(1) GENERAL PRINCIPLES OF ANGIOSPERM SEED FORMATION

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Based on Copeland & McDonald (1995); McDonald & Copeland (1996); Marcos Filho (2005)

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(2) Reproduction Processes in Plants

Plant reproduction is central to survival of the species and is accomplished either sexually or asexually. **Sexual** multiplication constitutes reproduction *per se* since it involves the development of a new individual from a mature individual and an active participation of sexual cells or nuclei. This process promotes the renewal of individuals from the fusion of male and female gametes.

Vegetative propagation or asexual multiplication often is the result of modification of plant vegetative structures such as stolons, rhizomes, bulbs, tubers, tillers, bulbils that possess the ability to regenerate the mother plant. This is also accomplished by plant cells or tissues (micro propagation) and apomixis (production of seeds and vegetative propagules by asexual methods).

This is the way to produce <u>clones</u>, i.e. a group of individuals or plants of common ancestry that have been vegetative propagated by mitotic division. This means that there is no fusion of sexual cells.

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(3) Floral Induction

The ability to support reproductive processes requires significant energy. Often, many crops do not begin to form flowers, and eventually seeds, until substantial vegetative growth has been accomplished. In some cases, as with most annuals, this is at the end of the life cycle, but in other cases the plant may not become reproductive for several growing seasons as with many fruit trees.

The plant reproduction process starts with the transition from a vegetative to reproductive stage when there are physiological changes in the activity of terminal buds. This occurs at a growth stage in which the plant acquires the ability to perceive and assimilate environmental stimuli. This stage depends on each plant. For example, in onions and carrots, this stage depends on the size of the bulb or root; in corn or tomato, on a specific node.

Floral initiation is influenced by plant age, environmental conditions, level of photosyntate accumulation (dry matter production) and other specific factors.

Plant growth originates within the buds in regions known as meristems. These are undifferentiated tissues located at the tips or growing points of vegetative or reproductive organs capable of undergoing cell division and elongation; these processes produce tissues that soon develop into specific plant parts. Within each meristem are minute primordia that enlarge and differentiate into recognizable plant organs.

Floral induction is a physiological change that permits the development of reproductive primordia. This change may precede actual flowering by several days, weeks, or even months.

Flowering may be induced by specific conditions of temperature, water availability, photoperiod, nutritional status, chemical stimulus or interaction among those factors. Besides the well known influence of floral induction in response to **day length** (short-day or long-day plants), many plants require exposure to relatively **low temperatures** (5^oC to 10^oC) for 10 to 100 days depending on the species. This is called vernalization, which means the promotion of flowering in some winter plants by cold treatment of specific plant organs such as in onion, carrot, rye, sugar beet and others.

The influence of **water** is also important to induce flowering in some species, such as coffee; some days after sufficient rainfall, bud dormancy is overcome and flowering induction occurs. Literature documents the action of water in metabolic processes that affect plant flowering, including hormone synthesis.

Certain **natural and synthetic compounds** can also cause floral induction. Some are auxin-like compounds such as indoleacetic acid. Others are gibberellic acid, cytokinins, and ethylene whose use is becoming commercially important in manipulating flowering and fruit development in certain crops.

In floral induction, the nutritional status of the plant is also important since the construction of the flowering parts and the whole reproduction process is dependent on food availability, translocation and assimilation.

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(4) Floral Initiation

Floral initiation is the morphological expression of the induced state and occurs more or less within the plant meristems.

There are generally three differing types of floral production:

- *Annuals*: these plants flower and die in one season. Grain crops are typical examples.
- *Biennials*: these plants live for most or all of two seasons. They are characterized by vegetative growth during the first season and reproductive growth in the second season after floral induction. Examples include onion, carrot, sugar beet, cabbage.
- *Perennials*: these plants flower and produce seed each year after they have passed the juvenile stage. Examples include coffee, cocoa, and several fruits.

Flowering only occurs when the plant has reached a minimum vegetative developmental stage and then acquires the ability to respond to external stimuli. Plants not sensitive to photoperiod usually flower after the accumulation of a certain amount of thermal energy, expressed in thermal units such as ^{o}C/day.

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(5) Types of Inflorescences

An inflorescence is the arrangement of flowers on a plant. The main axis of the inflorescence is the rachis and the branch on which the flower is found is the pedicel. Inflorescences can be either determinate or indeterminate. For determinate inflorescences, the terminal flower is the first to form and prevents further elongation of the inflorescence. In contrast, indeterminate inflorescences contain simultaneous reproductive and vegetative structures with flowers forming first on the oldest part of the rachis. Indeterminate growth exhibits a lack of uniformity. Important examples include:

- *Solitaire*: the simplest expression of a determinate inflorescence.

- *Head*: an inflorescence where the rachis and the pedicels are tightly clustered, surrounded by a group of flower-like bracts called an involucre. Example: sunflower.

- *Spike*: the flowers arising along the rachis are essentially sessile, and are attached to the rachis. Example: wheat.

- *Umbel*: an inflorescence in which the lateral branches arising from the rachis originate form the same location. Examples: carrot and celery.

- *Compound umbel*: is similar to an umbel except that each pedicel is branched bearing multi-branched individual flowers.

(6) - *Panicle*: an inflorescence in which the lateral branches arising form the rachis produce flower-bearing branches instead of single flowers. Examples: rice, oat, male inflorescence of corn.

- *Raceme*: the basic type of inflorescence in which pedicels arise laterally on a long central rachis. Examples: legumes such as soybean and field bean.

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(7) Types of Flowers

The typical flower of an angiosperm, or plant whose seeds are enclosed in an ovary, is composed of petals, sepals, stamens, and a pistil. These are ***complete*** flowers. ***Incomplete*** flowers lack any of these four parts.

The ***perfect*** flower contains both stamens and pistil, for example, this flower is a hermaphrodite. The ***unisexual or imperfect*** flowers are either staminate or pistilate.

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(8) Types of Flowers and Plants According to Sex

This plant is classified as a ***hermaphrodite*** when all flowers are perfect such as cotton, rice, coffee, and citrus. Species such as corn, cucumber, *Pinus*, which have both male and female flowers in the same plant are known as ***monoecious***; those that have unisexual flowers on different plants such as papaya, pecan, spinach, *Asparagus, Araucaria* are ***dioecious***.

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(9) Parts of a Complete Flower

The flower is a branch that usually has limited growth found in the axils of leaves, whose parts are adapted to the formation and development of the reproductive cells, fruits, and seeds.

Angiosperm plants show different types of flowers, but usually they are found in the same parts of the plant and vary in number, shape and disposition. The component parts of a complete flower are shown in this Figure.

The *peduncle* is the axis connected to the branch and supports all flower parts. The petals, often the most conspicuous and colored parts, collectively are called the *corolla*. Sepals, usually (but not always) less conspicuous, are know collectively as the *calyx*. Stamens are the male pollen-bearing structures and each consists of an anther and filament; each anther has two longitudinal pollen sacs.

(10) The set of stamens is known as the *androecium*. The pistil, usually the component of the *gynoecium*, is the female part of the flower and consists of the stigma, which receives the pollen, the style, and the ovary.

(11) The anther usually contains four pollen sacks. The ovary may be composed of one or more carpels, which may be considered highly modified leaf-like structures. When only one carpel forms the ovary, it is termed simple and usually contains only one locule or cavity. A compound ovary is made up of two or more united carpels and may contain one or more locules, depending on their arrangement.

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(12) Microsporogenesis and Microgametogenesis

Pollen grains are formed in the anther. This is a part of the stamen composed of cell layers and specialized tissues responsible for reproductive pollen grain formation and non-reproductive nutritional and dehiscence functions, each performing specific activities.

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(13) Phases of Pollen Grain Formation

The anther primordium consists of uniform, homogeneous meristematic cells. Within this phase of development, the anther has four lobes that contain the longitudinal pollen sacs.

The period of flower development when the stigma is ready to receive the pollen is known as anthesis. Pollen is usually produced in four sacs or microsporangia in the anther. Within the sporangia, certain cells become the *archesporial cells* that differentiate and give rise to the *microspore mother cells* and undergo a two-step reduction division or meiosis or microsporogenesis to yield four *microspores*, each being haploid or 1N.

Each of the four microspores is usually functional and undergoes two divisions, known as microgametogenesis, giving rise to a microgametophyte or mature pollen grain. Each mature pollen grain consists of a double cell wall (exine and intine), a vegetative nucleus and at least one sperm nucleus known as the generative or reproductive nucleus which is haploid or 1N.

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(14) The Surface of the Pollen Grain

The outer layer of the pollen grain double wall, i.e., the exine, has irregularities that promote adherence to the stigma. The exine is thick and contains sporopollenin, a compound extremely resistant to decomposition that contributes to increasing pollen longevity.

The exine surface is not continuous and is porous so the growth of the intine (a thin membrane) and consequent formation of the pollen tube can easily occur.

(15) Megasporogenesis and Megagametogenesis

Angiosperm seeds originate from the meristematic tissues of the ovary wall called ovule primordia. The main tissue of the carpel is the nucellus, which is completely surrounded by the growth of the ovule integuments (primine, the outer, and secundine, the inner) except for a very small opening known as the micropyle. The nucellus provides nutrients to support the complete development of the female gametophyte or embryo sac.

(16) Within the nucellus are specialized tissues of the carpel; one cell, known as the archesporial cell, and is 2N develops characteristics that distinguish it from adjacent cells. As this cell increases in size, its nucleus becomes larger and its cytoplasm grows denser in preparation for cell division. The first division is mitotic and results in a megaspore mother cell and a parietal cell; this cell remains undivided and soon deteriorates.

The megaspore mother cell is diploid or 2N. However, it soon undergoes meiosis giving rise to four haploid or 1N megaspores, but only one is functional and the other three degenerate. The development of the female gametophyte or embryo sac from the functional megaspore is known as megagametogenesis, which is a process of successive nuclear divisions within an enlarging cell that becomes the embryo sac.

Three successive mitotic divisions occur culminating in eight haploid nuclei. Soon, these nuclei arrange themselves within the enlarging embryo sac and cell walls form, resulting in three antipodal cells at one end, two polar nuclei (without cell walls) in the center, and the egg cell between the two synergid cells closer to the mycropilar end. After the two polar nuclei fuse to form a diploid nucleus, the resulting seven-celled structure is the mature female gametophyte or emrbyo sac or megagametophyte.

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(17) Pollination

Anther dehiscence frees the pollen grains; the transfer of the pollen grain from the anther to the stigma is known as pollination. There are two main types of pollination: self-pollination and cross-pollination.

Self-pollination occurs when pollen from the anthers of a flower is transferred to the stigma of the same flower or to different flowers of the same plant. In most cases, flowers do not open until pollination and fertilization are finished if the flower is a complete flower. Examples include soybean, rice, field bean, cotton, peanut, citrus, eggplant, lettuce, tomato, okra, tobacco, wheat, barley, and pea.

Cross-pollination occurs when pollen from one flower is transferred to the stigma of a flower of another plant. Unlike self-pollination, where progeny are genetically similar, cross-pollination results in progeny that are more dissimilar. This evolutionary approach produces a population of individuals that are more adapted to a wide array of environmental conditions. Maize, rye, *Crotalaria juncea*, sorghum, onion, carrot, castorbean, sunflower, cucurbits, alfalfa, pearl millet, brássicas, mango, papaya, bell pepper and others.

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(18) Pollination/Agents: wind

In most agricultural crops, cross-pollination occurs by two principal methods: wind (anemophily) and insects (entomophily). Other less important methods include birds, bats, water and humans.

In grass flowers where cross-pollination occurs, the anthers are connected to relatively long filaments, making it easier for wind to transfer the light pollen grains. After anther dehiscence, the pollen grains land on the receptive stigmas which provide easier contact and adherence of the pollen grains. Male inflorescences of wind-pollinated plants produce abundant numbers of pollen grains; in corn plants, for example, each male inflorescence produces from 20 to 50 million pollen grains.

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(19) Pollination/Agents: insects

In legumes and many other plant species such as cotton, sunflower, onion, cabbage, cucumber, passion flower, and *Crotalaria juncea*, pollen transfer is accomplished by honey bees and other insects which visit flowers to collect nectar and, after contact with the dehiscent anthers, carry the pollen to other flowers by touching their stigma.

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(20) Pollination: Other Agents

Pollination is also provided by bats, birds such as hummingbirds, water and humans (controlled pollination). An example of water pollination occurs in *Vallisneria spiralis*; the female flowers are supported by relatively long peduncles which elongate to reach the water surface and touch the short peduncles of the male flowers. After anther dehiscence, the pollen grains are transferred to the stigma.

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(21) Pollination/Difficulties

The morphological characteristics of the flower and genotype may create difficulties in pollination or fertilization and consequently seed formation. One example is the genetic or morphological self-incompatibility which occurs in cabbage, *Crotalaria juncea*, passion flower, sunflower, radish, rye and other species.

Another example is dichogamy which occurs when flowers have pistils and stamens that mature at different times. Protandry is an example of a flower that has the anthers release their pollen before the stigma is receptive as occurs in maize, carrot, onion and pecan. Protogyny is characteristic of flowers where the stigma is receptive to pollen before the pollen is shed from the anthers as found in mango, pearl millet, and cauliflower.

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(22) Pollinization/Importance: genetic purity

A sound knowledge of the type and agents of pollination is fundamental to the production of large quantities of high quality seeds with respect to genetic purity, especially for cross-pollinated plants.

Among the practices adopted to guarantee genetic purity are crop isolation, differences in the sowing time for the male and female lines known as the “split” in hybrid production, the use of cytoplasmic male-sterility and self-incompatibility widely used in ***Brassica*** vegetables.

In addition, it is important to know the dispersal characteristics of the pollen grain and its fertility to determine the proper proportions between the male and female lines to assure the highest yields as a result of efficient pollination.

Other significant examples of the importance of the pollination process are found in the technology adopted for hybrid cucumber seed production. The parental lines of this species produce monoecious, androecious or gynoecious flowers. Depending on the desired characteristics to be incorporated in the hybrid, it is possible to change sex expression by applying specific compounds to the seedlings. For example, the application of ethylene in androecious lines favors the formation of female flowers; in contrast, seedling treatment with silver thiosulphite in gynoecious lines promotes its reversal into an androecious line and the consequent formation of male flowers.

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(23) Pollination/Importance: ”Split”

Here, you see the release of male pollen and female maize inflorescences. This species exemplifies protandry.

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(24) Pollination/Importance: proportion of male and female lines for the production of hybrids

These are examples of a landscape of flowering crops of maize, sorghum **(25)** and pearl millet hybrids.

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(26) Pollination/Importance: quantity produced

Seed production fields of insect-pollinated species must be located in regions where there are many specific pollinators. This frequently occurs in woodlands, but sometimes it is necessary to provide insect colonies so adequate populations are available to ensure effective pollination.

At the same time, the layout of the field is related to the efficiency of pollination since the insects must stay inside this area to promote effective transfer of pollen grains to specific stigmas. If these aspects are ignored, seed production will be compromised and yields will be low.

Pest control during flowering and anthesis is also important in insect-pollinated species to avoid killing useful insects such as honeybees. This precaution is routinely adopted in sunflower and onion seed fields. It must also be emphasized that insecticide application during flowering can cause damage to the stigma and affect pollen tube development.

Rainfall also influences seed yield and quality. For example, high rainfall during flowering impairs pollination and seed set in onion and other insect-pollinated crops. In addition, it also affects pollen dispersal in anemophilous plants such as maize. Conversely, drought and high temperature such as >32°C increase the number of abnormal and sterile pollen grains in many cereals thus reducing seed set; the same occurs during the period of photosynthate transfer with negative effects on seed quality and yield. These facts emphasize the importance of the proper selection of sowing times to minimize these events.

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(27) Pollination/Importance: production of tomato hybrid seed

Tomato flowers are hermaphroditic and have a negligible degree of allogamy. Hybrid seed production requires the controlled pollination of previously selected parental lines, the determination of an adequate ratio of male to female plants, differences in the sowing time for the male and female lines (the male parent is generally planted earlier).

(28) To maintain genetic uniformity in self-fertilizing crops since male-sterile lines usually are not available, most seed companies utilize manual emasculation and pollination techniques of the female parent flowers. This practice, pollen collection and manual pollination, usually represents about 40% of tomato hybrid seed production costs.

All these comments are useful to illustrate the importance of a consistent knowledge of pollination to produce large quantities of genetically pure seeds.

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(29) Fertilization: formation of the pollen tube

When the pollen grain lands and adheres to the stigmatic surface, it absorbs the stigmatic liquid and germinates, producing a pollen tube whose formation is a consequence of intine growth. The pollen tube grows down the style, through the mycropyle and into the embryo sac closely following the tube apex.

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(30) Fertilization

The pollen tube vegetative nucleus which is 1N soon degenerates, but the two pollen tube sperm cells, each being 1N, enter the embryo sac; one fuses with the diploid polar nucleus to form a triploid or 3N ***endosperm nucleus***.

(31) The other sperm nucleus fuses with the egg cell, a process known as syngamy, to form a diploid ***zygote*** or fertilized egg.

The process of fertilization is very important because it not only results in the formation of a seed, but also dictates the level of genetic diversity present in the zygote and the future embryo.

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(32) Embryogeny

After sexual fusion, or syngamy, a brief period of reorganization occurs during which the zygote cytoplasm becomes more homogeneous and the nucleus larger. The duration of this period varies among species, but it is usually about four to six hours before the zygote begins to divide. Lines of polarity in preparation for future division and growth already exist in the embryo sac, having been established in the unfertilized egg, but initially, cell division of the zygote does not begin until at least a small amount of endosperm has formed.

The first cellular division of the zygote is not symmetrical, resulting in a terminal cell next to the mycropyle and a basal cell at the distal end. Of the first two cells formed, the one adjacent to the mycropyle is elongated and more prominent than the other terminal cell. This large cell undergoes a series of mitotic divisions to form a multicellular tissue known as the suspensor attached to the proembryo. Plant species may be classified according to this pattern of cell division, which results in different proembryo types. Each part of the mature embryo arises from the special parts of this structure, but it may vary in size and shape.

Although the mature embryos of monocotyledons and dicotyledons appear considerably different, their patterns of embryogeneny are similar. The size of the suspensor varies. Initially, it was thought that the function of the suspensor was to push the developing proembryo into the endosperm to enable easy access and ready digestion of the energy-rich endosperm tissue. More recently, there is evidence that the primary function of the suspensor is to secrete enzymes that digest the endosperm, absorb nutrients and transfer them to the developing embryo. By the time the embryo is mature, the suspensor has become an inconspicuous tissue.

The terminal cell of the first division ultimately develops into the embryo. The few-celled stage of the embryo is known as the proembryo. The development of this structure in dicot seeds typically undergoes four discrete stages: globular, heart, torpedo and mature, each corresponding to different developing stages of embryo formation, such as the radicle/hypocotyl, cotyledons, and plumule or epicotyl.

The cotyledons of many dicot seeds vary in shape. Endospermic seeds such as castorbean and rubber tree tend to have thin, delicate, leaflike cotyledons while nonendospermic seeds such as legumes possess cotyledons that are bulky and represent as much as 90% of the seed's dry weight.

Monocots also undergo the development of a globular embryonic stage. However, since only one cotyledon is formed, they do not form the remaining stages of proembryo development characteristic of dicots. Instead, monocot embryos begin development lateral to the axis of the seed as growth of the proembryo continues beyond the globular stage. The scutellum is considered as the equivalent cotyledon structure in the grass seed embryo; the embryo axis is protected by the scutellum as well as the plumule or the primary leaves by the coleoptile and the radicle by the coleorhiza.

The mature embryo possesses all the main parts of the future plant in different degrees of differentiation in relation to size, shape, position and vascularization, depending on the species.

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(33) Endosperm Development: endospermic seeds

After double fertilization, the endosperm begins its development before the embryo. It acquires the energy for growth by haustoria that penetrate into the adjacent maternal tissue to enhance nutrient absorption as well as by direct absorption of nutrients through diffusion from surrounding tissues, especially the nucellus.

The endosperm can develop in a variety of ways that involve an organized sequence of endosperm nuclear divisions followed or not followed by cell wall formation. **Endosperm** differentiation includes the deposition of reserves transferred from the mother plant.

Mature seeds in which there is a well-formed endosperm are known as <u>endospermic</u> and contain reserves to be used in germination such as in grasses, castorbean, rubber tree, tomato, coffee, beet, onion and others.

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(34) Maize, example of an endospermic seed

Maize is an example of an endospermic seed where 80% of the seed dry weight is represented by the endosperm.

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(35) Endosperm Development: nonendospermic seeds

Seeds lacking or possessing minimal endosperm are called <u>nonendospermic</u> and such seeds typically possess large embryos in relation to the whole seed as found in legumes, cotton, cucurbits, brássicas and many other dicots. In those seeds, the reserves are typically stored in the cotyledons because the endosperm is gradually degraded just after its formation to support this enhanced embryo growth.

As a consequence, food reserves stored in the endosperm or the cotyledons, depending upon the species, are used during germination and initial seedling growth until the plant starts the photosynthetic process and becomes autotrophic.

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(36) Field bean, example of a nonendospermic seed

Field bean is an example of a nonendospermic seed. Note the large cotyledons and lack of endospermic reserves.

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(37) Parts of the Embryo

The mature embryo contains different parts that occur with differing degrees of differentiation which vary among species. The most important parts are the following:

a) *radicle*: embryonic tissue that forms the primary root of the seedling;

b) *hypocotyl*: part of the embryonic axis below the attachment of cotyledons and above the radicle which develops into the initial elongating stem of the developing seedling;

c) *cotyledon(s)*: modified leaves in most dicots containing food reserves or a structure known as the scutellum responsible for the absorption of the endosperm and transferring nutrients to the germinating embryo as in grasses or a structure which protects the embryo as in many monocots;

d) *plumule*: mass of meristematic cells, is the major leaf bud of the seed or seedling. That part of the embryonic plant axis above the cotyledons, also known as *epicotyl;*

e) *coleorhiza*: a transitory membrane covering the emerging radicle in some grass seeds;

g) *coleoptile*: a transitory membrane covering the shoot apex of certain species that protects the plumule as it emerges through the soil;

h) *seminal roots*: occur in the cotyledonal node in grass seeds;

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(38) Perisperm development

After fertilization, the nucellus usually is degraded during embryo and/or endosperm development. In some species, such as coffee and sugar beet, the endosperm ceases development early and the nucellus becomes filled with food reserves not digested by the endosperm. This energy-rich tissue serves as a primary energy source during germination for these species. At the time of seed maturation, the remaining nucellar tissue is known as the ***perisperm***.

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(39) Seed Coats

Seeds usually have one or more external seed coat layers that develop simultaneously with the embryo and endosperm. The outer ovule integument, the primine, forms the external seed coat or the ***testa*** and the inner integument is known as the ***tegma***.

Seed coats accomplish important functions such as:

a) Maintaining a protective role around seed parts to ensure their interaction and normal vital functions.

b) Protection against harmful biotic and abiotic factors (physical, mechanical or chemical).

c) Regulation of water uptake and gas exchange with the surrounding ambient environment.

e) Regulation of germination and influencing the intensity of dormancy expression.

g) Control of seed dispersal favored by appendages such as wings, aculeus, hairs, mucilage in the seed coat surface.

Seed coat structure may differ markedly among species; some of them possess two or more seed coat layers such as occurs in legume seeds. In contrast, there is essentially no integumentary tissue remaining in a fully developed corn caryopsis; both ovule integuments are consumed leaving it naked inside the surrounding pericarp.

Differentiating seed coat appendages may be also found in seeds that include arils, caruncles, raphes, and callus that originate from the ovary or ovule integuments.

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(40) Fruit and Seed

The botanical definition of a fruit is much broader than that conveyed by popular usage of the term. A fruit is defined as a mature or ripened ovary that usually contains one or more ovules that develop into true seeds. Legume pods, lettuce and sunflower achenes and cereal grains are fruits.

The pericarp or ovary wall of angiosperms fruits is composed of three layers which are more or less distinct in various species: the exocarp, or outer layer; the mesocarp or middle layer, and the endocarp or inner layer. The relative development of each in various species often determines fruit structure and morphology.

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(41) Dry Fruits

Dry fruits are developed from an ovary of one or more locules and usually possess a thin pericarp that is dry at maturity. Visually, a one-seeded dry fruit looks the same as a true seed.

Dehiscent dry fruits often prematurely split and open at maturity and release mature seeds, such as legumes, follicle, capsule (cotton), silique (brássicas). This is known as “shattering” in seed production.

- Indehiscent fruits do not open at maturity. Examples include caryopsis, achene, samara, nuts, and schizocarp as found in carrot seeds.

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(42) Apomixis

Apomixis is the production of seeds and vegetative propagules by asexual methods. Apomictic seed structure is similar to those produced sexually following the fusion of the egg and sperm cells.

The main features of apomixis are:

- it substitutes asexual propagation for sexual reproduction;
- it occurs in parts of the plant normally concerned with the sexual process such as the flowering parts;
- it occurs without fusion of egg and sperm cells

This process represents a transition between plant propagation and reproduction in which there is the formation of “seeds” by different mechanisms with or without a pollination stimulus that usually results from the division and differentiation of nucellar cells. As a consequence, apomictic seeds are similar to clones and produce genetically identical plants.

In general, apomixis is not complete within a plant and its proportion varies according to the season and production location. For instance, the mean rate of apomixis seed formation in *Panicum maximum* is around 5%.

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(43) Examples of Seed Structure

The following slides depict differing examples of seed structure for **(44)** pea, **(45)** pumpkin, **(46)** castor bean, **(47)** and onion.

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(48) Seed Maturation

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(49) Importance

The process of seed development is genetically controlled and involves an organized sequence of many types of changes from ovule fertilization to the stage in which seeds become independent from the mother plant.

Seed development includes a whole set of successive morphological stages in preparation for successful seed germination. It is characterized by the synthesis and accumulation of reserves subsequently mobilized during germination that direct the resumption of growth and formation of a seedling.

Detailed studies of the seed development process provide basic information on seed maturity and the proper time to harvest with minimum seed loss from shattering or excessive maturation. Premature or harvest delays are usually detrimental to seed quality and yield.

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(50) Concept

Seed maturation is a process which includes a sequence of morphological, physical, biochemical and physiological changes from ovule fertilization to the stage when the seed becomes physiologically independent of the parent plant.

Alterations During Seed Development: moisture content

(51) Moisture content just after ovule fertilization is around 80% both for monocots and dicots.

(52) After sexual fusion, moisture content gradually declines, but remains relatively high during the majority of the maturation period to support increased seed weight through photosynthate accumulation.

Dehydration is accelerated at the final maturation stages primarily after maximum seed dry weight is attained; at this stage, orthodox seeds possess 30-35% (monocots) to 50-55% (dicots) moisture content. This decrease continues until hygroscopic equilibrium is attained; from this stage, seed moisture content varies according to fluctuations in relative humidity of the environment.

Decreases in moisture content during seed maturation are more intense in dry fruits; seeds within fleshy fruits dry slowly and possess higher moisture content at maturity. In addition, recalcitrant seeds do not exhibit drastic decreases in moisture content during seed development which remains around 60% or more during the seed development process.

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(53) Alterations During Seed Development: seed size

The fertilized ovule is a small structure compared to the mature seed. The first stage of embryogenesis is characterized by numerous cell divisions and elongation and significant increases in seed size; the maximum size is reached around the middle of the seed reserve accumulation period.

Afterwards, seed size is gradually reduced until the end of the maturation period following the most pronounced decreases in seed moisture content. These size decreases are most evident in legume seeds compared to grass seeds.

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(54) Alterations During Seed Development: seed dry weight

Immediately after fertilization, seed development begins and seeds become the primary recipient or sink for assimilates from the plant. There are four general stages that can be characterized during seed formation. The first two stages comprise intense cell division and elongation with slight increases in seed dry weight. The third stage is characterized by a rapid increase in seed weight when nutrition is supplied through the funiculus by the parent plant. At this point, the seed reaches its maximum dry weight, the funiculus degenerates and the seed becomes physiologically independent from the parent plant and the seed still contains a high moisture content.

The fourth and final stage is when the seed undergoes further dehydration after physiological maturity.

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(55) Alterations During Seed Development: seed germination

Seeds of several species including grasses are capable of germinating by protruding a primary root a few days after fertilization although seedling growth is usually poor at this point. Germination percentage and seedling vigor increase with further maturation and reache a maximum near or at the point of seed maximum dry weight. In addition, changes in seed vigor usually accompany any changes in seed dry weight. The more changes in seed dry weight, the less the seed vigor.

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(56) General Alterations during Seed Maturation

Here is an overall graph demonstrating changes in moisture content, seed size, vigor, dry weight and germination during seed maturation.

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(57) Determination of Physiological Maturity

The concept of physiological maturity is controversial in the scientific literature. Among the different opinions are:

a) Seeds attain physiological maturity at the time of maximum dry weight formation;

b) Physiological maturity is characterized by the absence of further significant increases in seed dry weight;

c) Seed is physiologically mature when it possesses its maximum dry weight, germination and vigor.

There is little doubt that seed development ceases at the point of maximum seed dry weight. However, this concept is often not understood because it is frequently associated with identifying the best time to harvest seeds. A typical example is illustrated by the use of terms such as “harvest maturity”, “morphological maturity”, “mass maturity”, “agronomic maturity” and others

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(58) Identification of Physiological Maturity

- The development of a “black layer” in the placental-chalazal region of maize and sorghum seeds and the progressive development of the “milk line” in maize seeds as a result of milky endosperm solidification beginning at the caryopsis apex and ending at the base are considered good morphological parameters to identify physiological maturity. Complete formation of the black layer and the milk line (75% of the seed’s length) corresponding to stage 4 in corn development are proven indicators of maize seed maturity.
- In soybean, the initiation of seed shrinkage and loss of green color from the pods and seeds coincide with the attainment of maximum seed dry weight. At this point, seeds are at 50%-55% moisture content.
- In wheat, physiological maturity occurs with the loss of green color in the leaf closest to the spike or ”flag leaf”. Oat and barley seed physiological maturity is identified by the loss of the green color in the pedicel.
- Vegetable and fruit seed maturity is usually recognized by fruit color such as with tomato, bell pepper, egg plant and others.

The identification of physiological maturity is very important because it identifies when the seed is physiologically independent from the mother plant. Even when it is not possible to mechanically harvest high moisture seeds, it is important to emphasize that after physiological maturity, seeds are exposed to harmful environmental conditions and must be harvested as soon as possible. If reliable visual parameters to identify physiological maturity are not available, it is impossible to determine the ideal time for harvest. This identification may also assist in establishing the best time to apply plant desiccants prior to harvest to avoid losses in seed quality.

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(59) Identification of Physiological Maturity of Maize Seeds

Here are examples of maize seeds showing black layer and milk line formation that assist in identifying physiological maturity.

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(60) Physiological Maturity x Harvest Time

Seed moisture content and some morphological seed and plant characteristics are common parameters used in identifying the best harvesting time. However, both vary in response to environmental changes so caution is needed to avoid serious mistakes in the timing of harvest. Seeds are typically harvested at moisture contents from 15% to 22%, but maize ears are usually harvested at 30%-35% moisture content.

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(61) Conclusion

A knowledge of seed formation and maturation is useful to establish a basis for efficient procedures during different phases of seed production and processing such as:

- Determination of the best sowing time according to the environment at different plant developmental stages. This also influences the efficiency of harvesting and determination of optimum yield.
- Identification of symptoms of seed weakness and injuries that assist in their diagnosis and problem solving.
- Establish optimum processes for pollination, seed production and maintenance of genetic purity.
- Development and improvement of seed quality tests
- Somatic embryos and artificial seed technologies are also dependent on a knowledge of seed development and maturation.