

Block

4

ENDOSPERM AND EMBRYO

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Course Design Committee

Prof. A.K. Bhatnagar (Retd.)
Department of Botany,
University of Delhi, Delhi-110054

Dr. Eklavya Chauhan
Sr. Consultant,
SOS, IGNOU, New Delhi-110068

Dr. Bhupinder Dhir
Consultant,
SOS, IGNOU, New Delhi-110068

School of Sciences, IGNOU

Prof. M.S. Nathawat, Director, (Ex.)

Prof. Amrita Nigam

Prof. Jaswant Sokhi (Retd.)

Block Preparation Team

Prof. Amrita Nigam
SOS, IGNOU, New Delhi-110068

Dr. Bhupinder Dhir
Consultant,
SOS, IGNOU, New Delhi-110068

Dr. Kumkum Chaturvedi
Consultant,
SOS, IGNOU, New Delhi-110068

Editor

Dr. A.K. Kavathekar (Retd.)
Department of Botany,
Sri Venkateswara College,
University of Delhi,
New Delhi-110001

Course Coordinator: Prof. Amrita Nigam

Production

Mr. Hemant Kumar
SO(P), MPDD, IGNOU

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BLOCK 4 : ENDOSPERM AND EMBRYO

In block 4 you will study four units which include process of fertilization which leads to development of an ovule that later forms seed while the mature ovary develops into fruit. The embryo undergoes various changes in different stages of development and finally forms the plantlet. Some plants lack the normal course of sexual reproduction i.e. do not show fertilization to form embryo. This phenomenon of apomixis is a reproductive mechanism in which plant clones itself through seed without undergoing sexual reproduction. Reproduction occurs by special generative tissues without fertilization. It has been considered as a bypass of normal sexual process.

Unit 12 deals with endosperm its importance to the development of seeds. Endosperm is the part of a seed that stores food for the young seedling. It is a tissue produced inside the seeds of most of the flowering plants following double fertilization, where one of the gamete fuses with the egg cell (female gamete) and other one fuses with the polar nuclei or secondary nucleus in the central cell to form primary endosperm nucleus. The fertilized egg cell forms the zygote which develops into an embryo while the primary endosperm nucleus divides and develops into endosperm. Endosperm is triploid ($3n$) in most of the species. However it is diploid in all members of Onagraceae and pentaploid in *Fritillaria*.

Next Unit 13 describes process of double fertilisation is well-known in flowering plants and involves fusion of one of the male gametes with the egg (syngamy). This results in the formation of zygote which develops into the embryo. The process of growth and differentiation leads to formation of mature embryo. Embryogenesis is the process of development of embryo from the zygote. The cells of the embryo later on differentiate to form various tissues which develop into various organs.

In this Unit 14 you will appreciate the distinctive process of apomixis and polyembryony in plants. In certain plants embryos develop without sexual reproduction or fertilization. In these plants, the embryos develop from unfertilized eggs or from other cells of the embryo sac or ovule. This means that embryos are not produced as the result of syngamy but via process of apogamy or apomixis. The present unit will provide you an overview of apomixis and polyembryony.

In unit 15 you will study about the development of fruit and seed. Seed can be defined as a unit of reproduction having embryo and nutritive tissue called endosperm. It is enveloped by seed coat derived from the integuments of the ovule. After pollination the ovary develops into fruit. The fruit encloses the seeds. The fruit protects the seeds and help in their dispersal. Seeds of many plants remain viable in soil for long periods. They may undergo the period of dormancy and germinate only when conditions especially of temperature and moisture become suitable for their germination.

Objectives

After studying this block, you would be able to :

- ❖ describe the development of embryo through various stages (globular, torpedo stage, heart shape);
- ❖ specify the role of endosperm and its importance in embryo development ;
- ❖ describe the phenomenon of apomixis and polyembryony and discuss their significance and applications; and
- ❖ summarize the various events involved in the development of seeds, fruits and their dispersal.

UNIT 12

ENDOSPERM |

Structure

12.1	Introduction	12.7	Endosperm Variants
	Objectives		Composite Endosperm
12.2	Development of Endosperm		Ruminate Endosperm
12.3	Structure of Endosperm		Mosaic Endosperm
12.4	Nature of Endosperm	12.8	Functions of Endosperm
12.5	Types of Endosperm	12.9	Summary
	Nuclear Type	12.10	Terminal Questions
	Cellular Type	12.11	Answers
	Helobial Type		
12.6	Endosperm Haustoria		
	Endosperm with Chalazal Haustoria		
	Endosperm with Micropylar Haustoria		
	Endosperm with Micropylar and Chalazal Haustoria		

12.1 INTRODUCTION

In the previous units you have studied about the structure of anther and ovule, gametogenesis, pollination and fertilisation. In this unit you will study about the structure and development of endosperm in detail. Endosperm is the part of a seed that stores food for the young seedling. It is a tissue produced inside the seeds of most of the flowering plants following double fertilisation. Flowering plants are unique in exhibiting double fertilisation. In double fertilisation, two male gametes are delivered to the embryo sac through the pollen tube. One of the gamete fuses with the egg cell (female gamete) and other one fuses with the polar nuclei or secondary nucleus in the central cell to form primary endosperm nucleus. The fertilized egg cell forms the zygote which develops into an embryo. The primary endosperm nucleus divides and develops into endosperm. Endosperm is triploid ($3n$) in most of the species. However, it is

diploid in all members of Onagraceae and pentaploid in *Fritillaria*. It surrounds embryo and provides nutrition to the developing embryo. It is consumed entirely or partially by the developing embryo. When the seed germinates, endosperm nourishes the early seedling growth till it becomes capable of producing its own food by photosynthesis. In this unit you will be studying the process of endosperm development, types of endosperm and variations in their structure.

Objectives

After studying this unit you would be able to:

- ❖ explain the process of endosperm development;
- ❖ describe the structure of endosperm;
- ❖ list various types of endosperm and endosperm haustoria;
- ❖ exemplify the functions of endosperm;
- ❖ identify the morphological nature of endosperm; and
- ❖ enumerate the endosperm variants.

12.2 DEVELOPMENT OF ENDOSPERM

Endosperm is a nutritive tissue that helps in development of seed. At the end of the nineteenth century, with the discovery of the female gametophyte and the double-fertilisation process in flowering plants, several theories/hypotheses to explain the evolutionary origin of the endosperm were suggested. One hypothesis proposed a supernumerary (extra) embryo as the origin of endosperm. According to this model, production of two genetically identical individuals (organismal duplication) by double fertilisation favored the functional divergence of the two embryos. As a result, one of the embryos acquired a novel nourishing function to the benefit of the sibling. Later phylogenetic studies indicated that in *Ephedra* (Gnetales), Gymnospermae, production of twin zygotes showed that fertilisation of a binucleate egg can indeed produce two embryos in this genus. Embryology of basal angiosperms is phylogenetically closer to ancestral gymnosperm species. This is because most basal angiosperms possess a four-celled embryo sac and produce a diploid endosperm. Hence, this could be a remnant of the paleo-embryonic origin of the endosperm.

Second hypothesis predicted that the endosperm is a homolog of the gymnosperm female gametophyte that develops into endosperm after fertilisation. This hypothesis is supported by the observations that angiosperm endosperm development is proliferative and invasive as that of the gymnosperm female gametophyte. According to modern day concept, the origin of endosperm is basically linked to double fertilisation. It is produced by the fusion of polar nuclei (secondary nucleus) and sperm nucleus. The primary endosperm nucleus present in the embryo sac divides and forms the nutritive tissue called endosperm. It is a triploid ($3n$) structure. Endosperm can be absent in some families such as Podostemaceae, and short-lived in species

such as Orchidaceae. It can be maintained in the mature seed (as in wheat, castor and coconut), or absorbed by the developing embryo (pea, bean and *Arabidopsis*).

Endosperm cells are rich in food reserves, and are compactly arranged without intercellular spaces. The cells contain reserves such as carbohydrates, protein, and lipids though ratio of these components varies depending on the species. Endosperm plays a nutritive role during the development of embryo. It provides nourishment to the embryo from the proembryo stage till it becomes self sufficient and completes its development. Endosperm tissue is the source of growth regulators like gibberellins and cytokinins. Endosperm derives nutrition from the nucellus and integuments. In some families, development of endosperm haustoria leads to partial or entire absorption of nucellus and integuments.

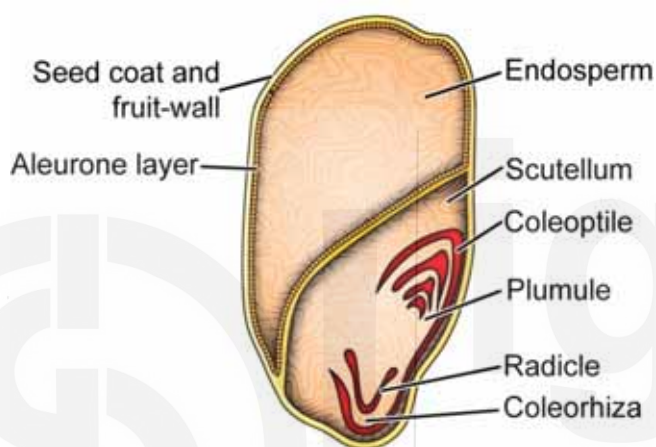


Fig 12.1: L.S. of Maize grain showing endosperm.

Different plants show different levels of endosperm persistence during seed development. In cereals, endosperm is formed and retained as a reserve tissue in the mature seed. In several dicotyledonous species, endosperm gets degraded by the time the embryo matures. Peas show presence of non-persistent endosperm which gets absorbed in the free-nuclear state. In the family Orchidaceae, endosperm nuclear divisions are terminated early in seed development or do not occur at all.

12.3 STRUCTURE OF ENDOSPERM

You know that endosperm is a triploid structure formed as a result of double fertilisation in angiosperms. A male gamete fuses with the polar nuclei or the fusion product of the polar nuclei, the secondary nucleus and forms the primary endosperm nucleus. The repeated divisions of the primary endosperm nucleus results in the formation of endosperm (Fig. 12.1). In some plants it shows variation in the ploidy due to difference in the number of polar nuclei which may be 1, 2, 4 or 8 depending upon the type of embryo sac. The number of polar nuclei contributing to the formation of endosperm is one in *Oenothera* leading to formation of diploid endosperm. In *Peperomia* eight polar nuclei, contribute to the endosperm development, hence the endosperm is $9n$. During further development the endosperm may undergo further polyploidization due to endomitosis and nuclear fusion. Highest level of ploidy has been noted in *Arum* where the nucleus of endosperm becomes $24576n$.

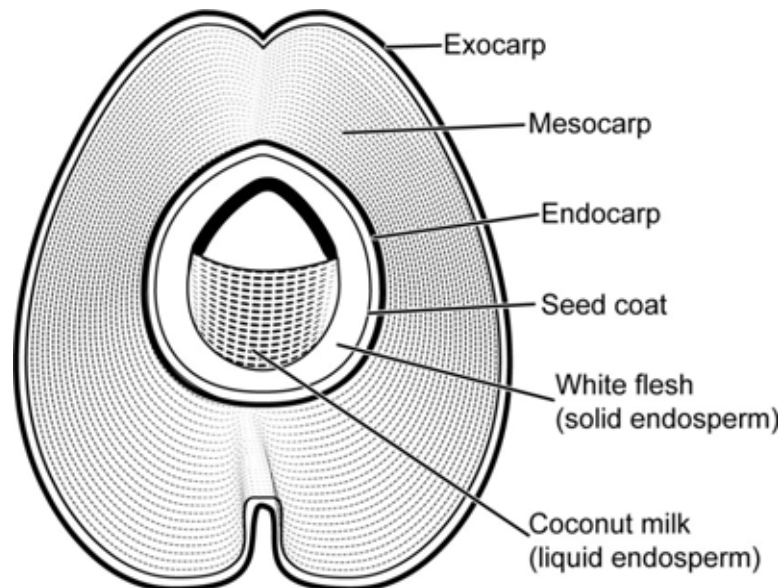


Fig 12.2: L.S. of *Cocos nucifera* fruit with seed.

The cells of the endosperm are thin-walled, large, isodiametric and store large food materials. The storage of starch, oil and proteins has been noted in the cells. The nuclei of these cells become disorganized due to deposition of food reserves. In mature seeds the endosperm represents an inactive tissue. Endosperm in some species is rich in starch (e.g., wheat, rice) or protein (gram, whereas in others it is forged with lipids (e.g., castor, sesame, coconut).

Coconut fruit has an exocarp impervious to water, fibrous mesocarp (source of coir) and hard endocarp. Inside, a thin seed coat surrounds solid white endosperm (edible part) with some liquid endosperm inside. At maturity only solid endosperm is present which is a source of coconut oil (Fig. 12.2).

Usually the endosperm is non-chlorophyllous. However, in some plants such as *Crinum* of Amaryllidaceae the seed coat as well as fruit wall are much diminished during seed development, allowing some light to penetrate and reach green endosperm for photosynthesis. In some cases the outermost layer of the endosperm becomes suberised and protective in function. In members of the family Poaceae (Graminae) the outermost layer of the endosperm become specialised and forms the aleurone layer. During maturation the cells of the outermost peripheral layer lose their meristematic activity, become enlarged and thick walled. These cell become filled with aleurone grains. The aleurone grains contain two types of inclusions-globoids containing phytin and lipids and protein carbohydrate bodies. During seed germination the cells of aleurone layer secrete certain enzymes like amylases and proteases which convert the stored food materials of endosperm to make it suitable for the developing embryo.

Endosperm is a nutritive tissue. It provides nutrition to the developing embryo and regulates its pattern of development. The mature endosperm serves as a reserve of carbohydrates, proteins and fatty acids. The developing endosperm derives nutrients from food reserves stored in the nucellus and integuments. Chalazal and micropylar haustoria helps in absorbing nutrients from the surrounding cells.

SAQ 1

- a) Fill in the blanks with appropriate words:
- In *Fritillaria* endosperm is.....
 - Endosperm is short lived in members of family
 - In *Peperomia* nuclei contribute in development of endosperm hence it is.....
 - In members of family Poaceae the outermost layer of the endosperm becomes specialized and forms the layer.
 - The developing endosperm derives nutrients from food stored in and
- b) State whether the following statements are true or false:
- In members of family Podostemaceae very prominent endosperm is found. []
 - In castor, wheat and maize endosperm constitutes the edible part of the fruit/seed. []
 - The aleurone grain contains lipids, proteins and carbohydrates. []
 - Endosperm absorbs nutrients from the surrounding cells with the help of integuments. []
 - Usually endosperm is non- chlorophyllous but in *Crinum* it is chlorophyllous. []
- c) Draw a neat, well labelled diagram of L.S. of maize seed.

12.4 NATURE OF ENDOSPERM

Endosperm is haploid i.e., a continuation of the gametophyte tissue or a diploid or triploid tissue or a second embryo of abnormal size and shape is still debatable. The fusion of the second male gamete was termed as vegetative fertilisation by earlier workers such as Strasburger (1900). In gymnosperms, the endosperm is a gametophytic (haploid) tissue as it develops directly by the continued free nuclear divisions of the functional megaspore while in angiosperms, it develops from the primary endosperm nucleus which is normally formed by the fusion of polar nuclei and a male nucleus, hence is neither haploid nor diploid but generally triploid. Many embryologists have considered endosperm as the second or distorted embryo. The most agreeable view regarding the morphological nature of the endosperm in angiosperms is that it is undifferentiated tissue that shows different degrees of polyploidy and its function is to provide nutrition for growth of the embryo. Thus, endosperm in angiosperms is similar to gymnosperms in function (nutrition), but is different in origin (triploid). The evolutionary advantage is that in angiosperms endosperm develops only if embryo has also developed in the seed, unlike in gymnosperms where gametophytic endosperm develops even if there is no embryo, causing some wastage.

12.5 TYPES OF ENDOSPERM

You have studied nature, structure and development of endosperm. Depending upon the mode of development, three main types of endosperms have been recognised in angiosperms these are:

- Nuclear type
- Cellular type
- Helobial type

12.5.1 Nuclear Type

In this type the primary endosperm nucleus undergoes free nuclear divisions (without formation of wall). The endosperm remains free- nuclear at the beginning but becomes cellular at a later stage. The nuclear divisions are synchronous in the beginning but later become non-synchronous i.e. nuclei may be seen in different stages of mitosis. The free nuclei formed remain suspended in the cytoplasm of the central cell. Later on the nuclei become gradually pushed towards the periphery by the expanding central vacuole. The nuclei increase in size either by fusion of two or more or by their independent growth. The wall formation is centripetal. It starts from the periphery and proceeds towards the centre of the embryo sac, or development initiates at the micropylar end and proceeds towards chalazal end. A single layer of uninucleate cells is formed. The anticlinal and periclinal divisions of these cells lead to complete cellularisation of the endosperm (Fig. 12.3). In some plants one or two peripheral layers of the cells develop while rest of the cells remains in the free nuclear state (without cell wall formation). In some plants wall formation does not take place and the cell remain in free nuclear state. Most of the cells are uninucleate but in some cases they become multinucleate by undergoing division. Nuclear endosperm development involves coenocytic, cellularization, differentiation, and maturation stages

The differentiated endosperm contains four major cell types: starchy endosperm, aleurone, transfer cells, and the cells of the embryo surrounding region. Recent research has demonstrated that coenocytic and cellularisation phases of endosperm development occur via mechanisms that are conserved among all groups of angiosperms. This includes nuclear migration during the coenocytic stage and anticlinal cell wall deposition. Complete cellularisation of the endosperm coenocyte is achieved through centripetal growth of cell, extending to the center of the endosperm cavity. Cells over the main vascular tissue become transfer cells and all interior cells become starchy endosperm cells.

The nuclear type is prevalent in economically important species including the cereals. In coconut when the fruit is young, the embryo sac is filled with a clear liquid containing numerous free endosperm nuclei. It is called as liquid syncytium Later on the periphery becomes jelly-like containing several cells. As the fruit matures the cellular endosperm along with the periphery becomes massive while the central part containing sweet liquid shows presence of large number of nuclei. The cellular endosperm constitutes the edible part of the

coconut. In betel nut and fruits of several other palms, the cellular endosperm occupies the entire cavity of embryo sac and becomes hard and woody. Various stages in the development of nuclear type of endosperm are shown in Fig. 12.3.

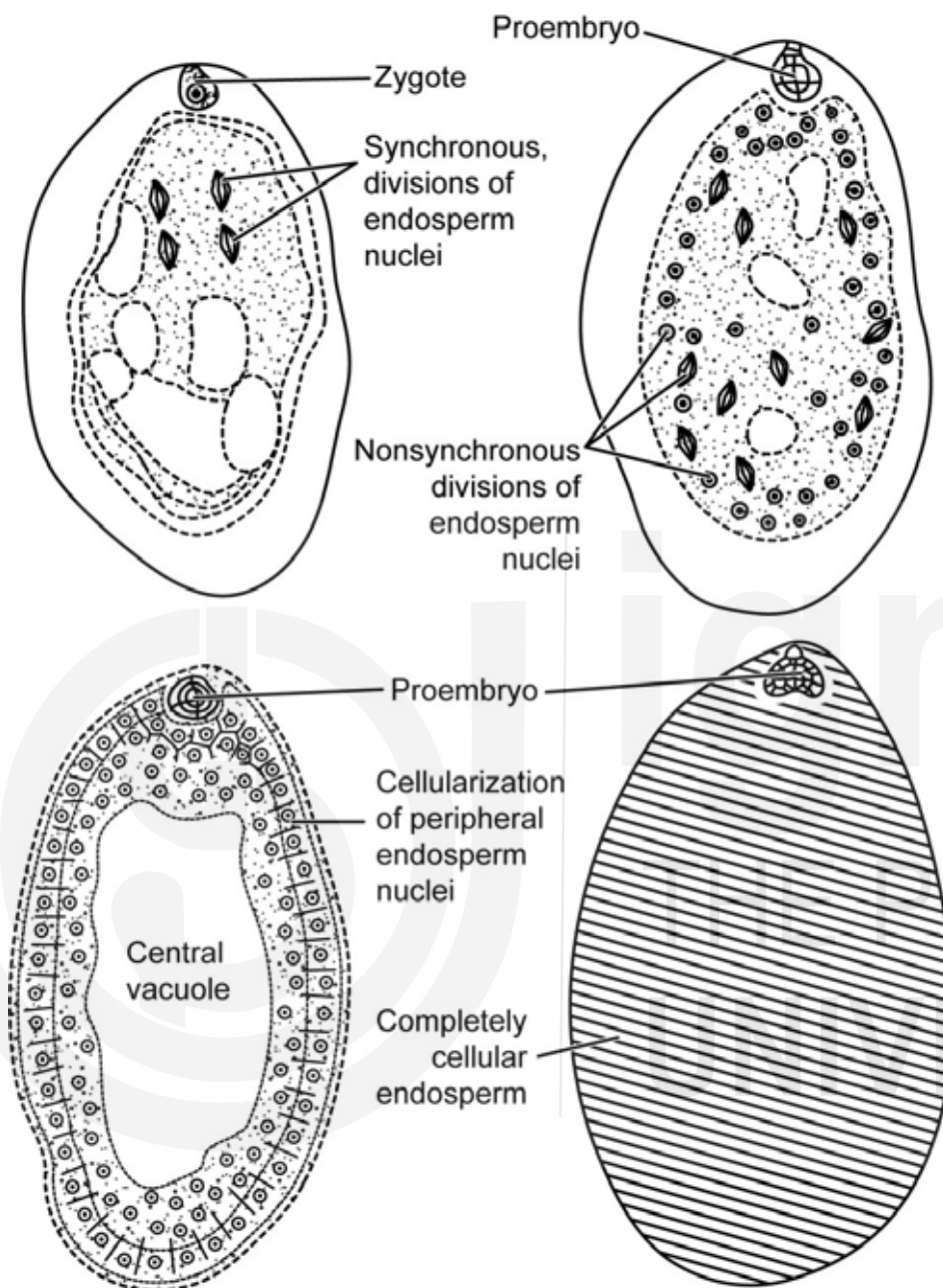


Fig.12.3: Different stages in the development of nuclear type of endosperm.

12.5.2 Cellular Type

The primary endosperm nucleus divides and the division is immediately followed by wall formation. The wall is usually transverse but sometimes longitudinal or oblique division also occurs. It divides the embryo sac into two cells. By further transverse division in two cells four celled linear endosperm is formed. Later these cells divide by repeated divisions and the tissue having irregularly shaped cells is produced. No free nuclear stage is seen in this type of endosperm. As a result the embryo sac contains cellular endosperm from the very beginning (Fig. 12.4). The examples of cellular type of endosperm include Balsam, *Pitunia*, barley, grasses, *Utricularia* etc.

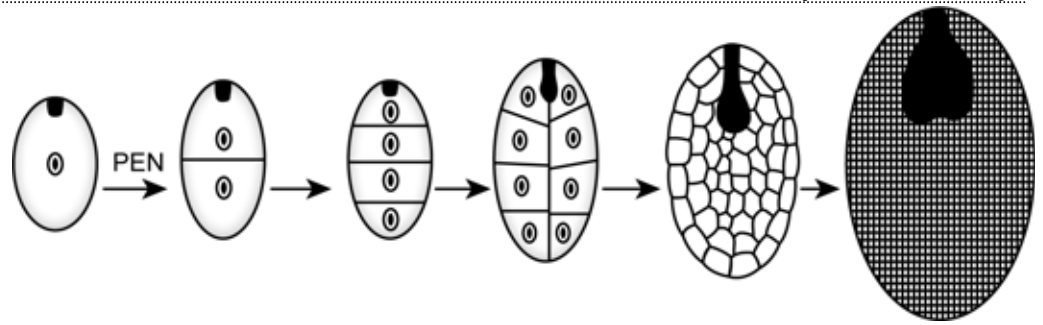


Fig.12.4: Different stages in the development of cellular type of endosperm (PEN = Primary endosperm nucleus).

12.5.3 Helobial Type

The primary endosperm nucleus moves to the chalazal end of the embryo sac, divides followed by transverse wall formation. This divides the embryo sac into two parts, a large micropylar chamber and a small chalazal chamber. Free nuclear divisions occur in the micropylar chamber. The wall formation takes place in the cells of this part. In the chalazal chamber, the nucleus either remains undivided or divides only few times. The chalazal chamber eventually becomes crushed or disintegrates at later stages (Fig. 12.5).

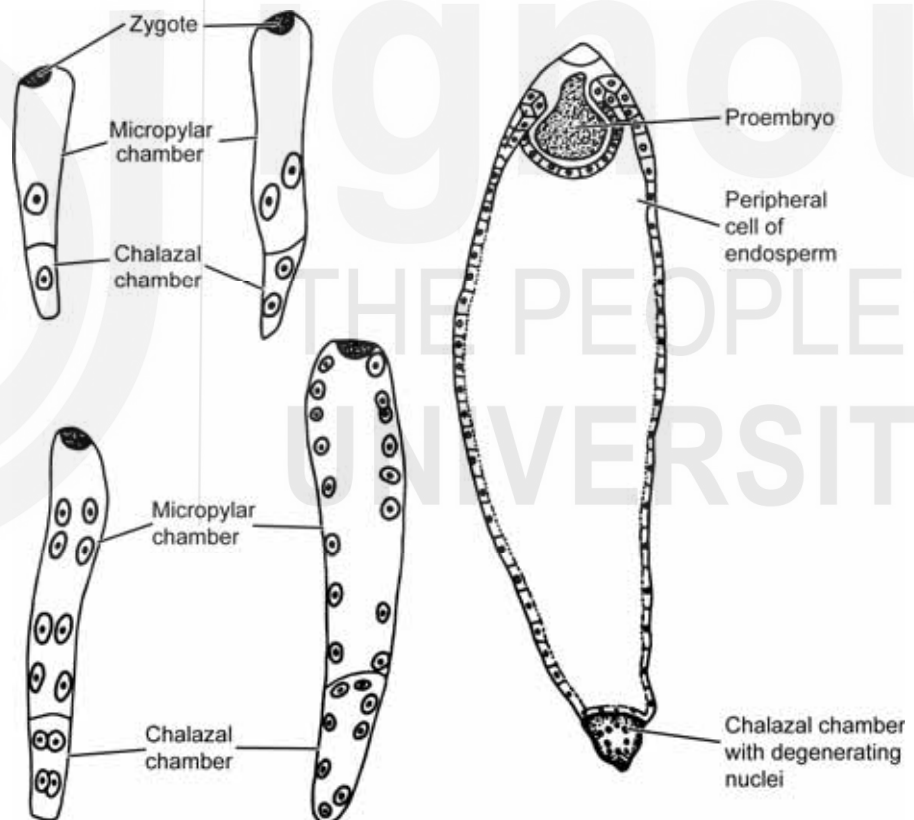


Fig.12.5: Different stages in the development of Helobial type of endosperm.

This type of endosperm represents an intermediate between nuclear and the cellular type. It is present mainly in monocots especially in members of Helobiales. However, typical type of endosperm has been observed in dicotyledonous families, such as Santalaceae and Saxifragaceae.

The three types of endosperm i.e. Nuclear, Cellular and Helobial are randomly distributed in the primitive and advanced families of angiosperms. The Nuclear type of endosperm is commonly noted in Polypetalae, Cellular type is reported in Sympetalae while the Helobial type is seen mostly in the monocotyledons.

The Nuclear type of endosperm has been noted in large number of taxa, hence it may be considered the most primitive type of endosperm. The comparative depiction of these three types of endosperm is given in Fig. 12.6.

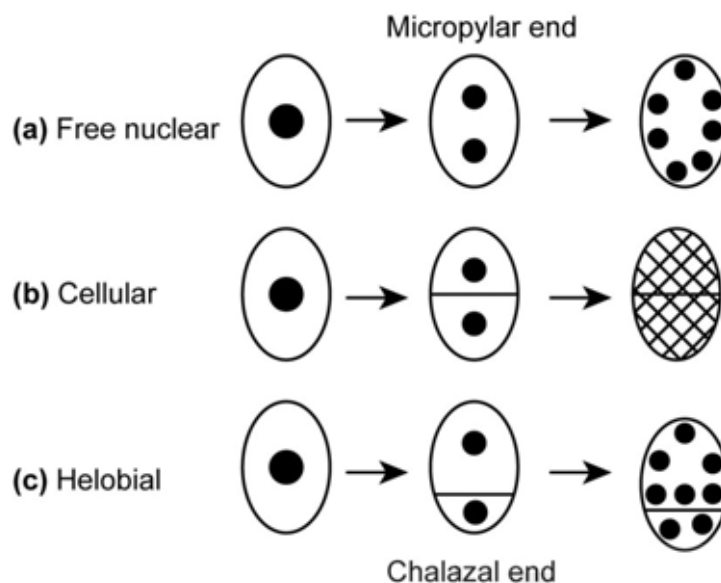


Fig. 12.6: Comparative depiction of different types of endosperm a) Nuclear; b) Cellular; c) Helobial.

SAQ 2

- a) Endosperm is a triploid structure, explain.
- b) Fill in the blanks with the appropriate words:
 - i) Endosperm plays a role and helps in the development of
 - ii) In young fruit of coconut embryo sac is filled with clear liquid containing free endosperm nuclei and it is known as.....
 - iii) No free nuclear stage is seen in..... type of endosperm.
 - iv) The chalazal chamber is disintegrated in type of endosperm.

12.6 ENDOSPERM HAUSTORIA

All the three types of endosperm described above may develop special structure called haustoria (singular - haustorium). Haustoria are the elongated structures of endosperm that remain free nuclear and invade the tissue in the developing seed and placenta. The occurrence of haustoria is a common feature of endosperm. They are believed to absorb, transport nutrients from the parent sporophyte and use it for the development of the endosperm. Micropylar haustorium has been noted in plants like *Impatiens*, *Nemophila*, *Frankenia hirsute* and chalazal haustoria have been seen in members of family Cucurbitaceae, Leguminosae and Euphorbiaceae. The development of both micropylar and chalazal haustorium has been noted in Lauraceae, Scrophulariaceae and Orobanchaceae.

12.6.1 Endosperm with Chalazal Haustoria

In this type of endosperm, the upper part is free nuclear but later on becomes cellular. The haustorium develops from the chalazal part which remains free nuclear. The lower part develops into coenocytic coiled worm like structure called vermiform appendage. The haustorium is aggressive, invades the chalazal tissue and transports nutrients to the main endosperm. This type of endosperm haustoria has been reported in *Macadamia ternifolia*, *Magnolia obovata*, *Iodinia rhombifolia*, *Crotolaria* etc (Fig. 12.7). The longest endosperm haustorium is found in *Echinocystis lobata* of the family Cucurbitaceae. In *Lomatia* besides the chalazal haustorium several finger like projections arise from the upper cellular endosperm. These penetrate the nutritive nucellar tissue and help in increasing the absorptive surface of the endosperm.

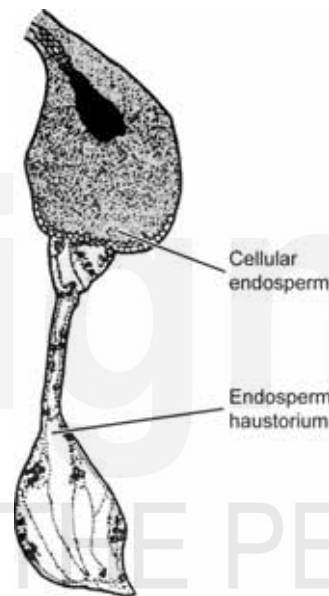


Fig. 12.7: Endosperm with chalazal haustorium in *Crotolaria*.

In species of *Crotolaria* and *Gravillea*, the wall formation is confined to the upper region and the free nuclear chalazal region elongates and behaves like a haustorium (Fig.12.7 & 12.8).

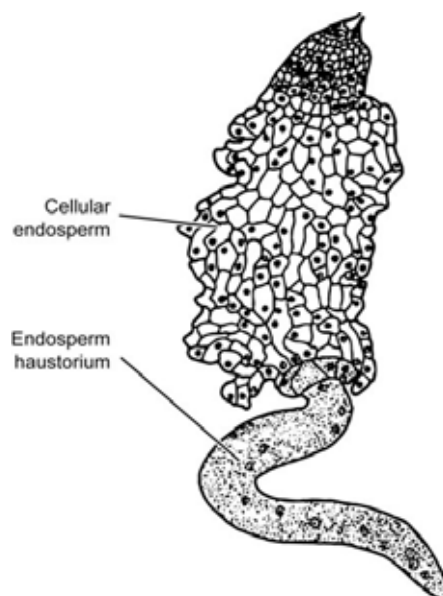


Fig.12.8: Endosperm with chalazal haustoria in *Gravillea*.

12.6.2 Endosperm with Micropylar Haustoria

In this case, the division of the primary endosperm nucleus is followed by transverse wall. This results in formation of upper small chamber and lower large chamber. The terminal part of the upper chamber develops into an extensive, branched haustorium. Its branches extend deep into the funiculus and derive nutrition (Fig.12.9). This type of haustoria is present in species of *Impatiens* and *Hydrocera*.

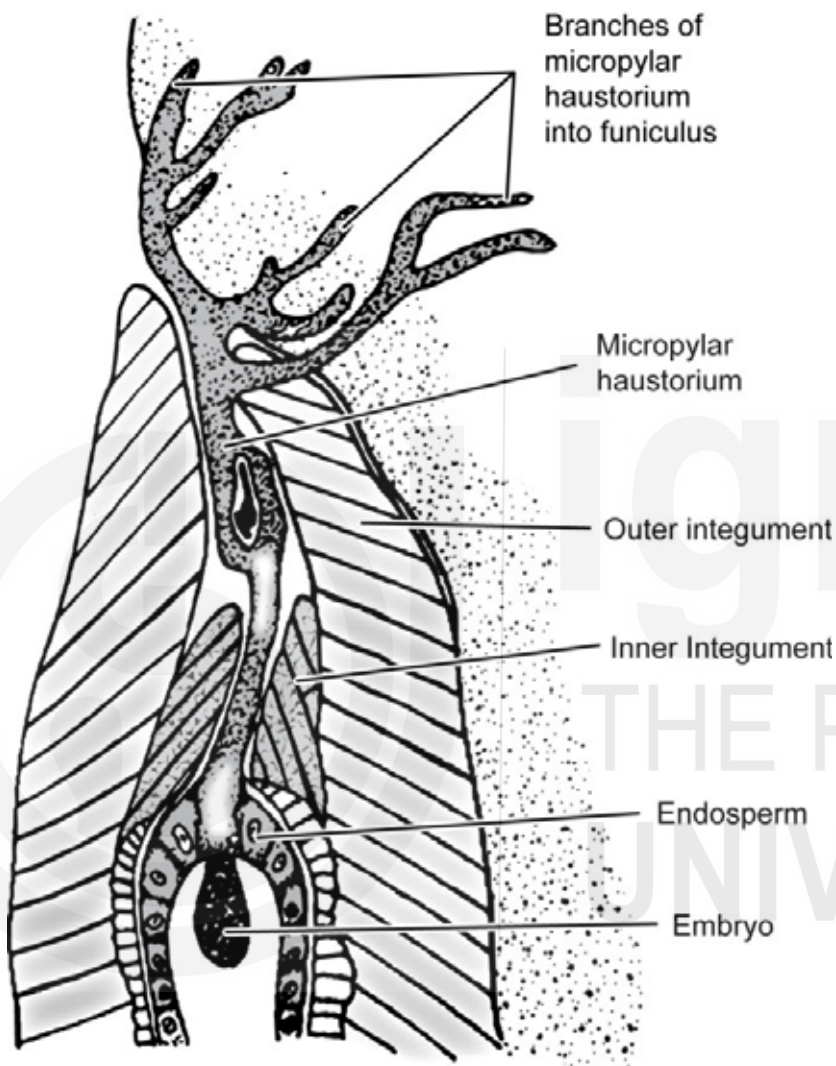


Fig 12.9: Micropylar haustorium in *Impatiens*.

12.6.3 Endosperm with Micropylar and Chalazal Haustoria

Some species show the presence of haustoria both at the micropylar and chalazal end of the endosperm e.g., *Nemophila* (Fig. 12.10 & 12.11). The chalazal haustorium gives out a prominent lateral branch which grows towards the funiculus and comes in direct contact with the placenta. In *Melampyrum*, the micropylar haustorium consists of a single cell with many tubular processes that enlarge and invade the tissue of the integument and funiculus (Fig. 12.12). The chalazal haustorium is short and confined to the nucellar tissue. In *Klugia notoniana* chalazal haustorium grows laterally and its branches enter the subepidermal cells of integuments (Fig. 12.13).

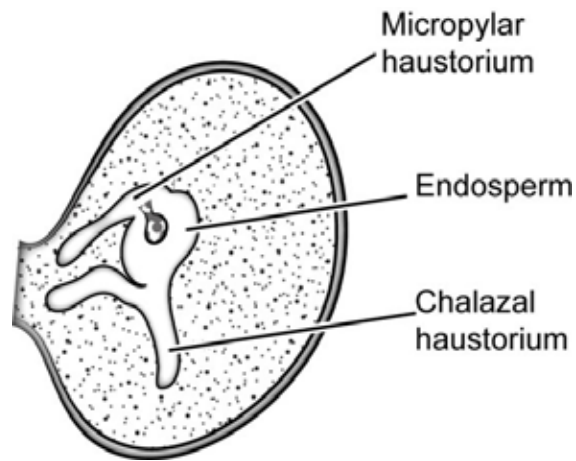


Fig.12.10: L.S. of ovule in *Nemophila* showing micropylar and chalazal haustoria.

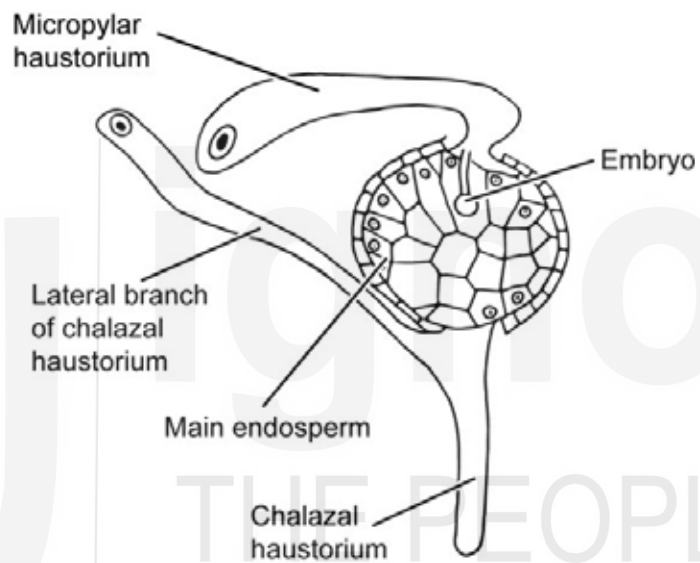


Fig.12.11: Enlarged endosperm in *Nemophila* showing micropylar haustorium and chalazal haustorium with lateral branch.

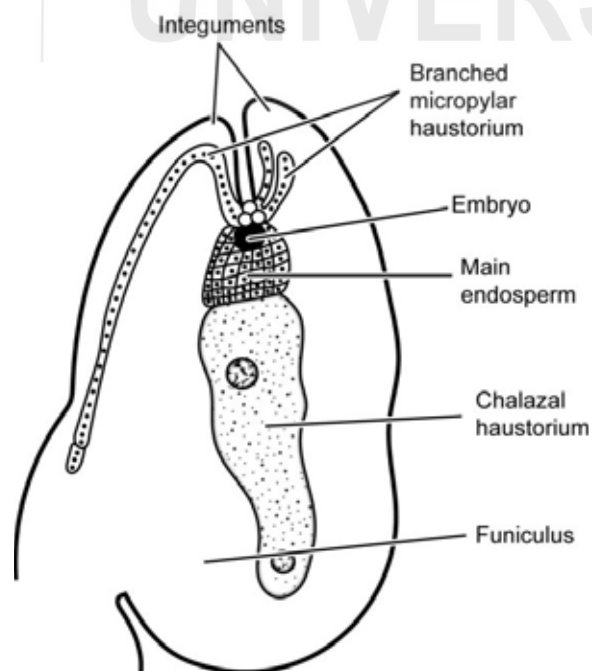


Fig.12.12: L.S. of Ovule of *Melampyrum* showing chalazal and micropylar haustorium.

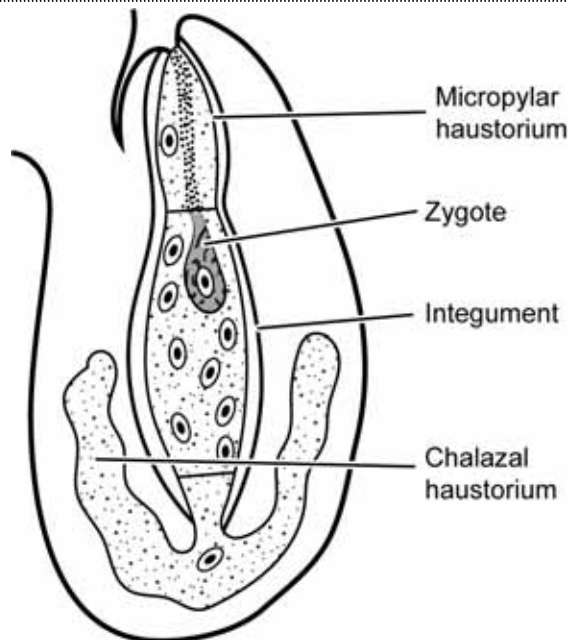


Fig.12.13: L.S. of ovule of *Klugia* showing micropylar and chalazal haustorium; note the branches of chalazal haustorium that enter the integuments.

Secondary haustoria : In *Centranthera* the micropylar and the chalazal haustoria are ephemeral. A certain number of cells of the endosperm close to the micropylar region develop tubular outgrowths that extend into the nucellus tissue and serve as secondary haustorium.

Lateral haustoria : In some species where the endosperm development is helobial type, the haustorium is neither micropylar nor chalazal but it is lateral. The chalazal chamber contains few nuclei. The micropylar chamber shows active nuclear divisions and develops lateral outgrowths that extend like a skirt on either side of the chalazal chamber. These grow downwards and function as active haustoria invading the chalazal tissue.

Perisperm : The nucellus is generally consumed by the developing endosperm but it persists in certain families such as Amaranthaceae, Portulacaceae, Zingiberaceae where it acts as the reservoir of food materials. The persistent nucellus is called as the perisperm that provides nutrients to the developing embryo. In black pepper endosperm is diminutive, confined to the vicinity of the embryo. Most of the seed is occupied by perisperm rich in nutrients.

12.7 ENDOSPERM VARIANTS

Variants have also been observed at later stages of the endosperm development. These include composite endosperm, ruminant endosperm and mosaic endosperm.

12.7.1 Composite Endosperm

In Loranthaceae, the development of embryo sac is unique. The ovary lacks ovules. The sporogenous tissue located at the base of the ovary develops several embryo sacs which elongate and enter the style. The primary endosperm nucleus of each embryo sac moves to the basal part where it divides to form cellular endosperm. During further development endosperm all

the embryo sacs elongate and fuse to form a composite endosperm mass (Fig. 12.14). Several proembryos belonging to individual embryo sacs with long suspensors develop but only one survives and attains maturity, with the expansion of developing endosperms in several embryo sacs, the intervening ovarian tissue is crushed.

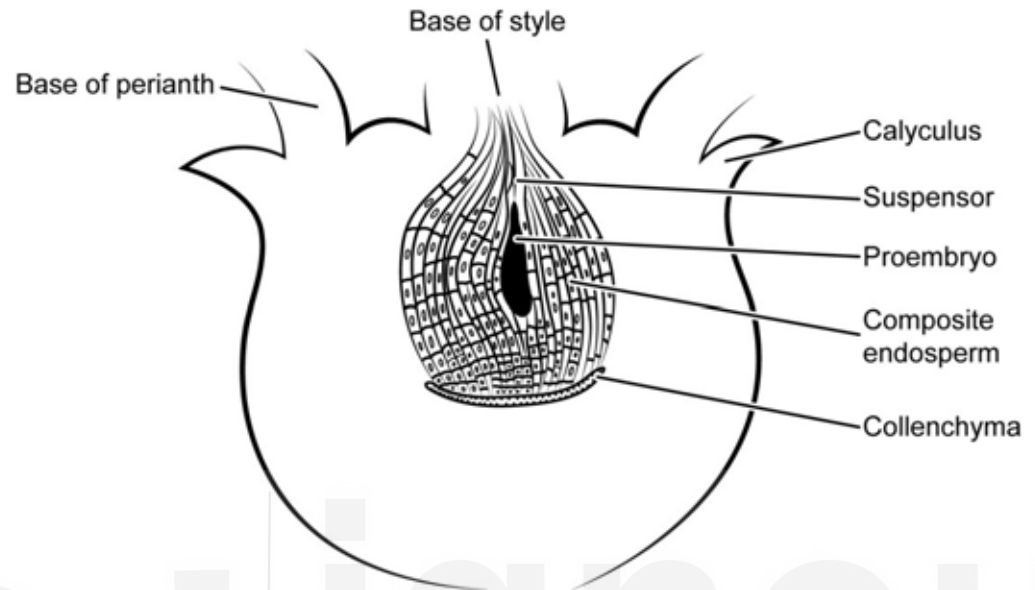


Fig 12.14: Composite endosperm in Loranthaceae.

12.7.2 Ruminant Endosperm

In this type of endosperm, the endosperm is dissected by ingrowths of seed coat. Ruminant endosperm is characterized by high degree of irregularity, unevenness on its enlarged surface (Fig. 12.15). This gives rise to a ruminated appearance. The ruminations are caused due to inward intrusion of the seed coat via meristematic growth. In palms the growth of the seed coat may intrude the young endosperm. If a betel nut is cut into two halves, the ruminations can be easily seen intruding from the seed coat into endosperm. In Acanthaceae, asymmetrical development of the central cellular endosperm forms the basal apparatus, primary and secondary haustoria and ruminations. Ruminant endosperm occurs in *Annona*, *Passiflora*, *Coccoloba* and *Myristica*.

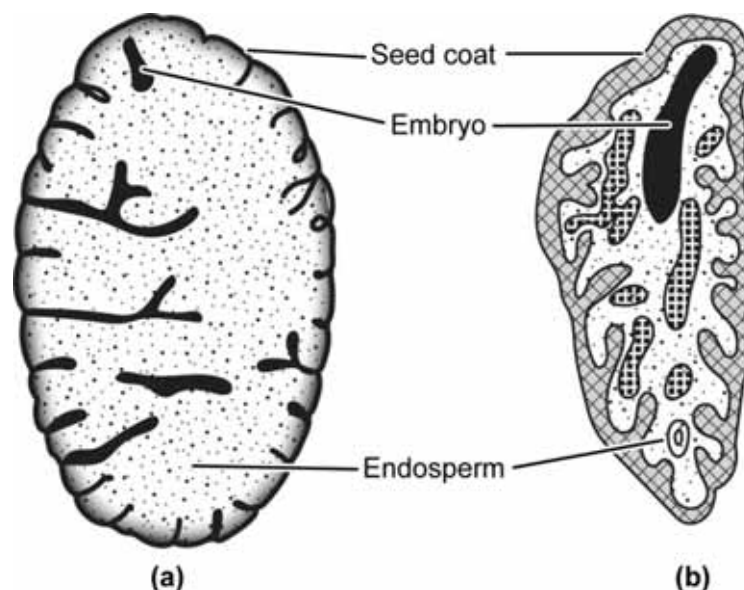


Fig. 12.15: Ruminant endosperm in a) *Asimina triloba*; and b) *Hedera helix*.

12.7.3 Mosaic Endosperm

In some plants tissue of endosperm appear in patches of two different colors providing a mosaic appearance. It has been postulated that formation of such endosperm occurs due to aberrant behavior of the chromosomes during mitosis or somatic mutations. In maize, red and white patches of tissues are seen in the grain. This type of endosperm has been reported in *Petunia*, *Lycopersicon* and *Acorus*

SAQ 3

- a) Enlist the differences between the composite and ruminant endosperm.
 - b) State whether these statements are true or false:
 - i) When the endosperm appears in patches of two different colours it is called as ruminant endosperm.
 - ii) The longest endosperm haustorium is found in *Echinocystis lobata*.
 - iii) Chalazal haustorium is observed in some members of Cucurbitaceae.
 - iv) Composite endosperm is characterized by its unevenness and shrunk growth.
-

12.8 FUNCTIONS OF ENDOSPERM

Most of the seeds possess endosperm as reserve of food material. The young endosperm is rich in food materials. It regulates the precise mode of embryo development and nourishes the developing embryo. During seed germination the food reserves stored in the mature endosperm get digested to support the developing embryo that forms the seedling. In some plants the seed coat and the fruit wall are consumed by the endosperm. The exposure to sunlight results in development of chlorophyll in species which have thin seed coat and fruit wall. Endosperm is found in most of the angiospermous plants.

In Orchidaceae, endosperm fails to develop beyond a few nuclear divisions. In legumes it is used by the embryo and the mature seed has no traces of it (exalbuminous). In legumes, the mature seed food reserves are present in the cotyledons rather than endosperm. In castor seeds endosperm is laden with fatty substances.

In monocotyledons it persists in the seed (albuminous). In cereals the mature endosperm is made of different tissues. The outer aleurone layer consists of living cells. The endosperm usually occupies major portion of the grain (87%) and aleurone forms 10% of the total endosperm. The aleurone layer stores lipids and protein. During seed germination, hydrolytic enzymes are produced in the aleurone layer and are released in the starchy endosperm for digestion and use of embryo and seedlings.

In barley and other cereals grains soaked in water release gibberellins from the scutellum of the embryo that diffuse in the endosperm. The aleurone layer responds to the condition by breaking down the protein reserves and secreting enzymes (α amylase) into the starchy endosperm.

Endosperm has a very important role in the development of embryo .in most of inter-varietal and interspecific crosses embryos fail to form because failure of endosperm formation.

SAQ 4

- a) What are albuminous and non-albuminous seeds?
 - b) Endosperm plays a very crucial role during embryo development. Discuss.
-

12.9 SUMMARY

- Endosperm is a triploid structure found in most of the angiosperms. It acts as a nutritive tissue and supports the development of embryo, on seed germination it nourishes the seedling till it becomes independent. Seeds or grains of cereals are full of starch. However, in mature seed of legumes no trace of endosperm is seen as most of it gets used up by the developing embryo.
- On the basis of development endosperm can be of three types: Nuclear, Cellular and Helobial. In some species endosperm may develop haustoria. Haustoria can develop at the chalazal end, micropylar end or it may be present at both the ends.
- Some variants in endosperm are also reported. These include composite, ruminant and mosaic endosperm.
- Mostly the endosperm is triploid in nature but in some species it can be diploid or polyploid in nature.
- Histologically endosperm is made up of thin walled isodiametric cells which store large amount of reserve food materials.

12.10 TERMINAL QUESTIONS

1. Explain the formation of aleurone layer in the endosperm?
2. Discuss the ploidy level variation in the endosperm?
3. Name a few families in which endosperm are not present.
4. Differentiate between endosperm of gymnosperms and angiosperms.
5. What are endosperm haustoria? Describe the different types of endosperm haustoria.

12.11 ANSWERS

Self-Assessment Questions

1.
 - a)
 - i) pentaploid
 - ii) orchidaceae
 - iii) 8, 9n
 - iv) aleurone
 - v) nucellus, integuments
 - b)
 - i) False
 - ii) True
 - iii) True
 - iv) False
 - v) True
 - c) See to Fig. 12.1.
2.
 - a) It is a triploid structure because it is formed as the result of double fertilisation where the male gamete (n) fuses with the two polar nuclei (secondary nucleus) (2n) and forms the primary endosperm nucleus (3n). The repeated division of the primary endosperm nucleus results in the formation of endosperm.
 - b)
 - i) nutritive, embryo
 - ii) liquid syncytium
 - iii) cellular
 - iv) helobial
3.
 - a) Composite endosperm - In this type sporogenous tissue located at the base of the ovary develops several embryo sacs which elongate and enter the style. The primary endosperm nucleus of the embryo sac moves to the basal part where it divides to form cellular endosperm. All the embryo sacs elongate and fuse to form a composite endosperm mass. This type of endosperm is noted in members of Lorantheaceae.

Ruminate endosperm - In this type of endosperm, the surface of the mature cellular endosperm shows a high degree of irregularity and unevenness. The endosperm shows ruminations caused due to localised activity of the seed coat or endosperm. Ruminate endosperm occurs in *Annona*, *Passiflora*, *Cocoloba*, *Myristica*, *Areca* and members of Acanthaceae.

- b)
 - i) False
 - ii) True
 - iii) True
 - iv) False
- 4. a) Endosperm is found in most of the angiospermous plants. Endosperm is utilized for growth of the embryo. When no traces of endosperm are seen in mature seed, the seed is called as exalbuminous or non endospermous. Moreoften, endosperm persists and remains present in the seeds, hence the seeds are called as albuminous or endospermous seeds.
- b) The young endosperm is rich in food materials. It provides nourishment to the developing embryo. During seed germination the food reserves stored in the mature endosperm get digested to support the developing embryo that forms the seedling.

Terminal Questions

1. Endosperm is usually non-chlorophyllous. However in some plants the seed coats and fruit wall becomes thin and translucent during seed development. The endosperm gets exposed to light and becomes green. Example - *Crinum* (Amaryllidaceae). The outermost layer of the endosperm may become suberised and protective in function. In some plants the outermost layer of the endosperm become specialised and forms the aleurone layer. The cells are rich in protein e.g., Poaceae. During maturation the cells of the outermost peripheral layer lose their meristematic activity, become enlarged, thick walled and seeds become filled with aleurone grains.
2. The endosperm develops from the primary endosperm nucleus formed by the fusion of male gamete with two polar nuclei. The repeated division of the primary endosperm nucleus results in the formation of endosperm. In some plants it shows variation in the ploidy which occurs due to change in the number of polar nuclei. The polar nuclei can be 1, 2, 4 or 8 depending upon the type of embryo sac. The endosperm in *Oenothera* is diploid because there is only one polar nucleus in this case. The number of polar nuclei is 8 in *Pepromia*, hence the endosperm is 9n.
3. Endosperm is absent in families such as Orchidaceae, Podostemaceae and Trapaceae.
4. The endosperm in gymnosperms is haploid while the endosperm in angiosperms is triploid. In gymnosperms, the endosperm gets differentiated before fertilisation from gametophytic tissue, whereas in angiosperms the endosperm differentiation occurs after fertilisation by fusion of a male gamete with polar nuclei in the central cell.
5. Haustoria are the elongated structures made up of extension of endosperm that invade the tissue in the seed and placenta. The occurrence of haustoria is a common feature of endosperm in some

families. They absorb nutrients and metabolise them for the developing endosperm. The haustoria can be micropylar or chalazal. Rarely, both micropylar and chalazal haustoria are present in a species.

In the endosperm with chalazal haustoria, the upper part is free nuclear but later on becomes cellular. The lower part remains free nuclear and develops into coenocytic coiled worm- like structure. It acts as an aggressive haustorium, invades the chalazal tissue and transports nutrients to the main endosperm. This type of endosperm haustoria has been reported in *Macadamia ternifolia*, *Magnolia obovata*, *Iodinia rhombifolia*, Cucurbitaceae, Leguminosae and some Euphorbiaceae.

In some cases, the division of the primary endosperm nucleus is followed by transverse wall formation. This results in formation of upper small chamber and lower large chamber. The terminal part of the upper chamber develops into an extensive, branched haustorium. Its branches extend deep into the funiculus and derive nutrition. This type of haustoria is present in *Impatiens* and *Hydrocera*.

Some species show the presence of haustoria both at the micropylar and chalazal end of the endosperm e.g., *Nemophila*, and members of family Lauraceae Scrophulariaceae and Orobanchaceae. The chalazal haustorium gives out a prominent lateral branch which grows towards the funiculus and comes in direct contact with the placenta.

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EMBRYO |

Structure

13.1	Introduction Objectives	13.4	Structure of Mature Embryo Dicotyledonous Embryo Monocotyledonous Embryo
13.2	Development of Embryo (Embryogenesis) Types of Embryogeny	13.5	Summary
13.3	Differentiations of Embryonal Tissues Genetic Regulation of Embryo Development Role of Auxin in Embryo Development Suspensor	13.6	Terminal Questions
		13.7	Answers

13.1 INTRODUCTION

In the previous units you have studied about various developmental events in plants, including the processes of male and female gametogenesis, double fertilization and development of endosperm that nourishes the embryo and embryo formation. The process of double fertilization is well-known in flowering plants and involves fusion of one of the male gametes with the egg (syngamy). This results in the formation of zygote which develops into the embryo. The process of growth and differentiation leads to formation of mature embryo is referred as embryogenesis. The cells of the embryo later on differentiate to form various tissues which develop into various organs.

Objectives

After studying this unit you would be able to :

- ❖ explain various stages of embryo development starting from the zygote;
- ❖ describe various stages of differentiation of embryonal tissues; and
- ❖ enlist the major differences between monocotyledonous and dicotyledonous embryo.

13.2 DEVELOPMENT OF EMBRYO (EMBRYOGENESIS)

The process of development of embryo from a zygote is called as embryogenesis. The zygote is located at the micropylar end of the embryo sac. Its basal or micropyle end is attached to the embryo sac wall, while the apical part or chalazal part projects in the central cell. The zygote undergoes a resting phase after its formation. The resting period varies with the species and depends upon the environmental conditions. With the passage of time, cell wall is formed all around the zygote and the cytoplasm shows a more polarized appearance. The micropylar part becomes vacuolated while the chalazal part shows presence of prominent nucleus. The density of the cytoplasmic organelles such as dictyosomes, endoplasmic reticulum (ER) and plastids increases. The density of ribosomes and polysome also increases in these cells indicating high metabolic activity.

In most of the angiosperms, the division in the zygote is transverse resulting in formation of a small apical cell and a large basal cell. In some angiosperms groups the division is vertical or oblique. In a two-celled proembryo the basal cell (towards the micropylar end) remains undivided or undergoes transverse division to form two cells. The apical cell divides vertically or transversely, forming a four celled proembryo having a linear or T- shaped configuration of cells. In the linear four-celled proembryo, the two apical daughter cells undergo two vertical divisions at right angles to each other to give rise a quadrant and then to an octant having two superposed tiers of four cells each. In T- shaped proembryo a vertical division at right angles to the first vertical division in the apical cell produces a quadrant. Rarely, as in the families such as Loranthaceae and Piperaceae the division of the zygote is vertical. A transverse division in each cell then goes on to produce an octant similar to one produced by four celled linear proembryo. Generally the octant possesses two superposed tiers of four cells each. Octant developing from either linear or T-shaped four-celled proembryos which occur in both dicotyledons and monocotyledons while those divisions are taking place in apical cell of the two-celled proembryo. The basal cell usually divides transversely, and some of its derivatives give rise to the suspensor which connects the embryo to the embryo sac wall.

Tangential divisions in the cells of the octant lead to differentiation of three wall layers. The outer **dermatogen** layer which forms the epidermis, middle **periblem** which gives rise to cortex of the stem and root, and inner **plerome** which gives rise to vascular tissue and pith. All the eight cells can also divide periclinally. The outer derivatives form the dermatogen while the inner cells undergo further division to form the cortical, vascular and pith regions. The process of differentiation of cell layers is called as **histogenesis**.

Organogenesis or differentiation of organs begins in the globular stage of the proembryo so that cotyledons (form leaves), epiphysis (form stem apex) and hypophysis (forms root cap and root cortex) are produced.

At this stage the embryo is **globular** in shape. By this stage derivative of the basal cells or its micropylar derivatives form a row of 6 to 10 suspensor cells. Some of the intermediate cells of the four celled proembryo also contribute to

the suspensor. The upper part of the suspensor becomes vesicular, forming finger-like ingrowths typical of cells involved in absorption of nutrients. It thus attains a haustorial function and provides nutrition to the developing embryo. The lower most cells placed between the suspensor and embryonal mass is referred as hypophysis. Hypophysis undergoes a transverse division followed by two longitudinal divisions at right angles to each other forming a group of eight cells. Out of these eight cells, inner four cells give rise to initials of the root cortex while the outer give rise to root cap and root epidermis (Fig. 13.1).

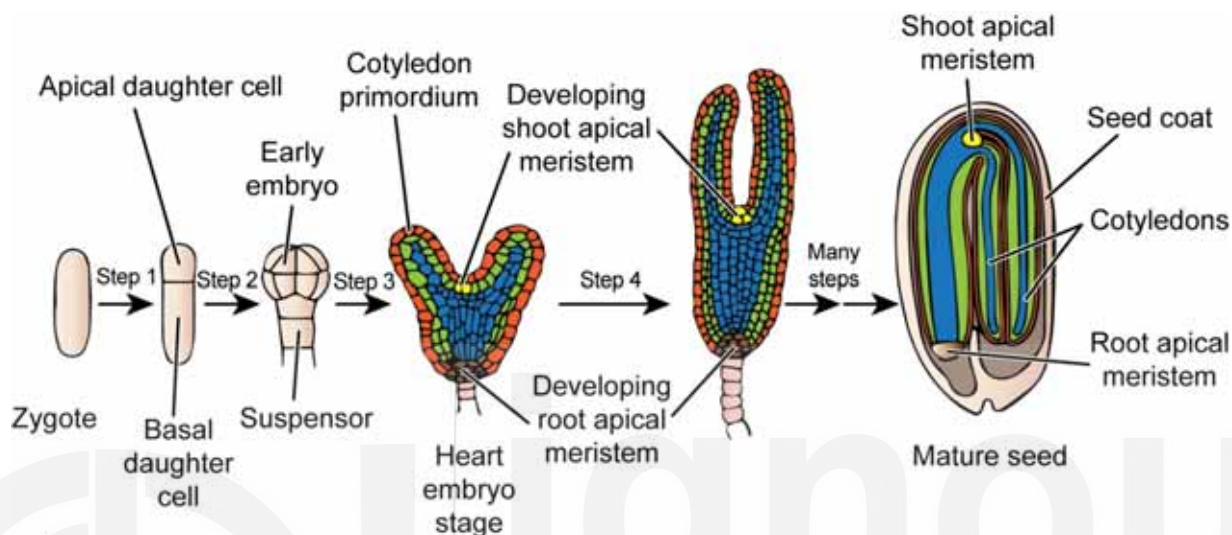


Fig. 13.1: Various stages of embryo development (embryogenesis) in plants.

The globular proembryo undergoes further cell multiplication and forms two cotyledons. The stage at which the development of cotyledons is initiated is referred as **cordate or heart shaped**. A wedge group of cells is cut off between the two cotyledons. The cotyledons and the hypocotyls enlarge to form a **torpedo shaped** embryo. Further development leads to the extension of cotyledons which remain straight as in cotton and or castor or become curved like horse shoe shaped as noted in *Cypselia* or *Brassica* (Fig. 13.1).

In some taxa exceptions have been noted during the development of embryo. The embryo remains small, reduced and lacks cotyledons and apical meristems. The embryo remains undifferentiated. The embryos of *Orobancha* remain globular or ovoid with no histogens except dermatogens.

13.2.1 Types of Embryogeny

Based on the plane of division of the apical cell and contribution of the basal and apical cell in the formation of embryo, six types of embryogeny have been categorised

1. The division of the zygote is vertical or obliquely vertical. Example - *Triticum*.
2. Apical cell of the 2 celled pro-embryo divides vertically to form T shaped four celled proembryo. The basal cell does not divide. The suspensor is derived from the apical cell.
3. The apical cell of the two celled proembryo divides transversely so that four celled linear proembryo is formed.

4. Basal cell plays no or insignificant role in the development of proembryo. This has been noted in members of the families- Brassicaceae and Ranunculaceae.
5. The basal cell and apical cell both contribute to the development of the embryo. This has been well-known in members of the families- Asteraceae and Violaceae.
6. Basal cell plays no or insignificant role in the development of embryo.
7. The basal cell forms the suspensor. This has been noted in members of family Solanaceae.

SAQ 1

a) Fill in the blanks:

- i) The stage of the development of cotyledons in embryo is
- ii) The fertilised embryo is located at the end of the embryo sac.
- iii) The division of the zygote by traverse wall results in formation of small cell and large cell.
- iv) In Loranthaceae and Piperaceae, the division of the zygote is
- v) Root cap and root apex are formed from
- vi) Organogenesis or differentiation of organs begins in the stage of the proembryo.
- vii) is the study of the development of embryo from a zygote.

b) State whether these statements are 'True' or 'False':

- i) In the embryo sac, zygote is located at the micropylar end.
- ii) As the development of zygote to form embryo progresses, the density of the cytoplasmic organelles increases.
- iii) The first division in the zygote is tangential in most angiosperms.
- iv) In T- shaped proembryo a vertical division at right angles to the first vertical division in the apical cell produces a quadrant.
- v) The outer derivatives of the octant give rise to periblem.

c) Answer in one word:

- i) The process of differentiation of cell layers in octant.
- ii) Some of the intermediate cells of the four celled proembryo contribute to the formation of a structure that attains haustorial function and provides nutrition to the developing embryo.
- iii) The stage of embryo at which the development of cotyledons is initiated.
- iv) The stage of embryo at which cotyledons and the hypocotyls enlarge.

13.3 DIFFERENTIATIONS OF EMBRYONAL TISSUES

Embryogenesis follows a simple and predictable pattern in *Arabidopsis*, hence has been studied as an ideal model to understand tissue development in plants. The embryonic cell division follows a linear pattern in this plant. The plant possesses small genome size and short life cycle.

A zygote is a **totipotent** cell. The zygote gets transformed into a mature embryo by the end of embryogenesis. The globular stage is a crucial stage in embryo development that regulates many morphogenetic processes: At this developmental stage, all tissues obtain their identities. The cells function is specified and tissues obtain their identities during this stage of embryo development. Formation of outer and inner layers, vascular and ground tissues, determination of shoot and root axis gets initiated during this stage. At this stage formation of all the basic tissues gets initiated, hence this developmental stage regulates cell division and cell-cell communication in flowering plants. Many components of the genetic pathways get activated during this period and genes involved in cell fate maintenance have been identified.

The embryo in *Arabidopsis*, follow a simple, highly regular and predictable pattern of cell division. The embryo undergoes a highly ordered sequence of cell divisions followed by differentiation into specific tissues. Embryogenesis begins with fertilization of the egg cell with one of the two sperm cells delivered by the pollen tube. After fertilization, the zygote quickly elongates along the apical-basal axis. It undergoes asymmetric division and produces a smaller apical and a larger basal cell. The apical cell forms the entire embryo except its basal portion. The basal cell undergoes a series of transverse divisions that ultimately generates seven to nine cells. Of these cells, the uppermost cell forms the extra-embryonic suspensor. After the first asymmetric division, the apical cell undergoes a series of rapid cleavage divisions. It undergoes two longitudinal divisions at right angles to one another to produce a quadrant of four cells of equal size. This is followed by a transverse division resulting in two tiers of four cells each, generating the octant stage proembryo (Fig. 13.2). At the octant stage, cells in both tiers undergo a tangential division aligned along the apical-basal axis giving rise to two cell populations with very different identities - the protoderm and the inner cells. This protoderm acts as the precursor of the epidermis while the inner cells form the precursor of the ground and vascular tissues.

In the later stages, orientation of cell division and volume is very regular in the lower half of the embryo. The outer protodermal cells divide anticlinally to extend the outer layer. In contrast, the inner cells divide longitudinally. The four basal cells form larger, outer ground tissue precursors and smaller inner vascular precursors. The uppermost cell of the suspensor is specified as the hypophysis and divides asymmetrically to form a smaller lens-shaped cell (precursor of the quiescent centre) and a larger basal cell (precursor of the distal stem cells of the root meristem).

13.3.1 Genetic Regulation of Embryo Development

The specification of cell identities during embryogenesis is controlled by specific molecular pathways and is often marked by the onset of specific gene expression patterns. The studies indicated that various transcription factors play an important role in the process of embryogenesis. The cellular and molecular events that take place during the formation of outer (protoderm) and inner layers, the specification of vascular and ground tissues, determination of shoot and root domains and the establishment of the first stem cells have been well studied in *Arabidopsis*.

WUSCHEL-RELATED HOMEODOMAIN (WOX) transcription factors have been implicated in this process. Tangential division during the embryo development is regulated by these genes as shown by the fact that tangential divisions get disturbed in *wox* mutants. The role of various transcription factors that play an important role during embryogenesis has been elucidated (Table 1).

The octant stage proembryo undergoes two rounds of cell division. Upper tier of cells contribute to the formation of aerial tissues while the lower tier of cells develops hypocotyl and root tissues. These two domains are fundamentally different. The cell division patterns are more regular in the lower domain as compared to upper domain. *WOX2* is expressed in the apical domain, whereas *WOX8* is expressed in the suspensor, including the part likely to be developed in hypophysis. *WOX9* is activated in the basal domain.

Embryonic root apical meristem (RAM) formation is initiated at the globular stage. At this stage, the uppermost cell of the suspensor divides asymmetrically to form a smaller lens-shaped cell and a larger basal cell. The upper cell of the suspensor develops into hypophysis. Both the hypophysis and its lens-shaped descendant express the *WOX5* marker. The role of hypophysis is specified. It triggers the initiation of the root meristem. After asymmetrical division of the hypophysis, the small descendant cell gives rise to the quiescent center (QC), which maintains identity of cells surrounding the RAM to produce a set of differentiated tissues. WUS-RELATED HOMEODOMAIN 5 (*WOX5*), a putative homeodomain transcription factor is required in the QC to maintain columella cells. Mutants that fail to form the hypophysis often produce rootless seedlings.

The expression of PLETHORA (PLT) family members viz. *PLT1* and *PLT2* initiates in the lower tier cells at the octant stage. Ectopic expression of *PLT1* or *PLT2* induces all organ identities that originate from the basal region of the embryo, i.e. hypocotyl, root and root stem cell niche, demonstrating a dominant role for *PLT1* and *PLT2* in basal cell fate determination. Auxin also regulates the expression of PLT genes. PLT genes are known to regulate formation of the shoot apical meristem (SAM) pattern in the embryo, the boundary between the SAM and the cotyledons, and pattern of leaves during post-embryonic development.

At the transition from the octant to the dermatogen stage, outer cells express epidermis-specific genes. The inner cells are marked by the expression of *MP*, the auxin efflux carrier PIN-FORMED 1 (*PIN1*) and *ARGONAUTE 10* [*AGO10*] also known as *PINHEAD* (*PNH*). Upper and lower inner halves of the embryo

are specified through independent mechanisms. This is because the division patterns in the upper half are very different from those in the lower half. The upper and lower inner tiers express different gene sets.

At the early globular stage, the longitudinal division of the inner cells leads to the formation of vascular and ground tissue precursor cells. The ground tissue specification in the embryonic root is regulated by GRAS family transcription factor SHR. *SCARECROW (SCR)* is found to be indispensable for the periclinal division of the ground tissue daughter cells that generates separate endodermis and cortex layers (collectively called ground tissue). SHR is expressed in the stele in both the nucleus and the cytoplasm. Plants use endoplasmic reticulum-containing channels called plasmodesmata to form cytoplasmic continuities between cells in order to exchange molecules. Two closely related leucine-rich repeat (LRR) receptor-like kinases viz. RPK1 and RPK2 (also known as TOADSTOOL 2 (TOAD2)) are expressed in globular stage. *CLAVATA3 (CLV3)* is involved in the regulation of meristem maintenance. At the early globular stage, the onset of localised auxin biosynthesis in the proembryo is required for PIN1 polarization in the inner proembryonic cells.

Table 1: Role of various transcriptional factors in embryo development.

Transcription factors/genes	Function	Stage at which expressed
<i>ARABIDOPSIS THALIANA</i> <i>MERISTEM LAYER 1 (ATML1)</i>	control anatomical delineation of the outer layer and inner cells	
<i>PROTODERMAL FACTOR 2 (PDF2)</i> (close homologue of <i>ATML1</i>)	Regulates specification of epidermal cells in the shoot	in four-cell stage proembryos
<i>WUSCHEL (WUS)</i>	marker for the shoot apical meristem (SAM)	initiates in the upper tier inner cells
<i>TARGET OF MONOPTEROS 5 (TMO5)</i> and <i>TMO7</i>	Marker of the root apical meristem (RAM)	initiates in the lower tier inner cells.
RECEPTOR-LIKE PROTEIN KINASE 1 (RPK1) and RPK2 [also known as TOADSTOOL 2 (TOAD2)]	Help in separation of outer and inner cells	globular stage proembryo
<i>SCARECROW (SCR)</i>	periclinal division of the ground tissue that generates endodermis and cortex layers (ground tissue)	early globular stage
<i>MONOPTEROS (MP)</i> or <i>AUXIN RESPONSE FACTOR 5 (ARF5)</i>	encode transcription factors that assist in root initiation	early globular stage
<i>SCHIZORIZA (SCZ)</i>	ground tissue patterning	heart shape stage

All root vascular tissues are derived from four provascular initial cells in the early globular stage proembryo. The provascular initial cells undergo several rounds of periclinal divisions to create a vascular bundle. *MONOPTEROS (MP)* also known as *AUXIN RESPONSE FACTOR 5 (ARF5)*] target genes

encoding transcription factors act downstream to assist in root initiation. Auxin activates the expression of *MP*, which in turn triggers the expression of its target genes such as *TMO5*. *MP* regulates formation of vascular tissue and controls specification of hypophysis. *MP* activates its downstream targets including *TMO7* in vascular and ground tissue cells. *TMO7* moves from the provascular cells to the uppermost suspensor cell. *MP* promotes PIN1-dependent auxin transport to the uppermost suspensor cell. Cytokinin (CK) plays a role in root vascular patterning. Auxin-CK interaction promotes periclinal cell division.

Ground tissue patterning defects have been noted in *scz* mutants at the heart stage in embryos. *SCZ* expression is found in ground tissue cells from the heart stage onwards. The *PLT3* and *BABYBOOM (BBM)* genes initiate expression from the heart stage onwards, with highest expression occurring in the provascular cells and the lens-shaped cell. The *plt1* mutant significantly impairs RAM formation and produces rootless seedlings.

13.3.2 Role of Auxin in Embryo Development

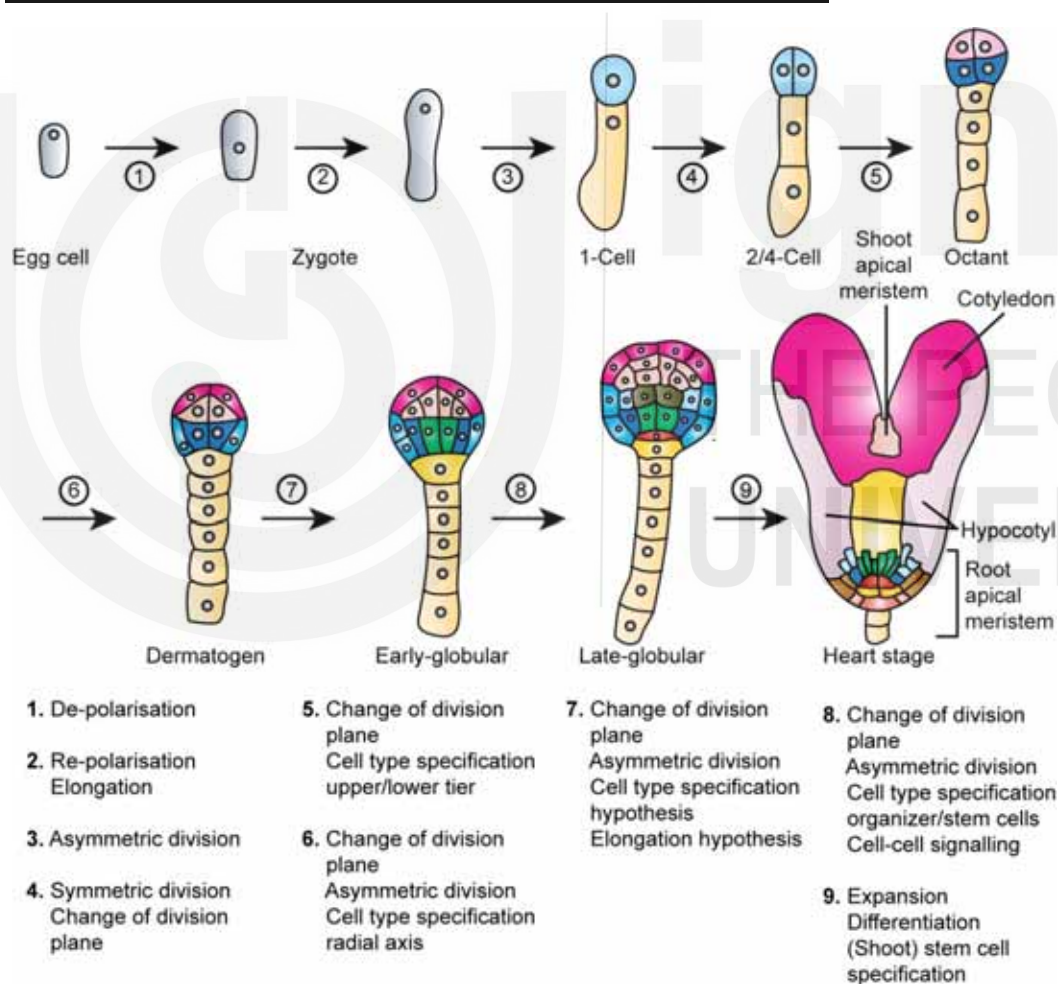


Fig. 13.2: Stages of development of embryo in *Arabidopsis*. Embryogenesis depicts various stages. Embryo with a single cell, embryo with 2 cells, Octant stage having four of eight cells in two tiers, Dermatogen stage- A tangential division of octant cells, early globular stage, Triangular stage showing polarized pattern of major elements with two symmetrically positioned cotyledon primordia and radially patterned cylinder. Heart stage showing cotyledon outgrowth, Mid-torpedo stage showing enlargement of cotyledons and hypocotyl and Bent cotyledon stage embryo with elaborated radial pattern in different organs. [Taken from Bosca et al. (2011) and Wendrich and Dolf Weijers, (2013)].

Auxin distribution changes dynamically at key steps of embryo development. Hypophysis specification is regulated by the plant hormone auxin. The mutations in components of auxin biosynthesis cause defects in hypophysis division and RAM formation in embryo. Auxin flow directionality mainly depends on the polarised subcellular localization of the PIN-FORMED (PIN) auxin transporters. Auxin regulates its own transport by controlling the expression of PIN genes. Expression of PIN1 in the basal cell membrane in the provascular cells next to the hypophysis actively transports auxin into the hypophysis. Auxin is produced in the cells of the suspensor.

13.3.3 Suspensor

The basal cell of the zygote and its derivatives develop into a nutritive tissue, the suspensor. It is ephemeral structure at the radicular end of the embryo. At initial stages, the suspensor grows faster than the embryonal part and attains its maximal size by the globular and heart- shaped stage. In mature seed, only remains of the suspensor are seen (Fig. 13.3). The suspensor anchors the embryo to the embryo sac wall and pushes it deep into nutritionally favourable environment of the endosperm. The presence and size of the suspensor is variable depending upon the functional requirement. In some plants no suspensor (*Viola*, *Tilia*) is reported. In some plants (Brassicaceae, Loranthaceae), a long filamentous suspensor is present. In most of the legumes, the suspensor is poorly developed. In *Cytisus laburnum*, the cells of the suspensor are clustered like bunch of grapes. In *Pisum sativum* the suspensor is composed of four large multinucleate cells. Plants of the families Orchidaceae and Trapaceae lack the endosperm formation. In absence of endosperm, the embryo develops suspensor haustorium. In Orchidaceae, the suspensor haustorium may be single- celled, vesicular or sac- like (*Dendrobium*), uniseriate filament of 5-10 cells which form haustorial branches, like bunch of grapes (*Epidendrum*), consisting of eight cells, formed by vertical division of the suspensor initial .In *Vanda*, or an irregular mass of cells situated towards the micropylar region which elongate to form tubular structure (*Cymbidium*). Suspensor haustoria have also been seen in members of families Crassluaceae and Fumariaceae. In these families the haustoria can be single celled or may enlarge to become conical, tubular, cyst- like or branched. Suspensor haustoria having finger like ingrowths similar to transfer cells support the absorption of nutrients from various ovular and extraovular tissues.

In *Capsella bursa-pastoris*, the micropylar cell of the uniseriate suspensor is large and haustorial. The wall of the cell show finger- like ingrowths which helps in withdrawing nutrients. The cell wall separating individual suspensor cells are transversed by plasmodesmata. The cytoplasm of the suspensor cell possesses well developed endoplasmic reticulum, large number of ribosomes, mitochondria and plastids. The suspensor is also considered as an important source of growth regulators such as auxins, gibberellins and cytokinins. These hormones are supplied at different stages of embryo development. The suspensor cells show high degree of endopolyploidy or polyteny. The suspensor cells start degenerating from the heart shaped stage of the embryo. Then cells show disorganisation in cytoplasm and ruptured vacuolar membranes. After disorganization of suspensor, the embryo depends upon

endosperm for its nutrition. Endosperm surrounds the embryo and provides it with nutrition during its development. It plays a role in differentiation of epidermal cells during embryogenesis.

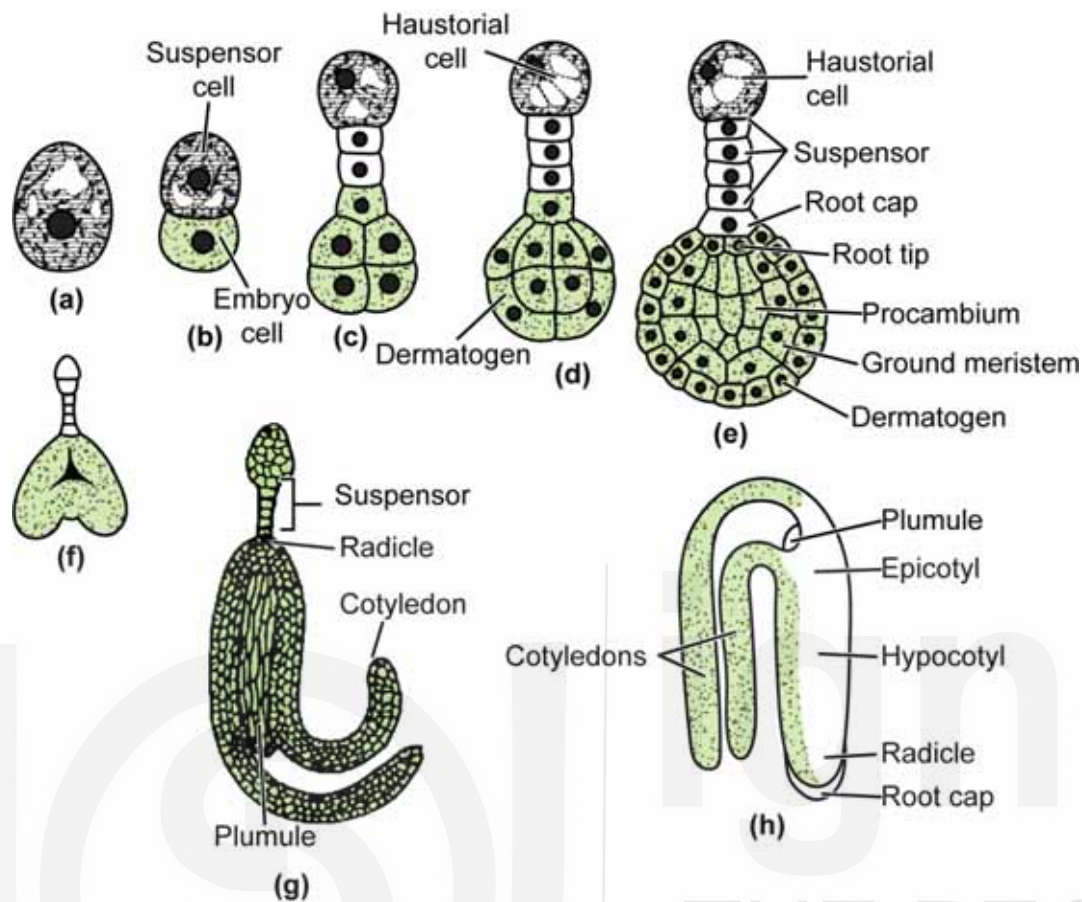


Fig 13.3: Development of suspensor in embryo.

SAQ 2

a) Fill in the blanks:

- cell forms the entire embryo.
- The basal cell undergoes a series of transverse divisions to form a structure called
- The stage is crucial stage in embryo development and regulates many morphogenetic processes.
- The uppermost cell of the suspensor gets specified as
- surrounds the embryo and provides it with nutrition during its development.

b) Define the following terms:

- Dermatogen
- Histogenesis
- Suspensor

13.4 STRUCTURE OF MATURE EMBRYO

The development of the proembryo is similar in both monocotyledons and dicotyledons. After the octant stage the destiny of the various cells of the proembryo differs in two groups. Hence both types of embryo show differences. The dicot embryo possesses an apical shoot apex and two lateral cotyledons whereas the monocot embryo possess one cotyledon and laterally placed shoot apex (Fig.13.4). In dicotyledons, the derivatives of the two opposite cells of the terminal quadrant give rise to two cotyledons, while in monocotyledons derivatives of one cell of the quadrant contributes to the cotyledons.

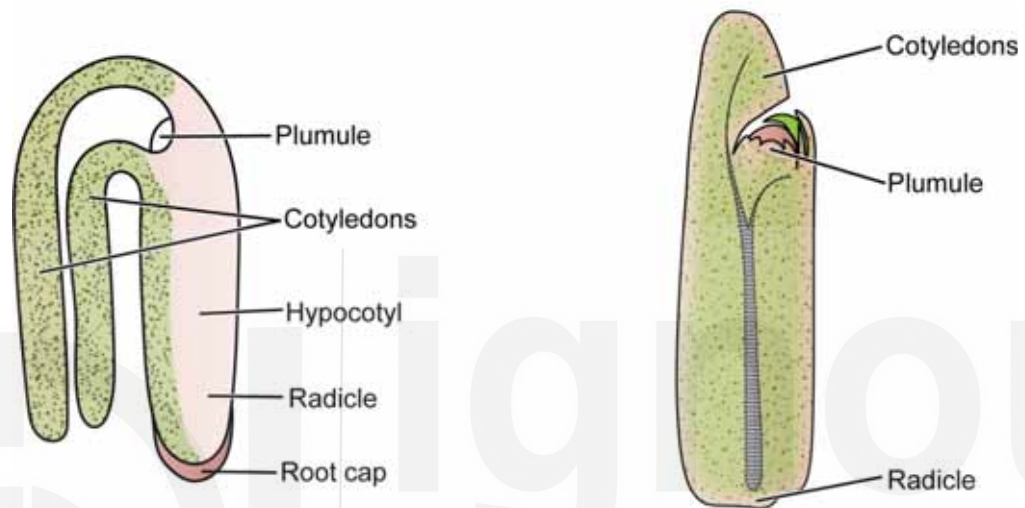


Fig. 13.4: Structure of a dicot and monocot embryo.

13.4.1 Dicotyledonous Embryo

The structure of the dicot embryo can be studied with the help of plant species such as *Capsella bursa-pastoris* which belongs to the same family as *Arabidopsis* (Brassicaceae). The division of the embryo is transverse resulting in a basal cell and terminal cell. The basal cell divides transversely while the terminal cell divides longitudinally. The four celled proembryo looks inverted T-shaped. The two terminal cells divide to form vertical wall oriented at right angles to the first, forming a quadrant. The cells of the quadrant divide transversely to form an octant. The lower cells of the octant give rise to stem tip and cotyledons (Fig.13.5).

The upper cells of the octant form the hypocotyl. All the eight cells divide periclinally. The outer derivatives form the dermatogen while the inner cells undergo further division to form the cortical, vascular and pith regions. At this stage, the embryo is globular in shape. All this development occurs in the terminal cell. The derivatives of some basal cells divide to form a row of 6 to 10 suspensor cells. The upper part of the suspensor becomes vesicular and attains a haustorial function. Some of the intermediate cells of the four-celled proembryo also contribute to the suspensor. The lower most cells placed between the suspensor and embryonal mass is referred as hypophysis. The hypophysis undergoes a transverse division followed by two longitudinal divisions at right angles to each other forming a group of eight cells. Out of these eight cells, inner four cells give rise to initials of the root cortex, while the outer cell give rise to root cap and root epidermis.

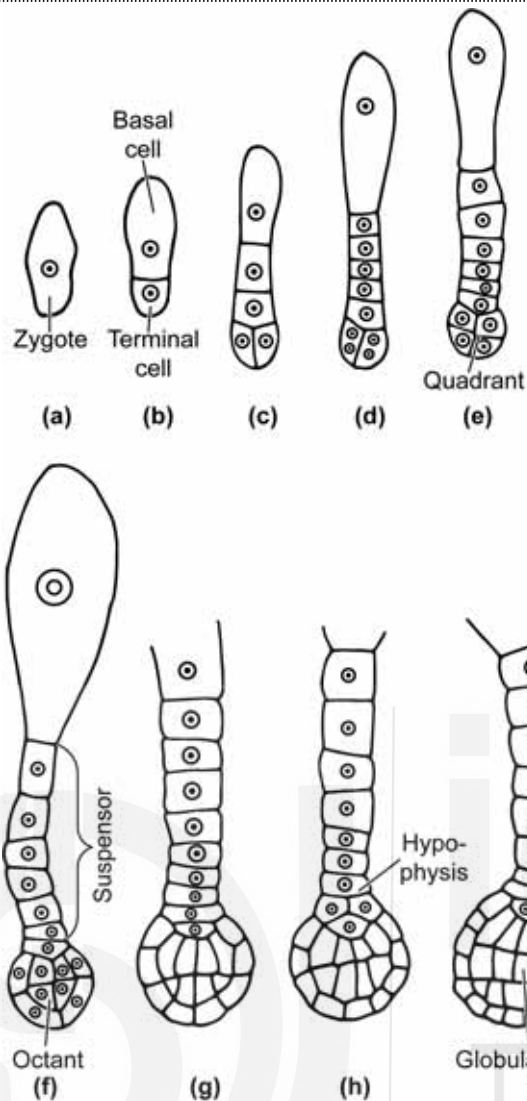


Fig. 13.5: Stages in development of dicot embryo in *Capsella bursa-pastoris*.

The globular proembryo undergoes further cell multiplication and forms two cotyledons (Fig.13.5). The stage at which the development of cotyledons is initiated is referred as cordate or heart shaped. A wedge group of cells is cut off between the two cotyledons. This represents the region of the epiphysis, the forerunner of the shoot tip. The cotyledons and the hypocotyls elongate to form a torpedo- shaped embryo. Further development leads to the elongation of cotyledons which become curved like horse shoe in *Capsella*.

The dicotyledonous embryo when seen in longitudinal section consists of an embryonal axis having two cotyledons. The portion of the embryonal axis above the cotyledons is termed as epicotyl which forms the plumule or stem tip. The cylindrical portion below the level of cotyledons is called hypocotyl and it forms the radical or root tip.

13.4.2 Monocotyledonous Embryo

The early development of the proembryo in this type remains similar to that in dicot embryo. At the time of differentiation of the cells in the globular stage, certain differences are noted. In monocots, one half of the terminal cell and its derivatives show a retarded growth. The other half grows rapidly to form one cotyledon. Asymmetric growth results in development of stem tip which appears lateral in position. The difference in both the embryo (dicot and

monocot) arise due to difference in the number and position of the cells of the terminal quadrant of the proembryo which contribute to the formation of the cotyledonary and epicotyl regions (Fig. 13.6).

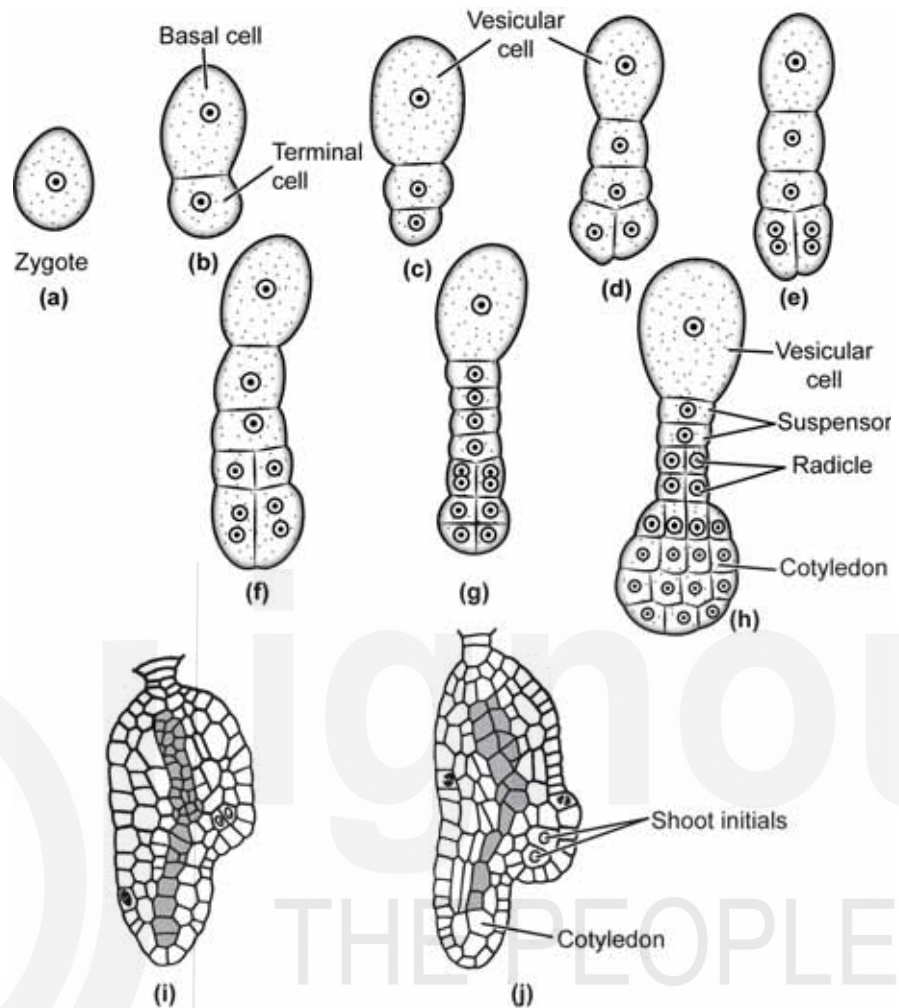


Fig. 13.6: Stages in development of a monocot embryo in *Sagittaria*.

The embryo of the monocotyledons possesses only one cotyledon. In grasses a single cotyledon is present in the form of scutellum which appears laterally attached to the embryonal axis (Fig 13.7).

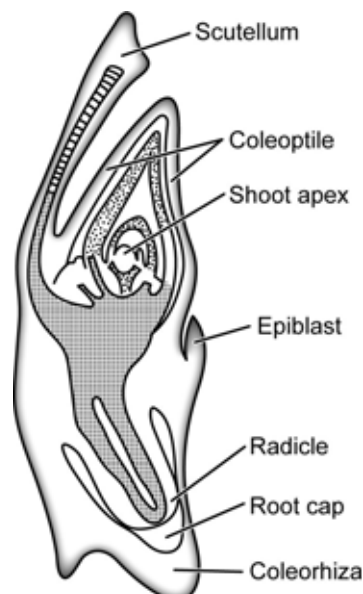


Fig 13.7: Median longitudinal section of monocot embryo.

The lower end of the embryonal axis has a radical and root cap enclosed in an undifferentiated part of the embryo called coleorrhiza. On one side of coleorrhiza a small outgrowth called epiblast is present. The portion of the embryonal axis above the level of attachment of scutellum is referred as epicotyl. It has a shoot apex with leaf primordial enclosed in a hollow foliar structure called coleoptile. The embryo remains embedded in the endosperm when present inside the seed. In dicotyledons, the derivatives of the two opposite cells of the terminal quadrant give rise to two cotyledons, while in monocotyledons the number of cells of the quadrant that contribute to cotyledons varies.

SAQ 3

a) Complete the sentence:

- i) Suspensor is an ephemeral structure developed at the end of the embryo.
- ii) At the stage of embryo, formation of all the basic tissues gets initiated.
- iii) Suspensor haustoria have been seen in the families
- iv) The destiny of the various cells of the proembryo differs in two groups after the stage.
- v) The structure of dicotyledonous embryo when seen in longitudinal section consists of an embryonal axis having two
- vi) In grasses a single cotyledon is present in the form of which appears laterally attached to the embryonal axis.
- vii) Apical cell development after the zygote formation requires the presence of hormone

b) The development of dicotyledonous embryo is different from monocotyledonous embryo. How?

c) Auxin plays a role in embryo development. Explain the statement.

13.5 SUMMARY

- The process of development of embryo from a zygote is referred as embryogenesis. The fertilized embryo is located at the micropylar end of the embryo sac.
- Embryogeny has been categorized into different types on the basis of plane of division of the apical cell and the contribution of the basal and apical cell in the formation of embryo.
- Zygote divides to form two celled structure which further undergoes divisions to form a four - celled proembryo and then quadrant. The cells of the quadrant divide transversely to form an octant. The lower cells of

the octant give rise to stem tip and cotyledons. The upper cells of the octant form the hypocotyl. The proembryo at this stage undergoes several divisions in various planes. The tangential divisions in the cells of the octant lead to differentiation of three histogen layers. The outer **dermatogen** layer forms the epidermis, middle **periblem** which gives rise to cortex of the stem and root, and inner **plerome** gives rise to vascular tissue and pith. The proembryo becomes globular shaped.

- The globular proembryo undergoes further cell multiplication and forms two cotyledons. The development of cotyledons is initiated at cordate or heart shaped stage. The cotyledons and the hypocotyl elongate to form a torpedo- shaped embryo. Further development leads to the elongation of cotyledons which become curved like horse shoe or remain straight. The destiny of each cell and its derivatives is regulated by expression of specific genes in a sequential manner.
- The development of the proembryo is similar in both monocotyledons and dicotylenous. After the octant stage the destiny of the various cells of the proembryo differs in two groups. The dicot embryo possesses an apical shoot apex and two lateral cotyledons whereas the monocot embryo possess one cotyledon and laterally placed shoot apex. The difference the embryo in both of dicots and monocots arise due to variation in the number and position of the cells of the terminal quadrant of the proembryo which contribute to the formation of the cotyledonary and epicotyl regions.

13.6 TERMINAL QUESTONS

1. Enumerate different types of embryogeny known in plants.
2. Name some of the important genes and factors regulating the development of embryo in Arabidopsis.
3. What is suspensor? What role does it plays during embryo development?

13.7 ANSWERS

Self-Assessment Questions

1. a) i) cordate or heart shaped
 ii) micropylar
 iii) apical, basal cell
 iv) vertical or oblique
 v) hypophysis.
 vi) globular
 vii) embryogenesis
 b) i) True; ii) True; iii) False; iv) True; v) False.

- c)
 - i) histogenesis
 - ii) suspensor
 - iii) cordate or heart shaped
 - iv) torpedo shaped
- 2. a)
 - i) apical cell
 - ii) suspensor
 - iii) globular stage
 - iv) hypophysis
 - v) endosperm
- b)
 - i) Refer to Section 13.2.
 - ii) Refer to Section 13.2.
 - iii) Refer to Section 13.3.
- 3. a)
 - i) micropylar
 - ii) globular
 - iii) Crassulaceae, Fumariaceae
 - iv) octant
 - v) cotyledons
 - vi) scutellum
 - vii) auxin
- b) Refer to Section 13.4.
- c) Refer to Section 13.4.

Terminal Questions

1. Refer to Section 13.2.
2. Refer to Section 13.3.
3. It is ephemeral structure at the radicular end of the embryo. It is considered as a nutritive tissue. At initial stages, the suspensor grows faster. It attains its maximal size by the globular and heart shaped stage. The suspensor anchors the embryo to the embryo sac and pushes it deep nutritionally favourable environment of the endosperm. In some plants no suspensor (*Viola*, *Tilia*) or reduced suspensor is reported (*Euphorbia*, *Bryonia*). In some plants (Brassicaceae, Loranthaceae), a long filamentous suspensor is present. In some plants such as *Cytisus laburnum*, the cells of the suspensor are clustered like bunch of grapes. In *Pisum sativum* the suspensor is composed of four large multinucleate cells. In families such as Orchidaceae, the suspensor forms the haustorium which may be single celled, vesicular, sac like or like bunch of grapes. Suspensor haustoria support the absorption of nutrients from various ovular and extraovular tissues.

APOMIXIS AND POLYEMBRYONY

Structure

14.1	Introduction	14.5	Parthenogenesis
	Objectives	14.6	Polyembryony
14.2	Apomixis		True Polyembryony
	Sporophytic		Pseudo-Polyembryony
	Gametophytic	14.7	Types of Polyembryony
14.3	Types of Apomixis		Causes of Polyembryony
	Recurrent Apomixis		Uses of Polyembryony
	Non-Recurrent Apomixis	14.8	Summary
	Adventive Embryogeny	14.9	Terminal Questions
14.4	Causes of Apomixis	14.10	Answers
	Importance of Apomixis		

14.1 INTRODUCTION

In the previous units you have studied about the process of fertilization and embryogenesis in detail. As you have studied that during the process of double fertilization, one of the male gametes fuses with the egg to form zygote, which undergoes divisions in certain planes to form a proembryo. The proembryo undergoes further divisions to form globular, heart and torpedo shaped embryo which finally develop into mature embryo from which the plantlet develops. In certain plants embryos develop without sexual reproduction or fertilization. In these plants, the embryos develop from unfertilized eggs or from other cells of the embryo sac or ovule. This means that embryos are not produced as the result of syngamy, but via a process of apogamy or apomixis. Sometimes there is the production of more than one embryo in a seed which is called polyembryony. These embryos may be produced as the result of multiple syngamy (result of fertilization) or by the process of apogamy or apomixis. Occurrence of polyembryony due to fertilization of more than one egg is called simple polyembryony. The

phenomenon is commonly noted in angiosperms for examples- onion, groundnut, mango, lemon and orange. The present unit will provide you an overview of apomixis and polyembryony.

Objectives

After studying this unit you would be able to :

- ❖ define apomixis and list the various reasons for the development of apomicts;
- ❖ describe parthenogenesis;
- ❖ describe polyembryony and its various types; and
- ❖ discuss the significance and applications of apomixis and polyembryony.

14.2 APOMIXIS

Apomixis is defined as the process of formation of a seed from the maternal tissues of the ovule asexually without the process of fertilization. The term apomixis was introduced by Winkler (1908) for “substitution of sexual reproduction by an asexual multiplication process without nucleus and cell fusion.” It is also referred as asexual seed formation. In this process, the plant bypasses the fundamental aspect of sexual reproduction i.e. meiosis and fertilization (Fig. 14.1).

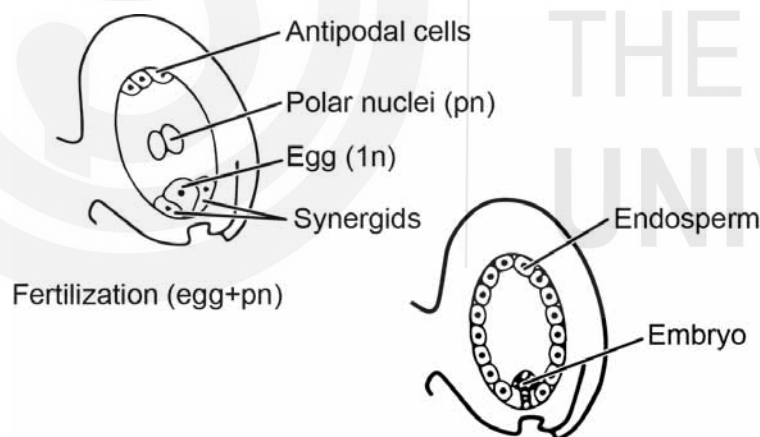


Fig 14.1: Sexual reproduction.

Seed produced without fertilization germinates into a plant. Since embryo is formed from a diploid maternal cell without meiotic reduction, gamete formation or fertilization, the progeny produced is genetically identical to the maternal parent. Hence, we can say that the plant represents a maternal clone. Some scientists give a broad definition of apomixis to include vegetative reproduction, where the propugule is parts of the plant other than seed i.e., stem, leaf or root. However, it is now more accepted to restrict the term apomixis for propagation through seed in which embryo has developed without intervention of meiosis or syngamy.

Endosperm development can occur without fertilization of the central cell. Apomixis is rare but relatively prevalent among angiosperms. It is represented

both in monocotyledonous and dicotyledonous plants. It has been described in about 400 flowering plants species representing 40 families.

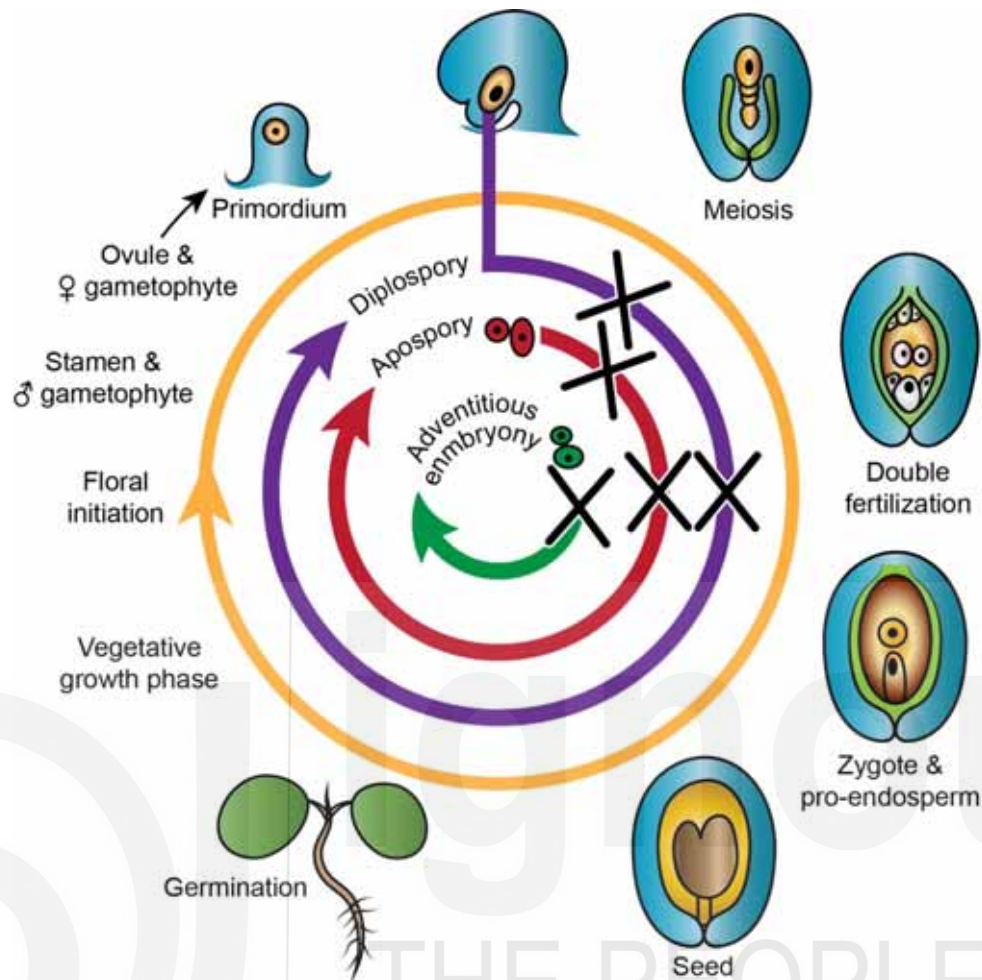


Fig .14.2: Initiation and Progression of Apomictic Mechanisms Relative to Events in the Sexual Life Cycle of Angiosperms.

Apomicts have been commonly noted in families such as Asteraceae and Poaceae. The process of apomixis was first noted in a lone female plant of *Alchornea ilicifolia* (syn. *Caelebogyne ilicifolia*) from Australia which continued to form seeds when planted at Kew Gardens in England (Smith, 1841). On the basis of development of embryo, apomixis mechanisms are divided into two types- gametophytic and sporophytic. Gametophytic apomixis means development of embryo via a cell of the gametophyte (embryo sac), and sporophytic means development of embryo directly from diploid somatic (sporophytic) cells within the ovule (Fig 14.2).

14.2.1 Sporophytic

In this type of apomixis, development of an embryo sac follows typical sexual pathway. During mitosis in the functional megaspore to form embryo sac, the diploid somatic cells of the ovule surrounding the embryo sac differentiate and form one or more embryos. The embryo initial cells form globular-shaped embryos that develop to maturity (Fig 14.3). The sexually and asexually produced embryos share the nutritive endosperm. This type of apomixis can lead to formation of a seed containing multiple embryos. It is commonly noted in citrus and mango.

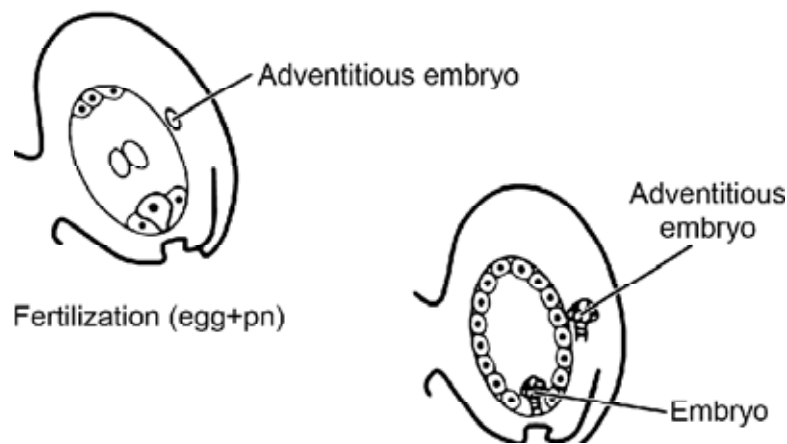


Fig 14.3: Sporophytic apomixis.

14.2.2 Gametophytic

In this type of apomixis an embryo sac is mitotically formed from a diploid cell in the ovule without undergoing meiosis. Embryo development in this type of apomixis occurs independent of fertilization. Another term for such embryo sac development is **apomeiosis**. Gametophytic apomixis is commonly noted in herbaceous and tree species which possess dehiscent fruits. Example - Poaceae, Asteraceae and Ranunculaceae.

Based upon the origin of the diploid precursor cell that ultimately gives rise to the mitotically derived embryo sac, apomeiotic embryo sac development is further subdivided into two types - **diplospory** and **apospory**. In *apospory*, the progenitor of embryo sac develops directly from a sporophytic cell of the ovule, and in *diplospory* meiosis is omitted, restituted, or preceded by endoreplication in the megaspore mother cell.

In **diplospory**, the megaspore mother cell (MMC) or a cell with apomictic potential is the progenitor cell of the unreduced embryo sac (Fig. 14.4). That cell may enter meiosis but it is not completed so that further derivatives are not haploid, but are diploid. Further development proceeds by mitotic division to achieve embryo sac formation (meiotic diplospory). Alternatively the MMC might undergo direct mitosis to form an unreduced embryo sac (mitotic diplospory). Diplospory has been observed in species of *Taraxacum officinale* (dandelion), *Ixeris denrata*, *Erigeron annuus* and *Tripsacum dactyloides*.

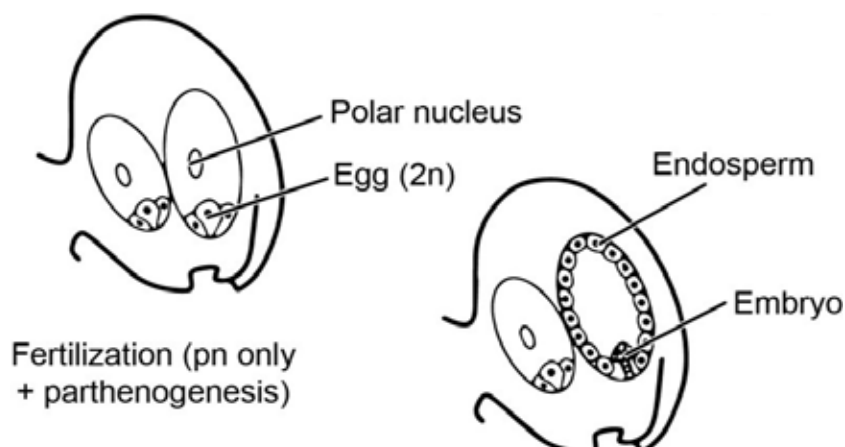


Fig 14.4: Apospory.

In **aposporous** apomicts, one or more somatic cells of the ovule give rise to an unreduced embryo sac. The development of the embryo sac occurs via mitosis of a diploid somatic cell positioned adjacent to the megaspore mother cell (Fig 14.4). This cell is termed as the aposporous initial cell. This initial undergoes mitosis and the nuclei become cellular. Meiotically reduced and aposporous embryo sacs may coexist in the ovule, or the aposporous embryo sac may continue development while the reduced sexual embryo sac degenerates. Apospory is seen in many species of *Pennisetum*, *Panicum* and other grasses.

In both cases i.e. diplospory (14.5) and apospory, true clones of the mother plant are formed. This is because chromosome restitution happens before crossing-over has initiated, and after endoreplication sister-chromosome pairing occurs.

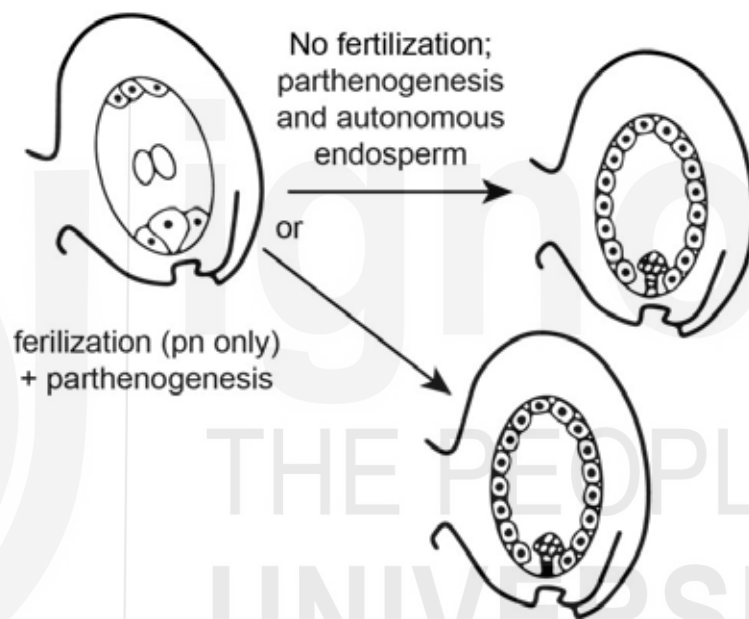


Fig .14.5: Diplospory.

Embryo development from the diploid egg formed in embryo sacs occurs without fertilization. Endosperm development in these plants may be either spontaneous (autonomous) or fertilization induced (pseudogamous). In pseudogamous aposporous species ovule-derived embryo sacs develop next to the reduced embryo sac, for example- *Paspalum*.

Most apomicts produce viable pollen. The presence of viable pollen provides the possibility of fertilization of unreduced eggs. In apomicts such as *Taraxacum*, *Poa*, *Parthenium*, *Tripsacum*, and *Hieracium piloselloides*, embryo formation is precocious i.e. initiates before anthesis or even before the opening of the flower, limiting the possibility of unreduced egg cell fertilization. In the aposporous apomict *Pennisetum ciliare*, a complete cell wall forms around the unreduced egg cell before the arrival of the pollen tube containing the two sperm cells. Development of complete cell wall around the egg serves as a means to avoid fusion of the second sperm cell with the unreduced egg cell at the time of fertilization-induced endosperm formation. Summary of apomictic embryo formation is given in Figure 14.6.

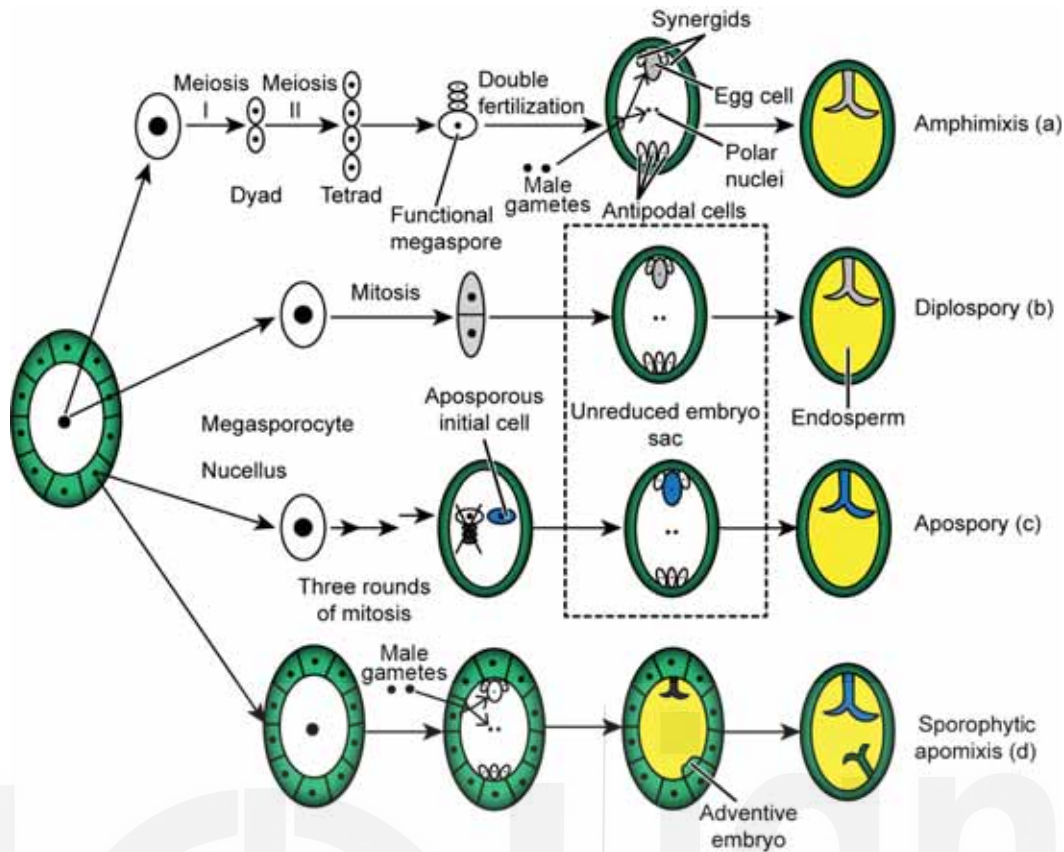


Fig. 14.6: Diagrammatic representation of the normal sexual reproduction leading to embryo and endosperm formation and various ways of development of apomicts including sporophytic apomixis, apospory and diplospory.

SAQ1

- a) Complete the sentence:
 - i) The term apomixis was introduced by
 - ii) Gametophytic apomixis is commonly noted in
 - iii) In sporophytic apomixis development of embryo occurs directly from
 - iv) In both, ... true clones of the mother plant are formed.
 - v) Apomicts have been commonly noted in families such as
- b) Define the following:
 - i) Aposporous apomicts.
 - ii) Diplospory
 - iii) Apomixis
- c) State whether the statements are true or false:
 - i) Apomixis is the process of formation of a seed from the maternal tissues of the ovule sexually with the process of fertilization.
 - ii) Most apomicts produce viable pollen.

- iii) The diploid embryo sacs are formed from the cells of the nucellus or integument.
- iv) Reduced embryo sacs relates to the development of haploid embryos without fusion of gametes.
- v) In some apomicts, endosperm is a result of triple fusion, but syngamy fails to occur.

14.3 TYPES OF APOMIXIS

Maheshwari (1950) classified apomixis into three types :

1. Recurrent (in non-reduced embryo sacs) (Fig 14.7)
2. Non-recurrent (in reduced embryo sacs)
3. Adventive embryony

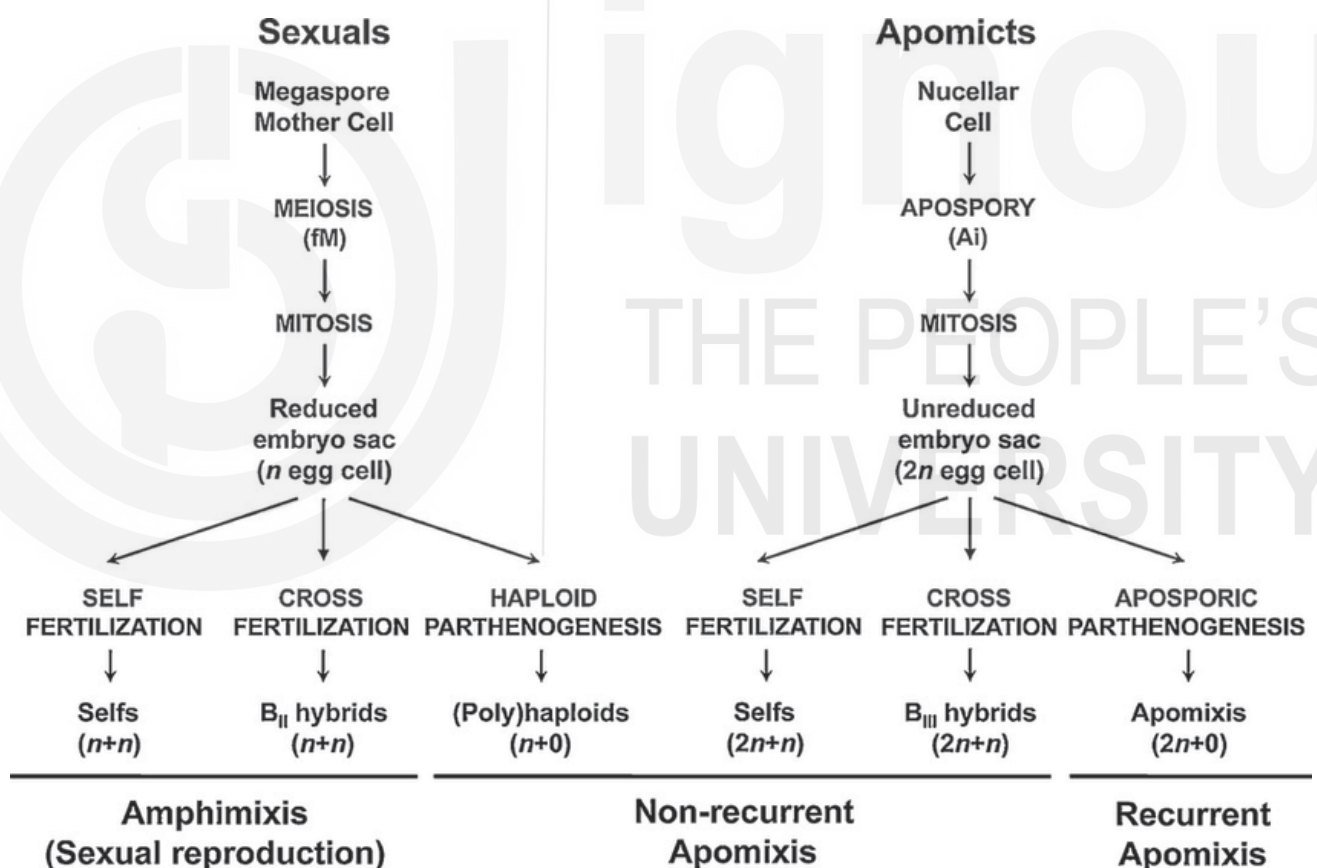


Fig.14.7: Flow diagrams showing the differences in normal sexual reproduction and apomixis.

14.3.1 Recurrent Apomixis

In this type of apomixis, an embryo sac is developed from the megaspore mother cell without the process of meiosis. Subsequently the embryo develops directly from the diploid egg cell without fertilization. The embryo sac arises from the cell of the archaesporium (generative apospory) or some other cell of the nucellus (somatic apospory) e.g., *Crepis*, *Taraxacum*, *Poa*, *Allium*.

Apospory may be classified into two types :

Generative apospory : The diploid embryo is developed from the diploid cells of the archaesporium. *Parthenium argentatum* is a common example of generative apospory. In some varieties of this plant, the nucleus of the megaspore mother cell undergoes normal meiotic divisions but does not form dyad. Instead it enlarges and develops to form an embryo sac. In this embryo sac the egg develops into embryo without fertilization. There is no coordination between the development of embryo and endosperm.

Aneuspory (Diplospory) : It includes taxa in which meiotic division is irregular during mega spore formation. Depending upon the extent of irregularity in meiosis, it is divided into four types

- i) **Antennaria type** - Two unreduced nuclei undergo two mitotic divisions to produce an eight-nucleate embryo sac of Polygonum type. This is also seen in *Datura*
- ii) **Taraxaccum type** - The first meiotic division ends in a restitution nucleus, meiosis II produces unreduced cells and ultimately an eight-nucleate embryo sac. The egg produces embryo as in *Taraxaccum*.
- iii) **Ixeris type** - A binucleate gynospore (megaspore) with restitution nucleus undergoes three mitotic divisions leading to the formation of an eight-nucleate embryo sac as in *Ixeris*.
- iv) **Allium type** - A premeiotic endomitotic doubling makes meiotic prophase to start with a double chromosome number, so that following meiosis an unreduced embryo sac with 8 nuclei is produced as seen in *Allium*

Somatic apospory : The diploid embryo sacs are formed from the cells of the nucellus or integument. The somatic cells of the chalaza or nucellus act as the embryo sac initial. *Hieracium* is a common example of somatic apospory. The megaspore mother cell undergoes meiosis and gives rise to megaspore tetrad. At this stage, a somatic cell situated at the chalazal end of the ovule becomes enlarged and vacuolated. It eventually forms an aposporic embryo sac. The embryo sac is diploid. The unfertilised eggs of such embryo sac give rise to diploid embryos e.g., *Malus*, *Ranunculus*. When the megaspore mother cell does not undergo meiosis but functions directly as the embryo sac initial it is referred as **gonial apospory**. Three successive mitotic divisions result in an eight-nucleate embryo sac *Antennaria alpina*. The different forms noted in this type of apospory include:

Unreduced embryo sacs: The fate of the nucleus in the embryo sac depends upon its position. Many irregularities in the disposition of the nuclei in early polarisation have been recorded. The mature embryo sac shows normal organisation with two synergids, three antipodal, an egg and a central-cell. Embryo development in unreduced embryo sac takes place as a result of pollination. These taxa are called eugamous, semigamous, or pseudogamous. The taxa in which the egg develops to form embryo without stimulus are called parthenogenic.

Eugamy : Normal fertilization of the apomictic egg takes place to produce zygote, for example *Hypericum perforatum*.

Semigamy : The male gamete penetrates into the egg but does not fuse with the egg nucleus. Both the nuclei divide independently but the division of the male nucleus stops early e.g., - *Rudbeckia speciosa*.

Unreduced pseudogamy : The male gamete degenerates either inside or outside the embryo sac. The egg develops without fertilization, for example *Zephyranthes texana*.

Agamospermy : Agamospermy is the formation of seed with the embryo formed without meiosis and syngamy. Agamospermy can be recurrent or non-recurrent. In non-recurrent type, the embryo is haploid. The seed having this type of embryo is non-viable. In recurrent agamospermy all the cells of embryo sac are diploid. This type of embryo is formed directly either from a nucellar cell (apospory) or diploid megaspore mother cell (diplospory). The diploid egg or diploid cells of embryo sac grow into normal embryos.

Reduced embryo sacs: This relates to the development of haploid embryos without fusion of gametes. In reduced embryo sac, egg can develop into an embryo without pollination stimulus and there is no fertilization. This type refers of embryo development in reduced embryo sacs.

Reduced psuedogamy : The reduced egg develops in a pseudogamous and parthenogenic manner. The pollen tube enters normally but the male gamete fails to fuse with the egg and disintegrates in the cytoplasm, e.g., *Triticum monococcum*.

Reduced parthenogenesis: Embryo development occurs from egg of reduced embryo sac. It is accomplished by heat or cold treatment to flowers e.g., - *Datura stromium*.

Androgenesis : The egg nucleus degenerates. The sperm nucleus functions in the cytoplasm of the egg and produces embryo e.g., *Poa alpina* x *P. pratensis*.

14.3.2 Non-Recurrent Apomixis

In this type of apomixis, the megaspore mother cell undergoes meiotic division and one of the megaspores thus formed develops into haploid female gametophyte i.e., embryo sac. There is no fertilization and embryo develops either from the unfertilised egg (haploid parthenogenesis) or from some other cell of embryo sac (haploid apogamy).

Haploid parthenogenesis: It is the development of embryo from an unfertilised egg of an embryo sac. This has been seen in *Solanum* species. The stigma of *Solanum nigrum* when pollinated with pollen of *S. luteum*, the male nucleus penetrates the egg but no nuclear fusion occurs. The male nucleus disintegrates but the egg gets activated and forms the embryo. In species such as *Orchis maculate* and *Platenthera chlorantha* sometimes the pollen tube does not enter the ovule, or enters very late so that the fertilization does not take place. The egg divides to form haploid embryo without fertilization.

According to Maheshwari, (1950) the egg fails to fertilize because the pollen tube is absent, pollen tube is not able to discharge its contents, early degeneration of sperms, or non-synchronization of egg and sperm maturation, so that syngamy fails to occur. Formation of embryo directly from diploid egg without fertilization is called diploid parthenogenesis for example - Rubus, Apple, Poa.

Haploid apogamy: It is the development of embryo from any cell of the embryo sac apart from the egg. Twin proembryo are noted in *Lilium martagon* and *Bergenia delavaysi*. One of the embryos develops from egg by normal fertilization, while the other develops from a haploid synergid cell.

14.3.3 Adventive Embryogeny

In this one or more diploid sporophytic cells divide and grow to form mature embryos inside normally developed sexual embryo sac. A zygote may also be formed from the egg which may degenerate or compete with apomictic embryos.

14.4 CAUSES OF APOMIXIS

The development of apomicts occurs because of various reasons such as:

- i) bypassing of meiosis during embryo sac formation (apomeiosis),
- ii) development of an embryo from egg independent of fertilization (a process known as parthenogenesis), and
- iii) formation of viable endosperm by fertilization-independent process or after fertilization with a sperm cell.

Apomicts show irregular meiosis. A set of genes control the apomixis trait which is genetically inherited. Apomixis is governed by three recessive genes (aabbcc). The genes determine the breeding behaviour. In the homozygous condition 'a' forms the unreduced eggs, 'b' prevents fertilization and 'c' promotes egg development without fertilization. Thus aaBBCC will have unreduced egg but cannot develop without fertilization. AAbbCC produces reduced egg but embryo development cannot take place because fertilization is prevented. AABBcc shows normal sexual behaviour because the gene C has no effect in the presence of A and B.

Inheritance in apomicts was studied by Gregor Mendel (1869) in *Hieracium*. The F₁ hybrids of *Hieracium* showed extensive segregation whereas the F₂ "hybrids" did not segregate and uniform progeny was obtained. Inheritance of gametophytic apomixis has been reported to be associated with the transfer of either a single locus or a small number of loci in most of the systems. Either one locus or a small number of loci are involved in the inheritance of apomixis. Studies proposed that a single dominant locus controlled apomixis in most species. Genetic analysis proved that apomixis is inherited as a dominant trait. The components of apomixis i.e. meiotic avoidance, parthenogenesis, and fertilization-independent endosperm development are controlled by independent loci. Two independent loci have been identified to control diplospory and parthenogenesis. Apospory locus (called *LOSS OF*

APOMEIOSIS or *LOA*) has been identified in plants. An additional locus responsible for fertilization-independent seed development (called *LOSS OF PARTHENOGENESIS* or *LOP*) has been developed. Deletion of either *LOA* or *LOP* returns the sexual pathway. Plants with no *LOA* do not produce diploid embryo sacs via apospory as they lack apomeiosis function.

Dominant inheritance has been reported for apospory in the dicotyledonous plants such as *Ranunculus* and *Hieracium*. The presence of varied apomictic mechanisms and the phylogenetic positioning of apomictic species throughout many angiosperm families suggest that apomixis has evolved independently multiple times in different groups.

14.4.1 Importance of Apomixis

At one time apomixis was regarded as an evolutionary dead end, with no prospect of adaptation or improvement. However, this feature is now regarded important for generic improvement and commercial success of hybrids of crop plants. Apomixis results in production of seeds without involving the process of meiosis and syngamy. It plays an important role in hybrid seed production. Apomixis prevents the loss of specific characters in the hybrid so that the hybrid can be propagated from seeds without conducting hybridization again and again. Apomixis does not involve meiosis; hence no segregation and recombination of chromosomes occur. The useful characters can be preserved for long. Interestingly, apomixis (like vegetative reproduction) is more common in plants growing in specialized habitats such as deserts, high altitude and aquatic conditions. In such situation, selection has favoured sustenance of adaptations that have evolved in each species.

Apomixis plays an important role in the enhancement of crop species because it leads to the formation of large genetically uniform populations with better hybrid vigor. Agronomic advantages of apomixis include rapid generation and multiplication of superior forms through seed germplasm. Adventive embryos are useful in agriculture and horticulture because of genetic uniformity and superior disease resistance.

SAQ 2

- a) Answer in one word:
- In this type of apomixis, development of an embryo sac follows typical sexual pathway.
 - In this type of apomixis, the megaspore mother cell (MMC) or a cell with apomictic potential is the progenitor cell of the unreduced embryo sac.
 - In this process diploid embryo sacs are formed from the cells of the nucellus or integument.
 - In this type of apomixis, an embryo sac is developed from the megaspore mother cell without the process of fertilization.
 - In this process, embryo develops from an unfertilized egg.
- b) Discuss the importance of apomixis in agriculture.
-

14.5 PARTHENOGENESIS

The process of embryo development from an unfertilized egg is called parthenogenesis. It is a form of reproduction in which an egg in the embryo sac develops into an embryo without being fertilized by a sperm. The development of embryo via parthenogenesis has been noted in apomictic grasses. Parthenogenesis is sometimes described as an 'incomplete form of sexual reproduction'. This is because the offspring of parthenogenic species develop from gametes. Gametes are reproductive cells that result from meiosis (or reduction division).

Parthenogenesis can operate on either a haploid or a diploid cell. In haploid parthenogenesis, an offspring develops from haploid egg to produce haploid adult. On the other hand, the process of diploid parthenogenesis proceeds along two pathways. Automixis (automictic parthenogenesis) is a postmeiotic process in which a haploid cell may either duplicate its chromosomes or join with another haploid cell. Diploid zygote develops and grows into diploid adult. A second form of diploid parthenogenesis, is apomixis (apomictic parthenogenesis). In this meiosis is absent but instead, two genetically identical diploid egg cells are produced from a parent cell through mitosis. One or more of these daughter cells which are diploid and clones (genetically identical) of the original parent cell develop into a diploid offspring. Parthenogenesis is usually found in combination with *apomeiosis* (the omission of meiosis) and *pseudogamous* or *autonomous* (with or without central cell fertilization) endosperm formation, together known as *apomixis* (clonal seed production) in plants.

SAQ 3

Discuss the importance of parthenogenesis.

14.6 POLYEMBRYONY

Polyembryony is the production of more than one embryo in a seed. These embryos may be produced as the result of multiple syngamy (result of fertilization) or by the process of apogamy or apomixis. Occurrence of polyembryony due to fertilization of more than one egg is called simple polyembryony. The phenomenon is commonly noted in angiosperms for examples- onion, groundnut, mango, lemon and orange. It was first reported by Leeuwenhock (1719).

Johansen (1950) defined polyembryony as the means production of multiple embryos arising from zygote such polyembryony is caused due to cleavage of proembryo (Orchidaceae) and is called cleavage polyembryony. Polyembryony also results from development of many embryos from other cells of embryo sac besides the egg (*Argemone*) or formation of many embryos due to presence of more than one embryo sac in same ovule (*Citrus*), or formation of many embryos from cells outside the embryo sac (Mango, *Opuntia*).

Braun (1859) classified polyembryony into four types :

1. cleavage of zygote or zygotic embryos.

2. formation of embryos from the cells of the embryo sac other than the egg.
3. development of more than one embryo sac within the ovule.
4. activation of sporophytic cells of the ovule.

Depending upon whether the embryos arise in one or more embryo sacs in the ovule two types of polyembryony have been recognized. It has been categorized as "true" and "false" depending upon the condition whether the embryos arise in the same embryo sac or in different embryo sacs in the same ovule.

Schnarf (1929) divided polyembryony into two types - true and false

14.6.1 True Polyembryony

In true polyembryony, embryos may arise either by a splitting of the zygote or proembryo (cleavage polyembryony) or from cells of the embryo sac other than the egg (apogamy), or from nucellar or integumentary cells outside the embryo sac (adventives embryony). Polyembryony is also seen in few gymnosperms.

14.6.2 Pseudo-Polyembryony

Pseudo or False polyembryony involves fusion of two or more nuclei in an ovule or development of two or more embryo sacs within the same nucellus. Sometimes more than one embryo sacs are present in an ovule so that two zygotic embryos may arise in a seed. In case of *Poa pratensis* and *Casuarina equisetifolia* these may arise either from the derivatives of the same megaspore mother cell or from two or more megaspore mother cells. It has been found that in *Atraphaxis* and *Trifolium* the additional embryo sacs sometime arise from the cells of the chalaza.

Gustafson (1946) proposed that true polyembryony is the development of embryos derived from one or several embryo sacs present in the same nucellus, while false polyembryony is referred to cases where two or more nucelli each with its embryo sac fuse.

14.7 TYPES OF POLYEMBRYONY

Webbe (1940) classified polyembryony of angiosperms into three types

1. Simple polyembryony: In the case of this type, a number of embryos develop as a result of the fertilization of several archegonia (in gymnosperms).
2. Cleavage Polyembryony: In the case of this type, a single fertilised egg (zygote) gives rise to a number of embryos.
3. Rosette polyembryony: Additional embryos develop from the rosette cells in certain gymnosperms as this type of polyembryony is termed rosette polyembryony.

Simple polyembryony - In this type, embryos arise in one or more embryo sacs in the ovule. Embryos also arise from budding or cleavage of the proembryonal or suspensor of the zygotic embryo. Embryos can also be produced without fertilization. In gymnosperms it results from the fertilization of the egg in several archaegonia in a female gametophyte (archegonial polyembryony).

Cleavage polyembryony - It results from the cleavage of the zygote or early stages of its development (proembryo) into two or more units. This type has been commonly noted in conifers (gymnosperms), but sporadically in the angiosperms such as *Nicotiana rustica*, *Isotoma longiflora*, and *Erythronium americanum*. In *Erythronium* first division of the zygote is transverse and results in the formation of a large basal cell and a small terminal cell. The former increases in size without undergoing any division or may undergo repeated divisions to form a group of cells from which embryos originate. As the volume of the cell increases, out-growths arise at its lower end which is referred as embryogenic mass. From embryonic mass, many cells at distal end form separate embryos. The filamentous proembryo becomes branched and each of the branches give rise to an independent embryo. The embryo gives off buds or out-growths which may themselves function as embryos. In *Isotoma* and *Exocarpus*, additional embryos are formed from suspensor cells of proembryo.

Rosette polyembryony

In this type, additional embryos develop from the rosette cells of the suspensor. This type is commonly noted in gymnosperms.

Embryos can be produced from various other cells present in the embryo sac or in the ovule include:

A. Embryos arising from the cells outside embryo sac

Cells of the nucellus and integuments also develop into embryos for example- *Citrus*, *Eugenia* and *Mangifera*. In *Spiranthes*, embryos develop from inner cells of inner layer of integument. Such embryos subsequently come to lie in the embryo sac and are nourished by the endosperm. Embryos obtained by nucellus are superior to those obtained by vegetative propagation because they are disease free and maintain their superiority for a long time.

B. Embryos from cells of embryo sac other than egg

Synergids embryos

The embryo may appear from synergids and antipodal cells in the embryo sac. The synergids may be fertilised by sperms from an additional pollen tube or develop without such fusion. Fertilization of the synergid usually occurs after entry of the additional pollen tube in the embryo sac. The unfertilised synergid is also stimulated to divide and form an embryo (Fig 14.8) like structure. These embryos are haploid in nature. The synergid embryos grow along with zygotic embryos in the embryo sac e.g., *Argemone Mexicana* and *Phaseolus vulgaris*. Embryos from antipodal cells develop less frequently (Example - *Ulmus americana*, *Allium odorum*) but these embryos are not viable.

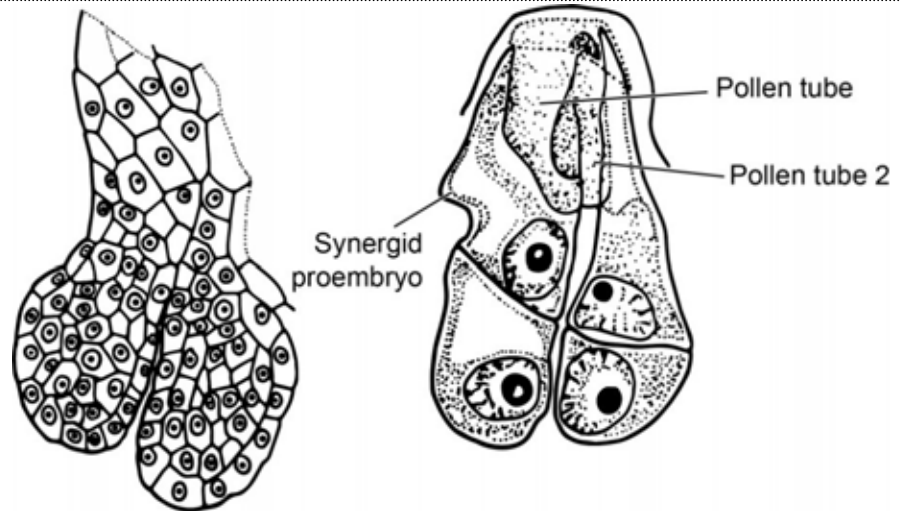


Fig. 14.8: Synergid polyembryony : *Tamarix ericoids* and *Dioscorea composite*.

Zygotic embryos

Cleavage of the apical cells of the globular or filamentous proembryo produced by the zygote results in two or more embryos (*Cocos nucifera*, *Primula auriculata*) (Fig 14.9).

Suspensor embryos

In members of Acanthaceae, the buds or new embryos arise from uniseriate suspensor of the young proembryo. The embryos that develop from proembryonal cells or suspensor cells are diploid (Fig 14.9).

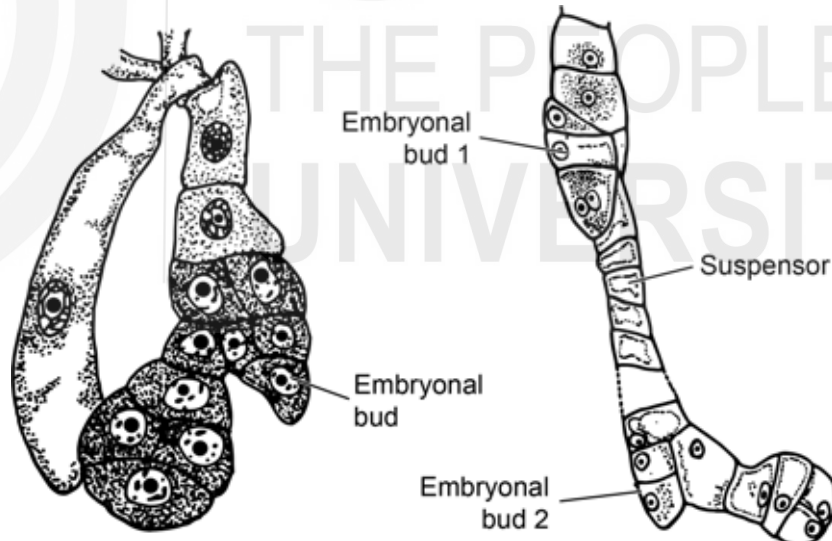


Fig. 14.9: Zygotic or suspensor polyembryony. Budding of an embryo from a globular proembryo and proembryo with embryo bud arising from uniseriate suspensor.

In *Citrus* a seed has 2-40 embryos, one zygotic and the rest adventive, mostly nucellar. In *Allium odorum*, there are 5 embryos, all developed by different methods, one from zygote, one from synergid, 2 from antipodal cells and one from integument of ovule.

14.7.1 Causes of Polyembryony

Two theories have been proposed to explain the occurrence of polyembryony.

Necrohormone theory

Haberlandt (1921, 1922) suggested that degenerating cells of the nucellus act as a source of stimulus to the adjacent cells to divide and form adventive embryos. There is no evidence to support the theory.

Kappert (1933) suggested that polyembryony is a recessive genetic character and is controlled by multiple genes. During hybridization, genes recombine in plant and this result in polyembryony. Firetti-Leggieri et al. (2013) suggested that polyembryony is associated with polyploidy

14.7.2 Uses of Polyembryony

Adventive embryos produced by the process of polyembryony are useful in agriculture and horticulture because of genetic uniformity and superior disease resistance compared to vegetative propagules. These embryos provide uniform seedlings same as the parental type. Nucellar adventive polyembryony is of great significance in horticulture. The plantlets produced by them are vigorous, free from disease (viruses) and endowed with well developed root system. The seedlings obtained from such embryos show more vigour and embryos are uniform in appearance.

Agronomic advantages of apomixis include rapid generation and multiplication of superior forms through seed from novel germplasms; the reduction in cost and time of breeding; the avoidance of complications associated with sexual reproduction (such as pollinators and cross-compatibility) and the avoidance of viral transfer in plants that are typically propagated vegetatively. Apomixis is very poorly represented among crop species. It has been well studied in subtropical fruit trees such as mango, *Citrus* (Fig 14.10) and tropical forage grasses, such as *Panicum*, *Brachiaria*, *Dichanthium*, and *Pennisetum*.

Earlier polyembryony was considered to have great potential in horticulture for these reasons. However, with the development of tissue culture technique, the value of polyembryony is much less exploited. However biotechnologists are interested in transferring genes for apomixis into other crop hybrids so that these can be propagated without resort to hybridization process for each generation.

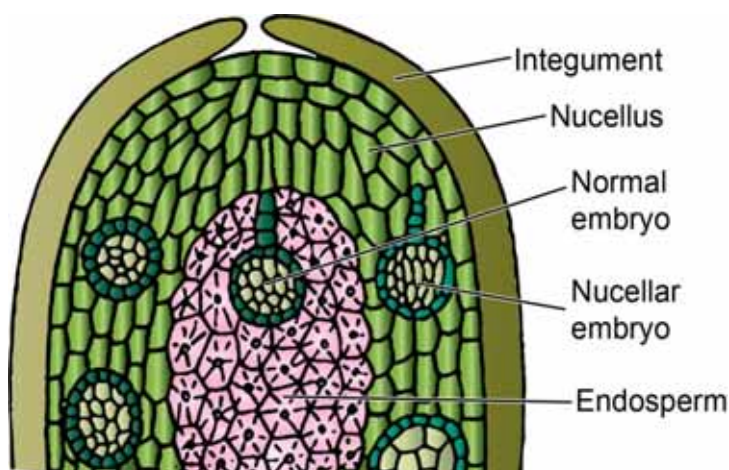


Fig 14.10: Citrus ovule section showing normal and nucellar embryos.

SAQ 4

- a) Differentiate between true and false polyembryony.
- b) Fill in the blanks :
 - i) The process of embryo development from an unfertilized egg is called
 - ii) In the process embryos are produced from diploid cells of the ovule lying outside the embryo sac i.e. nucellar or integumentary cells of the ovule.
 - iii) is the production of accessory embryos from two or more embryo sacs in the same ovule.
 - iv) polyembryony is commonly noted in conifers, gymnosperms.
- c) Discuss the applications of polyembryony in horticulture.

14.8 SUMMARY

- The process of formation of a seed from the maternal tissues of the ovule asexually without the process of fertilization is referred as apomixis. It is also called as asexual seed formation. Seed produced without fertilization germinates into a plant that develops as a maternal clone.
- Apomixis is divided into gametophytic and sporophytic types on the basis of development of embryo via a gametophyte (embryo sac) or directly from diploid somatic (sporophytic) cells within the ovule.
- Apomixis has been classified into two types- recurrent (in non-reduced embryo sacs) and non-recurrent (in reduced embryo sacs). The latter relates to the development of haploid embryos without fusion of gametes. In reduced embryo sac, egg can develop into an embryo without pollination stimulus and there is no fertilization. Non-recurrent type refers of embryo development in reduced embryo sacs.
- The process of embryo development from an unfertilised egg is called parthenogenesis. It is a type of reproduction in which an egg develops into an embryo without being fertilised by a sperm. It occurs during diplospory and apospory. The parthenogenesis has been noted in apomictic grasses.
- Polyembryony refers to the production of more than one embryo in a seed. The embryos are not produced as the result of multiple syngamy (result of fertilization) but by the process of apogamy or apomixis. It has been categorized as true" and "false"-according to whether the embryos arise in the same embryo sac or in different embryo sacs in the same ovule.

- In true polyembryony, embryos may arise either by a splitting of the zygote or proembryo (cleavage polyembryony) or from cells of the embryo sac other than the egg (apogamy), or from nucellar or integumentary cells outside the embryo sac (adventive polyembryony).
- Cleavage polyembryony results from the cleavage of the zygote or earlier stages of embryo development (proembryo) into two or more units examples- *Nicotiana rustica*, *Isotoma longiflora*, *Lobelia*, *Erythronium*. Cleavage polyembryony is common in gymnosperms, but it is of rare occurrence in angiosperms.
- In adventive polyembryony, the embryos are produced from diploid cells of the ovule lying outside the embryo sac i.e. nucellar or integumentary cells of the ovule. These embryos are called adventive or sporophytic. In other words, in this type embryo develops directly from a diploid cell other than egg like that of nucellus and integument.
- Apomixis plays an important role in the enhancement of crop species because it leads to the formation of large genetically uniform populations with better hybrid vigour. Agronomic advantages of apomixis include rapid generation and multiplication of superior forms through seed germplasm. Adventive embryos are useful in agriculture and horticulture cause of genetic uniformity and superior disease resistance as compared to vegetatively multiplied plants.

14.9 TERMINAL QUESTIONS

1. Enlist the differences between cleavage and rosette polyembryony.
2. How is gametophytic apomixis different from sporophytic apomixis?
3. What is adventive polyembryony?
4. Define :
 - i) apospory
 - ii) diplospory
 - iii) apomixis
 - iv) multiple polyembryony
 - v) apomeiosis
 - vi) recurrent apomixis
 - vii) parthenogenesis

14.10 ANSWERS

Self-Assessment Questions

1. a) i) Winkler in 1908
ii) herbaceous and tree species which possess dehiscent fruits.

- iii) diploid somatic (sporophytic) cells within the ovule.
 - iv) cases i.e., diplospory and apospory
 - v) Compositae and Poaceae
- b)
- i) In aposporous apomicts, one or more somatic cells of the ovule give rise to an unreduced embryo sac.
 - ii) In diplospory, the megaspore mother cell (MMC) or a cell with apomictic potential is the progenitor cell of the unreduced embryo sac.
 - iii) Apomixis is defined as the process of formation of a seed from the maternal tissues of the ovule asexually without the process of fertilization
- c)
- i) False; ii) False; iii) True; iv) True; v) False
2. a)
- i) Sporophytic
 - ii) diplospory
 - iii) somatic apospory
 - iv) recurrent
 - v) haploid parthenogenesis
- b)
- It plays an important role in hybrid seed production. Seed produced by the process develops into a plant which acts the maternal clone. The progeny derived from apomixis are clones which are genetically identical to the maternal parent. The ability to generate maternal clones in desirable genotypes in crop species accelerates agricultural breeding practices. It acts as a cost-effective method for producing hybrid seeds. Apomixis has an advantage of producing individuals with desired qualities in large numbers.
3. Parthenogenesis is sometimes described as an 'incomplete form of sexual reproduction'. Parthenogenesis can operate on either a haploid or a diploid cell. An offspring develops from egg to produce adult. The clones (genetically identical) of the parent cell develop into a diploid offspring. The process is like unisexual reproduction which involves one parent hence there is no production of viable seeds.
4. a)
- False polyembryony involves fusion of two or more nucelli or development of two or more embryo sacs within the same nucellus. Polyembryonate condition may also be due to the occurrence of multiple embryosacs within the ovule. Sometimes more than one embryo sac is present in an ovule so that two

zygotic embryos may arise in a seed. Example - *Poa pratensis*, *Casuarina equisetifolia*. These may arise either from the derivatives of the same megaspore mother cell or from two or more megaspore mother cells. It has been found that in *Atraphaxis* and *Trifolium* the additional embryo sacs sometime arise from the cells of the chalaza.

In true polyembryony the embryos arise in the embryo sac either by cleavage of the zygote (cleavage polyembryony), or proembryo or cells of the embryo sac other than the egg (apogamy), from the synergids and antipodal cells, or from nucellar or integumentary cells outside the embryo sac (adventives embryony).

- b)
 - i) Parthenogenesis
 - ii) Adventive embryony
 - iii) Multiple polyembryony
 - iv) Cleavage polyembryony
- c) The multiple embryos produced through polyembryony can be haploid, diploid or triploid. The haploid embryos can be used for producing homozygous diploids by doubling the chromosome number. Haploids and homozygous diploids can be of great use in breeding superior crop varieties and hybrids. Adventive embryos are useful in horticulture because of genetic uniformity and superior disease resistance. These embryos provide uniform seedlings similar to the parental type. The nucellar embryos have great significance in horticulture. This is because the plantlets produced by them are vigorous, free of diseases, virus and possess well developed root system. The seedlings obtained from such embryos show more vigour and are uniform in appearance.

Terminal Questions

1. Cleavage Polyembryony - In the case of this type, a single fertilized egg gives rise to a number of embryos.

Rosette polyembryony : Additional embryos develop from the rosette cells of embryonal suspensor in certain gymnosperms and this type of polyembryony is termed rosette polyembryony. This type has been commonly noted in conifers. Although common in gymnosperms, cleavage polyembryony occurs only sporadically in the angiosperms.
2. Sporophytic - The development of an embryo sac follows typical sexual pathway. The diploid somatic ovule cells surrounding the embryo sac differentiate and have an embryogenic cell fate. These embryo initial cells form globular-shaped embryos that develop to maturity. The sexual and asexual embryos share the nutritive endosperm. This type of apomixis leads to formation of a seed containing multiple embryos. It is commonly noted in *Citrus*.

Gametophytic - This type of apomixis relates to mechanism where an embryo sac is mitotically formed from a diploid cell in the ovule without undergoing meiosis. Embryo development in this type of apomixis occurs independent of fertilization and endosperm formation may or may not require fertilization. Such type of embryo sac development is called as apomeiosis. It is further subdivided into two types - diplospory and apospory based upon the origin of the diploid precursor cell that ultimately gives rise to the mitotically derived embryo sac.

3. Refer to Section 14.6 and 14.7.
4.
 - i) Apospory : The gametophyte develops directly from a sporophytic cell of the ovule. In these apomicts, one or more somatic cells of the ovule give rise to an unreduced embryo sac. Apospory involves development of the embryo sac via mitosis from a diploid somatic cell positioned adjacent to the megaspore mother cell. This cell is termed as the aposporous initial cell. This initial undergoes mitosis and the nuclei become cellular. Development of the aposporous embryo sac may lead to the demise of the sexually derived embryo sac. Aposporous embryo sacs might coexist in the ovule, or continue development while the reduced sexual embryo sac degenerates. True clones of the mother plant are formed.
 - ii) Diplospory : In diplospory meiosis is omitted, restituted, or preceded by endoreplication in the megaspore mother cell. The megaspore mother cell (MMC) or a cell with apomictic potential is the progenitor cell for the unreduced embryo sac. This cell may enter meiosis but aborts. The development proceeds by mitotic division to achieve embryo sac formation (meiotic diplospory). Alternatively cell might undergo direct mitosis to form an unreduced embryo sac (mitotic diplospory). Diplospory has been observed in species including *Taraxacum officinale* (dandelion), *Boechera* spp., *Erigeron annuus* and *Tripsacum dactyloides* true clones of the mother plant are formed.
 - iii) Apomixis : It is defined as the process of formation of a seed from the maternal tissues of the ovule asexually without the process of fertilization. It is also referred as asexual seed formation and is the result of plant's ability to bypass the fundamental aspect of sexual reproduction i.e., meiosis and fertilization.
 - iv) Multiple polyembryony : This type of polyembryony involves the production of accessory embryos from two or more embryo sacs in the same ovule. Example- In *Gossypium* the fertilization of egg in one embryo sac stimulates of embryo from an unfertilized egg in the adjacent embryo sac within the same ovule.
 - v) Apomeiosis : When an embryo sac is mitotically formed from a diploid cell in the ovule without undergoing meiosis, embryo development occurs independent of fertilization and endosperm formation may or may not require fertilization.

- vi) Recurrent apomixis : In this type of apomixis, an embryo sac is developed from the megaspore mother cell. The egg-cell is diploid. The embryo subsequently develops directly from the diploid egg-cell without fertilization. The embryo develops directly without the process of fertilization. Example- *Crepis*, *Taraxaccum*, *Poa*, *Allium* (onion).
- vii) Parthenogenesis : The process of embryo development from an unfertilized egg is called parthenogenesis. It also referred as a form of reproduction in which an egg in the embryo sac develops into an embryo without being fertilized by a sperm. It occurs during diplospory and apospory. Parthenogenesis is sometimes described as an 'incomplete form of sexual reproduction'. This is because the offspring of parthenogenic species develop from gametes. Gametes are reproductive cells that result from meiosis (or reduction division).

Acknowledgements

Fig 14.2 : (https://www.plantcell.org/content/plantcell/14/suppl_1/S228/F1.large.jpg .Ross A. Bicknella and Anna M. Koltunowb,1 a Crop and Food Research, Private Bag 4704, Christchurch, New Zealand b Commonwealth Scientific and Industrial Research Organization, Plant Industry, Adelaide, Glen Osmond, South Australia 5064, Australia).

SEED AND FRUIT|

Structure

15.1	Introduction	15.5	Dispersal of Seeds
	Objectives		Autochory
15.2	Parts of a Seed		Anemochory
15.3	Development and Structure of the Seed		Hydrochory
	Nucellus		Zoochory
	Integuments	15.6	Types of Fruits
	Appendages in Seed	15.7	Fruit Development and its Structure
15.4	Stored Metabolites in Seed	15.8	Parthenocarpy
		15.9	Summary
		15.10	Terminal Questions
		15.11	Answers

15.1 INTRODUCTION

In earlier units you have studied about the process of sexual reproduction by means of pollination and fertilization. You have also studied that process of double fertilization leads to the formation of zygote which develops into an embryo and primary endosperm nucleus which eventually forms the endosperm. In this unit you will study about the development of fruit and seed. Seed can be defined as a unit of reproduction having embryo and nutritive tissue called endosperm. It is enveloped by seed coat derived from the integuments of the ovule. After pollination the ovary develops into fruit. The fruit encloses the seeds. The fruit protects the seeds and help in their dispersal. Seeds of many plants remain viable in soil for long periods. They may undergo the period of dormancy and germinate only when conditions especially of temperature and moisture become suitable for their germination.

Objectives

After studying this unit you would be able to :

- ❖ explain the development of seed from the ovary and its structure;
- ❖ describe different types of modifications in seed structure for their dispersal;
- ❖ list the various types of appendages found in seeds;
- ❖ know the reserve materials present in the seed which provide nourishment to the young sporophyte during germination;
- ❖ describe the structure and development of fruit;
- ❖ classify different types of fruits; and
- ❖ discuss the interesting phenomenon of parthenocarpy for development of seedless fruits.

15.2 PARTS OF A SEED

Seed is a mature ovule enclosing an embryonic plant and stored food material. It is covered by seed coat formed from one or two integuments. The size, shape, texture and colour of the seed show a lot of diversity. The seeds of most of the plants are a few millimeters (e.g., mustard, guava, poppy) to few centimeters (e.g., Castor, groundnut, cucumber) in diameter. Orchids have very small seeds just like dust particles. Tropical trees and lianas have fruits that possess large seeds. The seeds may possess smooth surface or it can be wrinkled, ribbed or furrowed. The surface can also be glossy (in linseed and castor), fleshy or pulpy (in *Magnolia*). Many seeds have hairs, as in cotton and milkweed.

In fruits, seeds are attached to a fruit wall by a stalk called funiculus. The funiculus gets prolonged, running along the seed and terminating at the chalaza to form a structure called raphe. When the seed gets separated from the funiculus, a scar is left at the point of attachment called the hilum. Close to the hilum at one end of it is situated a minute pore called micropyle. During seed germination water is absorbed mainly through this pore and the radicle also comes out through this pore (Fig.15.1).

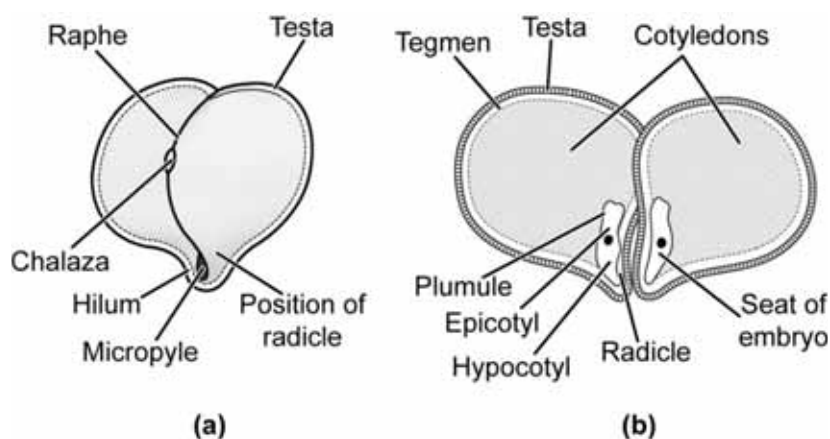


Fig. 15.1: a) Parts of a dicot seed; b) Parts of a monocot seed.

15.3 DEVELOPMENT AND STRUCTURE OF THE SEED

A seed is a specialised structure that protect the embryo, nourishes it maintain dormancy till the conditions are favourable for germination (rainy season), ensures wider propagation through effective biotic or abiotic dispersal, and finally provides nutritional support to the seedling till it becomes capable of manufacturing its own food by photosynthesis. To achieve these functions seed show several adaptations in different species.

With the development of embryo and endosperm, the integuments and nucellus in the ovule also undergo certain changes resulting in the formation of seed.

15.3.1 Nucellus

In most of the flowering plants, the nucellus gets gradually utilized by the embryo or endosperm so that hardly any remains of nucellus are seen in the seed. The nucellus degenerates completely in the leguminous seeds. In some species such as *Euphorbia* the nucellar cells near the micropylar and chalazal end persist for a longer period in the mature seed. In some seeds, the major volume is occupied by the persistent nucellus which is also the main food storage tissue. Example - black pepper. This persisting nucellus is termed as perisperm (Fig. 15.2).

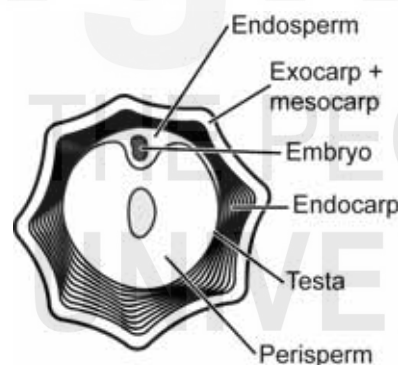


Fig.15.2: Black pepper: Fruit with seed cut in longitudinal section.

15.3.2 Integuments

The ovule usually possesses one or two integuments. The cell layers of one or both of the integuments show proliferation after fertilization. The integument in which number of cell layers increase is called as multiplicative. In some plants, the number of cell layers in integument remains same as in the mature ovule. It is called as non-multiplicative. Normally, in most cases majority of the cell layers degenerate or get compressed as the seed matures. Some of the cell layers in one or both integuments persist and become hard to form a protective sheath called the seed coat. These cells enlarge and their walls become lignified or superseded. Such a layer of hard cells is described as sclerotic, mechanical, palisade - like or Malphigian layer.

In seeds developing from the ovule having two integuments (bitegmic), the persisting outer integument is called as testa and the inner integument is termed as tegmen. In contrast, in seeds developing from ovule having one

integument i.e. unitegmic, the seed covering is termed as testa. Seeds with testa are referred as testal while those having prominent tegmen are called as tegmic. Seeds in which the outer layers of outer integument constitute the mechanical layer are called as exotestal, while those having hardened inner portion are called endotestal. Similarly seeds with outer part of the inner integument modified as sclerotic zone are exotegmic and those with inner layers forming the protective sheath are referred as endotegmic. Mostly where, the fruit wall is stony or tough, the seed coat is thin and soft. Example - Coconut, almond, groundnut. In species with soft or fleshy fruit, the seeds are hard and stony e.g., Apple and guava.

Various histological changes takes place during the formation of seed coat. This could be understood with the help of following examples.

In cotton, the ovule possesses two integuments (Fig.15.3).

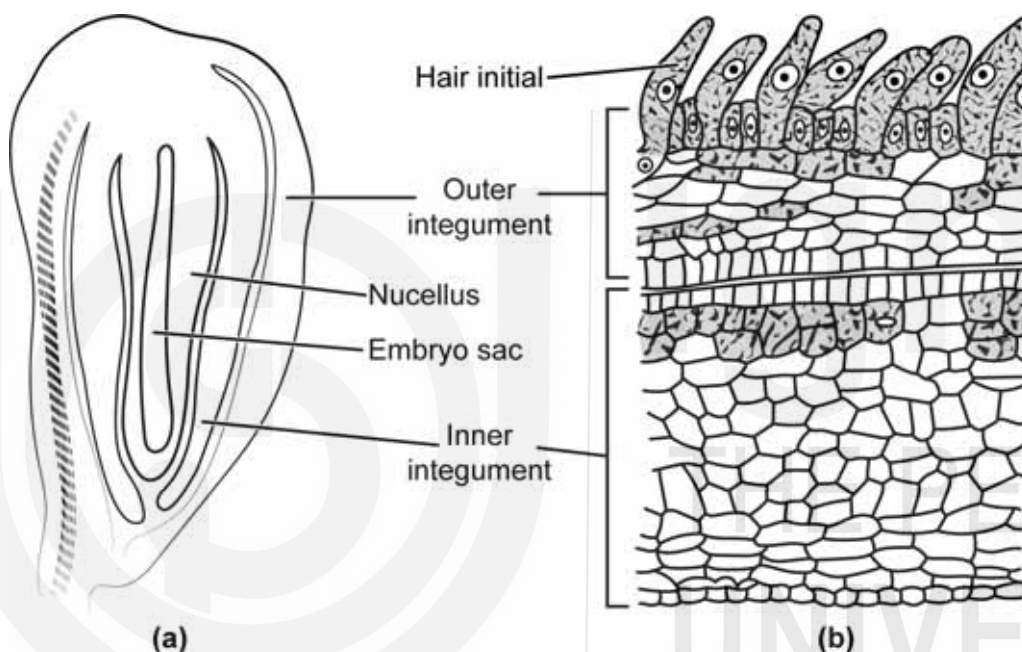


Fig. 15.3: Seed coat development in cotton a) L.S. of ovule showing mature embryo sac; b) A portion of integuments from ovule after 2-3 days of pollination.

Both the integuments participate in the formation of seed coat. The outer integument is 4-6 cells thick and the inner integument is 8-15 cells thick at the mature embryo sac stage. The inner integument is multiplicative. After pollination, outer integument gets distinguished in three zones. i) outer epidermis, ii) outer pigmented zone which is 2-5 layers thick and contains starch and tannin filled cells, iii) inner epidermis. In the inner integument, cells of the outer epidermis start elongating radially. The cells enlarge many times of their original size and their walls become thick. This layer forms the sclerotic layer of the mature seed coat. In mature seed, the inner integument possess four zones- i) outer palisade- like layer, ii) a pigmented zone having 4 or 5 layers, iii) inner colorless zone having 9 or 10 layers and iv) inner epidermis. Some of the outer epidermal cells of the outer integument enlarge and elongate outward to form hairs during the development of seed coat. These hairs (the cotton of commerce) are single celled, thin walled and can reach up to a size of 40 mm (Fig. 15.4). These form the cotton fibre of commerce.

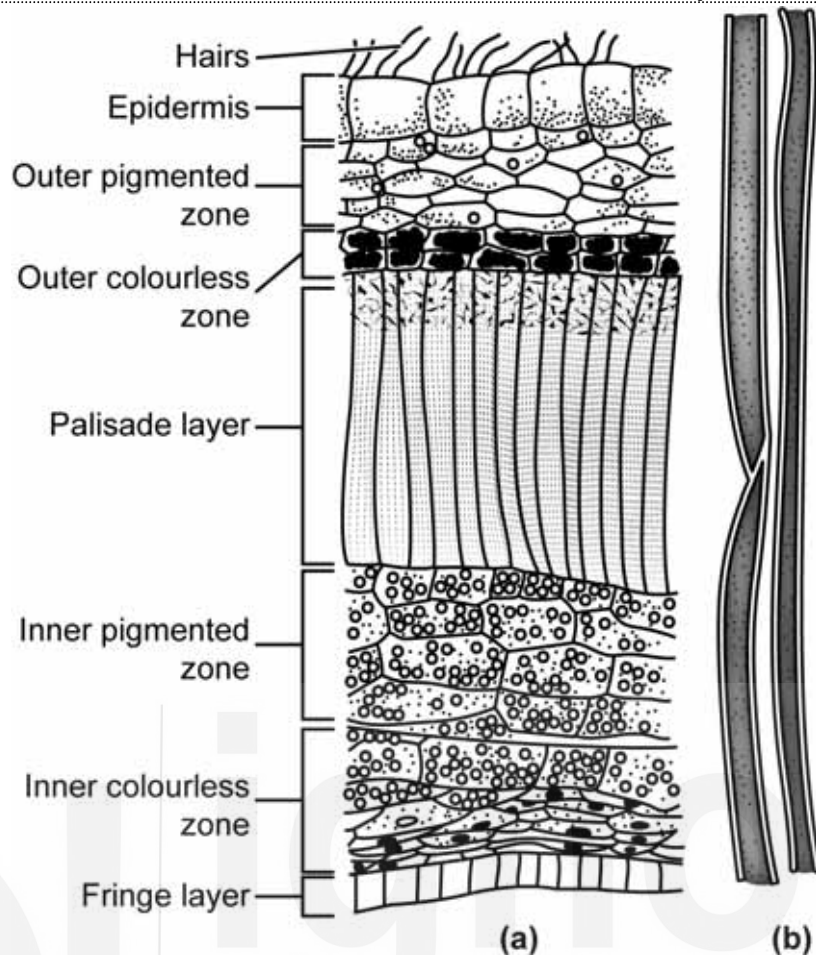


Fig. 15.4: Structure of integuments of cotton a) Mature seed coat; b) hairs of cotton.

In mustard, the outer integument possesses 2 to 5 layers of cells, and the inner integument has 9 or 10 layers of cells. Cells of the outer integument become large and get filled with mucilage. The subepidermal layers possess tangentially elongated cells which later become crushed. Inner epidermis of the outer integument forms the sclerotic layer. The inner integument gets reduced, only its inner epidermis forms a pigmented layer in the seed.

In leguminous seeds, the seed coat is derived from the outer integument whereas the inner integument degenerates. The outer epidermis of the testa forms the palisade layer. The cells refract light in the middle and near the outer wall of cells. The orientation of microfibrils that constitute the wall thickenings are responsible for refraction. The subepidermal layer of cells differentiates to form funnel-shaped cells. Thin walled parenchymatous tissue with vascular bundles is present below this region. The attachment of the funicle in seed forms a disc-shaped structure which fits into the depression called hilum. The outer layer of cells of the funicle head also forms the palisade layer (counter-palisade) which is attached to the palisade layer of the testa. Both palisade and counter palisade get interrupted in the center by a groove that acts as an air passage in the ripening seed. The groove also possesses group of tracheids called trachiedal bar. On both the sides of tracheidal bar aerenchyma is present. Testa is impermeable to water, hence the tracheidal bar serves as hygroscopic valve providing moisture during seed ripening and germination (Fig. 15.5).

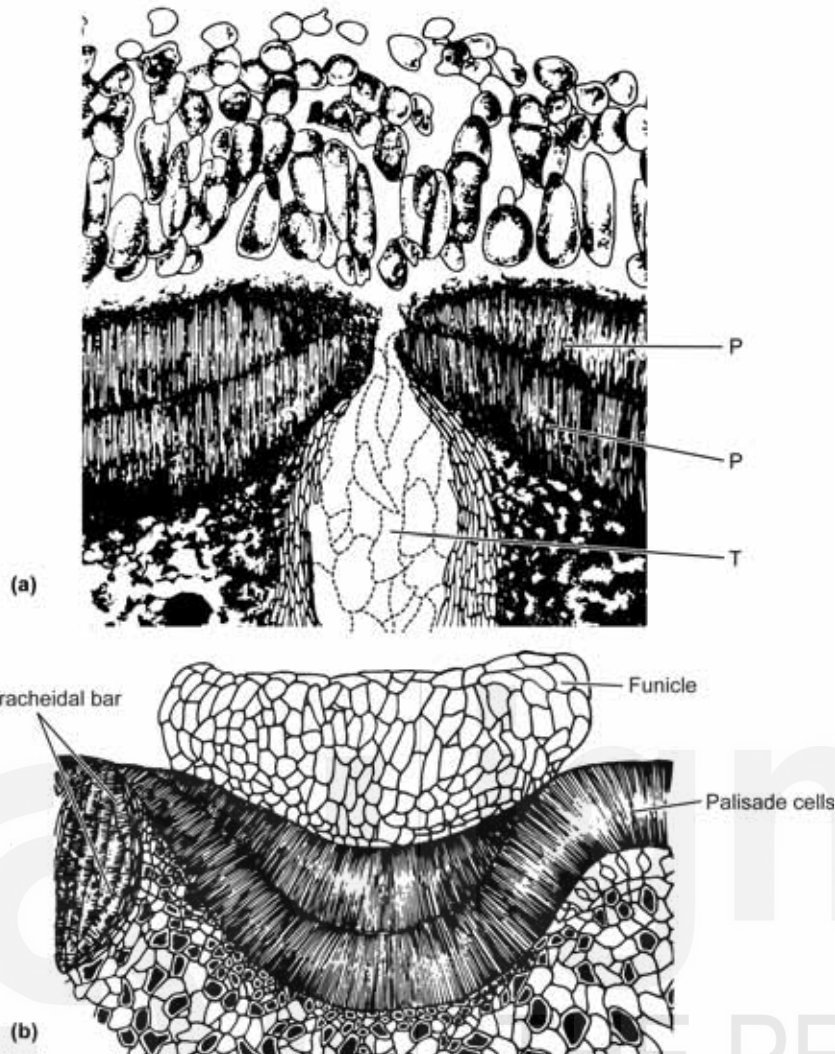


Fig. 15.5: Median L.S. of seed coat through hilum of *Phaseolus aureus* seed a) photograph of the region of hilum; b) diagrammatic representation of funicle region.

The seed coat of certain plants is fleshy or juicy. In pomegranate, the outer epidermal cells of testa become radially elongated and filled with sweet sap under turgor pressure. This layer forms the juicy edible part of the seed. The inner part of the testa is hard and the tegmen is membranous (Fig. 15.6).

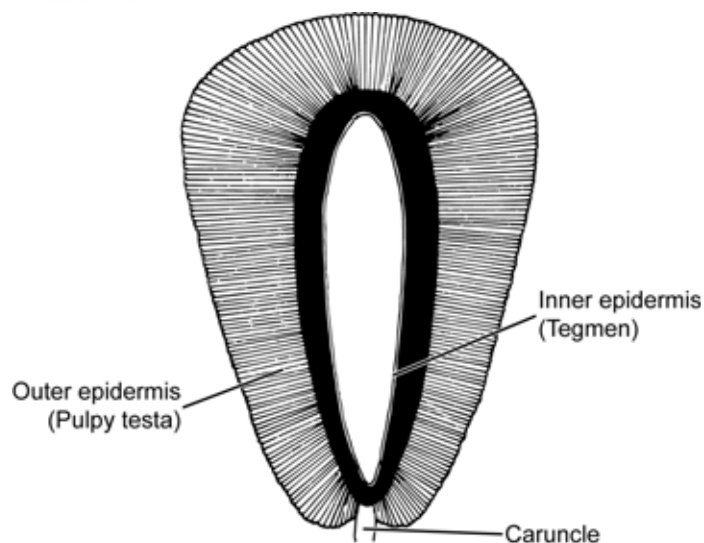


Fig. 15.6: diagrammatic representation of the L.S. of seed of pomegranate showing outer epidermis of testa with radially elongated cells and solid black inner portion of outer integument made up of sclerenchyma.

SAQ 1

- a) What is the sclerotic or Malpighian layer?
- b) Fill in the blank spaces with appropriate words:
 - i) The seed of cotton is
 - ii) Seeds of flowering plants are always enclosed in a
 - iii) In the majority of seeds the constitute the nutritive tissue.
 - iv) In seeds of pomegranate seedcoat is and
 - v) In coconut the fruitwall is and seed coat is
 - vi) Trachiedal bar serves as providing moisture during germination.

15.3.3 Appendages in Seed

Seeds of certain species have specialised outgrowths or envelopes. These structures develop from parts of the ovule or funicle after fertilization.

Aril - It is an outgrowths that arises from funicle or the testa near the raphe. It covers the seeds partially or completely. It is also referred as the third integument. It is fleshy and brightly colored. The cells of aril contain oil, starch, sugar, pigments and aroma containing compounds. The edible part of litchi is aril (Fig. 15.7). In *Myristica fragrans* the hard seed is covered by a thin, irregular and bright orange aril (that gives the spice mace). It is supposed to be consumed by birds and in the process seeds get scattered.



Fig.15.7: Aril of litchi.

Caruncle - It is a white, collar- like structure borne on the micropylar end of the seed. It is found in members of the family Euphorbiaceae. Example - Castor (*Ricinus communis*) (Fig.15.8). The soft outgrowth capping the hard seed is formed by proliferation of cells at the tip of the outer integument. It is

rich in starch and sugars. Insects such as ants consume the caruncle and in the process help in the dispersal of the seeds by carrying them away to a far off places. It is believed that caruncle also help in seed germination by absorbing moisture due to its hygroscopic nature.

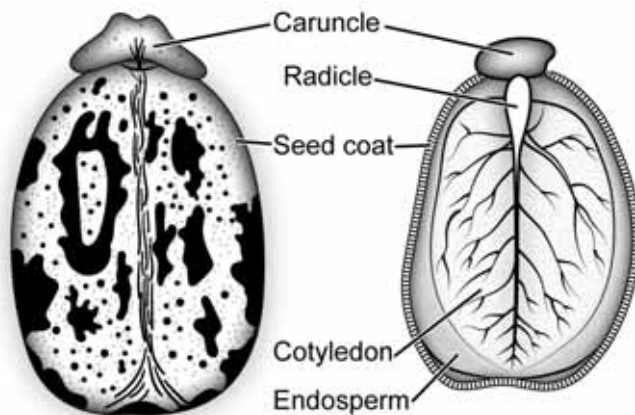


Fig. 15.8: Structure of castor seed showing caruncle, and L.S. of seed.

Operculum - It is a plug- like structure formed in the micropylar portion of the seeds by proliferation of cells at the tip of the inner integument or nucellus. Operculum has been noted in seeds of monocots belonging to families Commelinaceae, Musaceae, Lemnaceae and Zingiberaceae and some dicot families like Bignoniaceae and Nymphaeaceae. The cells of the operculum are thick- walled and contain an orange red substance. The operculum becomes detached from the rest of the seed during germination process and help in coming out of embryo.

Wings and hairs - In some plants the epidermal outgrowths or the folds/projections of the integuments appear as wings. In *Oroxylon* disc like transparent, thin, round wings spreads on two lobed seeds. In *Moringa oleifera* the seeds show presence of three wings. The wings provide large surface area and strength to the seed. Seed coat of *Oroxylon indicum* expands to form a large wing which helps in dispersal . The winged seeds get arranged compactly in the fruit. These seeds travel long distances along with the wind. Some seeds also show the presence of hair like structures. Seeds of *Calotropis procera* (milkweed) posses tuft of hairs at one pole (Fig. 15.9). Hairs provide large surface area without corresponding increase in weight thereby facilitating the dispersal of seeds by air. In aquatic plants like *Nymphaea* the seed hairs are filled with air and provide buoyancy to the seed to float on water.



Fig. 15.9: Milkweed seed showing tuft of hairs at one pole.

SAQ 2

- a) State whether the following statements are true or false:
 - i) Aril is also called as third integument.
 - ii) In *Ricinus communis* caruncle is found at the chalazal end of the seed.
 - iii) Wings provide large surface area and strength to the seed.
 - iv) In aquatic plants seed hairs are filled with air and thus provide buoyancy to the plant.
 - v) The edible part of litchi is caruncle.
 - vi) In *Oroxylon* seeds have hairs for dispersal.
- b) Fill in the blanks with appropriate words:
 - i) Operculum is formed by proliferation of cells at the tip of or
 - ii) Caruncle is involved in seed dispersal by
 - iii) In the drumstick (*Moringa oleifera*) fruit seed has wings.
 - iv) In many members of family Euphorbiaceae a white collar like structure is present at micropylar end that is called as
 - v) In cotton is present on entire surface of seedcoat.

15.4 STORED METABOLITES IN SEED

In seeds of most of the plants, the food is stored in the cells of the endosperm. For example in coconut, wheat, castor bean endosperm stores bulk of food reserves. The food stored in the endosperm is utilized during development of embryo and germination of seed. The endosperm surrounds the embryo and nurtures embryo till the seedling begins to photosynthesize and become autotrophic. Perisperm is another nutritive tissue found in some seeds. It is the part of the persisting nucellus. It is mostly seen in monocots such as ginger and turmeric but also found in few dicots, such as in black pepper and lotus. In *Canna*, the chalazal cell divides repeatedly to form starch containing tissue called chalazosperm. You can recall from Unit 12 (Endosperm) that mature seeds containing persistent endosperm are called albuminous, and those lacking it are called exalbuminous. Leguminous seeds lack endosperm. In these plants, the function of the storage of the food is taken up by cotyledons of the embryo.

In a germinating seed, the embryo gets energy for the metabolic events through the stored lipids and carbohydrates. Carbohydrates are generally stored in the thick walls of the endosperm (coffee and date palm) or cotyledons (balsam and *Nasturtium*). Starch grains are present in cells of

cotyledons and endosperm. Seeds also possess protein reserves for supplying nitrogenous compounds to the young seedling till it becomes capable of absorbing nitrogen from the soil with the help of roots. Seed proteins occur in the form of discrete protein bodies called aleurone grains. These are present in the endosperm and embryo of most plants. In cereals, the aleurone grains are concentrated in the outer layer of the endosperm, forming a specialised layer called aleurone layer. (Fig. 15.10) The aleurone protein bodies become active during seed germination. Their action gets triggered by the gibberellins released by the embryo. The enzyme α amylase gets released during this time which helps in the breakdown of the starch present in the endosperm. Legumes are rich in reserve proteins. Groundnut contains about 25 percent and soybean contains nearly 40 percent protein.

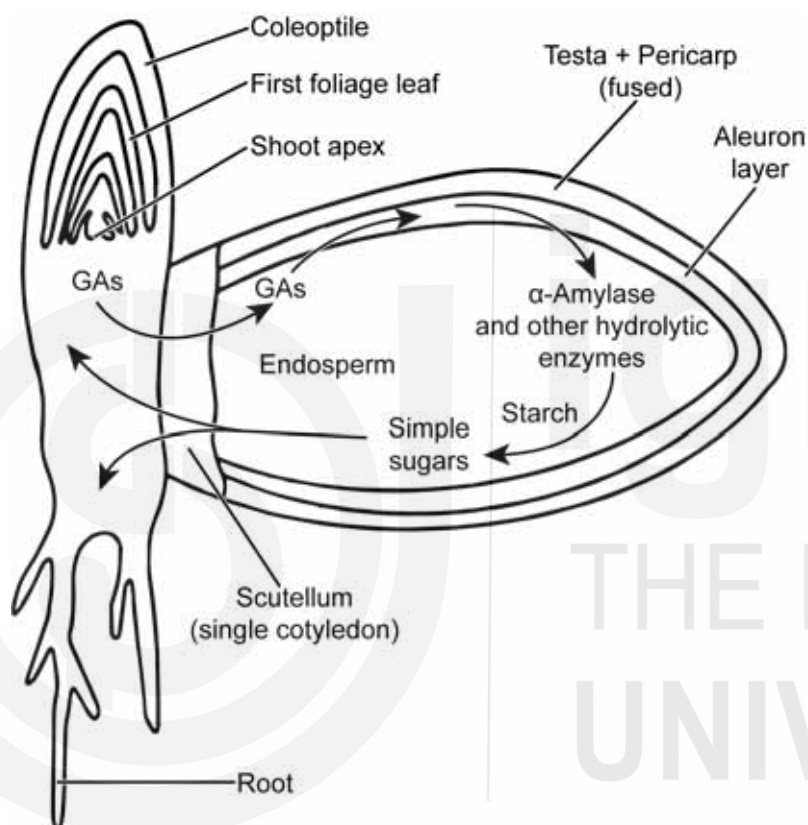


Fig 15.10: Stored food reserves in germinating barley grain.

SAQ 3

State whether the following statements are true or false:

- In leguminous seeds well developed perisperm is found.
- Seeds of castor are exalbuminous.
- Proteins occur in only those seeds that lacks starch and lipids.
- Enzymes responsible for digestion of starch during seed germination are produced in seed itself.
- In majority of seeds endosperm is the main reservoir of food.
- In monocots like ginger and turmeric perisperm is found which is also a nutritive tissue.

15.5 DISPERSAL OF SEEDS

A plant usually bears many fruits and innumerable seeds. If all the seeds produced by the plant germinate at one place, the resulting seedlings would compete with each other for space, light, water and minerals. The seedlings will become vulnerable to attack by pests and pathogens. There will be more chances for backcrossing resulting in production of genetically inferior progeny. To overcome these drawbacks, seeds have evolved several mechanisms for dispersal of seeds over a wider areas. Fruits of some plants possess some inbuilt mechanisms for dispersing seeds to long distances. This is termed as autochory. External agencies such as air, water and animals also help in dispersal of seeds which are referred as anemochory, hydrochory and zoochory respectively.

15.5.1 Autochory

This is a self dispersal mechanism. In it forceful expulsion of seeds occurs from the fruit because of turgidity or dessication of the pericarp cells. Example - in *Impatiens*, the fruit is a cylindrical capsule formed by the fusion of five carpels. Fruit wall comprise of three regions. The middle region is made up of radially elongated cells. The cells possess high turgor pressure. This zone is termed as expansion zone. When the fruit matures and starts drying the cells of the expansion zone come in the state of tension. Inner portion of the pericarp consisting of 2 or 3 layers of collenchyma that offers resistance. At this stage a mild jerk or touch can result in separation of carpels. The carpels curl inward resulting in the dispersal of seeds up to distance of 2 metres. In *Euphorbia* as the mature capsule dries up, its three compartments open up with a force along longitudinal slits, throwing the seeds a metre or more away.

15.5.2 Anemochory

The seeds of certain plants are carried to long distances through air currents. The seeds are provided with special structures such as wings or hairs that help in their dispersal to far away places., Anemochorus plants usually produce large number of seeds since many seeds get wasted in the process of dispersal to long distances. For example- Orchids produce several hundred million seeds per plant. The seeds are very tiny and get blown away like dust particles. The seeds possess undifferentiated embryo and lack endosperm. Hairy seeds of milkweed, *Calotropis procera* and semal, *Bombax ceiba* can be seen carried away by strong summer winds.

15.5.3 Hydrochory

Plants growing in and near the water bodies use water as agency for dispersal of seeds and fruits. For example- *Cocos nucifera* (coconut) has spread to various continents because of its ability to float over hundred to thousand kilometers. The fruit has a smooth, water proof exocarp followed by a fibrous and air filled mesocarp and a hard endocarp. The seed retains its viability for more than three months. It is believed that seeds of sweet potato have been carried across continents by oceanic water currents.

15.5.4 Zoochory

It is the dispersal of fruits and seeds by animals. Some fruits are eaten by animals and the seeds are passed out with the excreta. For example - fruits of plum, figs, grapes, guava are eaten by birds. The fleshy part of the fruit is digested by the birds and the hard seeds are given out along with the droppings. The seeds of the plants such as neem, maulsari are large. The birds eat the pulp and discard the seeds below their perch. The seeds/fruits of some plants stick to the body parts of animals and get carried away to distant places. Seeds of *Viscum album* (mistle toe) are dispersed through birds eating its fruits by adhering to their beak. Fruits of some plants belonging to Asteraceae bear spines and hooks which help in attaching them to body parts of animals. Sheeps, goats and cow also play an important role in seed dispersal. Humans also serve as agent of dispersal by raising plants of their use in different parts of world. Animals like monkeys, langurs, lizards and squirrels are very effective dispersers of seeds.

15.6 TYPES OF FRUITS

A fruit developed solely from the ovary and its contents is known as a true fruit e.g., mango (Fig.15.11). A fruit developed from the ovary, its contents and additional parts of the flower such as the receptacle, petals and sepals is known as false fruit e.g., apple, strawberry (Fig.15.12). The wall of the fruit is called as pericarp. Generally mature pericarp is made up of 3 distinct regions. In mango outer peel represents the exocarp, middle fleshy and juicy part is mesocarp and inner stony part is the endocarp.

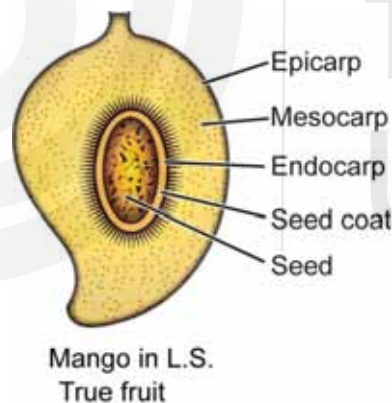


Fig. 15.11: L.S. of mango (a true fruit).

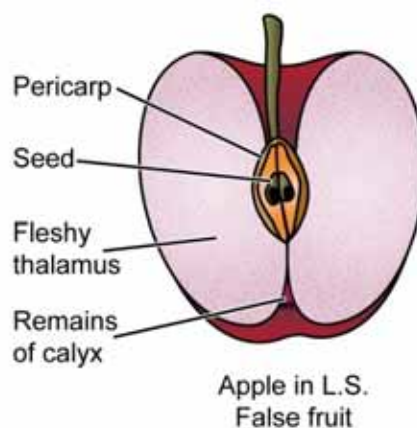


Fig. 15.12: L.S. of apple (a false fruit).

Fruits display huge diversity in their size, shape, colour, structure, chemical constituents, dispersal mechanism and hardness. On morphological ground they are classified on the basis of degree of hardness of fruit wall and their ability to dehisce or remain intact after ripening. Based on these criterion classification of some important types of fruits is given below.

A. SIMPLE FRUITS

These fruits are formed from one carpel. On the basis of degree of hardness of fruit wall or pericarp, the fruits can be categorized as dry and hard or soft and fleshy.

A. Dry fruits

The seed coat becomes hard on maturity.

1. Indehiscent fruits

These include fruits that do not open at maturity to shed their seeds. Such fruits develop from a single carpel or from a compound gynoecium with several carpels. The major types of indehiscent fruits include :

- i) **Achene** - It contains one seed loosely arranged inside the fruit. The seed is attached to the fruit wall at a single point. Example- buttercup, sunflower.
- ii) **Caryopsis** - It is like achene but the pericarp and testa of the seed become fused. Example - wheat, corn.
- iii) **Samara** - It is a single seeded, winged achene dry indehiscent fruit. In this type of fruit a flattened wing of fibrous papery tissue develops from the ovary wall (Fig 15.13). Example - Maple. Fruits developing from gynoecium having many carpels.
- iv) **Nut** - A single seeded fruit that develops from ovary that initially possess several carpels but all of them degenerate except one. The mature fruit contains one carpel and one seed. Example - walnut, beech, chestnut, oak.

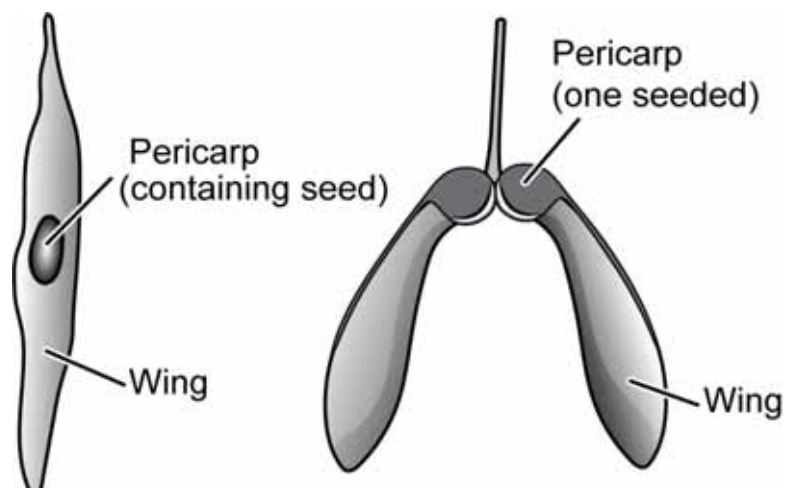


Fig. 15.13: Samara Fruit.

- vi) **Schizocarpic fruits** - These fruits develop from multilocular ovaries. On ripening they separate into individual achenes each representing a carpel. At maturity the carpels distinct as separate indehiscent fruits.
Example- *Malva*, *Abutilon*.

2. Dehiscent fruits

Fruits developing from a single carpel or from a syncarpous ovary with two or more carpels. Dry fruits in which pericarp splits open at maturity by definite natural means to release the contained seeds are called as dehiscent fruits. Three main type of dehiscent fruits are follicle, legumes and capsules (Fig. 15.14).

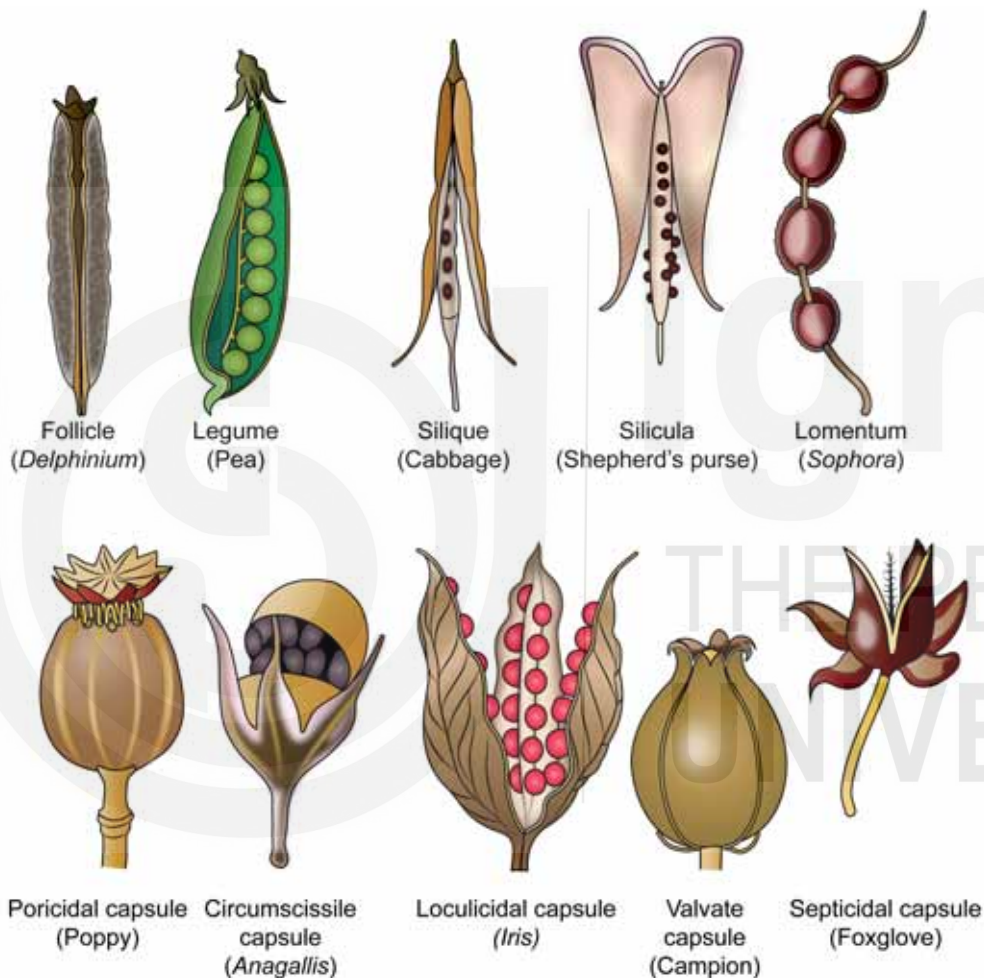


Fig. 15.14: Different types of dry dehiscent fruits.

- i) **Follicle** - A pod like dry dehiscent fruit splitting along only one suture. It may contain one or many seeds. Example- Larkspur, Delphinium, milkweeds.
- ii) **Legume** - It is the dry dehiscent pod that splits open on both ventral and dorsal side. Example- peas, beans, peanut.
- iii) **Lomentum** - It is a dry dehiscent legume constricted between the seeds. Example- *Sophora*, *Desmodium*.
- iv) **Capsule** - Capsule is a most common fruit type. It is a simple, dry, many seeded dehiscent fruit developing from multicarpellary, syncarpous

ovary. The dehiscence is along fusion lines of carpels or along dorsal lines of dehiscence or by splitting transversely into top and bottom portions or by small pores that develop in the pericarp. Example- *Iberis*, *Hypericum*.

On the basis of dehiscence capsules are of following types :

- a) Loculicidal capsule - A dry dehiscent capsule which splits along the locules (midrib of each ovary). Example- Lily, *Iris*.
- b) Septicidal capsule - A dry dehiscent capsule which splits along the septa and opens at the top. Example- Yucca, agave.
- c) Siliqua - a special long slender capsule of 2 fused carpels with length usually more than three times of its width. It is a pod like fruit having two carpels and a false septum that divides the locule. On ripening of fruit the two valves separate and the seeds remain attached to the septum. Example- Mustard, cabbage.
- d) Silicle - A silicle or silicula is a special short broad capsule of 2 fused carpels with width more than length. Example - Shepherds purse, *Iberis amara* (candytuft).
- e) Pyxis - a capsule that dehisce transversely by a lid that falls off to release seeds. Example plantain, *Amaranthus*.
- f) Poricidal capsule - A capsule which opens with round holes. Example Poppies.
- g) Circumscissile capsule - It is a dry dehiscent fruit opening by splitting along the centre of fruit, so that top of capsule lifts off like a lid. Example *Anagalis*.
- h) Valvate capsule - It is a dry dehiscent fruit in which the tips of the seed capsule split. Example - Campion, Primrose, Jacobs ladder (*Polemonium*).

B. Fleshy fruits

A fruit in which the wall becomes soft and fleshy as it matures (Figs. 15.15 to 15.19) .These include

- 1) **Berry** - In these fruits exocarp, mesocarp and endocarp are indistinguishable. The pericarp is fleshy and encloses one or many seeds (Fig.15.15). Example- Tomato, grapes.



Fig. 15.15: Berry of tomato; same in T.S.

Two special types of berry-like fruits may be singled out for special consideration.

- a) **Hesperidium** - This is a special type of berry in which a leathery rind is formed, the interior of the fruit is divided by septa, indicating the number of carpels (Fig. 15.16). Example *Citrus*.



Fig.15.16: Hesperidium of orange.

- b) **Pepo** - It is like a berry but the exocarp is hard so relatively hard rind is formed. The interior of fruit is not divided by septa (Fig.15.17). Example- Pumpkin, watermelon, gourds, squash.



Fig. 15.17: T.S. of Pepo of cucumber.

- 2) **Pome** - A false fleshy fruit formed by a group of carpels more or less firmly united with each other and surrounded by and united to the floral tube or receptacle (Fig.15.18). Example- Apple, Pear.

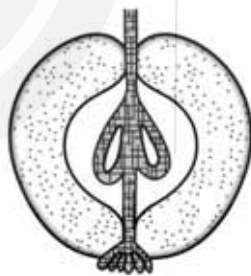


Fig.15.18: Pome of apple.

- 3) **Drupe** - It is like a berry with soft and fleshy exocarp and mesocarp but the endocarp is thick and hard (Fig.15.19). Example- Peach and mango. Coconut is also a drupe with exocarp impervious to water and mesocarp fibrous and airy, but hard endocarp.



Fig 15.19: Drupe of mango.

Other types of fruits are :

Aggregate Fruit - An aggregate fruit or etario consists of many individual small fruits that develop by merger of several separate ovaries within a single flower. The individual units may be berries or other specific types. Example - Raspberry, Strawberry.

Multiple Fruit - These fruits are formed from the cluster of flowers, each flower in the inflorescence produce a fruit but these fruits mature into a single mass. Example - Pineapple Mulberry.

SAQ 4

- a) Enlist the differences between dehiscent and indehiscent fruits.
- b) Fill in the blanks:
 - i) In fruits, seeds are attached by a stalk called
 - ii) The attachment of the funicle forms a disc shaped structure which fits into the depression called
 - iii) is an outgrowth that arises from funicle or the testa near the raphe.
 - iv) is a plug like structure formed in the micropylar portion of the seeds by proliferation of cells at the tip of the inner integument or nucellus. It has been noted in seeds of monocots.
 - v) Mature seeds containing persistent endosperm are called
- c) Match the name of fruits given in Column 1 with their type in Column 2:

Column 1

- i. Mulberry
- ii. Watermelon
- iii. Grapes
- iv. Lemon
- v. Apple
- vi. Peach

Column 2

- a. Hesperidium
- b. Drupe
- c. Pepo
- d. Multiple fruit
- e. Berry
- f. Pome

15.7 FRUIT DEVELOPMENT AND ITS STRUCTURE

Concurrent with the development of seed(s) mature ovary develops into fruit. The fruits protect the seeds which are progenitor of next generation. They also help in the dispersal of seeds. In primitive families like Magnoliaceae the fruits

open even when they are attached to the plant, but in majority of angiosperms the fruit completely encloses and protects the seeds. Fruit development is initiated by growth hormones produced by developing seeds. The fruit which develops from the carpel of the ovary is called as true fruit. False fruit – a fruit in which some or major fleshy part is not derived from the ovary, but from some adjacent structures such as the perianth and receptacle. Example- In strawberry, *Fragaria annassa* the floral receptacle extends to form the fleshy edible part of the fruit. In apple *Pyrus malus* the floral tube formed by the floral organs and the receptacle together constitute the fruit. In both the fruits, carpellary and accessory tissues form the edible part. In jackfruit, *Artocarpus integrifolia* the perianth and in pineapple, *Ananas comosus*, the bracts surrounding the flowers in an inflorescence contribute to the formation of fruit. When organs other than ovary participate in the formation of fruit, the fruit is termed as false fruit or pseudocarp. Some authors include the multiple and aggregate fruits also in the category of false fruits because of the inclusion of some or the other accessory parts or tissues in the fruits.

The wall of true fruit is called pericarp. The mature pericarp possesses three distinct layers or zones. The outer peel or skin represents the exocarp or epicarp. The fleshy and juicy middle portion is called mesocarp. The inner shell or stone is called endocarp. Example- Mango.

In some fruits the whole pericarp may be uniformly hard and these layers may not be distinct example- groundnut.

The development of fruit can also be studied with the help of some examples.

In Caryopsis fruit, carpel has one ovule and therefore the mature fruit has one seed. During maturation the ovary wall undergoes a few divisions. The pericarp and the remains of the integument get fused. In wheat caryopsis three main regions are seen :

1. the caryopsis wall which includes pericarp, seed coat and remains of the nucellus;
2. endosperm; and
3. embryo.

The pericarp is distinguished into five layers: i) epidermis; ii) hypodermis; iii) zone of thin walled cells; iv) cross cells; v) tube cells. The outer epidermis and hypodermis together form the exocarp. It is composed of thin walled compressed cells. Inside the exocarp are present a few layers of thin-walled parenchymatous cells. Next to it are present thick walled cross cells having pits elongated transversely to the cell. The tube cells form the inner epidermis of the pericarp. The tube cells possess thin walls but are pitted. In mature seed, the testa is absent but tegmen is present along with one or two layers of nucellus.

In legumes, the outer epidermis of the ovary forms the exocarp of the pod. Few layers of thin-walled parenchymatous cells constitute the mesocarp. The endocarp consists of sclerenchymatous and a few layers of parenchymatous cells. Vascular bundles are located in the mesocarp along with some

sclerenchymatous cells. Example - *Astragalus macrocarpus*. The shrinkage of the sclerenchymatous cells helps in opening of valves resulting in dispersal of seeds.

In berry fruit like tomato much of the pericarp is fleshy or juicy. The exocarp consists of an epidermis and 3 to 5 layers of collenchymatous cells. The epidermis is covered with cuticle. Mesocarp consists of large thin walled cells with abundant intercellular spaces. With the development of ovules the parenchymatous tissue of the placenta grows around the funiculi. It grows further and envelops the hard seeds completely. Several edible fruits such as grapes and guava are good example of a berry.

In drupe fruit like peach (*Prunus persica*) most of the cell divisions in the ovary wall occurs before fertilization or soon after it. Further growth of fruit takes place mainly by cell enlargement. Initially cell enlargement occurs in all directions but later its mainly in radial direction. At maturity the outer epidermis has thick cuticle and unicellular hairs. Mesocarp is loosely parenchymatous and endocarp has sclerieds and form the stone of the fruit.

15.8 PARTHENOCARPY

Generally the fruits develop after fertilization and contain fertile seeds in them. Fruits of some plants such as banana, tomato, orange and grapes etc. can develop without seeds. (Fig.15.20). In these fruits the ovules abort during fruit maturity and cells of septa along with pericarp proliferates to form pulp region. The phenomenon of formation of fruit without fertilization is called parthenocarpy. This type of fruit development can require pollination or may occur even without pollination. Parthenocarpy can be natural or induced artificially. Three types of parthenocarpy are identified in plants.

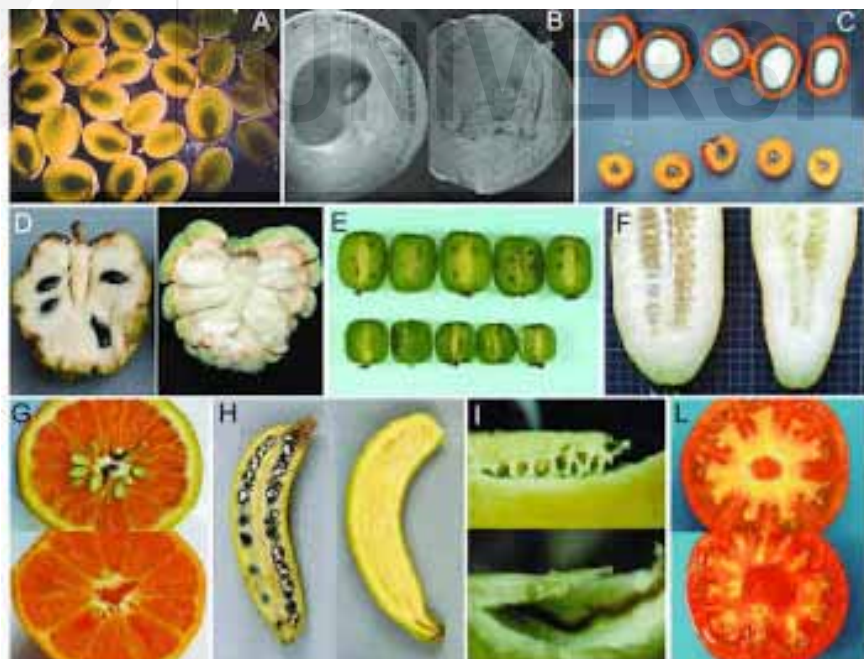


Fig.15.20: Parthenocarpic fruits.

Genetical Parthenocarpy - It is observed in many species cultivated for their fruits. It arises due to mutations or hybridization. In parthenocarpic fruits sterile pollen is present i.e. pollination stimulus is available but fertilization does not

take place. As a result seeds are not produced. Many cultivated varieties of orange, grapes and cucumber has been produced from mutation in axillary bud. The plant bears seedless fruits. Cultivated bananas are triploid natural hybrids and therefore sterile fruits are produced without fertilisation. Seedless watermelon are produced artificially by inducing triploid sterile plants in each generation.

Environmental Parthenocarpy - It results from the change in environmental conditions such as frost or low temperature. The change in temperature interferes with the normal reproductive processes in plants. For example- cultivation of tomato under low temperature and high light intensity produces parthenocarpic fruits.

Induced Parthenocarpy - This involves treatment of flowers with certain plant growth regulators. Low concentrations (10^{-6} to 10^{-7}) of auxins and gibberellins induce parthenocarpy in many plants that otherwise bear seeded fruits. Seedless guava, tomato and strawberry have been obtained by this method. Seedless papaya can be grown in green houses by preventing pollination and applying phytohormones.

Importance of Parthenocarpy - Parthenocarpic fruits are of importance in horticulture as they are easy to consume. They are also preferred by industries manufacturing jams, jellies and juices. Gibberellins cause fruit enlargement in grapes and also loosen the bunches. Parthenocarpy is desirable in fruit crops that are difficult to pollinate and fertilise like figs, tomatoes etc. In dioecious species like *Persimon* parthenocarpy increases fruit production because staminate trees need not to be planted for pollen production.

SAQ 5

Write short notes on :

- i) Genetical parthenocarpy
 - ii) Simple fruit
 - iii) Aggregate fruit
-

15.9 SUMMARY

- Seed is a mature, fertilised ovule enclosing an embryonic plant and stored food material. It is covered by seed coat formed by the integuments. It is attached to the fruit by a stalk called funiculus.
- The integuments and nucellus in the ovule undergo changes resulting in the formation of seed. Generally the nucellus gets utilized by the embryo/endosperm or degenerates. In some plant species the nucellar cells near the micropylar and chalazal end persist for a longer period in the mature seed. In some seeds, the major volume is occupied by the persistent nucellus called perisperm.

- One or both integument of the ovule may contribute to formation of seed coat. Part of seed coat derived from outer integument is called as testa, and from the inner integument tegmen. Seeds with testa are referred as testal while those having prominent tegmen are called as tegmic seeds. Seeds with outer part of the inner integument modified as sclerotic zone are called exotegmic and those having inner layers forming the protective sheath are referred as endotegmic seeds. Similarly, if outer part of testa is hard, the seed is regarded exotestal, and if inner is hard the seed is endotestal.
- Seeds of certain plants have specialized outgrowths or envelopes. These structures develop from parts of the ovule or funicle after fertilization. These include aril, caruncle, operculum, wings and hairs.
- In most of the seeds, food is stored in the cells of the endosperm which is utilized during development of embryo and germination of seed. In a germinating seed, the lipids and carbohydrates are available as the main storage compounds. Starch grains and oil droplets are present in cells of cotyledons and endosperm. Seeds possess protein reserves in the form of discrete protein bodies called aleurone grains.
- Fruits and seeds are variously adapted for dispersal. Fruits of some plants possess some inbuilt mechanisms for dispersing seeds to long distances. This is termed as autochory. External agencies such as air, water and animals also help in dispersal of seeds that is termed as anemochory, hydrochory and zoochory respectively.
- Fruits developed from the ovary are known as a true fruits, while those developed from the ovary, along with other parts of the flower such as the receptacle, petals, and sepals are known as false fruits.
- The fruits formed from single ovary with one or more carpels are called simple fruits. These fruits are categorized on the basis of their water content as dry and hard or soft and fleshy. The fruits formed from merger of more than one ovary are called aggregate fruits. The fruits are further classified as dehiscent and indehiscent, depending upon whether the fruits open up at maturity to shed seeds or not.
- Fruits of some plants develop without fertilization and seed formation. In these fruits the ovules degenerate during fruit maturity and cells of septa along with pericarp proliferates to form pulp region. The phenomenon of formation of fruit without fertilization is called as parthenocarpy.

15.10 TERMINAL QUESTIONS

1. Write a detailed note on various agencies involved in the dispersal of the seeds?
2. What are the different storage metabolites found in the germinating seeds?
3. Write a note on seed development and its structure.
4. Discuss about the various types of seed appendages.

5. Define parthenocarpy and discuss its types and importance.
6. Describe the development of fruit in caryopsis and berry fruits.

15.11 ANSWERS

Self-Assessment Questions

1. a) Sclerotic or malphigian layer is formed by certain cells of the seed coat which elongate in radial plane look like leaf palisade and become hard due to thick walls. These form the main protective layer of seed coat.
b) i) hairy
ii) fruit
iii) endosperm
iv) fleshy and juicy
v) hard, soft
vi) hygroscopic valve
2. a) i) True; ii) False; iii) True; iv) True; v) False; vi) False.
b) i) inner integument, nucellus
ii) ants
iii) three
iv) caruncle
v) hairs
3. i) False; ii) False; iii) False; iv) True; v) True; vi) True.
4. a) **Indehiscent fruits** - Fruits developing from a single carpel which do not open at maturity to shed their seeds. The major types are achene, caryopsis, samara, nut and drupe.
Dehiscent fruits - Fruits developing from a single or multiple fused carpels which open by definite natural means to shed the contained seeds at maturity. The major types are follicle, capsule, silique.
b) i) funiculus
ii) hylum
iii) aril
iv) operculum
v) albuminous

- c)
 - i) Multiple fruit
 - ii) Pepo
 - iii) Berry
 - iv) Hesperidium
 - v) Pome
 - vi) Drupe
- 5.
 - i) **Genetic parthenocarpy** is seen in plants grown for their fruits. It occurs due to mutations and hybridization. In these plants seedless fruits are formed. Many varieties of orange, banana and grapes are examples of genetic parthenocarpy.
 - ii) **Simple fruits** - These fruits are formed from one carpel. These fruits can be categorized as dry and hard or soft and fleshy on the basis of amount of water present and degree of hardness of fruit wall or pericarp.
 - iii) **Aggregate fruit** - A fruit that is formed by the development of a number of carpels of an apocarpous gynoecium from the same flower. The individual units may be berries or other specific types. Example - raspberry and strawberry.

Terminal Questions

1. Fruits of some plants possess some inbuilt mechanisms for dispersing seeds to long distances. This is termed as autochory. External agencies such as air, water and animals also help in dispersal of seeds which are referred as anemochory, hydrochory and zoochory respectively.

Autochory- This is a self dispersal mechanism. In it forceful expulsion of seeds occurs from the fruit because of turgidity or dessication of the pericarp cells. Example - in *Impatiens*.. In *Euphorbia* as the mature capsule dries up. Its three compartments open up with a force along longitudinal slits, throwing the seeds a metre or more away.

Anemochory- The seeds of certain plants are carried to long distances through air currents. The seeds are provided with special structures such as wings or hairs that help in their dispersal to far away places. The seeds are very tiny and get blown away like dust particles. Hairy seeds of milkweed, *Calatropis procera* and semal, *Bombax ceiba* can be seen carried away by strong summer wind.

Hydrochory - plants growing in and near the water bodies use water as agency for dispersal of seeds and fruits. For example- *Cocos nucifera* (*coconut*) float over hundred to thousand kilometers. The seed retains its viability for more than three months. It is believed that seeds of sweet potato have been carried across continents by oceanic water currents.

Zoochory - It is the dispersal of fruits and seeds by animals. Some fruits are eaten by animals and the seeds are passed out with the excreta. For

example- seeds of plum, figs, grapes and guava are dispersed by birds.. The seeds/fruits of some plants stick to the body parts of animals and get carried away to distant places. Squirrels, goats, langurs, lizards and monkeys also play an important role in seed dispersal. Humans also serve as agent of dispersal by raising plants of their use in different parts of world.

2. The food stored in the endosperm is utilized during development of embryo and germination of seed. The endosperm surrounds the embryo and nurtures it till the seedling begins to photosynthesize and become autotrophic. In a germinating seed, the embryo gets energy for the metabolic events through the stored lipids and carbohydrates. Carbohydrates are generally stored in the thick walls of the endosperm (coffee and date palm) or cotyledons (balsam and *Nasturtium*). Starch grains are present in cells of cotyledons and endosperm. Seeds also possess protein reserves for supplying nitrogenous compounds to the young seedling till it becomes capable of absorbing nitrogen from the soil with the help of roots. Seed proteins occur in the form of discrete protein bodies called aleurone grains. In cereals, the aleurone grains are concentrated in the outer layers of the endosperm, forming a specialised layer called aleurone layer. Legumes are rich in reserve proteins. Groundnut contains about 25 percent and soybean contains nearly 40 percent protein.
3. Refer to Section 15.3.
4. Seeds of certain plants have specialised outgrowths or envelopes called appendages. These structures develop from parts of the ovule or funicle after fertilization. These include :

Aril - It is an outgrowths that arises from funicle or the testa near the raphe. It covers the seeds partially or completely. It is also referred as the third integument. It is fleshy and brightly colored. The cells of aril contain oil, starch, sugar, pigments and aroma containing compounds. The edible part of litchi is aril.

Caruncle - It is a white, collar- like structure borne on the micropylar end of the seed. It is found in members of the family Euphorbiaceae. Example- Castor (*Ricinus communis*). The soft outgrowth capping the hard seed is formed by proliferation of cells at the tip of the outer integument. It is rich in starch and sugars. Insects such as ants consume the caruncle and in the process help in the dispersal of the seeds by carrying them away to a far off places.

Operculum - It is a plug- like structure formed in the micropylar portion of the seeds by proliferation of cells at the tip of the inner integument or nucellus. Operculum has been noted in seeds of monocots belonging to families Commelinaceae, Musaceae, Lemnaceae and Zingiberaceae and some dicot families like Bignoniaceae and Nymphaeaceae. The cells of the operculum are thick- walled and contain an orange red substance. The operculum becomes detached from the rest of the seed during germination process and help in coming out of embryo.

Wings and hairs - In some plants the epidermal outgrowths or the folds/projections of the integuments appear as wings. In *Oroxylon* disc like transparent, thin, round wings spread on two lobed seeds. The wings provide large surface area and strength to the seed. Some seeds also show the presence of hair like structures. Seeds of *Calotropis procera* (milkweed) possess tuft of hairs at one pole. Hairs provide large surface area without corresponding increase in weight thereby facilitating the dispersal of seeds by air. In aquatic plants like *Nymphaea* the seed hairs are filled with air and provide buoyancy to the seed to float on water.

5. Generally the fruits develop after fertilization and contain fertile seeds in them. Fruits of some plants such as banana, tomato, orange and grapes etc. can develop without seeds. In these fruits the ovules abort during fruit maturity and cells of septa along with and pericarp proliferates to form pulp region. This phenomenon of formation of fruit without fertilization is called parthenocarpy. This type of fruit development can require pollination or may occur without even pollination. Parthenocarpy can be natural or induced artificially. Three types of parthenocarpy is reported in plants.

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Acknowledgements

Fig 15.7 : : https://www.google.com/imgres?imgurl=https%3A%2F%2Fupload.wikimedia.org%2Fwikipedia%2Fcommons%2Fthumb%2Fe%2Fe3%2FARS_Litchi_chinensis.jpg)

Fig 15.9 : store.underwoodgardens.com
<https://cdn11.bigcommerce.com/s-q83qdckkjh/images/stencil/128>

Fig 15.20 : <https://www.google.com/imgres?imgurl=https%3A%2F%2Fwww.researchgate.net%2Fpublication%2F330483895%2Ffigure%2Ffig3%2FAS%3A716475413327872%401547832458074%2FExamples-of-seeded-and-seedless-fruits-in-parthenocarpic-species-A-Pastinaca-sativa.png>)



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GLOSSARY

Aberrant	: anything diverting from the normal type.
Acropetal	: developing upward, toward the apex.
Anticlinal	: at right angles to the surface of an organ or part.
Appressorium	: the flattened thickened tip of a hyphal branch by which some parasitic fungi attach to and penetrate their host.
Apomeiosis	: Production of a meiotically unreduced gametophyte.
Autotrophic	: an organism capable of synthesizing its own food.
Bract	: a specialized leaf or leaf like part usually situated at the base of a flower or inflorescence.
Carpel	: a simple pistil or a single member of a compound pistil.
Concentric	: anything having a common centre.
Concealed	: kept hidden inside, anything which cannot be easily seen
Convolute	: coiled, rolled up together or with one part over another.
Dimorphic	: occurring in two distinct forms.
Dispersal	: the process of distributing or spreading things over a wide area.
Dormancy	: the state in which a plant is not growing actively.
Edible	: anything that can be eaten.
Embayment	: a shape resembling a bay.
Ephemeral	: anything that is short lived.
Expulsion	: process of throwing something out with force.
Gurgitate	: to throw or pour back.
Histogenic	: phase in which growth and differentiation of cells/tissues occur.
Hypanthium	: a cup shaped or tubular expansion of the receptacle of a flower that surrounds the carpels
Hypanthodium	: a special type of inflorescence in which receptacle is fleshy and forms hollow ball like structure with an apical opening.
Hygroscopic	: substance that readily absorbs water from its surroundings.

Hypodermal	: lying beneath epidermis.
Inconspicuous	: a plant or plant part that is not prominent i.e. very small or hard to see.
Interveining	: happening/occurring between two events or activities
Mutualistic	: an association between two organisms of different species in which each member benefits.
Offsprings	: young ones borne to parents.
Ontogeny	: developmental events that occur during existence of a living organism.
Periclinal	: parallel to the surface of an organ or part.
Petalloid	: a part that looks like petal of a flower.
Primordial	: giving origin to something derived or developed.
Progeny	: descendants of a plant
Progenitor	: a part/plant body from which a plant descended or originated.
Proliferation	: rapid increase in the number or amount of a cell or part.
Receptive	: able to receive signals or stimuli.
Restitution	: restoration of something lost.
Ruminations	: deep in carvings.
Spatial	: uneven distribution of species within an area.
Tangential	: perpendicular to the axis.
Temporal	: relating to the sequence of time or to a particular time.
Thermogenic	: pertaining to the production of heat.
Transverse	: extending across something.
Wagging	: move rapidly to and fro.
Wriggling	: quick twist and turn movements.

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