but is known to have an indirect effect on maintaining auxin in its active state. Boron is also required for cell wall formation. Deficiency of Boron causes hypertrophy and hyperplasia of tissue.

Plant hormones better known as plant growth regulators also control and coordinate morphogenesis in plants. Auxin and cytokinin remain to be the most significant plant hormones, along with them ethylene is crucial for fruit ripening, Gibberellic acid for germination. Almost all the morphogenesis response or growth shown by plants is mediated by one or the other hormone.

7. Morphogenetic effect of genetic factor

Genes are known to have specific response to a specific environment. We are very well familiar with George Mendel’s law of genetics. In his first law called as Law of dominance he described how inheritance of genes governs formation of tall or short plants in *Pisumsativum*. Both types of plant (tall and short) can be easily differentiated from one another based upon their genetic composition. Transcription and translation of genes leads to synthesis of enzymes which directly regulate or control growth and morphogenesis in plants. Generally, any morphogenetic trait is not entirely controlled or affected by a single gene but many genes or polygenes collectively affect morphogenesis. One of the key effects of genes on morphology is seen in extent of growth as well as on distribution of growth. Several examples are available where shape of leaves, flowers, fruits is inherited and controlled by gene expression.

SAQ.2

a. Etiolation is an important effect of___________intensity.

b. _____________is a process of providing low temperature for induction or acceleration of flowering.

c. __________is essential constituent of all the proteins.

d. Deficiency of____________causes hypertrophy and hyperplasia of tissue.

Lamprent in his study found that in pea plant there is a long distance between first and second flower as compared to the total length of inflorescence. This is believed to be controlled by three genes. In corn grass due to a single gene dominant mutation results in formation of narrow leaves, many tillers and less number of male flower as compared to normal plant. In another plant *Aquilegia canadensis* a dwarf race with bushy and compact growth differs from normal plant by a single gene. There is another example of *Acetabularia* (marine alga) in which control of gene over form and morphology was determined. This alga has a branching, rhizoid base from this base rises a stalk which has a hat (umbrella-like structure). A single large nucleus is found to be located in the basal rhizoids.

There are two species of *Acetabularia* one is longer (*A. mediterranea*) and another shorter (*A. crenulata*). Both the species also differ in form of hat. In Hammering's grafting experiment stalk was excised (cut) from longer species and grafted onto the basal portion of shorter species, now a new hat formation will begin from the stalk, at initial stages the newly formed hat may look like the hat to the species to which stalk belongs but finally the hat formed was similar to the hat of species which contributed rhizoid (containing nucleus). Hence, it was clear that formation of hat in *Acetabularia* is controlled by gene present in nucleus **(Figure 9.2)**.

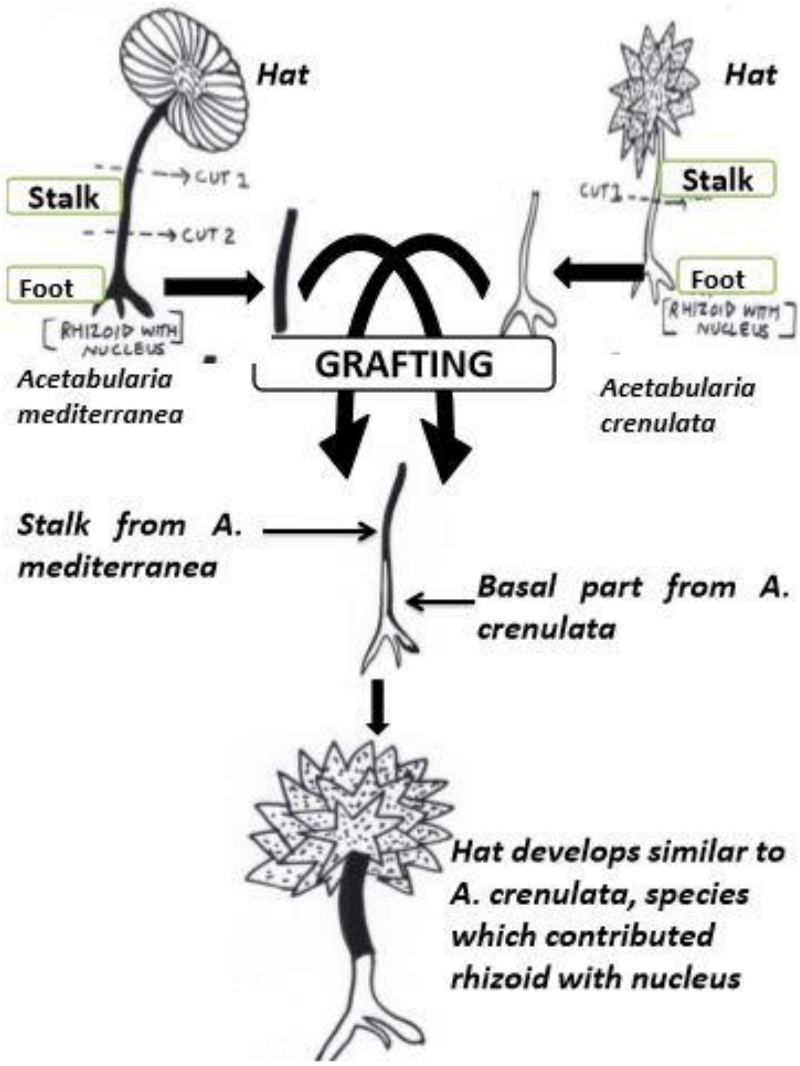


Figure 9.2: Demonstration of development of Hat in *Acetabularia* to be under genetic control

Some plants develop perfect or complete flower having both male (staminate) and female (pistillate) flowers. Such flowers are also known as hermaphrodite or bisexual and when male and female flowers develop on the same plant i.e. some flowers will be male and some flowers will be female such plant is called monoecious and the condition is known as monoecism whereas when male and female flowers develop on separate plant as seen in case of animals and the plant is called dioecious and the condition is known as dioecism In this case a male plant will develop only male flowers and female plant will develop only female flowers. Some common example of dioecious is strawberry (*Fragaria*). These types of sexual development in flowers are controlled by specific gene. However, environmental factors equally contribute to development of sex of flowers.

Genes also play a crucial role in production and distribution of growth substances which in turn affects morphology of plant. Genes also control photoperiodic effect which regulates flowering in plants. As a result of gene mutation, the flower time and season may get altered Most plant are haploid i.e. two sets of chromosome in each nucleus. In some plants number of sets of chromosome is multiplied. Such plants are called polyploids (triploid with three set of genes, tetraploid with four set of genes and so on). Polyploid plants are believed to exhibits better growth in terms of leaves size, enhanced number and size of fruits and flower etc. But this increase is restricted to certain level only. Plants with ploidy level higher than tetra or pentaploid show negative growth in terms of number and size of leaves, flower, fruit and other growth parameters.

9.4 Summary

- Morphogenesis is defined as a process concerned with formation and development of whole plant, a part of plant or a specific structure.
- During very early developmental stages polarity is established at the zygote stage.
- Different parts of plant have different type of morphology.
- This difference develops due to difference in growth pattern, growth rate and different dimension of growth.
- These factors can be environmental such as light, temperature, water etc
- Physical factors and mechanical factors also affect morphogenesis in plants.
- Beside environmental factor, genetic factor (genes) also control and regulate morphogenesis.
- Genes are considered to be the ultimate control agent of growth and development.
- However, genes alone do not control growth instead they interact with prevailing environmental conditions to regulate growth.
- Meristematic cells divide and differentiate to form different types of cells with specific structure and function.
- Differentiated cells loose their ability to divide.
- Structural changes occur inside a cell during the process of differentiation.
- These changes may occur in cell wall, protoplasm or both.
- Differentiated plant cells can undergo a process of dedifferentiation and can again become meristematic.
- Such dedifferentiated cells can again differentiate by a process known as redifferentiation.

- Different factors called as morphogenetic factors affect growth and development of plants.
- Light is one of the most crucial factors for growth, development and survival of plants.
- Light influences flowering, height, strength of stem, development of xylem and phloem etc.
- Plants also need an optimum temperature for growth and development. However, the optimum temperature may vary from one plant species to another.
- Physical factors such as compression, tension, bending and swaying, gravity also effect growth and development of plants.
- Chemical factors also affect morphogenesis in plants. Several elements are required by plants for normal formation and growth of tissues and organs.
- Nitrogen enhances differentiation in phloem and increases growth of sieve tube and vessels.
- The ratio of C/N is also known to affect morphogenesis.
- Phosphorus also promotes cell division in roots.
- Boron is also required for cell wall formation.
- Genes remain to be the most crucial factor governing growth and development as they control and regulate complete morphogenesis of plant stating from establishment of polarity, vegetative growth and reproductive growth.

9.5 Terminal Question

Q.1 Explain the meaning of morphogenetic factors. Mention about different types and function of morphogenetic factors?

Answer:---

Q.2 Differentiate between differentiation, dedifferentiation and redifferentiation?

Answer:---

Q.3 On what parameter effect of gravity differs from effect of other morphogenetic factors?

Answer:---

Q.4 Define the term correlation with reference to morphogenesis in plants?

Answer:---

Q.5 How does embryogenesis differ from rhizogenesis?

Answer:---

Short Questions

Q.6 Write short notes on:

1. Acclimatization
2. Callus
3. Etiolation
4. Genome
5. Hypertrophy

Q.7 Multiple choice questions:

1. Phosphorus:

(a) Promotes cell division in roots and enhance stem elongation

(b) Inhibits cell division in roots and enhance stem elongation

(c) Promotes cell division in roots and has little effect on stem elongation

(d) Inhibits cell division in roots & has little effect on stem elongation

2. Which of the following aspect of light influences morphogenesis:

(a) Duration
(b) Quality
(c) Intensity
(d) All of the above

3. Which of the following statement is false:

(a) Temperature significantly affects bud breaking
(b) Related growth occurs when insufficient light is supplied

(c) All the morphogenetic factor acts independently
(d) Blue light prevents cell elongation in plants

4. Choose the correct statement smaller:
(a) Under low hydrostatic pressure smaller size leaves develop
(b) Under high hydrostatic pressure larger size leaves develop row
(c) Hydrostatic pressure has no role in controlling size of leaves
(d) Both a and b are correct

5. Study the following statement and choose the correct one:
1. Different parts of same plant may respond differently to same temperature.
2. Thermoperiodism affects flowering but has no effect on fruit setting.
3. Shorter wavelength of light enhances elongation of cells
4. Exposure of high temperature results in reduction in length of root cells
(a) Only 2 is correct
(b) 1 and 2 are correct
(c) 1, 2 and 4 are correct
(d) 1, 3 and 4 are correct

9.6 Answers

Q. No. 7 1. (c) 2. (d) 3. (c) 4. (d) 5. (c)

SAQ.1

a. Totipotency**b.** Karl Willhelm**c.** Longer**d.**Secondary growth

SAQ.2

a. Light**b.** Vernalization**c.** Nitrogen**d.**Boron

Unit- X

Polarity

Structure

10.1 Introduction

Objectives

10.2Totipotency

10.3 Summary

10.4 Terminal Questions

10.5 Answers

10.1 Introduction

The term polarity means specific orientation of plant activity and morphogenesis in space. Plants are multicellular organisms made up of cells, tissue and organs. As we already know that in a multicellular organism cells, tissue and organs are integrated with one another to bring about overall functioning of an organism. There are many factors which regulate and control this integrated functioning. Among different factors polarity is one the most important factor of plant integrity.

Objectives

After studying this unit, you will be able -

- To know about how is polarity developed and how it affects morphogenesis
- To understand role of totipotency in growth of plants and in plant tissue culture

In plants axial polarity, dorsiventral polarity and radial polarity are known. However, when we talk of polarity in plants we generally refer to axial polarity. Axial polarity means presence of a well-defined longitudinal axis which bears lateral organs such as lateral branches, roots, leaves and flowers. The radial axis is most clearly evident in dicotyledonous species as the concentric rings of cell layers stem, hypocotyl and root with an increase in size across this axis can arise from the generation of new cell layers following divisions in the vascular cambium in the older plant.

There are several factors which influence polarity in plants. Physical factors like light, gravity, electric and magnetic field, chemical agents such as plant growth regulators and ions influence polarization in plants. Polarization is related to axial gradient of bioelectric potential (BEP) which develop from gradient of $Ca2+$, $K+$, $H+$ etc. Changes in membrane permeability to these ion generates a dielectric potential. Results obtained from studies conducted on plants such as *Arabidopsis*,*Capsella bursa-pastoris* have made it clear that apical-basal polarity is determined even before the first zygotic division in the egg.

Early events of zygote polarization have been very well studied in *Fucus* (brown alga). In *Fucus* polarization of zygote is initiated and influenced by various types of stimuli such as unidirectional light, temperature, electric field or chemical gradient. Axis formulation is associated with redistribution of plasma membrane components. Ca++ is the most important component which gets accumulated toward basal end during axial axis function.

In *Arabidopsis* during axial polarization, zygote divides by an asymmetric transverse division resulting in formation of two daughter cells of unequal size. One is the basal cell which is derived from vacuolar region and is larger in size and another cell is smaller upper cell which is derived from cytoplasmic region. Upper cell divides to form suspensor (containing six to nine cells). Only the upper most cell of suspensor called hypophysis is actually the part of embryo proper.

Although suspensor cells are known to have different functions such as they physically project the embryo into endosperm, avail a source of hormone and nutrient to the developing embryo, the suspensor cells undergo programmed cell death when embryo reaches its torpedo stage of development.

In *Fucus* the larger upper cell is known to form thallus cell from which develops the thallus structure of mature alga. On the other hand the small basal cell forms rhizoid which undergoes polarized growth. In ferns and mosses polarity can be induced by membrane bound biliprotein phytochrome.

There are two system under which induction of polarity in plants have been studied.

(A) The first system of polarity in plants is ROOT- RHIZOID POLARITY, this type of system studied in phaeophycean zygotes and in pteridophytic spores.

Development of polarity occurs parallel to ionic gradient of calcium, potassium and sodium. During polarization an increase influx of calcium ions occurs into the cell present in the future rhizoid pole. On the contrary a decreases influx of calcium ions occur in the opposite pole.

(B) Another system of polarity is SHOOT-ROOT POLARITY found in higher plants: (Development / induction of polarity in multicellular plants)

The earliest work related to shoot-root polarity was done by Marquis Duhamel du monceau in eighteenth century. In his work existence of two morphogenetic factors was proposed, one was a heavy root sap and another a light shoot sap. Both morphogenetic factors (shoot sap and root sap) were directed by gravity to their respective poles, where they got accumulated and shoot sap initiated formation of shoots and root sap gave rise to roots.

Zygote displays a specific cell polarity with a vacuolar pole present at micropylar site (which later develops into suspensor or root pole) and an opposed cytoplasmic pole (embryo pole). Establishing polarity is an important event for morphogenesis and development of plant. Particularly in plants polar differences can be identified at very early stage of development after the formulation of zygote. During the process of development of plant, polarity can also be seen in plant axis i.e. in shoot and root tips. This means that once a polarity is established it does not gets altered naturally. So if a part of shoot or root is existed and allowed to regenerate the end toward shoot tips always regenerates into shoot and the opposite end will develop roots. However, during the process of development either removal of one part of plant or changes in a part of plant significantly affect morphogenesis of one or more other parts of plant. This process is called as correlation and is generally mediated through nutrient and plant growth regulators.

10.2 Totipotency

1. Basic concept of totipotency

Totipotency refers to inherent genetic potential of a plant cell to regenerate into complete plant. Plant cells can follow a developmental pathway similar to that of a zygote resulting in formation of new plant. The concept of regeneration the entire plant from a single cell or tissue was conceptualized by G. Haberlandt in 1902, who is known as father of plant tissue culture.

F. C. Steward along with his colleagues developed a method for growing carrot tissue by taking small part, from the secondary phloem region of carrot root. This part was utilized as explants in the experiment. The explants were cultured by placing it onto a liquid medium under aseptic conditions. During the culture process the phloem tissue began to grow. Initially some single cells and some groups of cells became loosened from the surface of growing tissue and started growing separately. Some single cells developed somatic embryos or embryoids by a process now known as somatic embryogenesis. The embryo ultimately gave rise to shoot and root and the complete plant was regenerated **(Figure 10.1)**.

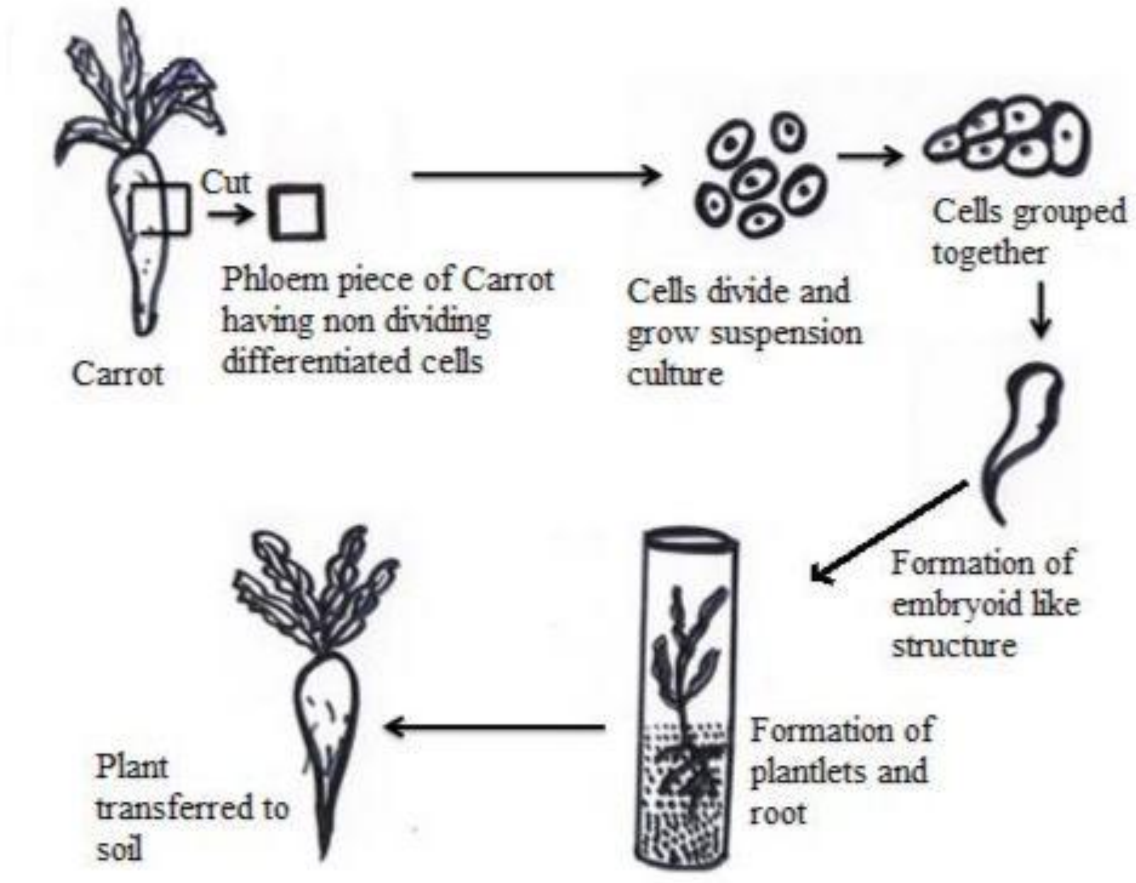


Figure 10.1: Regeneration of complete plant (carrot) from single cell

SAQ.1

a. The concept of____________the entire plant from a single cell or tissue was conceptualized by G. Haberlandt in 1902.

b. Some single cells developed somatic embryos or embryoids by a process now known as_________embryogenesis.

c. The embryo ultimately give rise to_______and________and the complete plant was regenerated.

2. Importance or significance of Totipotency

- The most important aspect/application of totipotency is reconstruction or regeneration of complete plant from any tissue or organ.

- Regeneration of plants from somatic cells through their ability totipotency has been utilized for vegetative propagation of many medicinal, aromatic and ornamental plants with economic importance.
- With the development of plant tissue culture technology large number of plants can be produced in short time interval. Totipotency is the underlying principle of regeneration of plants through plant tissue culture. Hence, endangered, rare and scarce plants can be mass propagated through the technique.
- Advancements made in plant science have resulted in development of genetically modified plants. Production of homozygous plants, haploid plants, somatic embryogenesis, somatic hybridization, protoplast (fusion and) culture etc. Totipotency is the basis of all the above mentioned developments made in plant science.
- In vitro regenerated cells, tissue, callus with totipotency potential can be preserved for long periods under liquid nitrogen. The process is known as cryopreservation. Whenever required these cells can be retrieved thawed and can be utilized for regeneration (since they are totipotent)

3. Totipotency and plant tissue culture

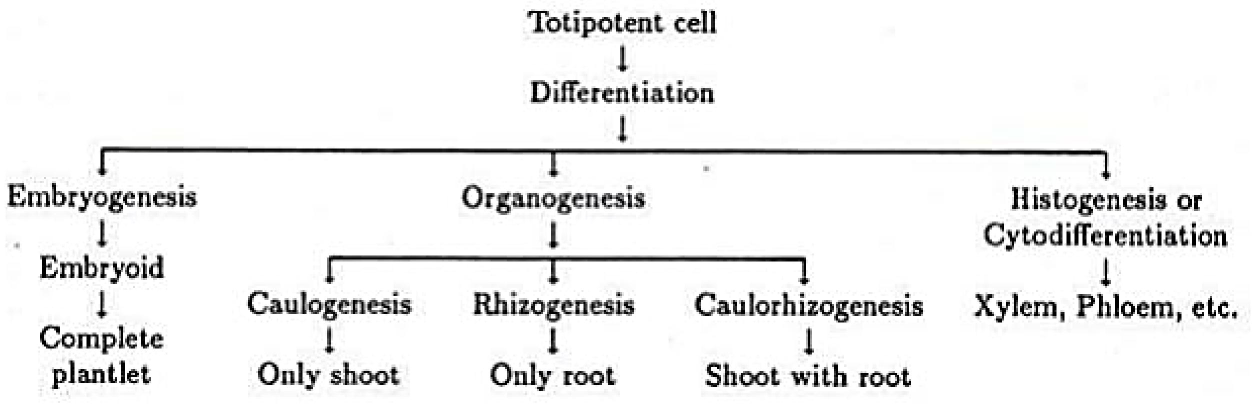
Plant tissue culture also known as in vitro micropropagation is a technique utilized for regeneration of plants under controlled conditions. The technique has been successfully utilized for regeneration, conversation of large number of medicinal, aromatic, ornamental and other plants on a large scale.

The entire success of plant tissue culture technology is based upon the totipotency of plant cells. Normally, we grow plants mainly through seeds or by methods of vegetative propagation including cutting, grafting, layering etc. But through the technique of tissue culture plants can be regenerated by culturing any part of the plant. The part of plant (cell, tissue, organ) excised to culture is called as explant. Explants are transferred to a culture medium aseptically. The cultures are then incubated under suitable temperature with proper light.

Now, during the process of incubation the explants which are differentiated tissue undergo the process of dedifferentiation and become undifferentiated and totipotent. Explants now undergo the process of redifferentiation and start growing to regenerate a new plant.

4. Different response of totipotent cells during in vitro culture process

When totipotent cells undergo the process of differentiation to form different types of cells and organ. There are basically three types of pathways which can be followed:



(a) Embryogenesis: Totipotent cells can divide and differentiate to give rise to embryoid structure. Formation of embryo is a bipolar structure and same structure give rise to root as well as shoot i.e. complete plant.

(b) Organogenesis: division and differentiation of totipotent cells may also result in formation of organs. If totipotent cell give rise to only shoot it is known as caulogenesis. However, rhizogenesis is process of formation of roots. In another process called as Caulorizogenesis formation of shoot as well as root occurs simultaneously.

(c) Histogenesis / Cyto differentiation: Totipotent cells may divide and differentiate and give rise to tissues like xylem, phloem etc**(Figure 10.2)**.

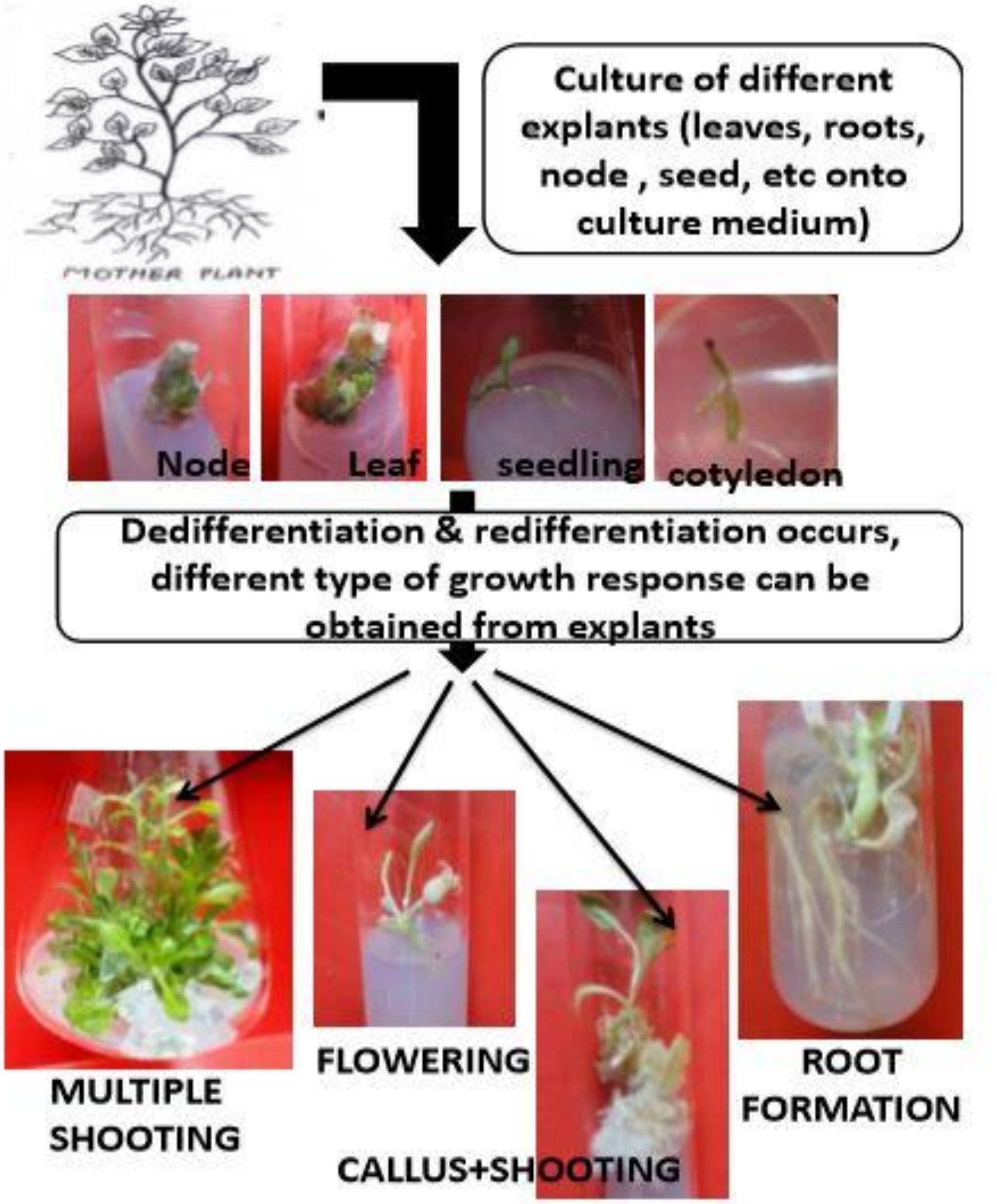


Figure 10.2 Depicting regeneration of different organs from different explant

In tissue culture process growth can be of two types direct and indirect. In direct growth formation of organs (shoots, roots or embryo) occurs directly from explant whereas in indirect growth first a callus (undifferentiated mass of cell) is formed. By further sub culturing of callus regeneration of shoot and roots can be obtained. The plant regenerated in laboratory conditions are then transferred to soil (natural conditions) through a process known as hardening or acclimatization.

Hence, totipotency forms the basis of plant tissue culture through which large number of plants can be regenerated in comparatively shorter duration of time.

There are several advantages of plant tissue culture.

1. Production of large number of plants.

2. Conservation of endangered species.

3. Production of hybrid plants.

4. Synthesis of secondary metabolites.

5. Production of virus resistant plants through meristem culture.

10.3 Summary

- During very early developmental stages polarity is established at the zygote stage.
- Due to this polarity difference at both the ends of zygote is established according to which different structures are developed at different poles.
- Axial polarity is most significant polarity pattern in plants which is represented by longitudinal axis which bears lateral organs such as lateral branches, roots, leaves and flowers.
- Totipotency is the ability of a cell to give rise to different types of cells and eventually lead to regeneration of a complete plant
- Totipotency is reconstruction or regeneration of complete plant from any tissue or organ.
- Totipotency forms the basis of plant tissue culture through which large number of plants can be regenerated in comparatively shorter duration of time.

10.4 Terminal Question

Q.1 Define polarity? Citing suitable examples mention about shoot root and root- rhizoid?

Answer:--

Q.2 Define totipotency? Elaborate upon the role of totipotency in plant tissue culture?

Answer:--

Q.3 Mention the significance & importance of totipotency.

Answer:--

Q.4 What is bioelectric potential?

Answer:---

Short Questions

Q.5 Write short notes on:

1. Differentiation, dedifferentiation and redifferentiation
2. Xeromorphy
3. Pluripotent cell
4. Symmetry

Q.6 Multiple choice questions:

1. Axial polarity represents:

a) Longitudinal axis with lateral branches and roots

b) Horizontal axis with lateral branches and roots

c) Both longitudinal and horizontal axis with branches roots and flower.

d) None of the above

2.Totipotency is:

a) Regeneration of complete plant from meristematic cells only

b) Regeneration of complete plant from any tissue or organ

c) Regeneration of complete plant from somatic cells only

d) Regeneration of complete plant from pluripotent cells

3. A differentiated cell:

a) Is pluripotent

b) Can divide and produce new cells

c) Cannot divide and produce new cells

d) Can give rise to different type of cell

4. Which of the following is not true?

a) Polarization is related to polarity

b) BEP develops from gradient of ions.

c) Ca^{++} ions is most crucial ion for development of polarity

d) All of the above

5. Choose the correct sequence:

a) Differentiation----Undifferentiated state----Dedifferentiation-----Redifferentiation

b) Dedifferentiation----Undifferentiated state----Redifferentiation-----Differentiation

c) Dedifferentiation----Differentiation----Redifferentiation-----Undifferentiated state

d) Differentiation----Dedifferentiation----Undifferentiated state-----Redifferentiation

10.5Answers

Q. No. 6 1. (a) 2. (b) 3. (c) 4. (d) 5. (d)

SAQ.1

a. Regeneration**b.** Somatic**c.** Root, shoot

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