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SEED DEVELOPMENT AND MATURATION

Howard C. Potts¹

The culmination of the life cycle of most higher plants is the development of its reproductive unit, the seed. The seed, in terms of sexual reproduction, is a mature, fertilized ovule consisting of the embryonic axis, food reserves and an outer covering.

The life of any seed can be divided into four stages: (1) its origin in the flower of the mother plant, (2) its development and maturation, (3) its resting stage, and (4) its resumption of growth or germination.

Seed Development and Morphology

At a specific time in the life cycle of all flowering plants, the physiological and biological processes change from the production of vegetative organs - leaves & stems - to the reproductive organs - the flowers. Despite differences in the appearances of flowers, those floral organs involved in the formation of seed are quite similar for most species. The male and female reproductive organs of most flowering plants are comparable. Typically, each flower is produced at the end of a stalk, the pedicle, which is modified and specialized for reproduction. The tip of the pedicle, where the floral organs are attached, is usually somewhat enlarged. This enlarged region is called the Receptacle. In a typical complete flower, the receptacle gives rise to the four basic floral organs - sepals, petals, stamens, and pistil.

The sepals and petals have no direct role in actual seed development, but serve as a protective organ and in some cases attract insects, necessary for pollination. The Stamens, the male reproductive organs of a flower, are located inside the petals. Each stamen is typically composed of a threadlike stalk, the Filament, which is terminated by an enlarged four-lobed, usually yellow organ - the Anther. The primary role of the filament is to position the anther so the pollen is dispersed in a manner typical of its species. The pollen grains are formed inside the anther. When mature, the anther ruptures and releases the pollen.

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The female reproductive organ, the Pistil, is located at the center of the flower. The enlarged base, which may rest on or be surrounded by the receptacle, is the Ovary. Extending from the ovary is the stalk-like Style, which terminates in an expanded portion called the Stigma (Figure 1).

Pistils and ovaries can be simple or compound. Within each ovary one or several ovules can be produced. The common bean is an example of a species with a simple pistil that produces several ovules (Figure 2). All species of the grass family have a simple ovary which produce only one ovule. A compound ovary is composed of two or more cavities or carpels. One or many ovules may be formed inside each cavity. Cotton and okra are examples of species having compound ovaries.

Some species produce flowers having no stamens or non-functioning ones. Such flowers are referred to as pistillate or male-sterile. The flowers of the female inflorescence or ear of maize have no stamen. When the pistil is absent, the flower or floret is referred to as staminate. The florets produced on the tassels of maize are normally staminate. Flowers and florets containing neither male nor female reproductive organs or containing non-functioning ones are sterile and, of course, are not involved in seed formation.

Some species, such as maize and cucumber, produce staminate flowers on one part of the plant and pistillate flowers on another part of the same plant. Such plants are referred to as being Monoecious. In a few species, individual plants produce only pistillate or staminate flowers. Such species are Dioecious. Papaya and date palm are examples of dioecious species.

Grass flowers are so small and inconspicuous that many people think grasses have no flowers. Because they are so different from flowers of most other plants, a separate terminology is applied to some of their floral organs. The complete perfect flower of a grass plant consists of a pistil with a single, simple ovary, two styles with featherlike stigmas, and three stamens (rice has six stamens). The reproductive organs of grasses are enclosed by two leaflike structures. The larger structure is the Lemma and the smaller the Palea. The Lodicules, two small saclike structures located inside the lemma and the palea, expand when the flower's reproductive organs are mature. Expansion of the lodicules causes the lemma and palea to separate and expose the stamens and stigmas. The lemma, palea, and enclosed organs are called a floret. Florets are produced individually or along a central axis in groups of two or more; they are connected by small stems, known as Rachillas. The individual or groups of florets are subtended by two leaflike structures called glumes (Figure 3).

The maize flower is a significant exception to the basic organization of grass florets. The female florets are arranged in paired rows

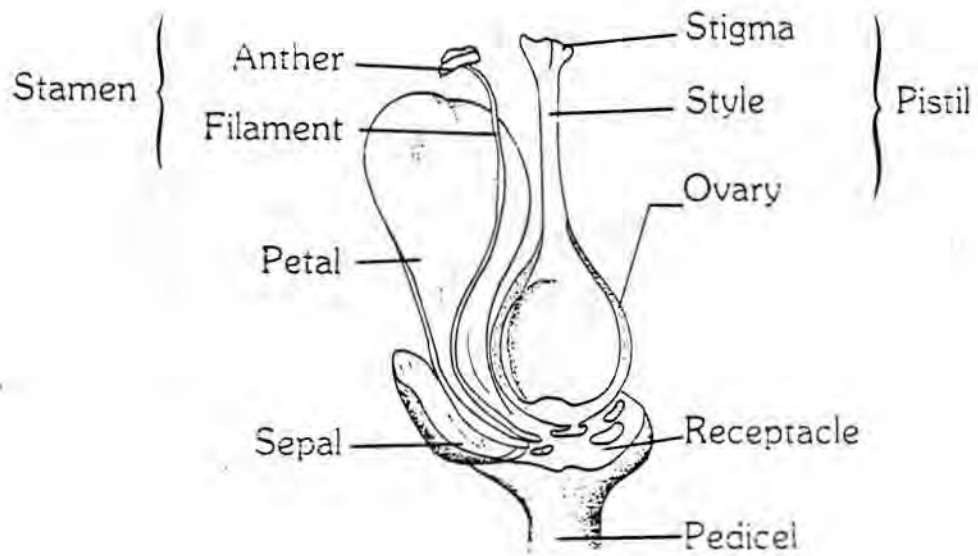


Figure 1. Diagram of a longitudinal section of a complete flower.

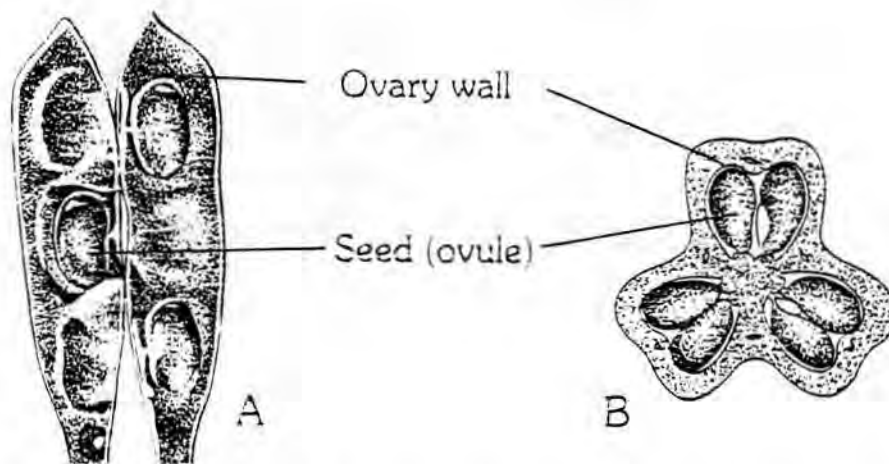


Figure 2. Comparison of simple pistil of the common bean, *Phaseolus vulgaris* (A), and sesame, *Sesamum indicum* (B), having a compound ovary.

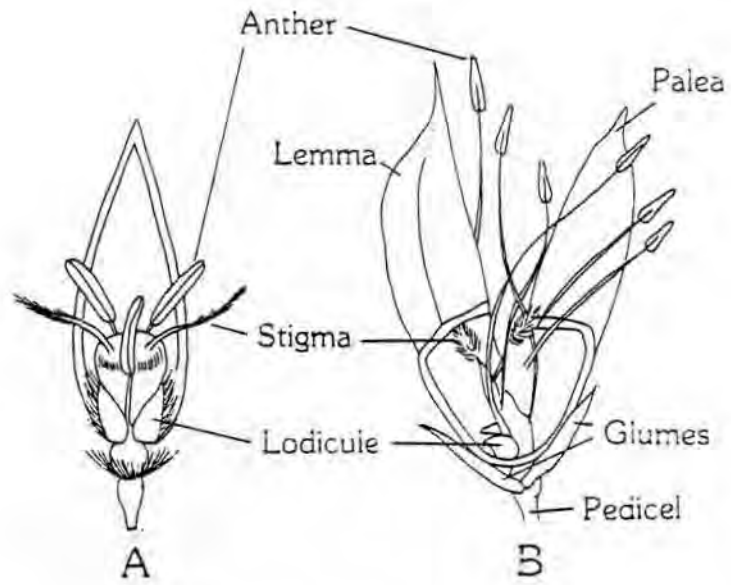


Figure 3. Open oat floret, *Avena sativa* (A) and rice spikelet, *Oryza sativa* (B).

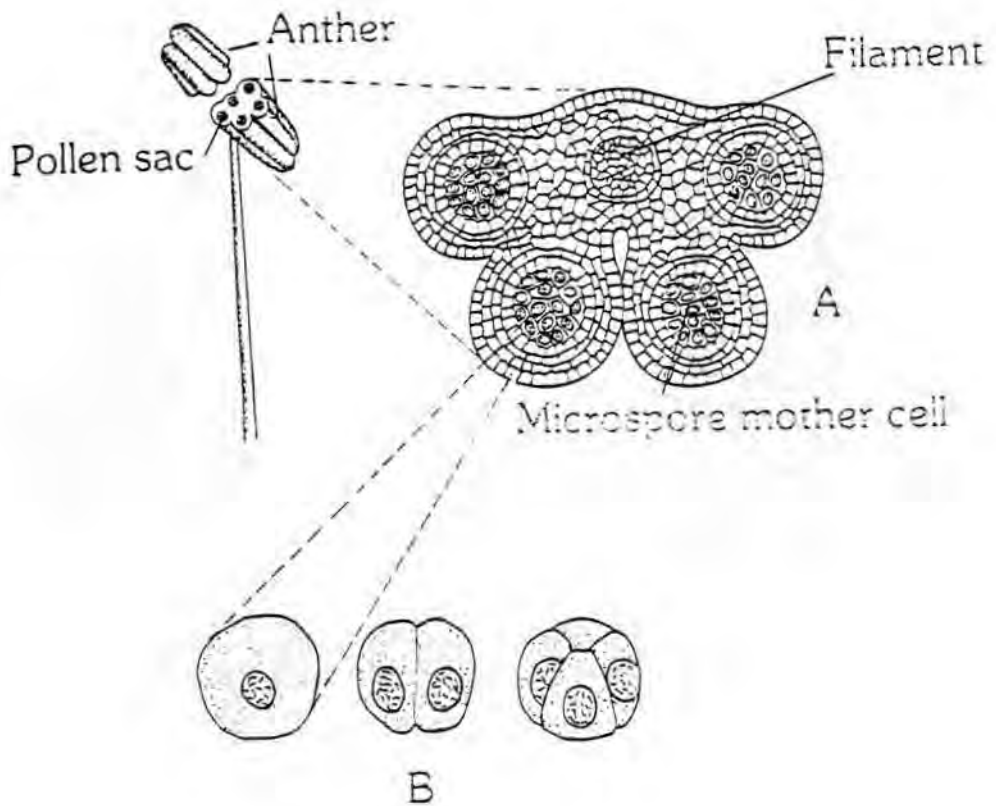


Figure 4. Development of a pollen grain from a microspore mother cell.

along a central axis, the cob, and each floret produces a long single stigma-style (the silk).

Only the essential parts of a flower - the pistil and stamens - are directly involved in seed formation. The process of pollen grain development is called microsporogenesis. A cross section of a developing anther reveals that each of the four lobes is filled with cells called microspore mother cells (Figure 4). Through meiosis, a cell division process by which the number of chromosomes is reduced, each microspore mother cell divides twice. These divisions result in the formation of four microspores, each containing half (1N) the chromosome number of the mother plant. The wall of the microspore becomes the wall of the pollen grain. Prior to being shed, this wall thickens and the outer surface usually becomes roughened with spines, pits, plates, or ridges, according to the species.

The ovules develop from cells of the placenta which line the inside of the inside of the ovary wall. Each ovule starts as a mass of cells, called the nucellus, which enlarges rapidly. This tissue is one to several cell layers in thickness and surrounds the single but much larger megaspore mother cell. The developing ovule is raised from the ovary wall on a short stalk called the Funiculus. As the funiculus elongates, one or more layers of cells, the Integuments, envelope the megaspore mother cell, except over a small opening called the Micropyle. The functional megaspore then divides mitotically three times, giving rise to an embryo sac containing eight genetically identical nuclei.

In the mature embryo sac the large cell near the micropyle is the Egg cell. The smaller cells at each side of the egg cell are called Synergids. The two nuclei near the center are the polar nuclei. The three cells at the end opposite the egg cell are the Antipodals. Thus, a mature ovule ready for fertilization consists of an embryo sac with generally six cells and two polar nuclei. The embryo sac is surrounded by the nucleus, which, except for the micropyle, is surrounded by the integuments. The entire structure is attached to the ovary wall by the funiculus (Figure 5).

When a pollen grain lands on a stigma of the same species, pollination has occurred. Mature pollen grains may be transferred from the anther to the stigma by gravity, wind, or various insects. When pollen is transferred to the stigma of flowers of the same plant, self-pollination occurs. When pollen is transferred to stigmas in genetically different plants, cross-pollination takes place.

Events occurring after pollination are similar for all flowering plants. Normally, the pollen grain germinates within a few hours after contacting the stigma, producing a pollen tube which grows through the style and the ovary wall. The tip of the pollen tube passes through the micropyle and penetrates the embryo sac where the pollen tube ruptures, discharging its two sperm nuclei. One of the sperm nuclei joins with

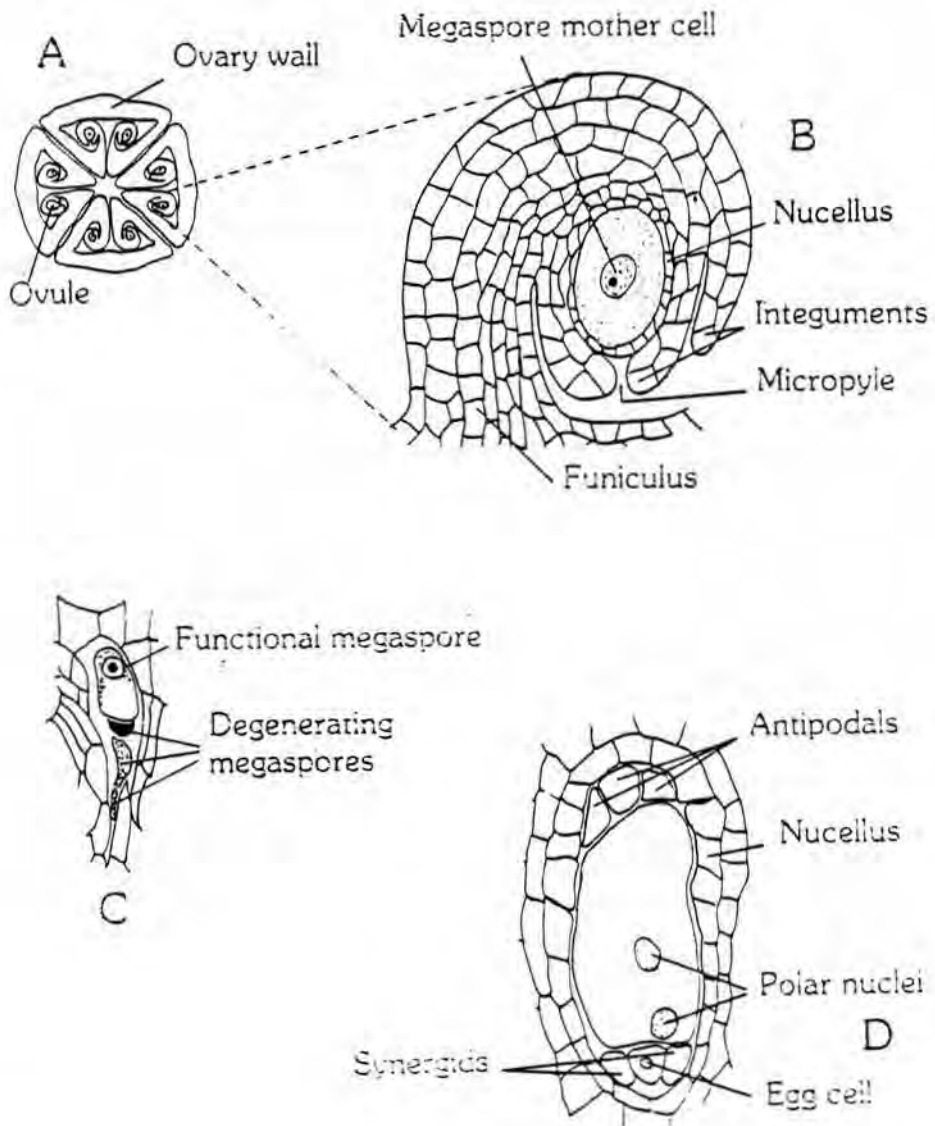


Figure 5. Diagram of embryo sac development.

and fertilizes the egg cell, forming the first cell of the new plant, the Zygote. The second sperm nucleus fuses with both polar nuclei to form the primary endosperm nucleus. Fertilization of the egg cell re-establishes the normal (2N) chromosome number of the species. The fusing of the three nuclei initiates the formation of the endosperm (3N). The two separate unions, sperm with egg and sperm with polar nuclei, are referred to as double fertilization, an event unique to the plant kingdom (Figure 6). Double fertilization must occur within every ovule in the ovary or the seed will not be formed.

In beans, for example, this means that, depending on the number of ovules, one or more pollen grains are required to fertilize the ovules produced in each ovary. In rice, only one pollen grain is necessary for fertilization because only one ovule is formed in each pistil.

Seed Development

Following fertilization, the newly formed cells, the zygote and endosperm, start dividing. The zygote produces a row of cells, the proembryo (Figure 7). After a few hours or days, the proembryo cell farthest from the micropyle enlarges and divides, forming the first cells of the embryo. Of the cells formed by this division, the cell nearest the micropyle gives rise to the roots and associated underground plant parts. The other cell gives rise to the above-ground parts: stems, leaves, and eventually flowers (Figure 8).

A few days after fertilization the first difference becomes apparent between embryos which will have two cotyledons (dicots) left and those which will have only one (monocots) right (Figure 9). As the seed continues its development, it increases in size and dry weight until growth is completed and germination capability is achieved. This point is generally referred to as physiological maturity of the seed. No further morphological development takes place.

The mature embryo of most dicotyledonous seed consists of an embryonic axis to which the two cotyledons are attached. The formation of these two structures utilizes most or all of the endosperm, depending on the species. At one end of the axis, above the cotyledonary node is the Epicotyl or Plumule which will produce the above-ground structures of the plant. At the other end of the embryonic axis is the Radicle which will develop into the primary root. Between the radicle and the cotyledonary nodes is an area called the Hypocotyl. The embryonic axis, cotyledons and endosperm (when not totally consumed in embryo formation) are completely covered by the Testa (seed coat) which is formed by drying and hardening of the integuments. The scar on the surface of the testa, the Hilum, is formed when the funiculus is broken from the now mature, fertilized ovule (seed) (Figure 10). The micropyle can be seen on the testa of some seeds. Examples of dicots includes beans and soybeans.

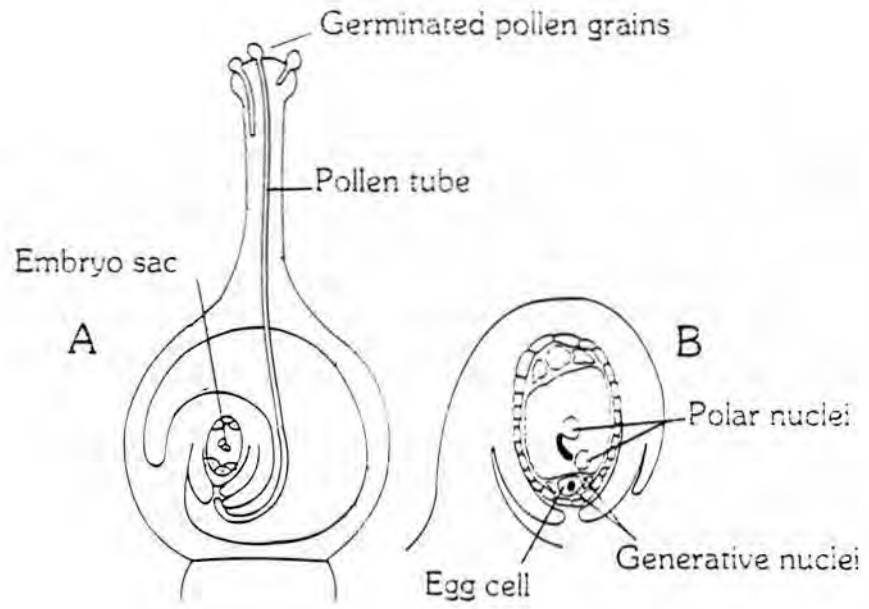


Figure 6. Double fertilization process.

Primary endosperm

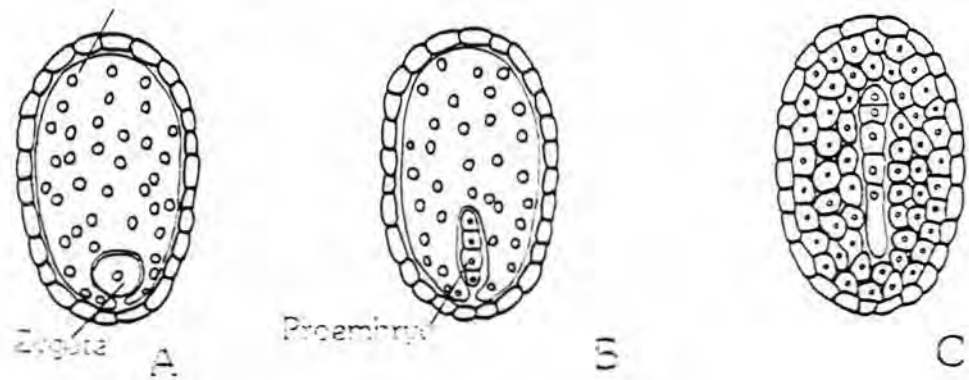


Figure 7. Development of the proembryo.

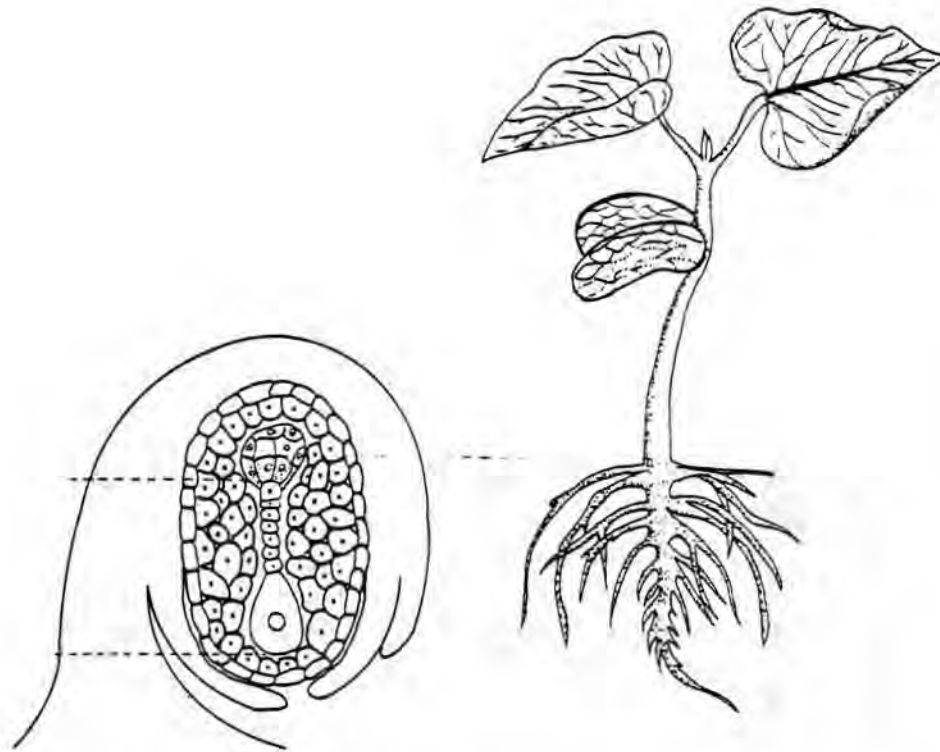


Figure 8. Relation between polarity of proembryo cells and the future seedling.

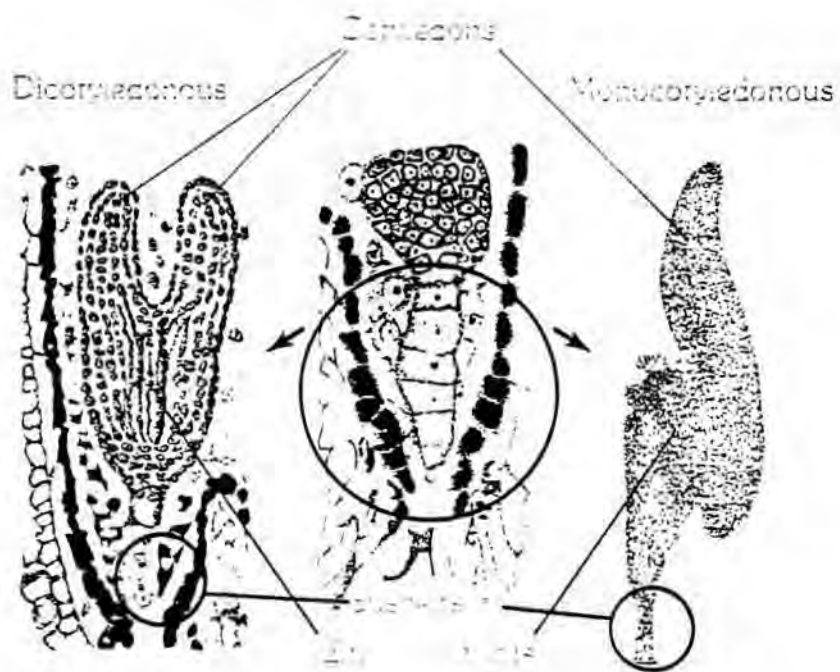


Figure 9. Differences between dicotyledonous and monocotyledonous embryos.

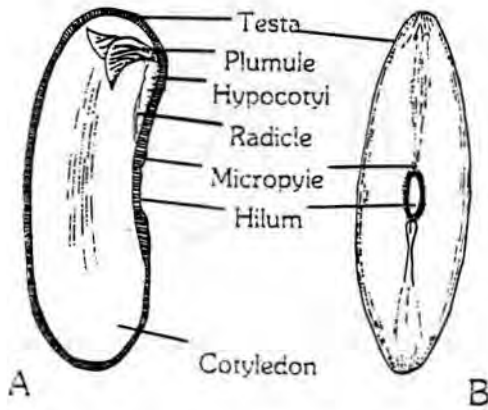
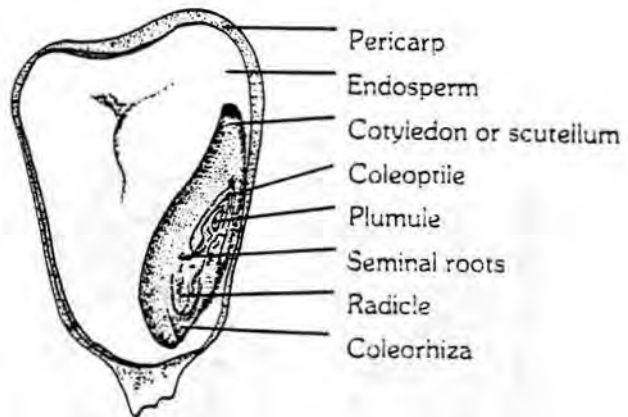


Figure 10.
Features of the mature embryo of a dicotyledonous plant.

Figure 11.
Longitudinal section of a caryopsis.



The development pattern of the monocot seed is very similar to that of a dicot seed except for the number of cotyledons. Also, in most economically important monocot species, the endosperm is not totally consumed during development of the embryo. Therefore, the mature monocot seed contains both cotyledonary and endospermic forms of stored food. Maize, wheat, and barley are examples of monocot seeds.

Seeds of the grass family are classed botanically as fruits. The embryo, as defined previously, is embedded in the endosperm. The ovary wall, or pericarp, rather than the integuments, functions as a protective layer outside the seed coat. This type of one-seeded fruit is called a Caryopsis. A longitudinal section of the embryonic axis reveals those structures common to all seed. The cotyledon in a caryopsis is called the Scutellum. In addition, there are protective tissues; the Coleoptile encloses the epicotyl, and the Coleorhiza encloses the radicle. Rudimentary seminal roots, located in the region of the cotyledonary node, can be seen in most grass species (Figure 11). The Mesocotyl is the region located between the epicotyl and the cotyledonary node.

It should be evident that for a seed to be valuable for reproductive purposes, its embryo must be alive. The longevity of any seed depends on many factors - the environment in which it is stored, its chemical composition, its physical structure, etc. It is important that we know the structure of the seed with which we work, not only for proper selection and use of equipment for harvesting, threshing, and handling seed but also to relate this structure to different stages of a quality control program. In purity tests, for example, it is necessary to know the seed characteristics of the species with which we are working to be able to separate it from the other seeds, weeds or inert matter. It is necessary to know the embryonic structure and its relation to the tissues of the future plants to evaluate results of germination, tetrazolium and other growth tests.

Summary

In summary, the four basic floral organs are sepals, petals, stamens, and pistil; the latter two are directly involved in seed formation. Pollen formation takes place in the anthers. When a pollen grain lands on a stigma of the same species, pollination has occurred. Then, a sperm nucleus fertilizes the egg cell, re-establishing the normal (2N) chromosomes number of the species. The seed or reproductive unit is a mature fertilized ovule comprised of the plumule, radicle, one or two cotyledons, food reserves, and an outer covering, the pericarp or testa.