Sexual Reproduction in Flowering Plants - Part 4

Objectives

After studying this module the students will be able to:

- Define double fertilisation and triple fusion
- Discuss the various post-fertilisation structures and events
- Explain the process of apomixis
- Discuss the process of polyembryony

Content Outline

- Double Fertilisation
- Post-fertilisation: Structures and Events
    - Endosperm
    - Embryo
    - Seed
- Apomixis and Polyembryony
- Summary

Double Fertilisation

After entering one of the synergids, the pollen tube releases the two male gametes into the cytoplasm of the synergid. One of the male gametes moves towards the egg cell and fuses with its nucleus thus completing the **syngamy**. This results in the formation of a diploid cell, the zygote. The other male gamete moves towards the two polar nuclei located in the central cell and fuses with them to produce a triploid primary endosperm nucleus (PEN) (Figure 1). As this involves the fusion of three haploid nuclei it is termed triple fusion. Since two types of fusions, syngamy and triple fusion take place in an embryo sac the phenomenon is termed double fertilisation, an event unique to flowering plants (Table 1). The central cell after triple fusion becomes the primary endosperm cell (PEC) and develops into the **endosperm** while the zygote develops into an embryo.

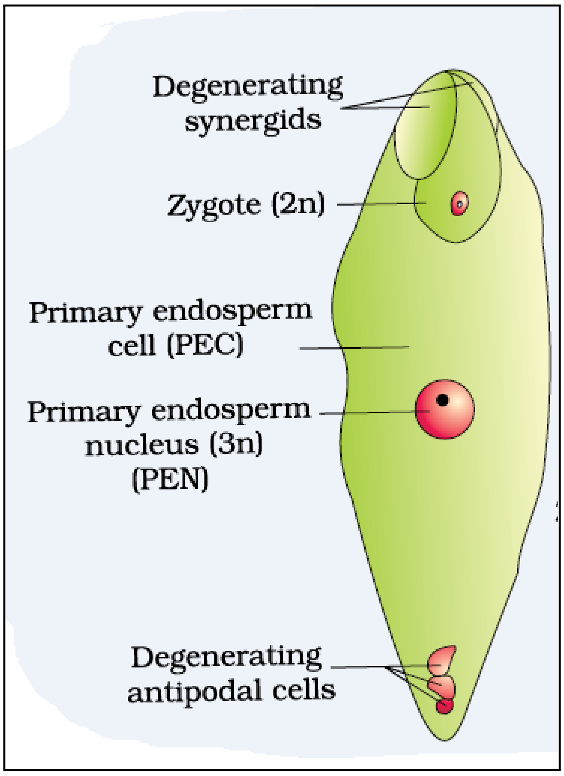

Figure 1: Fertilised embryo sac showing zygote and Primary Endosperm Nucleus (PEN)

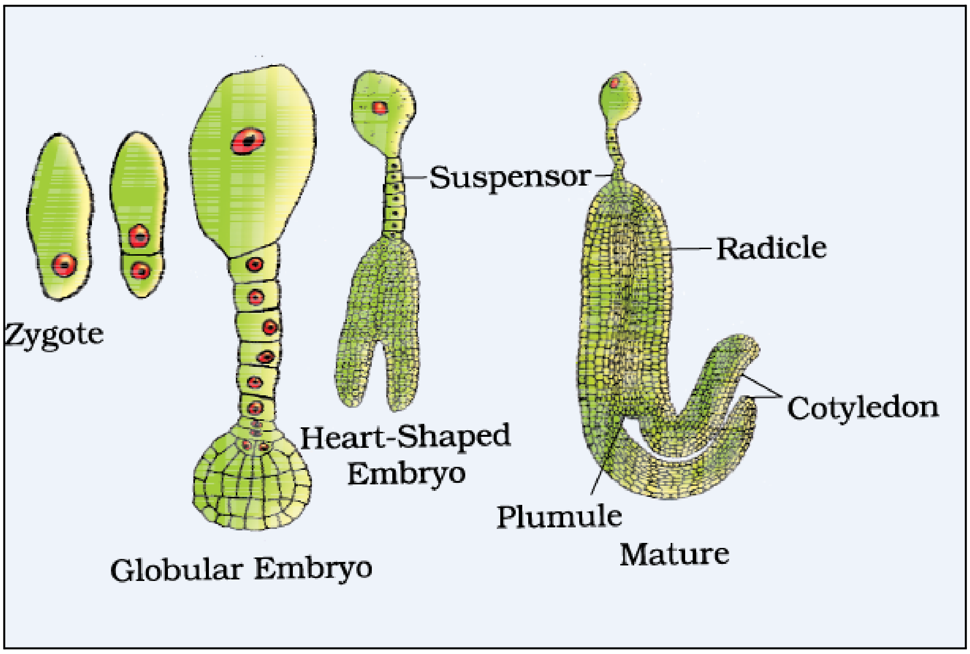

Figure 2: Stages in embryo development in a dicot

Table 1: Difference between fertilisation and double fertilisation in Angiosperms

Fertilisation	Double fertilisation
1. The union of two compatible gametes is known as fertilisation. 2. Fertilisation is commonly observed in all the eukaryotic organisms. 3. The ultimate outcome of the fertilisation event is the diploid zygote.	1. During the process of double fertilisation one male gamete fuses with the egg and the other male gamete fuses with the secondary nucleus of the same embryo sac. 2. The phenomenon of double fertilisation is observed in flowering plants only. 3. A diploid zygote and a triploid primary endosperm cell are produced due to the double fertilisation.

Post-fertilisation: Structures and Events

Following double fertilisation, events of endosperm and embryo development, maturation of ovule(s) into seed(s) and ovary into fruit, are collectively termed post-fertilisation events.

- **Endosperm**

  Endosperm development precedes embryo development. Why? The primary endosperm cell divides repeatedly and forms a triploid endosperm tissue. The cells of this tissue are filled with reserve food materials and are used for the nutrition of the developing embryo. In the most common type of endosperm development, the PEN undergoes successive nuclear divisions to give rise to free nuclei. This stage of endosperm development is called free-nuclear endosperm. Subsequently cell wall formation occurs and the endosperm becomes cellular. The number of free nuclei formed before cellularization varies greatly. The coconut water from tender coconut that you are familiar with, is nothing but free-nuclear endosperm (made up of thousands of nuclei) and the surrounding white kernel is the cellular endosperm.

  Endosperm may either be completely consumed by the developing embryo (e.g., pea, groundnut, beans) before seed maturation or it may persist in the mature seed (e.g., castor and coconut) and be used up during seed germination.

Types of endosperm development

The three main types of endosperm development in flowering plants are: Nuclear type, Cellular type, and Helobial type:

- **Nuclear type:** This is the most common type of endosperm. In the nuclear type of endosperm the first division of the primary endosperm nucleus and few subsequent nuclear divisions are not accompanied by wall formation (karyokinesis). The nuclei produced are free in the cytoplasm of the embryo sac and they may remain free indefinitely or wall formation takes place later. In the coconut, cell wall formation of endosperm is never found complete. In *Areca* and *Phoenix* the endosperm becomes very hard (Figure 3).

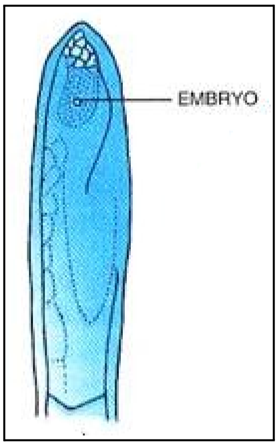

Figure 3: Nuclear endosperm

- **Cellular type:** In this case, there is cytokinesis after each nuclear division of the endosperm nucleus. The endosperm, thus, has a cellular form, from the very beginning because first and subsequent divisions are all accompanied by wall formation. It is a less common type and seen mostly in dicots. E.g., *Petunia*, *Datura*, *Adoxa*, *Annona*, *Peperomi*, etc. (Figure 4).

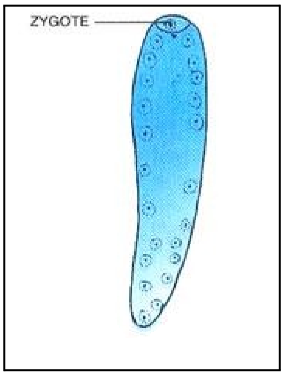

Figure 4: Cellular endosperm

- **Helobial type:** It is an intermediate type between the nuclear and cellular types. It shows features of both the nuclear and cellular type. The first division is accompanied by cytokinesis but the subsequent ones are free nuclear. The chamber towards the micropylar end of the embryo sac is usually much larger than the chamber towards the chalazal end. A large number of nuclei are formed in the micropylar chamber by free nuclear divisions while the nucleus of the chamber towards the chalazal end divides to form fewer free nuclei or may not divide at all. Helobial endosperm formation is commonly observed in monocotyledons. It is present in all the organisms belonging to the order Helobiales. E.g., *Asphodelus*, *Eremurus*, *Vallisneria*, *Linnophyton*, etc (Figure 5).

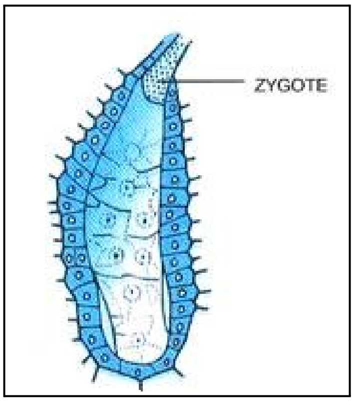

Figure 5: Helobial endosperm

Activity: Split open some seeds of castor, peas, beans, groundnut, fruit of coconut and look for the endosperm in each case. Find out whether the endosperm is persistent in cereals – wheat, rice and maize.

- **Embryo**

  Embryo develops at the micropylar end of the embryo sac where the zygote is situated. Most zygotes divide only after a certain amount of endosperm is formed. This is an adaptation to provide assured nutrition to the developing embryo. Though the seeds differ greatly, the early stages of embryo development (embryogeny) are similar in both monocotyledons and dicotyledons. Figures 1 and 2 depict the stages of embryogeny in a dicotyledonous embryo. The zygote gives rise to the proembryo and subsequently to the globular, heart-shaped and mature embryo.

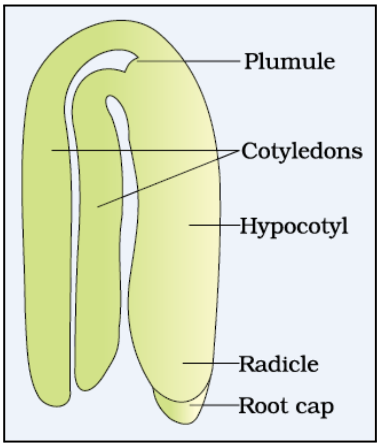

Figure 6: A typical dicot embryo.

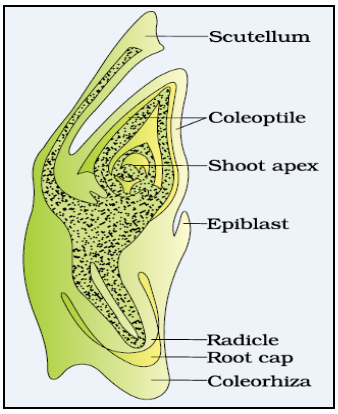

Figure 7: L.S. of an embryo of grass

A typical dicotyledonous embryo (Figure 6), consists of an embryonal axis and two cotyledons. The portion of the embryonic axis above the level of cotyledons is the epicotyl, which terminates with the plumule or stem tip. The cylindrical portion below the level of cotyledons is hypocotyl that terminates at its lower end in the radicle or root tip. The root tip is covered with a root cap.

Embryos of monocotyledons (Figure 7) possess only one cotyledon. In the grass family the cotyledon is called scutellum that is situated towards one side (lateral) of the embryonal axis. At its lower end, the embryonal axis has the radical and root cap enclosed in an undifferentiated sheath called coleorhiza. The portion of the embryonic axis above the level of attachment of scutellum is the epicotyl. Epicotyl has a shoot apex and a few leaf primordia enclosed in a hollow foliar structure, the coleoptile.

Activity: Soak a few seeds in water (say wheat, maize, peas, chickpeas, ground nuts) overnight. Then split the seeds and observe the various parts of the embryo and the seed.

- **Seed**

  In angiosperms, the seed is the final product of sexual reproduction. It is often described as a fertilised ovule. Seeds are formed inside fruits. A seed typically consists of seed coat(s), cotyledon(s) and an embryo axis. The cotyledons (Figure 8) of the embryo are simple structures, generally thick and swollen due to storage of food reserves (as in legumes). Mature seeds may be non-albuminous or albuminous. Non-albuminous seeds have no residual endosperm as it is completely consumed during embryo development (e.g., pea, groundnut, sunflower). Albuminous seeds retain a part of the endosperm as it is not completely used up during embryo development (e.g., wheat, maize, barley, castor). Occasionally, in some seeds such as black pepper and beet, remnants of nucellus are also persistent. This residual, persistent nucellus is the perisperm.

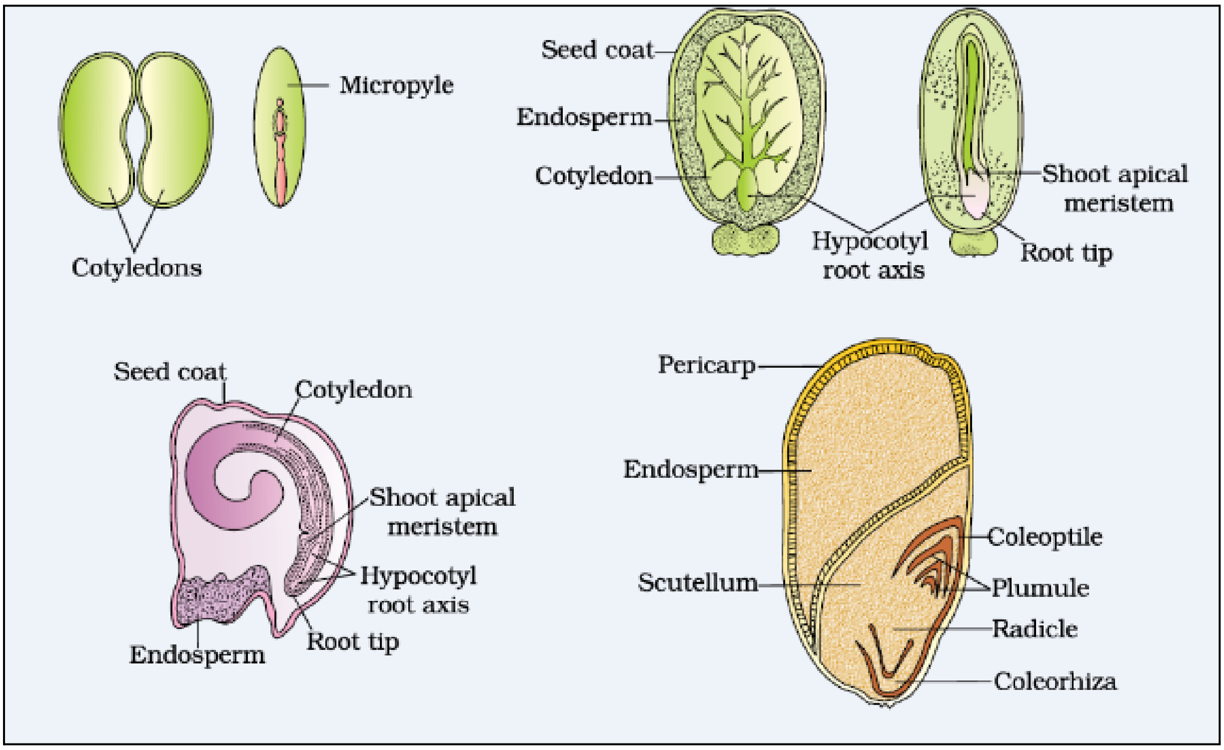

Figure 8: Structure of some seeds

Integuments of ovules harden as tough protective seed coats (Figure 8). The micropyle remains as a small pore in the seed coat. This facilitates entry of oxygen and water into the seed during germination. As the seed matures, its water content is reduced and seeds become relatively dry (10-15 per cent moisture by mass). The general metabolic activity of the embryo slows down. The embryo may enter a state of inactivity called dormancy, or if favourable conditions are available (adequate moisture, oxygen and suitable temperature), they germinate.

As ovules mature into seeds, the ovary develops into a fruit, i.e., the transformation of ovules into seeds and ovary into fruit proceeds simultaneously. The wall of the ovary develops into the wall of fruit called pericarp. The fruits may be fleshy as in guava, orange, mango, etc., or may be dry, as in groundnut, and mustard, etc. Many fruits have evolved mechanisms for dispersal of seeds.

Point to ponder: Recall the classification of fruits and their dispersal mechanisms that you have studied in an earlier class. Is there any relationship between the number of ovules in an ovary and the number of seeds present in a fruit?

In most plants, by the time the fruit develops from the ovary, other floral parts degenerate and fall off. However, in a few species such as apple, strawberry, cashew, etc., the thalamus also contributes to fruit formation. Such fruits are called false fruits (Figure 9). Most fruits however develop only from the ovary and are called true fruits. Although in most of the species, fruits are the results of fertilisation, there are a few species in which fruits develop without fertilisation. Such fruits are called parthenocarpic fruits. Bananas are one such example. Parthenocarpy can be induced through the application of growth hormones and such fruits are seedless.

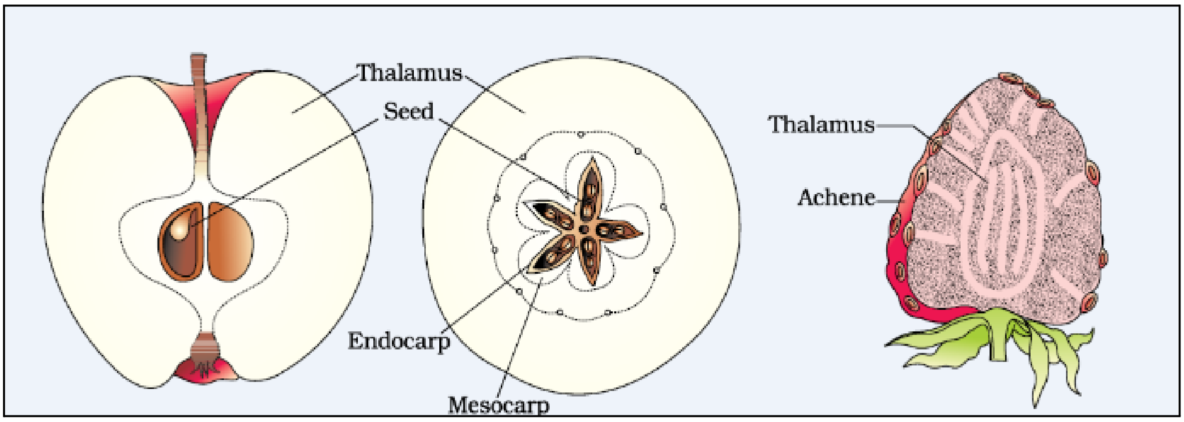

Figure 9: False fruits of apple and strawberry

Seeds offer several advantages to angiosperms. Firstly, since reproductive processes such as pollination and fertilisation are independent of water, seed formation is more dependable. Also seeds have better adaptive strategies for dispersal to new habitats and help the species to colonise in other areas. As they have sufficient food reserves, young seedlings are nourished until they are capable of photosynthesis on their own. The hard seed coat provides protection to the young embryo. Being products of sexual reproduction, they generate new genetic combinations leading to variations.

Seed is the basis of our agriculture. Dehydration and dormancy of mature seeds are crucial for storage of seeds which can be used as food throughout the year and also to raise crop in the next season.

As seeds mature their water content gets reduced and they become relatively dry. A reduction of 10-15% of moisture by mass is observed. Seeds show a temporary suspension of growth and this state of inactivity is known as dormancy. It is a resting state, during which a seed is physiologically inactive. Such seeds germinate only after the completion of their dormancy period and when favorable conditions like adequate moisture, oxygen and suitable temperature are available.

Viability is the living capacity of seed; it is the ability of the seed to germinate after a specific period of rest i.e., dormancy. Seeds remain viable till the onset of favorable conditions and then germinate to produce a seeding. The period of viability varies in different species. For example, seeds of some plants lose their viability within a few months, whereas some seeds retain their viability and remain alive for hundreds of years. The seeds generally lose their viability due to various causes like axhausen of the food around the embryo, damage to the embryo. Premature exhaustion of the RNAs or denaturation of the enzymes.

Point to Ponder: Can you imagine agriculture in the absence of seeds, or in the presence of seeds which germinate straight away soon after formation and cannot be stored?

How long do the seeds remain alive after they are dispersed?

Some seeds can remain alive for hundreds of years. There are several records of very old yet viable seeds. The oldest is that of a lupine, Lupinus arcticus excavated from Arctic Tundra. The seed germinated and flowered after an estimated record of 10,000 years of dormancy. A recent record of 2000 years old viable seed is of the date palm, Phoenix dactylifera discovered during the archeological excavation at King Herod’s palace near the Dead Sea.

After completing a brief account of sexual reproduction of flowering plants it would be worth attempting to comprehend the enormous reproductive capacity of some flowering plants by pondering on few points through asking the following questions:

Points to Ponder:

- How many eggs are present in an embryo sac?
- How many embryo sacs are present in an ovule?
- How many ovules are present in an ovary?
- How many ovaries are present in a typical flower?
- How many flowers are present on a tree? And so on...

Can you think of some plants in which fruits contain a very large number of seeds? Orchid fruits are one such category and each fruit contains thousands of tiny seeds. Similar is the case in fruits of some parasitic species such as Orobanche and Striga. Have you seen the tiny seed of Ficus? How large is the tree of Ficus developed from that tiny seed. How many billions of seeds does each Ficus tree produce? Can you imagine any other example in which such a tiny structure can produce such a large biomass over the years?

Apomixis and Polyembryony

Although seeds, in general, are the products of fertilisation, a few flowering plants such as some species of Asteraceae and grasses, have evolved a special mechanism, to produce seeds without fertilisation, called apomixis.

Point to Ponder: What is fruit production without fertilisation called?

Thus, apomixis is a form of asexual reproduction that mimics sexual reproduction. There are several ways of development of apomictic seeds. Apodictically produced offspring are genetically identical to the parent plant. Apomixis occurs in at least 33 families of flowering plants, and has evolved multiple times from sexual relatives. Apomictic species or individual plants often have a hybrid origin, and are usually polyploid.

In some species, the diploid egg cell is formed without reduction division and develops into the embryo without fertilisation. More often, as in many Citrus and Mango varieties some of the nucellar cells surrounding the embryo sac start dividing, protrude into the embryo sac and develop into the embryos. In such species each ovule contains many embryos. Occurrence of more than one embryo in a seed is referred to as polyembryony. Polyembryony is quite common in Onion, Groundnut, Mango, Lemon, Orange.

Point to Ponder: What is parthenocarpy?

Parthenocarpy (literally meaning virgin fruit) is the natural or artificially induced production of fruit without fertilization of ovules. The fruit is therefore seedless. Parthenocarpy (or stenospermocarpy) occasionally occurs as a mutation in nature; if it affects every flower the plant can no longer sexually reproduce but might be able to propagate by apomixis or by vegetative means (Figure 10).

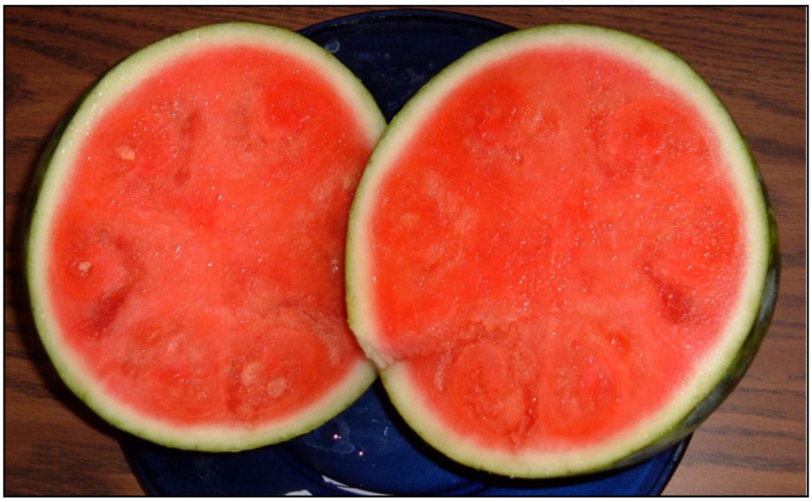

Figure 10: Seedless watermelon

Source: https://upload.wikimedia.org/wikipedia/commons/c/cc/Watermelon_seedless.jpg

Activity: Take out some orange seeds and squeeze them. Observe the many embryos of different sizes and shapes from each seed. Count the number of embryos in each seed.

Point to Ponder: What would be the genetic nature of apomictic embryos? Can they be called clones?

Hybrid varieties of several of our food and vegetable crops are being extensively cultivated. The cultivation of hybrids has tremendously increased productivity. One of the problems of hybrids is that hybrid seeds have to be produced every year. If the seeds collected from hybrids are sown, the plants in the progeny will segregate and do not maintain hybrid characters. Production of hybrid seeds is costly and hence the cost of hybrid seeds becomes too expensive for the farmers. If these hybrids are made into apomicts, there is no segregation of characters in the hybrid progeny. Then the farmers can keep on using the hybrid seeds to raise new crops year after year and he does not have to buy hybrid seeds every year.

Because of the importance of apomixis in the hybrid seed industry, active research is going on in many laboratories around the world to understand the genetics of apomixis and to transfer apomictic genes into hybrid varieties.

Summary

Angiosperms exhibit double fertilisation because two fusion events occur in each embryo sac, namely syngamy and triple fusion. The products of these fusions are the diploid zygote and the triploid primary endosperm nucleus (in the primary endosperm cell). Zygote develops into the embryo and the primary endosperm cell forms the endosperm tissue. Formation of endosperm always precedes development of the embryo.

The developing embryo passes through different stages such as the proembryo, globular and heart-shaped stages before maturation. Mature dicotyledonous embryo has two cotyledons and an embryonal axis with epicotyl and hypocotyl. Embryos of monocotyledons have a single cotyledon. After fertilisation, the ovary develops into fruit and ovules develop into seeds.

A phenomenon called apomixis is found in some angiosperms, particularly in grasses. It results in the formation of seeds without fertilisation. Apomicts have several advantages in horticulture and agriculture.

Some angiosperms produce more than one embryo in their seed. This phenomenon is called polyembryony.

Practice Questions

1. What is triple fusion? Where and how does it take place? Name the nuclei involved in triple fusion.
2. Why do you think the zygote is dormant for sometime in a fertilised ovule?
3. Differentiate between:

a. hypocotyl and epicotyl;
b. coleoptile and coleorhiza;
c. integument and testa;
d. perisperm and pericarp.

4. Why is an apple called a false fruit? Which part(s) of the flower forms the fruit?
5. What is meant by emasculation? When and why does a plant breeder employ this technique?
6. If one can induce parthenocarpy through the application of growth substances, which fruits would you select to induce parthenocarpy and why?
7. Explain the role of tapetum in the formation of pollen-grain walls.
8. What is apomixis and what is its importance?