
**DEVELOPMENT, DORMANCY AND GERMINATION OF SEEDS METABOLISM,
HORMONAL CONTROL AND GENETIC CONTROL**

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ABSTRACT

The seed is an important stage in the life cycle of higher plants, thus ensuring its survival. It is the plant's dispersal unit, which is able to survive the period between seed maturation and the establishment of the next generation as a seedling after germination. For this survival, the seed is mainly in a dry state, and well equipped to withstand long periods of adverse conditions. To optimize germination, the seed goes into a dormant state. Dormancy prevents germination before harvest. This seed dormancy allows the seeds to overcome unfavorable periods for seedlings. Several processes are known to be involved in the induction of dormancy and in the transition from dormant to germinal state. Many studies have been done to better understand how germination is controlled by various endogenous and exogenous factors. Thus, the biochemical and physiological factors linked to dormancy and the germination process as well as the role of phytohormones and genes involved in different tissues are described and discussed in this article.

Keywords: Seed, Development, Dormancy, Physiology, Germination, Chemical composition, Mobilization of reserves, Phytohormones, Genes.

1. INTRODUCTION

When seeds are brought to the soil surface and exposed to sunlight and sufficient moisture, changes in dormancy states and the germination requirements of non-dormant seeds interact to control the timing of germination. Dormant seeds that reach the soil surface must be extra-mature before they can germinate. If the seeds are non-dormant or conditionally dormant, the temperature should be within the range required for germination; otherwise, germination will be delayed. After germination, the growth of the future plant depends largely on the cell divisions that occur in the root and stem meristems within the embryo of the mature plant. Activation of the embryo root meristem is necessary for the initiation of root growth and is a key element in the establishment of a seedling (Nieuwland et al., 2016).

Activation of the mitotic cell cycle has been shown to occur in the shoot and root meristems during the final stages of seed germination and to be dependent on gibberellic acid (GA). Thus, many studies have identified crucial roles for GA and abscisic acid (ABA) during seed germination. The application of exogenous ABA inhibits germination, so mutants of *Arabidopsis thaliana* (*Arabidopsis*) deficient in ABA biosynthesis or signaling have increased germination efficiency. Mutants deficient in AG show delayed or no seed germination (Wang et al., 2016).

In addition, other hormones, such as ethylene, brassinosteroids, cytokinins and auxins, also influence germination (Rajjou et al., 2012). Besides phytohormones, other germination stimulants are known. Among them, compounds containing nitrogen (NO: Nitrogen monoxide; NO₂-: Nitrogen dioxide; NO₃-: Nitrate), which stimulate germination, as well as reactive oxygen

species (ROS) which exert germination control, most likely with NO, in order to regulate ABA catabolism and GA biosynthesis during seed imbibition.

In this study, events occurring during seed development, dormancy and germination will be detailed at the cellular and molecular levels.

2. DEVELOPMENT, ANATOMY AND MORPHOLOGY OF THE SEED

Spermatophytes, seed-producing plants that carry the embryo, are made up of gymnosperms and angiosperms. The seeds could be produced sexually, resulting in genetic diversity and, asexually, resulting in genetic uniformity. The sexually produced seeds result from fertilization and the developing embryo will be surrounded by a supply of food and a protective covering (Black et al.,

2006). Asexual reproduction is probably important for the establishment of colonizing plants in new areas.

In addition, their development can be divided into three stages:

1st phase: phase of formation of the various tissues within the embryo and surrounding structures (histodifferentiation, characterized by extensive cell divisions);

2nd phase: phase of predominant cell enlargement and expansion (weak cell division, increase in dry weight due to the deposition of reserves, decrease in water content);

3rd phase: during this phase the accumulation of dry matter slows down and stops at physiological maturity (Black et al., 2006). In many species physiological maturity is followed by drying as the seed loses water up to 7–15% moisture and becomes tolerant to desiccation (orthodox seeds) and therefore able to withstand environmental conditions unfavorable. At this stage, a seed is at rest (expressing low metabolic activity). In contrast, some species produce recalcitrant seeds which do not undergo drying during ripening and are sensitive to desiccation during excretion. These seeds quickly lose their viability when the water is removed by drying and are therefore difficult to store.

2.1 Seed development

A seed is defined as an embryo, which is an immature diploid sporophyte developing from a zygote, surrounded by nutritious tissue and enveloped by an integument. The embryo generally consists of an immature root called the radicle, an apical meristem called the epicotyl, and one or more young leaves called the cotyledons; the transition region between the root and the stem is called the hypocotyl. An immature, unfertilized seed is known as an ovum where the female gametophyte (embryo sac, megagametophyte) is located inside the pistil. It is surrounded by one or two integuments and the nucellus (megasporangium) (Black et al., 2006; Frohlich and Chase, 2007).

An ovum is therefore, in the developmental sense, an unfertilized immature seed precursor (Gasser et al., 1998) and, in a morphological and evolutionary sense, a mega-porporium surrounded by integuments. These integuments develop into the testa (seed coat), the outer cell layer of the outer seed coat of which usually forms a dead cover layer in mature seeds, while the inner cell layer (s) may remain alive (Windsor et al. , 2000; Haughna and Chaudhuryb, 2005).

In the nucellus, a megaspore develops into a haploid megagametophyte (female gametophyte). The megagametophytes of gymnosperms and angiosperms differ considerably (Floyd and Friedman, 2000; Baroux et al., 2002). The megagametophyte of mature gymnosperms is multicellular.

In most angiosperm species, the mature megagametophyte, also called the embryo sac, is seven-celled and eight-nucleated, referred to as Polygonum type (Berger et al., 2008; Friedman and Ryderson, 2009).

Less commonly, the mature megagametophyte is made up of four cells and four nuclei, called the Nupha/Schisandra type, which is found in basal angiosperms, namely

Nymphaeales and Austrobaileyales. It is believed to be the ancient type of embryo sac (Friedman & Ryderson, 2009).

A typical mature embryo is differentiated and has a developing polarity divided into radicle (embryonic root) and growing together with the cotyledon (s) (embryonic leaves). Gymnosperms have bare seeds; their seeds are not surrounded by an ovary and are usually found bare on the scales of a cone.

In a typical mature gymnosperm seed, the embryo is covered by two layers: the maternal haploid megagametophyte containing stored nutrients and the diploid tissue that develops in the testa. Unlike gymnosperms, angiosperm ova and seeds are covered; they are locked inside the ovary.

The ovary is the base of a modified leaf (carpel) or the fusion of several carpels into a pistil. A mature ovary contains one or more mature seeds and is called a fruit. A pericarp (husk of the fruit) develops from the wall of the ovary and may contain other parts of the flower. Seeds and fruits can be the dispersal units of angiosperms.

2.2 Pollination and fertilization (Double fertilization)

The reproduction of angiosperms is characterized by double fertilization; That is, in addition to the fertilization of the oocytes, a second fertilization event occurs in which the central cell nucleus of the megagametophyte is targeted by a second nucleus of the sperm (Friedman and Ryderson, 2009). This leads to the formation of the endosperm. Since the central cell of most angiosperm species has either one nucleus (Nuphar Schisandra type) or two nuclei (Polygonum type), the endosperm thus fertilized is diploid or triploid. The endosperm grows much faster than the embryo, initially due to an enlargement of cells associated with endopolyploidy (nuclear divisions without cytokinesis). Thus, the seed growth rate decreases in angiosperms at this stage (Sundaresan, 2005).

In angiosperms (Figure 1), the embryo sac is formed when a single diploid (2n) cell (megasporocyte) of the nucellus undergoes meiosis resulting in the production of four haploid megaspores. Thus, after pollination, the megasporocyte develops into the megasporangium of the ovum. The megasporocyte is a single cell that undergoes meiosis, producing a tetrad of four haploid megaspores, which in most extant seed plants are arranged in a straight line or linearly (Yadegari and Drews, 2004).

The three distal megaspores (far from the base of the ovum) abort; only the proximal megaspore (near the base of the ovum (Figure 2.1) continues to develop and undergoes mitosis three times, to produce an eight-nucleus haploid megaspore (Yadegari and Drews, 2004). cell walls form around these, resulting in a cellularized female gametophyte. During cellularization, two nuclei (one from each pole) migrate to the center of the embryo sac and fuse to form a central diploid cell. At pollination, the resorbed pollen grains transform into mature male gametophytes and form pollen tubes, which develop in the tissues of the megasporangium (Yadegari and Drews, 2004). Three cells that migrate to the micropylar end of the embryo sac become 1 egg apparatus with an ovum (the female gamete) in the center flanked by two synergids, and the other three are located at the opposite end (chalazal), forming cells. Male gametes (spermatozooids) are produced as pollen grains in the pollen sacs of the anthers (microsporangia). A mature pollen grain contains a large vegetative haploid cell (tube) and a smaller generative haploid cell that divides mitotically and produces two sperm (Figure 2.2) (Yadegari and Drews, 2004).

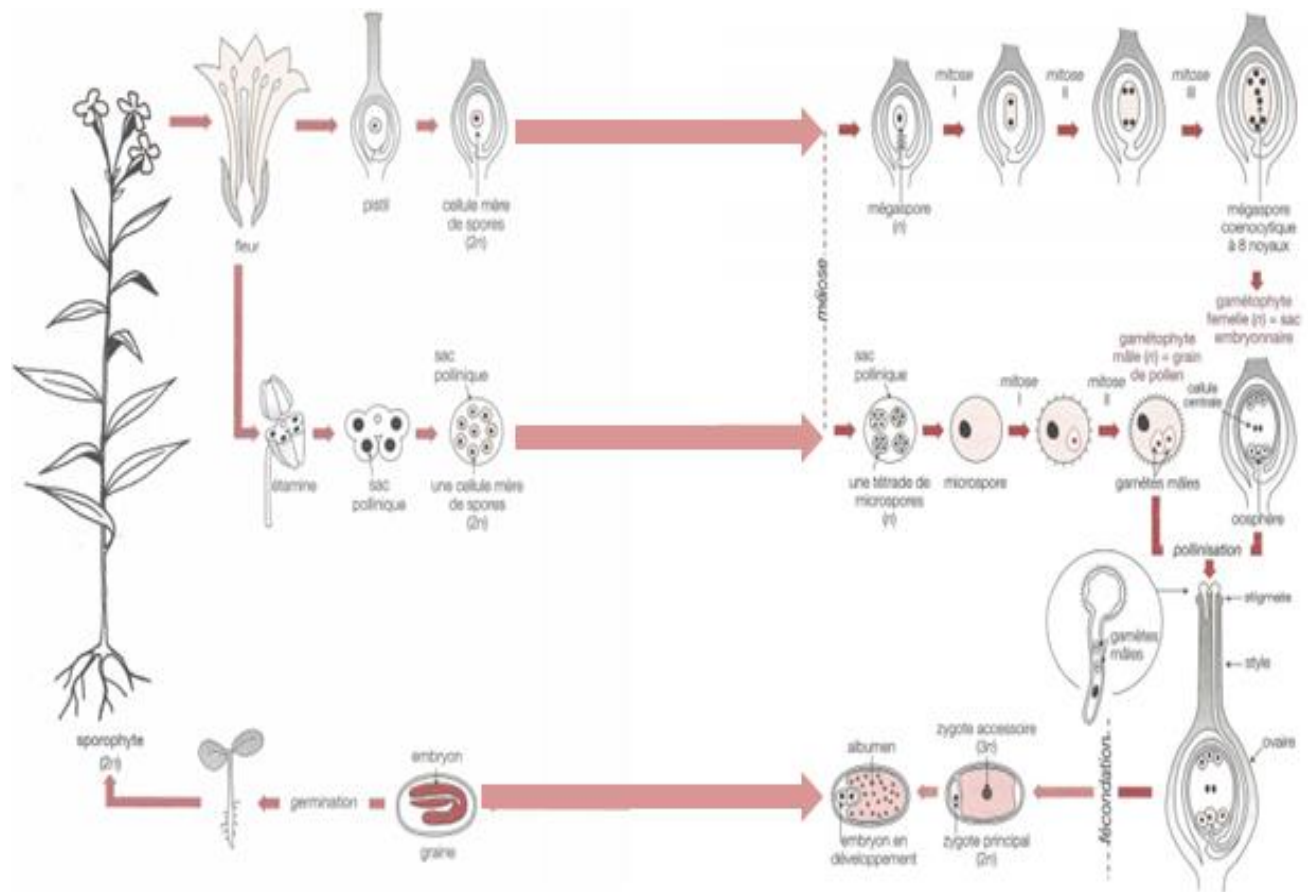


Figure 1. Development cycle of angiosperms (Kleiman, 2001).

Ripe seeds are the end point of seed development: two sperm are delivered through the pollen tube after reaching the female gametophyte in the mature egg. One sperm fuses with a haploid egg, while another fuses with a central diploid cell, forming the diploid zygote and the triploid endosperm, respectively. These events trigger seed development, where the zygote and endosperm develop in parallel to eventually produce mature seed. When complete, the mature dry seed consists of an outer layer of dead tissue, the testa, which is the remnant of the maternal egg seed coat that has collapsed during the seed's ripening phase. Below the testa is the endosperm, which remains as a unicellular layer surrounding the embryo (Baud et al., 2002).

The mature seed is a very resistant entity capable of withstanding long periods in the dry state until the conditions for germination are in place. The seeds transform plants into space-time travelers, which arguably explains the success of angiosperms among terrestrial plants in colonizing many habitats.

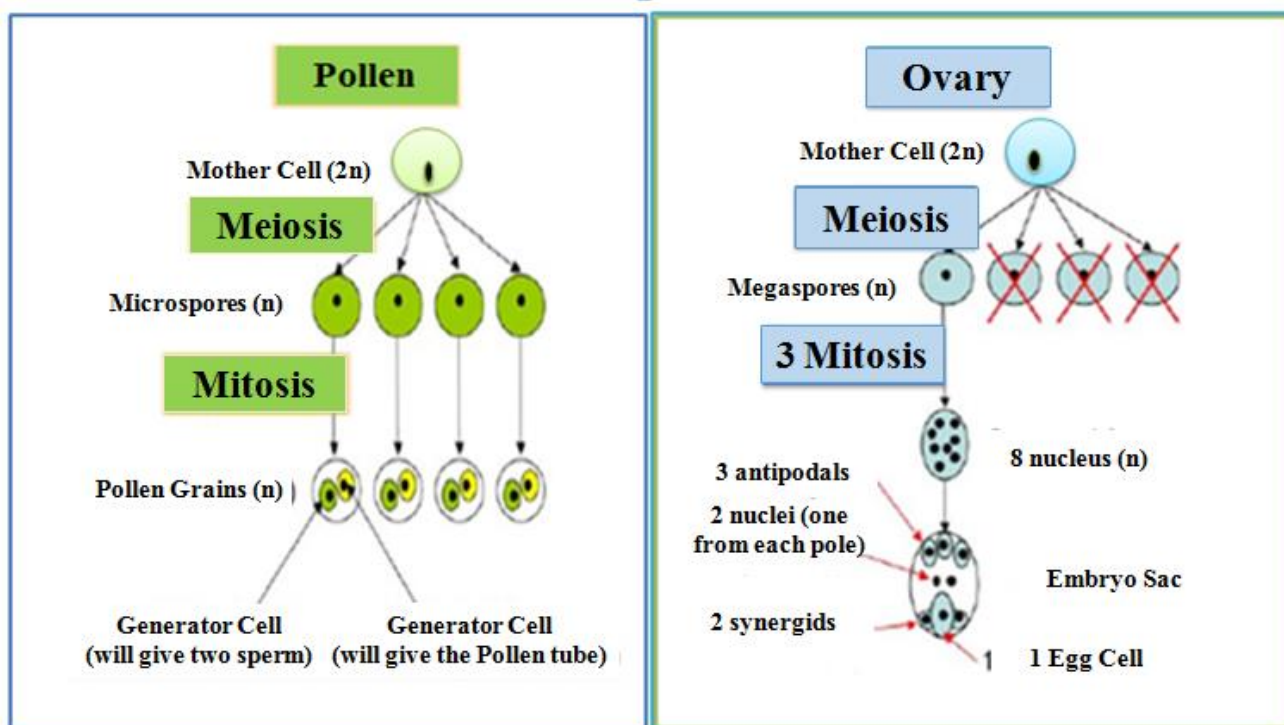


Figure 2.1. Fertilization in angiosperms.

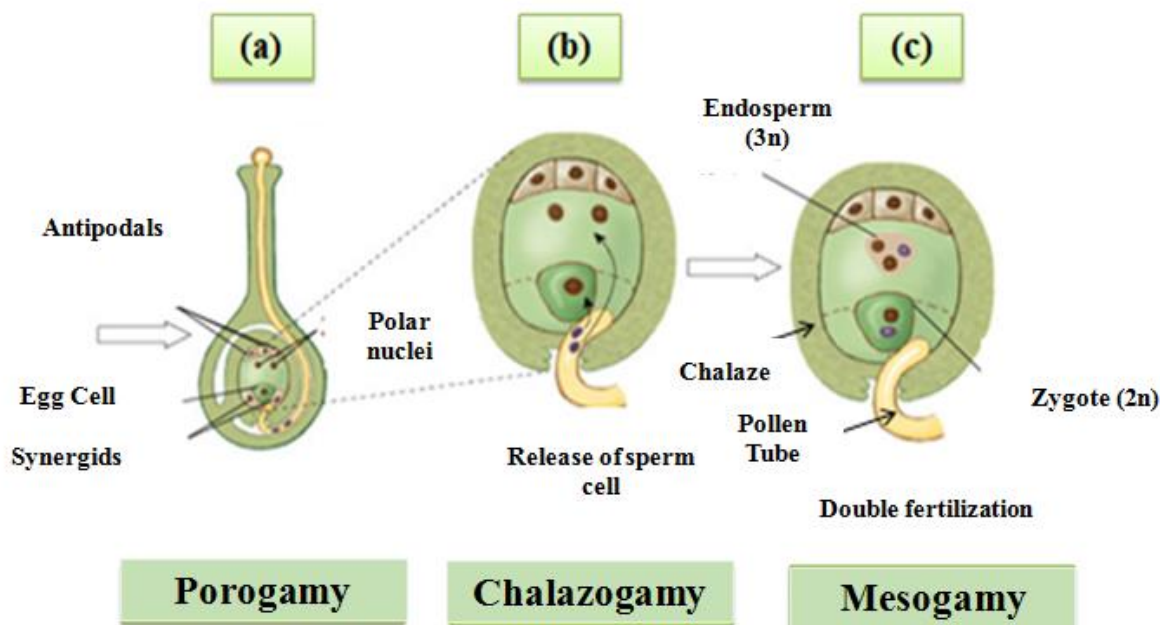


Figure 2.2. Double fertilization in an angiosperm egg. (a) Disposition of cells in the mature embryo sac and penetration of the pollen tube into the micropyle, with the release of two spermatozoa to effect double fertilization. (b) Sperm are released from the pollen tube into a degenerate synergistic cell surrounding the egg and (c) they migrate to the egg and central cell.

Pollination involves the transfer of pollen grains to the stigma, the receiving surface of the pistil, followed by the growth of a pollen tube through the style to the egg. Pollination can take place in the same plant (self-pollination, self-pollination) or the pollen can be delivered by a different plant (cross-pollination, allogamy).

Autogamy leads to the production of offspring that are faithful to nature; this is disadvantageous when the autonomous offspring possess recessive traits, but it may be advantageous for reproduction under unfavorable environmental conditions (Darwin, 1876). In addition, outcrossing can introduce traits that increase resistance to disease and predation, as well as seed and fruit yield.

To prevent self-pollination and promote the creation of genetic diversity, plants often exhibit self-incompatibility, causing pollen to be rejected from the same flower or plant.

Although pollination can be carried out by wind, water, or insects (sometimes by animals such as bats or birds), the majority (over 70% of angiosperms) depend on insects for cross-pollination. (Faheem et al., 2004). The effectiveness of pollinators depends on the characteristics of the flower such as color, smell, shape, size and production of nectar and pollen.

Wind pollination likely resulted from insect pollination in response to pollinator limitation and changes in the abiotic environment, especially in families consisting of small single flowers and dry pollen (Culley et al. , 2002).

When pollen comes in contact with the stigma, it adheres, hydrates and germinates, developing a pollen tube. The two immobile sperm are transported by the growth of the end of the tube into the embryo sac (Lord and Russell, 2002).

2.2.1 Development of the embryo and associated processes

Seed development consists of two main phases: embryo development and seed maturation. Embryogenesis is a phase that begins with the formation of a single cell zygote and ends at a stage when all the structures of the embryo have been formed (Mayer et al., 1991). This is followed by a growth phase during which the embryo fills the seed sac (Goldberg et al., 1994). At the end of the growth phase of the embryo, cell division occurs in arrests of the embryos (Raz et al., 2001). Subsequently, the seed, containing an embryo, undergoes maturation during which food reserves accumulate and thus develops tolerance to dormancy and desiccation (Goldberg et al., 1994).

During embryogenesis (Figure 3), the central part of the megagametophyte breaks down to form a cavity in which the embryo expands (Bewley and Black, 1994). The developmental time of the embryo varies between species and can range from a few days to several months or even years. It is also influenced by the prevailing environmental conditions. Early embryonic development includes the acquisition of apico-basal polarity, epidermal differentiation, and the formation of a shoot and root meristem (Dumas and Rogowsky, 2008). Polarity is established after the first division of the zygote. The polarity is generally perpendicular to the axis of the embryo and asymmetric; a basal and apical cell is created.

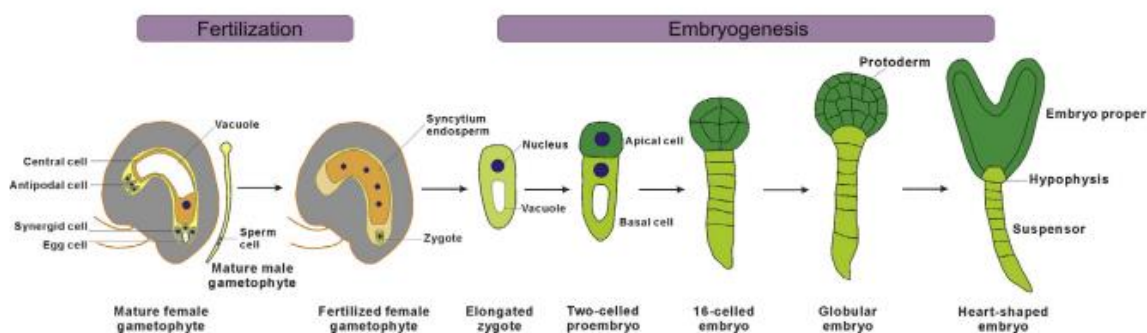


Figure 3. The embryonic development of a Dicotyledon from a fertilized egg (Zhao and Sun, 2015).

During development, the embryo progresses through the globular, heart and torpedo stages to maturity. During the transition from the red blood cell stage to the heart stage, the structure and number of cotyledons are established. The mature embryo consists of two cotyledons borne on a hypocotyl, the collar (hypocotyl-radicle transition zone) and the radicle; desiccation of the

seeds then occurs. In Poaceae (monocot), after the first division of the zygote, the basal cell does not divide but forms the terminal cell of the suspensor (Friedman and Ryderson, 2009). The other few suspensive cells and the embryo are produced from the axial cell. After further divisions, a globular shaped embryo is formed. It elongates club-shaped with radial symmetry and then becomes symmetrical on both sides by the differentiation of the absorbent scutellum and the coleoptile, which covers the first leaf of the foliage. During the coleoptile stage of development, the embryo axis and the suspensor are established. Later, at the leaf stage, the stem and root meristems are defined and the leaf primordia differentiate (Frohlich and Chase, 2007).

The embryonic cells stop dividing during maturation, the embryo dries up and becomes inactive. Mature grass embryos also contain a specialized thin tissue, coleorhiza, which covers the radicle (Haughna and Chaudhuryb, 2005; Gasser et al., 1998).

Species that mature at the end of seed development and remain viable in the dry state are called orthodox, but in some their seeds are unable to survive low moisture content and are called recalcitrant. Some of its mangroves show an extreme, for example: *Avicennia* spp. In which there is no maturation drying and the growth of the embryo continues from development to germination and early growth of seedlings while remaining on the mother plant (Black et al., 2006).

2.2.2 Development of the endosperm

The development of the endosperm is essential for the proper development of the embryo and for producing a viable seed. It usually precedes the development of the embryo; an interval between the first division of the endosperm nucleus and the embryo usually takes several hours, but it can be extended even to a few months (eg in *Colchicum*). Sometimes divisions in both the embryo and endosperm occur simultaneously (eg, some aquatic species) or zygotic division precedes division of the endosperm nucleus.

After fertilization of the central cell, the endosperm undergoes cell-like, nuclear or mixed-type development (Dumas and Rogowsky, 2008).

In cell development, the formation of the cell wall follows nuclear divisions. In nuclear development, which is the most common pattern in angiosperms, the nucleus of the endosperm repeatedly divides without cytokinesis or cell wall formation. This results in the formation of a single giant cell with a central vacuole surrounded by nuclei (coenocytic or syncytial endosperm).

Cellularization begins in the micropylar endosperm at final mitosis, progressing as a wave passing through the peripheral and chalazal endosperm (the region near the chalazal endosperm may not become fully cellular, for example in *Arabidopsis*). At this stage, the embryo is usually in the heart stage.

The fully developed endosperm consists of four main cell types: (i) those containing starch (starchy endosperm); (ii) cells of the aleuron layer; (iii) transfer cells; and (iv) those in the region surrounding the embryo (Black et al., 2006).

During seed filling, the starchy endosperm expands rapidly, is filled with starch granules, studded with protein storage vacuoles. When stores are synthesized, water is displaced from this region of the endosperm and cells undergo PCD. In contrast, cells in the aleuron layer (arranged in one to several layers immediately below the pericarp) do not store starch and retain their viability after ripening drying.

These cells can contain anthocyanins responsible for the color of the seeds. Transfer cells, which develop in the basal endosperm on the main vascular tissue of the parent plant, are responsible for the transfer of amino acids and sugars to the endosperm and the embryo from the conductive tissue when filling seed.

Cells early in the development of the endosperm line the cavity in which the embryo develops; they probably play a role in the transfer of nutrients to the embryo and / or in the creation of a physical barrier between the embryo and the endosperm. Unlike the endosperm found in grasses, the endosperm of many dicot species is ephemeral and is not a major component of mature (non-endospermic) seed (Black et al. 2006).

In seeds with a persistent endosperm, the cells usually live to maturity. In some species there is an endosperm which can be very hard when ripe; this is the case of certain legumes (carob (*Ceratonia siliqua*), Chinese senna (*Cassia tora*)), date (*Phoenix dactylifera*), coffee (*Coffea* spp.), nut palm (*Phytelephas macrocarpa*) and asparagus (*Asparagus officinalis*). This is due to the synthesis of (galacto) mannans deposited as thickened secondary cell walls that obstruct much of the interior of the cell, although some cytoplasm remains. In fenugreek (*Trigonella foenum graecum*), however, the cytoplasm is completely occluded except in a single outer layer of aleuron cells in which there is no thickening of the cell wall.

2.3 Morphology of ripe seeds

2.3.1 Embryo

The embryo of mature angiosperms consists of an embryonic axis with a single cotyledon (monocots) or a pair of cotyledons (dicots) (Black et al., 2006). The embryonic axis carries the radicle, hypocotyl, epicotyl and plumule. The radicle contains the root meristem and when germination is complete gives rise to the embryonic root. It is usually adjacent to the micropyle. The hypocotyl is a rod-shaped region of the axis bounded by the radicle at the basal end and by the cotyledon (s) at the proximal end; the epicotyl is the first growth segment above the cotyledons. Cotyledons may be well developed and serve as storage organs (non-endospermic seeds) for reserves, or thin and flattened (endospermic seeds) (Figure 4) (Bewley and Black, 1994).

2.3.2 Endosperm

The endosperm can have radial or anteroposterior (micropyle to chalaza) symmetry (Berger, 2003), as in most angiosperms. Radial symmetry distinguishes the outer layers of aleuron and sub-aleurone from the inner mass of the starchy endosperm. Along the AP axis, three regions are organized: (i) the micropylar endosperm (*Arabidopsis*) or the region surrounding the embryo (maize (*Zea mays*)); (ii) the greater central part of the endosperm; and (iii) the posterior transfer layer of chalazal (*Arabidopsis*) or endosperm (maize).

The micropylar endosperm (endosperm cap) encloses the tip of the radicle (Figure 4) which, in some species, slows down radicle emergence and imposes dormancy (for example, ferocious spruce (*Datura ferox*)) (Black et al., 2006). In some other species, such as Chinese senna or fenugreek, the micropylar endosperm has only a thin, unrestricted wall; on the contrary, they have much thicker cells in the lateral endosperm, surrounding the cotyledons (Gong et al., 2005).

The relative size of the endosperm varies considerably at maturity, depending on the amount of reserves transferred to the embryo during seed development (Black et al., 2006). In seeds with a peripheral embryo, the endosperm is abundant and loaded with starch, while starch is not the predominant reserve when the embryo is axial (except in some monocots) (Martin, 1946).

The fate of the chalazal and micropylar domains in development varies among endosperms of all basal angiosperm taxa and suggests that this may be a feature of its development in all angiosperms (Floyd and Friedman, 2000). Endosperm-embryo interactions and signaling are suggested by the fact that the bipolar pattern of endosperm development of most angiosperms is shared with the bipolar pattern of embryos.

For example, in all Nymphaeales (Nymphaeaceae, Cabomaceae, Hydatellaceae), the micropylar endosperm undergoes division and cellularizes, while the chalazal domain remains undivided and acts as a haustorium, sometimes extending to the perisperm (Floyd et al. Friedman, 2000; Rudall et al., 2008, 2009).

The Brassicaceae, *A. thaliana* and *Lepidium virginicum* are other examples of the development of the bipolar endosperm, in which a multinucleated "chalazal" region is formed, and at the same time, when the rest of the endosperm, including the micropylar domain, is dimensioned, this chalazal region remains multinucleated (Nguyen et al., 2000; Olsen, 2004).

The radicle is embedded in the micropylar domain of the endosperm (Figure 4), while the tip of the cotyledons is located in the chalazal endosperm domain of these Brassicaceae. Floyd and Friedman (2000) examined in detail the evolution of endosperm development patterns in basal flowering plants and the endosperm development of other angiosperms is summarized by Baroux et al. (2002). The genera *Arabidopsis* and *Lepidium* have been shown to be particularly well suited to interspecies work on seeds and fruits of the Brassicaceae family (Mummenhoff et al., 2009).

Regardless of its origin, contemporary endosperm tissues serve not only as a source of nutrients for the embryo during seed development, but also as an integrator of seed growth and development, which includes signaling reciprocal between seed compartments and parental effects caused by imprinting (Otho et al., 2009; Springer, 2009). Depending on the species, the endosperm is partially or totally shed when the seed matures. However, most angiosperm species retained an endosperm layer in their mature seeds (Floyd and Friedman, 2000).

In many cases, this endosperm in the mature seed also participates in the control of germination by constituting a barrier for the growing radicle. During germination, the micropylar endosperm weakens, allowing the radicle to protrude from surrounding tissue. The hypothesis that the

weakening of the seed cover layers is obtained by enzymatic action was first proposed by Ikuma and Thimann (1963).

The weakening of the endosperm was initially demonstrated for seeds of asteroid species with a thick layer of endosperm (tomato, tobacco, coffee) or a thin layer of endosperm (eg, lettuce; Ni and Bradford, 1993; Toorop et al., 2000).

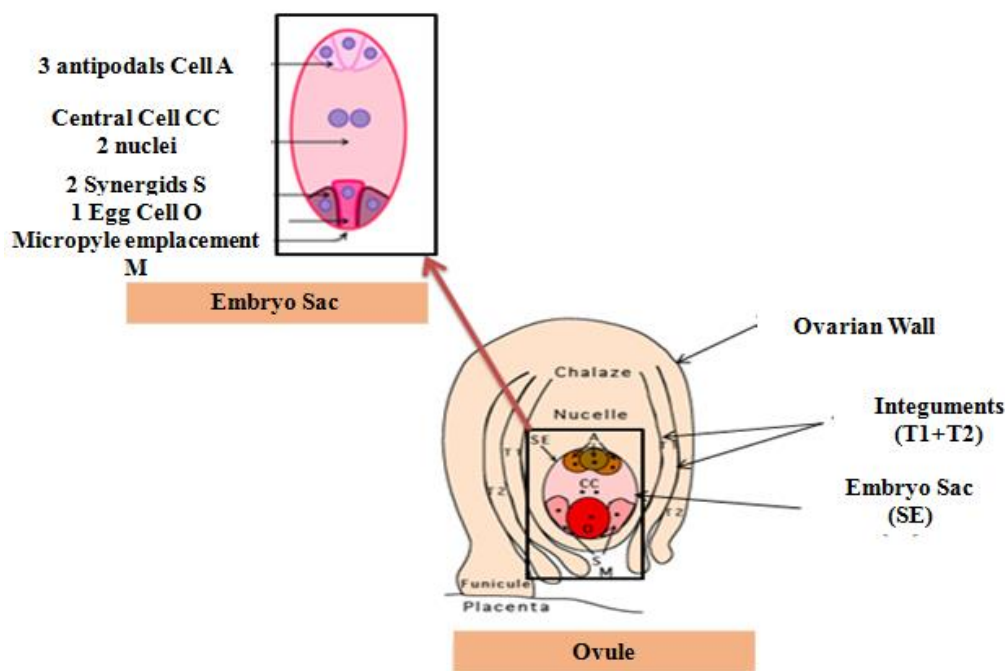
More recent work has shown that the weakening of the endosperm also occurs in the seeds of dew species. Brassicaceae *Lepidium sativum* and *A. thaliana* have a thin endosperm layer and the weakening of the micropylar endosperm has been quantified biomechanically during germination of *L. sativum* (Müller et al., 2006; Linkies et al., 2009).

2.3.3 Perisperm

In some species, the nucellar region of the egg gives rise to a storage tissue called the perisperm (Figure 4). It is generally present in mature seeds with the endosperm, in varying proportions, locations and forms (Black et al. 2006). A perisperm is present in some monocots (eg Zingiberaceae) as well as some dicotyledons (eg Piperaceae, Nymphaeaceae, Cactaceae, Amaranthaceae, Chenopodiaceae). In a few species it is the main source of storage reserves, the endosperm being absent (eg, Quinoa and *Yucca* spp.) (Bewley and Black, 1994).

2.3.4 The seed coat

The seed coat (testa) is maternal tissue that surrounds the embryo (Figure 4), endosperm, and perisperm (if present). It protects internal structures against stress



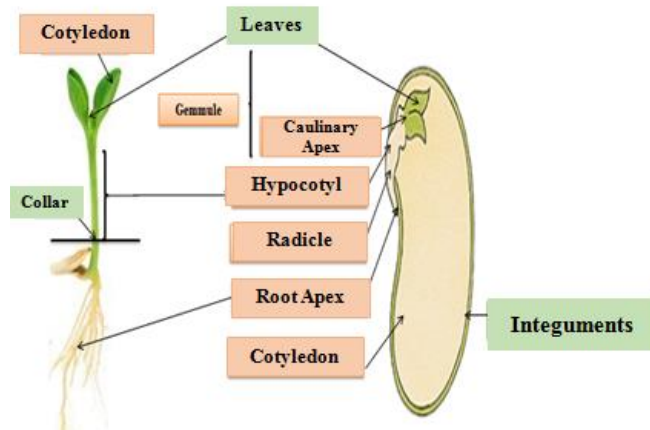
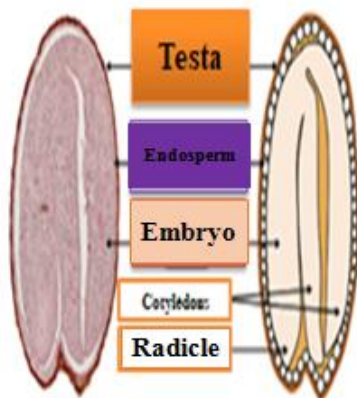
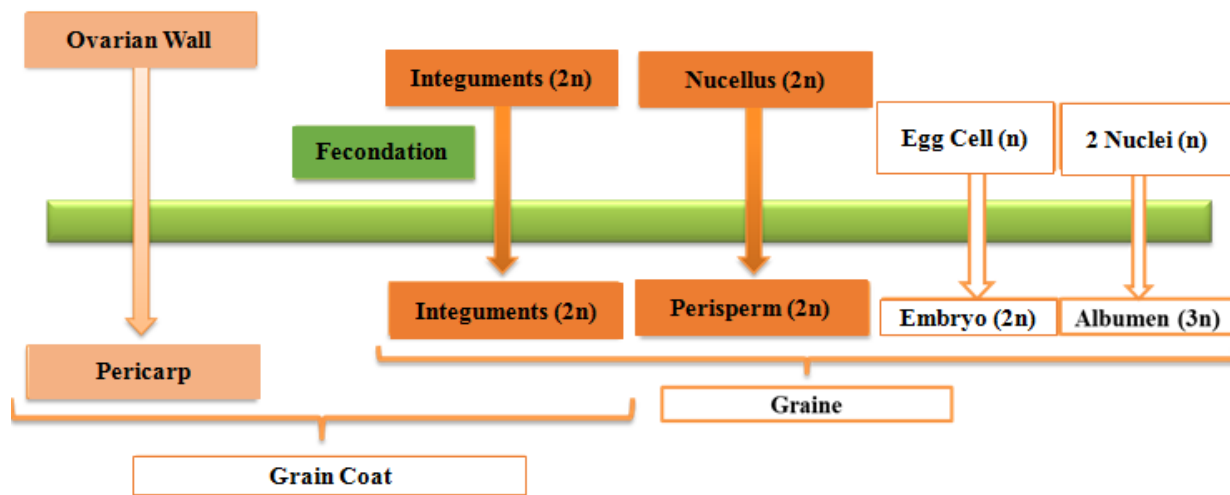


Figure 4. The different structures of the seed during the passage from an unfertilized ovum to a young planting (a) Structure of an ovum before fertilization (b) Fate of the different structures of a seed of a dicotyledon after fertilization (c) Structure of a mature seed of a dicotyledon (Chahtane et al., 2016) (d) Young seedling after germination.

3. Physiology of dormancy

Seed dormancy has been defined as the inability of a viable seed to germinate under favorable conditions (Bewley, 1997).

Seed dormancy can improve seedling survival by preventing germination under unfavorable or mayfly conditions (Bewley, 1997). It is an essential regulator of the seasonal timing of

germination by providing a temporal context for the perception of environmental cues, so that a signal perceived soon after its dispersal, when seeds are dormant, will not have the effect. same effect on the probability of germination as the signals perceived from time to time. After dispersal, when the seeds are dormant.

It is well known that factors inducing germination, such as water and permissible germination temperatures, interact with dormancy to regulate the timing of germination under natural conditions (Baskin and Baskin, 1998). How environmentally induced secondary dormancy alters this dynamic, however, is still poorly understood.

Physiologically dormant seeds are lost in the dormant state (Finch-Savage and Leubner-Metzger, 2006; Holdsworth et al., 2008) and dormancy is lost through a 'post-settling' process (Holdsworth et al., 2008). After ripening, germination can occur under a wider range of environmental conditions.

Seed dormancy is crucial for plant survival and ensures that seeds germinate only when environmental conditions are optimal. It is therefore an adaptive trait in many species of seed plants, allowing wild plants to survive under stressful conditions in nature (Finkelstein et al., 2008).

The ecological importance of seed dormancy includes preventing out-of-season germination and therefore reducing competition within species and ensuring the survival of plants under stressful conditions. As a complex and mysterious biological issue, seed dormancy has increasingly gained the attention of multidisciplinary researchers, including plant biologists, plant breeders, breeders and food scientists.

Seed dormancy guarantees seed germination at the right time. Therefore, during maturation, the embryo must be kept in a state of rest, mobilizing virtually no stored nutrients and undergoing no cell division or elongation. In this resting state, genes activated by germination are not actively expressed. Therefore, the radicle does not enter the testa and endosperm. It is now widely recognized that the structure of chromatin determines gene expression and thus regulates multiple developmental processes. In recent years, many genes associated with chromatin remodeling are thought to regulate seed dormancy and germination (Cho et al., 2012; Zheng et al., 2012).

Physical dormancy occurs when surrounding structures delay germination, usually by preventing water absorption or limiting the embryo's oxygen availability. This is due to the presence of one or more layers of sclerified palisade cells in the seed or the fruit mantle, as well as frequently to water repellent compounds, such as cutin, waxes and suberin.

Chemically induced dormancy is believed to be achieved by compounds such as abscisic acid in the mantle which inhibits embryo germination. The shell structure may slow or prevent their leaching upon imbibing until a sufficient volume of water is available to wash them, and be sufficient to support subsequent growth of the seedlings. Phenolic compounds are present in large quantities in the coats of some species, although their role in inhibiting dormancy is

questioned: they could play a more important role in deterring the attack of pathogens (Nonogaki et al., 2010).

Morphological dormancy concerns the loss of seeds in which the embryo is still immature and unable to germinate before the end of its development following imbibition of the dispersed seed.

Although dormancy is established during seed maturation, application of exogenous ABA (or even maternal ABA in the plant during seed development) only inhibits seed germination but does not induce dormancy; only ABA synthesized by the seed can establish dormancy (Kucera et al., 2005). Thus, ABA localized differently in plant tissues has distinct effects on seed dormancy or germination.

Seed dormancy is defined as an intrinsic blockage at the end of germination of a viable seed under conditions favorable to germination (eg temperature, humidity, light) of the corresponding non-standardized seed. Seed dormancy controls the timing of germination according to the seasons and plays an important role in the evolution of seed plants and adaptation to climate change (Baskin and Baskin, 2007). The timing of germination can strongly influence the rate at which species can expand their range and can play an important role in determining survival or extinction during climate change (Donohue, 2005).

Baskin and Baskin (2004) proposed a complete ecophysiological classification system comprising five classes for “whole seed” dormancy: physiological (DP), morphological (DM), morphophysiological (DMP), physical (DPY) and combinatorial (DPY + DP). These different classes and their distribution among angiosperms are also summarized by Finch-Savage and Leubner-Metzger (2006).

Morphological dormancy is evident in seeds with differentiated but very small embryos compared to the size of the whole seed. The embryo to semen ratio (I / O ratio) describes the relative size of the embryo in the seed. A high I / O ratio (e.g. 0.9) means that the embryo occupies most of the seed volume, while a low I / O ratio (e.g. 0.1) means that the embryo is tiny and the nutrient storage tissue (endosperm, perisperm, megagametophyte) occupies most of the seed volume (Forbis et al., 2002; Finch-Savage and Leubner-Metzger, 2006).

Seeds with low I / O ratios often have long germination periods (a month or more) and the presence of abundant megagametophytes (eg cycads, gymnosperms) or perosperms with endosperm (eg, Nuphar, basal angiosperms) is typical of seeds of class DM. Forbis et al. (2002) used ancestral continuous trait state reconstruction methods using I / O family means for 179 families, calculated from a large dataset including 1222 extant angiosperm species.

Their analysis showed that I / O ratios increased in derived angiosperms compared to ancestral angiosperms. They proposed, on the basis of these results, that a small embryo incorporated into an abundant endosperm/perisperm, and therefore classified in DM (and DMP), or the ancestral type of dormancy of angiosperms. This hypothesis is in agreement with the results of Baskin and Baskin (2004). DM simply delays the time of germination until the time the embryo must develop in the seed before germination can take place. Dispersing seeds with a small embryo that

needs time to develop could have become an old strategy for spreading germination times, as successful germination is highly dependent on environmental conditions.

Among angiosperms, seeds containing an abundant perisperm occupying more of the endosperm storage tissue are characteristic of existing and extinct nymphaeales (Nymphaeaceae, Cabomaceae, Hydatellaceae) (Friedman, 2008; Rudall et al., 2009) and Austrobaileyales (Trimeniaceae) (Yamada and Marubashi, 2003; Yamada et al., 2008). The presence of perisperm as the only nutritive tissue in the seed is rare. It is usually present with the endosperm in different proportions, locations and shapes.

Abundant perisperm is not limited to basal angiosperms and is not necessarily associated with DM. Abundant perispermation is typical of most seeds of Caryophyllales, such as sugar beet (non-dormant, Amaranthaceae; Hermann et al., 2007) and cacti (DP, Cactaceae; Stuppy, 2002).

Forbis et al. (2002) stated that the available gymnosperm embryo fossils were roughly the same shapes and sizes as extant gymnosperm embryos from related groups (see references cited in Forbis et al., 2002) and that they do not. There were no fossil gymnosperm seeds having an extremely small or extremely large size. Large I / O ratios. They therefore suggested that an unknown gymnosperm ancestor prior to these fossil specimens probably had a small scattering embryo. As several existing taxa have much larger embryos, they interpreted this to support the hypothesis of an increased I / O ratio in gymnosperms.

Taken together, there appears to be a general trend towards increasing relative embryo size during evolution (higher I / O ratio) for angiosperms and gymnosperms (Forbis et al., 2002; Baskin and Baskin, 2004). On this basis, Forbis et al. (2002) proposed that morphological dormancy is the ancestral type of dormancy among gymnosperms and angiosperms. This is consistent with the conclusion reached by Baskin and Baskin (1998, 2004). The evolution of the size of the larger embryos has probably resulted in the appearance of non-dormant seeds; the embryo does not need to develop before germination.

It is believed that an increase in the relative size of embryos is one of the main determinants (or requirements) of the evolution of other seed dormancy classes (Finch-Savage and Leubner-Metzger, 2006). Central eudicots tend to have less endosperm than more extant basal angiosperm species. At the same time, physiological dormancy has developed, thought to be linked to adaptation to seasonal climate change, as its release requires the seeds to perceive one or more specific environmental triggers. DMP is the most abundant type of dormancy and is found in seeds of all major clades of gymnosperms and angiosperms (Baskin and Baskin, 2004; Finch-Savage and Leubner-Metzger, 2006). The PD can be divided into different types; the most common form in angiosperms and gymnosperms is undiagnosed DMP. Embryos excised from seeds without PD will germinate normally and treatment with gibberellins (GA) breaks dormancy.

In addition, depending on the species, dormancy can be broken by scarification (abrasion or cutting of the coating layers), after maturation (period of dry storage) and by cold or hot stratification. Unbound DMP has been shown to be determined by physiological factors in both the embryo and the covering layers (broad 'integument') (Nonogaki, 2006; Bentsink and

Koornneef, 2008; Holdsworth et al., 2008) Layer dormancy is mediated by any of the cover layers (endosperm and testa (s)). Embryos excised from dormant seeds grow and develop easily.

Abscisic acid (ABA) is an important positive regulator of coat-related Parkinson's disease in the seeds of gymnosperms and angiosperms (Kucera et al., 2005). This suggests that gymnosperms and angiosperms share the same ABA-related molecular mechanisms that regulate dormancy and germination, and that ABA dependence is a plesiomorphic trait of angiosperms and gymnosperms.

The ABA-related transcription factor ABI/VP1 (ABA INSENSITIVE3 VIVIPAROUS1) is widespread among green plants and participates in the regulation of dormancy in seeds and buds of angiosperms and gymnosperms (Holdsworth et al., 2008). On the other hand, DOG1 (Delay Of Germination 1), a gene with a major quantitative trait more specifically involved in the dormancy and the time of seed germination, is only known to date in Brassicaceae and its relationship with ABA. is currently the subject of research (Bentsink et al., 2010).

Physiologically dormant and non-dormant seeds are distributed throughout the phylogenetic tree of gymnosperms, basal angiosperms and eudicots (Finch-Savage and Leubner-Metzger, 2006). Therefore, it has been suggested that the gain and loss of PD probably occurred multiple times during evolution (Baskin and Baskin, 1998; Finch-Savage and Leubner-Metzger, 2006). The course of Parkinson's disease also led to the appearance of MPD in seeds with a small embryo, which when it grew in embryo size and the concomitant loss of DM gave rise to seeds of PD (Finch-Savage and Leubner-Metzger, 2006). The most phylogenetically limited dormancy classes are PY and a combination of DPY and DP (Baskin and Baskin, 1998, 2004; Finch-Savage and Leubner-Metzger, 2006). DPY is characterized by impermeability of the seed or the fruit mantle to water. It is believed to be an adaptation of the plant to specialized living habitats (Baskin and Baskin, 2004). LaD PY is not found in gymnosperms, but only in seeds of angiosperms, indicating that this is a more derived form of dormancy.

3.1 Primary seed dormancy

Primary seed dormancy is an important adaptive trait of the plant that blocks seed germination under conditions that would otherwise be favorable for germination. This trait is found in newly produced mature seeds of many species, but not all.

Seed dormancy is a general phenomenon in plants, of which primary dormancy is a special case. Seed dormancy can be broadly defined as the blocking of germination of a viable seed under favorable germination conditions.

A non-dormant seed is a seed capable of germinating under all possible environmental conditions and normally compatible with seed germination for a given plant species.

Dormancy release is a term used to describe a dormant seed that has lost its dormancy.

Primary seed dormancy is the dormancy that develops during seed development in the parent plant (Finch-Savage and Leubner-Metzger, 2006).

The depth levels notably describe the growth behavior of the embryo excised from the dormant seed (Baskin and Baskin, 2004; Finch-Savage and Leubner-Metzger, 2006).

Sucrose transporters in the ovular integuments and endosperm are important for providing maternal nutrients to the embryo (Baud et al., 2005; Chen et al., 2014). The expression of

AtSUC5, encoding a sucrose transporter, is strongly induced early in seed development, specifically in the endosperm (Baud et al., 2005). Seeds of *atsuc5* mutants exhibit low levels of fatty acids and delayed embryonic development, suggesting that nutrient delivery via AtSUC5 is crucial for normal embryonic development.

A recent report provided direct evidence that maternal sucrose is deposited in developing seeds via the funicular phloem via specific SWEET transporters localized in the seed coat and endosperm (Chen et al., 2014). This is because *sweet11 / sweet12 / sweet15* triple mutant seeds have a low lipid content and show a high accumulation of starch in the seed coat, while starch levels in the embryo are low.

This indicated the presence of abnormal sugar efflux transport from maternal ovular tissues to the embryo via the endosperm (Chen et al., 2014). Taken together, these recent reports suggest that the endosperm may also serve as a food transmission tissue during Arabidopsis seed development. In mature seed, the endosperm plays a central role during seed imbibition to prevent germination of dormant primary seeds.

During the maturation phase, embryonic cells develop by accumulating high levels of lipids and storage proteins.

Fat and protein will make up up to 70% of the dry weight of mature seed and will support future germination and seedling establishment (Baud et al. 2002; Penfield et al. 2004). The endosperm and the embryo contain abundant reserves of nutrients, although most of them are stored in the embryo. In the later stages of seed maturation, metabolism decreases as the seed dries and acquires tolerance to desiccation, which involves a build-up of late embryonic abundance proteins conferring osmotolerance (Dekkers et al., 2015).

The mature seed is a very resistant entity capable of withstanding long periods in the dry state until the conditions for germination are in place. The seeds transform plants into space-time travelers, which arguably explains the success of angiosperms among terrestrial plants in colonizing many habitats.

The dormancy of primary seeds is a primary property of freshly produced seeds. The trait is functionally defined. A germination test is necessary to determine whether a mature, dry seed is in primary dormancy or not. Primary dormancy is released during the post-dry period, when seeds gradually acquire the ability to germinate when exposed to favorable germination conditions and therefore become non-dormant (Holdsworth et al., 2008). An unfavorable germination condition is one that invariably prevents germination of the seed, regardless of the age of the seed, without killing the embryo in the seed.

Germination conditions unfavorable to seed germination therefore cannot be used to assess primary dormancy.

Examples of unfavorable seed germination conditions include imbibing seeds in the dark, followed by a far red pulse (RF), imbibing at high temperatures and high salinity conditions.

Primary seed dormancy is established during maturation.

Indeed, Karssen et al. (1983) showed that seeds isolated at mid-ripening from developing fruits germinated, but not when isolated at later stages of ripening. Similar observations have been reported by Alboresi et al. (2005).

Primary dormancy, hereinafter called dormancy, can be illustrated by a population of *Arabidopsis* seeds collected immediately at the end of their maturation. This initial population is divided into subpopulations, which will experience increasing amounts of dry weather after maturation (Holdsworth et al. 2008).

A subpopulation of seeds of a given age is subjected to a germination test, in which the percentage of germination of seeds in the subpopulation is assessed after some time after the seed has been imbibed.

In the absence of post-ripening (that is, when the seeds have recently completed maturation in the parent plant), a subpopulation will likely be unable to germinate. This subpopulation is said to be dormant. As the dry weather after maturation increases, the germination of the seed subpopulation is tested and the percentage of seed germination gradually increases. Thus, the depth of dormancy in these subpopulations is said to decrease.

Eventually, there will be a dry period after maturation when the entire seed subpopulation will germinate, that is, the time when seed dormancy is completely released. The transient nature of seed dormancy can be used to define the depth of dormancy stored in a seed.

The longer the period after maturation required to lose the dormancy of a seed population, the greater the initial depth of dormancy in that population.

Therefore, primary dormancy prevents germination until the risk of summer drought. Such regulation of germination time is a major determinant of physical condition, and germination time has been shown to be subject to extremely strong natural selection (Donohue et al., 2010).

Primary seed dormancy is an important adaptive trait of the plant that blocks seed germination under conditions that would otherwise be favorable for germination. This trait is found in newly produced mature seeds of many species, but not all.

Once produced, dry seeds undergo a period of aging, called dry post-ripening, during which they lose their primary dormancy and gradually acquire the ability to germinate when exposed to favorable germination conditions. The dormancy of primary seeds has been widely studied not only for its scientific interest, but also for its ecological, phenological and agricultural importance.

However, the mechanisms underlying dormancy in primary seeds and their regulation after maturation remain poorly understood.

3.2 The dynamics of secondary dormancy depend on primary dormancy

Seed dormancy can prevent germination under unfavorable conditions reducing the chances of survival of seedlings. Freshly harvested seeds often have significant primary dormancy which

depends on the temperature of the maternal plant and which is released gradually by post-maturation (Figure 5).

Secondary dormancy is found in shallow DMP and is a term used with seeds that have lost primary dormancy to describe their behavior when exposed, especially for prolonged periods, to environmental signals unfavorable to germination, such as darkness or low temperatures (Hilhorst, 1998).

Induction of secondary dormancy was affected by the state of primary seed dormancy. Specifically, post-sag had a non-monotonic effect on the ability to be induced into secondary dormancy by stratification; first increasing sensitivity as post-maturation progresses, then decreasing after 5 months post-maturation and finally increasing again 18 months after maturation.

The temperature of seed ripening sometimes has effects independent of the expressed primary dormancy, so that seeds ripened at low temperatures, but showing germination proportions comparable to those of seeds ripened at higher temperatures, are more easily induced in secondary dormancy. Since seed maturation temperature is an index of seed maturation and dispersal, these results suggest that the interaction of seed maturation temperature, post-maturation and postdisperse conditions combine to regulate the period of seedling. year of seed germination.

Indeed, in response to such unfavorable signals, the seed will enter a state of "secondary dormancy" where germination will again be suppressed even under favorable germination conditions. Under natural conditions, seeds may enter or exit secondary dormancy several times depending on seasonal indices in order to optimize seedling establishment. Secondary dormancy has been studied less than primary dormancy. Although primary and secondary dormancy appear to share common underlying germination control mechanisms, including the involvement of the phytohormones gibberellic acid (GA) and abscisic acid (ABA), their understanding at the molecular level remains poorly understood (Cadman et al. al., 2006; Ibarra et al., 2016).

However, seeds can be induced into secondary dormancy if they encounter conditions or signs of future unfavorable conditions. If this induction of secondary dormancy is influenced by the conditions of seed maturation and if the primary dormancy has not been explored in depth. In this study, we examined the induction of secondary dormancy in seeds of *Arabidopsis thaliana* which matured under different temperatures and with different levels of post-maturation.

Seed maturation conditions, determined by flowering season and fruit set, influence the level of primary dormancy induced in seeds (reviewed in Gutterman, 1992; Donohue, 2009). For example, in *A. thaliana*, cold temperatures during seed maturation induce strong primary dormancy (Donohue et al., 2007). Cold-ripening seed temperatures occur in early spring or fall for genotypes that do not require vernalization to flower (Thompson, 1994; Donohue, 2009).

As such, the temperature of seed maturation provides information on the seasonal schedule; seeds ripened in cold weather may experience cold temperatures before summer, while seeds ripened in warmer temperatures may not be cold until after summer has passed. It is therefore

important to know how much seed ripening temperature influences responses to other seasonal signals, such as water availability and temperature fluctuations during imbibition, and whether it does so exclusively. by altering primary dormancy levels.

Even after the loss of primary dormancy, seeds can acquire secondary dormancy if conditions are still unfavorable for germination, and the dormancy cycle can occur under natural conditions (Footitt et al., 2011, 2013; Penfield et al., 2011, 2013; Penfield et al. Springthorpe, 2012). Secondary dormancy can be induced by specific environmental factors, such as humidity and temperature, which vary seasonally. Water limitation, which often occurs during summer in temperate climates, can induce secondary dormancy.

In naturalized populations of *Acacia saligna* seeds, for example, the induction of secondary dormancy is regulated by humidity, with its low moisture content inducing secondary dormancy (Tozer and Ooi, 2014). Low exposure to moisture due to the low moisture content of the soil can accelerate germination once moisture becomes available again. For example, seeds of *Polygonum aviculare* were induced into deep secondary dormancy by exposure to low humidity conditions, but after seed hydration, dormancy breaks were more pronounced in these seeds than in those found in consistently soil. wet (Batlla and Benech-Arnold, 2006; Batlla et al., 2007).

Exposure to wet incubation at different temperatures in the dark can also induce secondary dormancy. In *A. thaliana*, secondary dormancy can be induced by high temperature imbibition (Donohue et al., 2007) or by prolonged imbibition at low temperatures (Penfield and Springthorpe, 2012).

The seasonal context of these responses is poorly understood, but such responses are probably important determinants of the seasonal patterns of the dormancy cycle under natural conditions (Footitt et al., 2011, 2013) which ultimately determine the seasonal timing of germination of seedlings. seeds.

To understand how the environmental factors that regulate secondary dormancy actually influence the timing of seed germination under natural seasonal conditions, it is necessary to know how they interact with other factors that vary with the seasons, such as seed maturation and post-subsidence conditions. After ripening is an indicator of the time since seed dispersal, and the temperature of seed ripening is an index of when, during a season, the seeds have been dispersed.

Determining how the factors regulating secondary dormancy, which vary according to the season, interact with the temperature after ripening and seed maturation, will therefore provide important information on the mechanisms regulating the seasonal calendar of seed germination. .

Dormancy is believed to play a key role in resolving such unfavorable conditions, with dormant genotypes of populations being found in areas with warmer summers (Montesinos-Navarro et al., 2012), and more dormant alleles of the locus. butler DELAY OF GERMINATION- DELAY OF GERMINATION- 1 found in more arid locations (Kronholm et al. 2012). Thus, dormancy dynamics appear to play an important role in regulating the timing of germination under conditions of adequate humidity and permissive temperatures in this species.

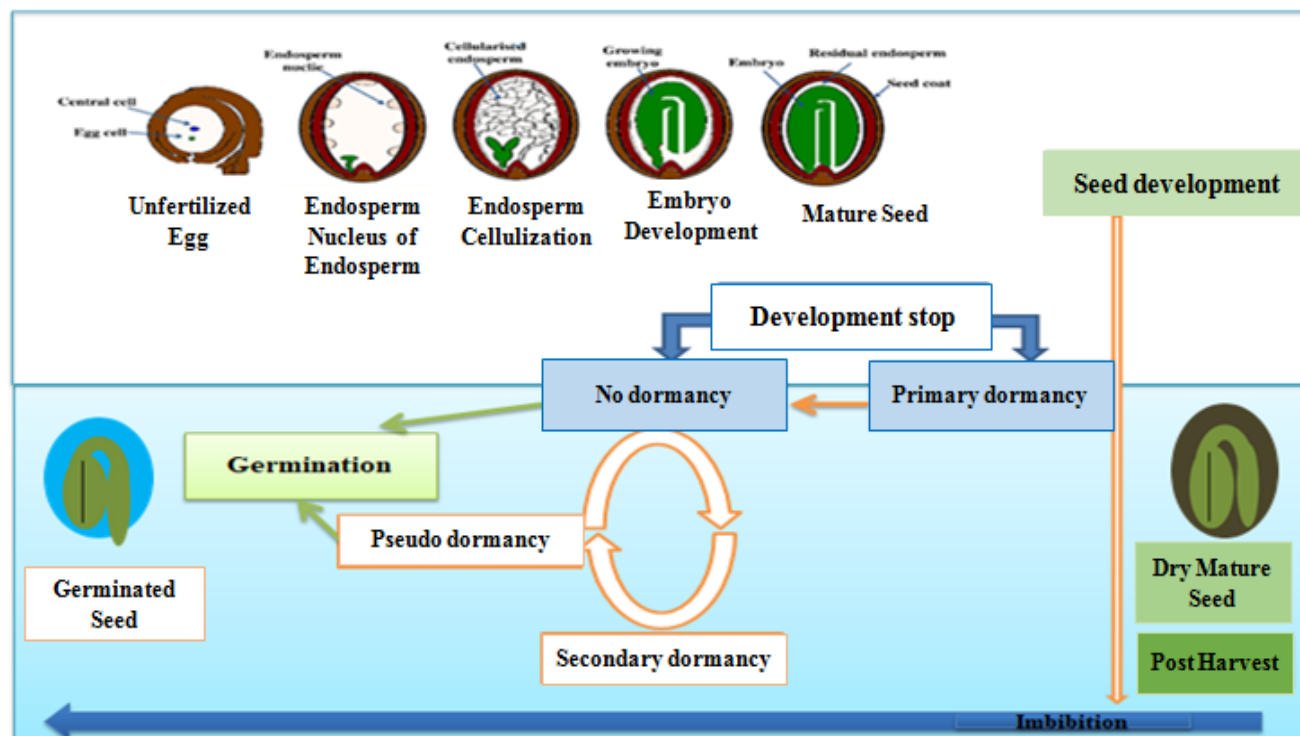


Figure 5. Schematic representation of the events that occur between the seed development phase (Savadi et al., 2017) and the germination phase passing through primary and secondary dormancy.

3.3 The causes of dormancy

Dormancy is either imposed by the seed coat or by the embryo, or a combination of the two (Nikolaeva, 1977). The dormancy imposed on the seed coat is due either to the impermeability of the mantle to water and / or gases, or to the mechanical prevention of radicle extension, or to the seed coat itself, which prevents inhibiting substances from leaving the embryo or providing inhibitors to the embryo.

When the embryo is dormant, hormonal, heat and / or light treatments are usually necessary, which can be satisfied naturally during a post-ripening period. When the two types of dormancy are combined, removal of the seed coat will not result in germination, but additional treatments related to the embryo are required. Since many plant families are dormant, understanding this type of dormancy and identifying natural ways to break it becomes economically important.

3.4 Factor acting on the regulation of seed dormancy

3.4.1 The ABA / AG balance

The ABA / AG balance (Figure 6) determines the output of a seed: high endogenous ABA content, with low AG levels leading to deep dormancy and low seed emergence, while low ABA levels and high promote germination before harvest.

Therefore, the ABA / AG balance should be strictly regulated. The ABA / AG balance has two major aspects: the balance of hormone levels and the balance of signaling cascades. ABA has been reported to be involved in suppressing AG biogenesis (Seo et al., 2006) and AG also negatively regulates ABA biogenesis during seed germination (Shu et al., 2006). al., 2013; Oh et al., 2007).

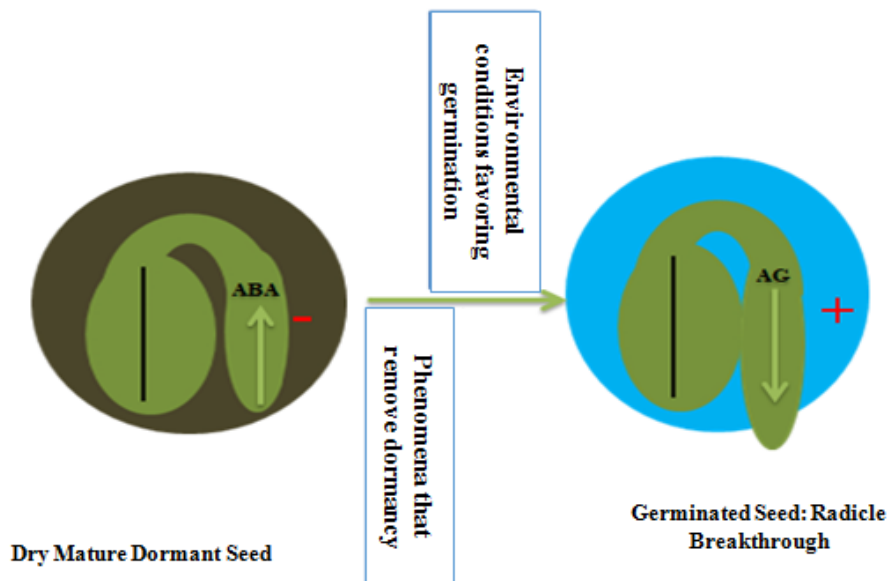


Figure 6. Schematic presentation of roles of ABA and AG in the transition from dormant to germinal state in a seed.

3.4.2 Auxin: a new master in seed dormancy

The application of exogenous auxin suppresses seed germination at high salinity (Park et al., 2011), indicating that this hormone plays an important role in seed dormancy and germination in response to environmental stimuli. Previous studies have shown that IAA (indole-3-acetic acid) can delay seed germination and inhibit preharvest germination in wheat (Ramaih et al., 2003).

ABA suppresses the elongation of the embryonic axis during seed germination, also by potentiating auxin signaling (Belin et al., 2009); and a forthcoming study suggested that release of treatment-induced dormancy after ripening is associated with decreased seed sensitivity to auxin (Liu et al., 2013). All of these observations suggest that auxin may play a role in regulating seed dormancy and germination.

Emerging genetic data shows that auxin protects and strictly regulates seed dormancy alongside ABA (Liu et al., 2013b).

3.4.3 The role of ABA: Exposing non-dormant seeds to ABA blocks their germination

ABA is a phytohormone that plays an essential developmental role in the proper maturation of seeds (Vicente-Carbajosa and Carbonero, 2005; Finkelstein, 2013).

Regarding the origin of ABA acting to promote dormancy during seed development, elegant genetic experiments led Koornneef et al. (1989) to conclude that the acquisition of seed dormancy involves ABA produced by seed tissues resulting from fertilization rather than that produced by maternal tissues (Karssen et al., 1983). These findings are also corroborated by a more recent study (Kanno et al., 2010).

In addition, unfavorable germination conditions suppress seed germination, which implies de novo accumulation of endogenous ABA (Kim et al., 2008).

In addition, the treatment of dormant seeds with norflurazone or fluridone, inhibitors of ABA synthesis (Figure 7), triggers seed germination during imbibition (Debeaujon and Koornneef, 2000; Lee et al., 2010). Taken together, these experiments clearly indicate that dormant seeds activate ABA synthesis and signaling upon imbibition, which blocks germination.

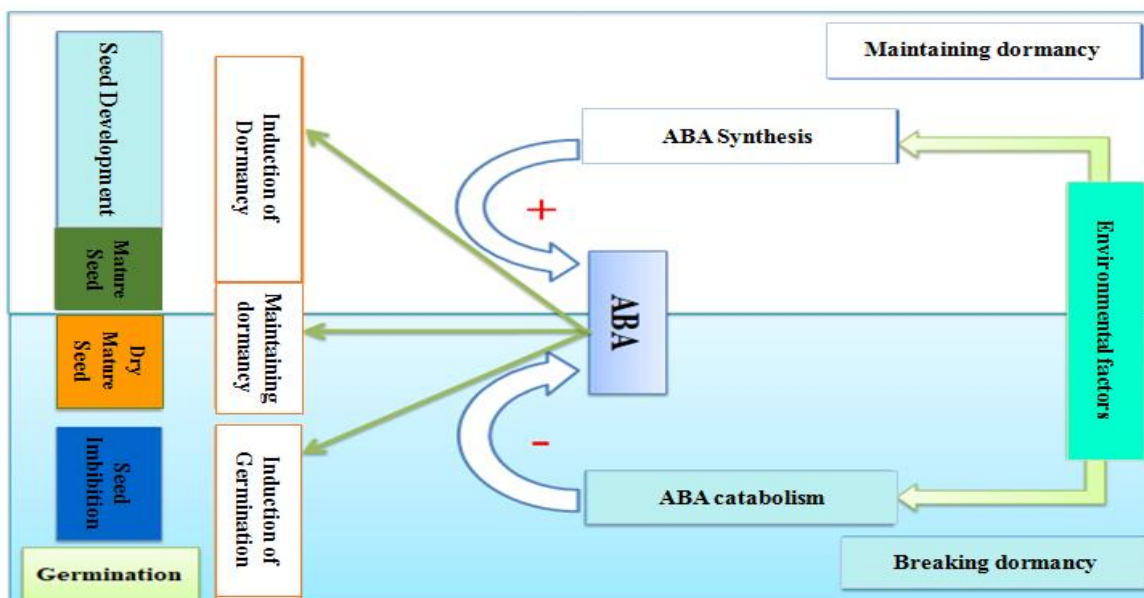


Figure 7. Schematic presentation of the role of ABA in the process of maintaining and removing dormancy.

3.4.4 The role of the GA

AG and ABA are often considered to be hormones that exert an antagonistic role in the control of seed germination (Ali-Rachedi et al., 2004; Lee et al., 2010).

Lee et al. (2010) showed that exogenous GA did not downregulate the accumulation of the GA response factor, RGA-LIKE 2 (RGL2), a seed germination repressor, in very dormant Cvi seeds, suggesting that dormant seeds of Cvi lack the capacity to respond to GA.

This is consistent with a recent report showing that sensitivity to GA increased during post-maturation (Hauvermale et al., 2015). An interesting topic for future research will be to explore how dormant seeds acquire the ability to signal in response to GA after maturation.

3.4.5 Other phytohormones involved in seed dormancy

In addition to ABA, GA, and auxin, almost all other phytohormones are probably involved in modulating seed dormancy and germination, including ethylene (ET), brassinosteroids (BR), jasmonic acid (AJ), salicylic acid (AS) and cytokinins (CTK) and strigolactones (SL).

ET interrupts seed dormancy and promotes seed germination by neutralizing the effect of ABA (Arc et al., 2013; Corbineau et al., 2014). Mutations in positive regulators of the ET signaling pathway cause deep dormancy, while seeds of the negative regulator *ctr1* (Constitutive Triple Response 1) germinate more many aspects of plant development, via the signaling pathway with D53 (DWARF 53) as a repressor (Umehara et al., 2008; Jiang et al., 2013; Zhou et al., 2013). SLs are host-derived germination stimulants for parasitic weed seeds (Cook et al. 1966). They also trigger seed germination in other species, obviously reducing the ABA / AG ratio (Toh et al., 2012). In addition, some key components of the SL signaling pathway affect seed germination, including *SMAX1* (plus axillary growth suppressor *e2 1*) in *Arabidopsis* (Stanga et al., 2013) and *OsD53* (Jiang et al., 2013; Zhou et al., 2013).), which is the homolog of *SMAX1* in rice. However, the precise regulatory mechanisms underlying MLs require further study.

In summary, these plant hormones, including ET, BR, AJ, AS, CTK, and SL, regulate seed dormancy and germination, most likely playing a role in ABA / AG balance. (Figure 8), although the interactions between these hormones and GA require complement, some known detailed mechanisms are only the tip of the iceberg. In addition to these phytohormones, other small molecular compounds, including ROS (reactive oxygen species) and NO (nitric oxide), are involved in the regulation of seed dormancy and germination. ROS and NO synergistically reduce seed dormancy and probably act upstream of ABA (Bykova et al., 2011; Arc et al., 2013).

Thus, hormones and signaling compounds precisely regulate dormancy and seed germination through an integrated network of interactions with the ABA / AG balance as a central node.

In addition to phytohormones, various environmental signals determine the appropriate time for seed germination, also by mediating the ABA / AG balance. Light is a major environmental factor during seed germination, increasing the expression of the anabolic AG genes, *GA3ox1* and *GA3ox2*, and repressing the expression of *GA2ox2*, an AG catabolism gene (Cho et al., 2012).

Previous studies have shown that blue light suppresses seed germination by enhancing transcription of ABA biosynthetic genes and altering the expression of ABA catabolic genes (Gubler et al., 2008; Barrero et al. , 2014). Post-maturation can also break seed dormancy, which downregulates ABA biogenesis. The level of transcription of the ABA catabolism gene, *CYP707A2*, increases after maturation (Millar et al., 2006).

Temperature is another environmental factor that influences seed dormancy both during seed maturation and in soil by regulating the balance of ABA / AG biogenesis (Footitt et al., 2011; Kendall et al. , 2011). Temperature variation during seed maturation affects primary seed

dormancy by regulating envelope permeability, a regulatory mechanism distinct from ABA / AG pathways (MacGregor et al., 2015).

Furthermore, although the detailed mechanisms underlying the preharvest TaMFT-RNAi plant germination phenotype are elusive, the TaMFT homolog in Arabidopsis, MFT, is a critical factor that helps refine the balance of ABA signaling. / AG (Xi et al., 2010; Nakamura et al., 2011).

Therefore, seed dormancy is the integrated result of endogenous and environmental factors that regulate the ABA / AG balance, whether it is hormone accumulations or hormone signaling cascades.

Control of phytochromes may involve cytokinin (CTK) effects on transmembrane cells (Thomas, 1992).

3.5 Effect of pretreatment on removal of seed dormancy

It should be noted that a number of treatments during imbibition could trigger germination of dormant seeds.

These treatments may affect the depth of dormancy present in the dry seed or the germination arrest program, or both.

Among the techniques employed to overcome seed dormancy, desiccation of the seed coat at the distal end (Yogeesha et al., 2005) or at the end of the radicle (Goldbach, 1979) has resulted in highest germination of the seed, no ungerminated seeds remain at the end of the test period.

The other methods, using HCl and acetone, could not completely eliminate seed dormancy (Yogeesha et al., 2005).

Germination of 93% was reported by Idu (1994) when seeds were scarified with H₂SO₄ for 15 minutes. The preliminary study by Yogeesha et al. (2005) on the treatment of seeds with sulfuric acid showed that treatment with hot sulfuric acid 75% for 4 minutes resulted in germination of (50%). In contrast, hot water treatments did not improve germination (Yogeesha et al., 2005).

Investigating the effects of different dormancy removal treatments on the germination of *Rhynchosia capitata*, a common annual summer weed. The seeds were soaked in thiourea, KNO₃, HCl, HNO₃ and H₂SO₄, and they were also mechanically scarified (sandpaper). The results showed that the seeds of *R. capitata* showed signs of physical dormancy mainly due to the impermeability of their husk. Mechanical scarification and acid scarification (soaking seeds in H₂SO₄ for 60 and 80 min and in HCl for 12 and 15 h) were very effective in breaking dormancy and promoting germination. Soaking seeds in HNO₃ for 1-5 days showed little effect, while various concentrations of thiourea and KNO₃ failed to break the dormancy of *R. capitata* seeds (Haider Ali et al., 2011).

4. PHYSIOLOGY OF SEED GERMINATION

Successful germination and seedling development is a critical step in the growth of a new plant.

Germination is a crucial developmental transition as it precedes seedling establishment. Normal germination requires imbibition with water and first involves the rupture of the testa, which is probably the result of the expansion of the cells of the micropylar endosperm, followed by the concomitant rupture of the endosperm and the root protrusion outside the testa (Dekkers et al., 2013; De Giorgi et al., 2015).

Unlike the mature seed, the juvenile plant is very fragile. It is therefore not surprising that germination control mechanisms have appeared during evolution (Lopez-Molina et al., 2001).

Seed germination is considered to be the initiation of the first developmental phase of the life cycle of higher plants and is followed by post-germination growth of the plant (Rajjou et al., 2012). A seed begins to germinate under conditions

favorable in response to environmental stimuli such as light, temperature, soil components (especially nitrate) and molecular mechanisms of a response which have been well characterized.

In the case of germination of a monocotyledonous plant seed, the coleorhiza is the first part to come out of the seed coat, while in the germination of a dicotyledonous plant seed, the radicle first develops from the seed coat. . In both groups, the progress of germination is strictly related to the rate of water uptake.

At first, there is a rapid imbibition of water by a dry seed (phase I) until the seed tissues are completely hydrated. This is followed by limited water uptake during phase II, while in phase III there is an increase in water uptake which is related to the completion of germination. Most important is phase II, which is associated with various cellular and biochemical events such as DNA repair and translation of stored and newly synthesized mRNAs. Phase II is characterized by increased metabolic and cellular activity. At the germination stage, the decision of embryonic cells to reenter the cell cycle or to remain inactive is crucial in determining seedling formation (Weitbrecht, 2011; Barroco, 2005). The cell cycle, which is arrested in a resting seed, is reversed during germination (Figure 8).

DNA replication is a relatively late event in seedling formation and occurs after a seed has soaked in water at the end of phase II. In most species, radicle protrusion does not require mitotic activity (Gendreau, 2008), although in tomato activation of cell division occurred before radicle protrusion (De Castro, 2000).

At the germination stage, cell cycle activation is crucial for seedling formation (Barroco, 2005). The cell cycle is a series of coordinated recurring events that occur between the ends of subsequent cell divisions, whereby cellular material is duplicated and divided into daughter cells. Cell cycle progression is controlled by reversible phosphorylation by protein kinases and phosphatases and by the activity of cyclin-dependent kinases (KDC) and their activating subunits, cyclins (CYC).

In plants, there are five groups of KDCs (KDC A to KDC E). Kinases of the CDKA group have a PSTAIRE motif in their amino acid sequence which is involved in their interaction with cyclins, while B KDCs contain another specific protein motif, PPTA / TLRE. KDC A play a role in G1 to S and G2 to M transitions, while proteins of the CDKB group are required to progress in mitosis (Gendreau, 2012; Inze, 2006).

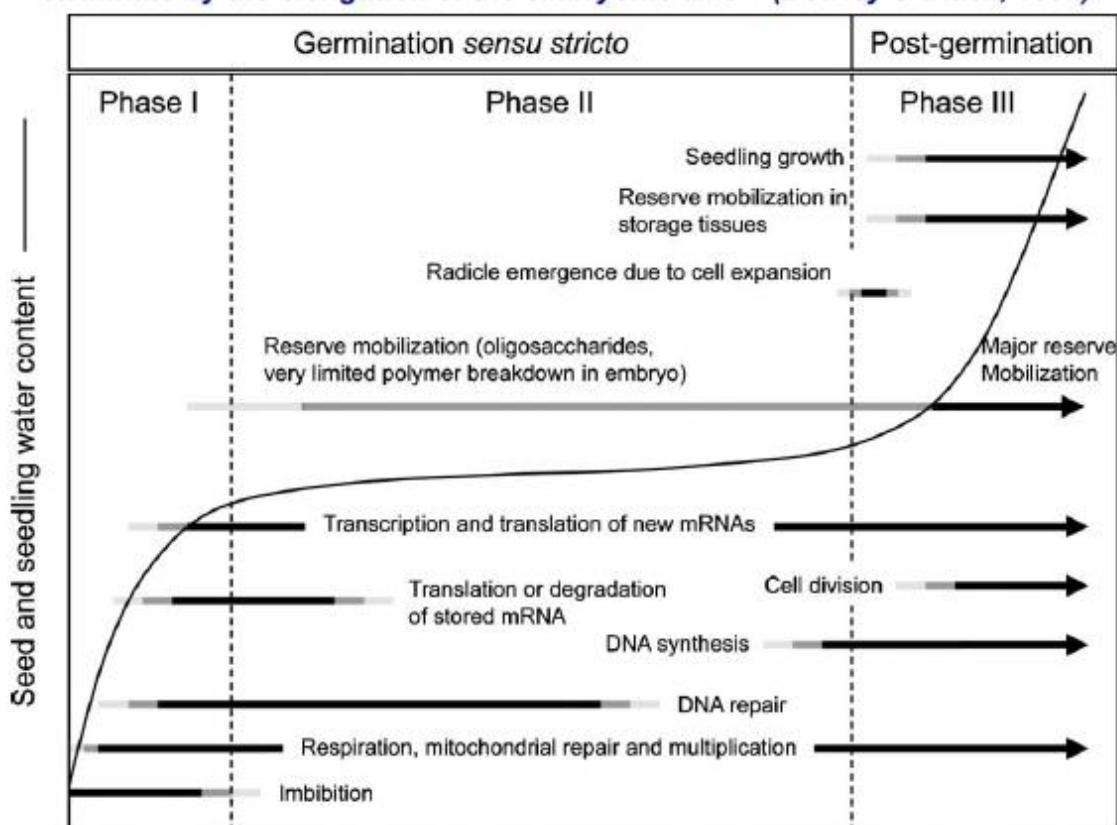


Figure 8. Germination includes the events that begin with water uptake by the quiescent dry seed and end with the elongation of the embryonic axis (Bewley and Black, 1994; Nonogaki, 2010).

4.1 Variability in seeds affects germination

Variability refers to the natural differences that exist between individuals in nature. In many cases, a species seeks to manage this natural variability to produce a constant phenotype (Lempe et al., 2013; Boukhibar and Barkoulas, 2016). In other cases, variability may be a positive element in the generation of various phenotypes (Blake et al., 2006; Fraser and Kaern, 2009).

Variability in seeds manifests itself at different scales, including interpopulation, intrapopulation, and cellular levels.

Thus, cells and organisms are found in highly variable environments which induce variability in response to heterogeneous and time varying conditions. Sources of variability are often described

as "intrinsic" or "extrinsic", describing, respectively, the processes inherent in the individual entity under consideration and the external influences originating from the individual's environment (Swain et al., 2002).

Intrinsic variability refers to the variability in individuals, usually at the cellular level. This variability notably includes transcription and translation events (Swain et al., 2002), which result from random collisions between various molecular components. It is widely believed that the random nature of biochemical reactions, particularly the expression of genes in cells, contributes to stochastic behaviors of cells and organisms (Raser and O'Shea, 2005). It is assumed that the transcription of genes within organisms explains a great variability and contributes to the phenotypic differences between individuals of genetically and genetically identical backgrounds (Raj and van Oudenaarden, 2008).

Extrinsic variability refers to the differences between individuals in a population. At the cellular level, influences such as fluctuating microenvironments, differences induced by unequal cell division and physical constraints induce differences in cell-to-cell behavior (Johnston, 2012).

On the other hand, plants are continually exposed to sources of extrinsic variability in the form of changes in the environment. The ability to produce a consistent phenotype in the face of fluctuations is called robustness (Kitano, 2004; Boukhibar and Barkoulas, 2016).

Thus, at the grain level, significant variability in germination rate and dormancy between different seed populations has already been reported in a wide variety of species (Kanno et al., 2010). In the context of agriculture, variability between seed lots is a major obstacle to uniform crop establishment and harmonization of seed behavior remains a key objective of this industry (Finch-Savage and Bassel, 2015).

Seeds have been shown to exhibit higher germination levels in association with reduced dormancy when growing under specific parent conditions, including periods of high temperature, drought and short days (Fenner, 1991). These maternal effects act as instructive signals for the next generation to calculate their germination based on the season in which they are produced.

Likewise, seed coat composition can directly influence seed germination and dormancy (Debeaujon, 2000), while maternal conditions affected the production of flavonoids in the developing seed coat (MacGregor et al., 2015). During low temperatures, the expression levels of the phenylpropanoid genes increased, leading to higher concentrations of flavonoids and increased seed dormancy.

Variable germination in a seed lot can be observed in seeds collected from mother plants that are grown under constant environmental conditions (Philippi, 1993). The mechanisms underlying the occurrence of this seed-to-seed variability within populations have already been explored at the whole plant level and linked to spatial characteristics derived from the mother.

The position of a seed in a plant can affect its subsequent germination performance (Susko and Lovett-Doust, 2000). This has been demonstrated in grasses, where seeds placed lower showed improved germination characteristics compared to those of the distal upper parts of the plant

(González-Rabanal et al., 1994), and in Brassica weed species. , *Alliaria petiolata* (Susko and Lovett-Doust, 2000). This has also been observed in seeds of the Umbelliferous family showing differences between primary and secondary inflorescences (Thomas et al., 1977).

In some species, the same mother plant can produce several morphologies (Silvertown, 1984). This occurs mainly in the Chenopodiaceae and Asteraceae families (Imbert, 2002).

These multiple morphologies can lead to contrasting germination behaviors within a seed lot and variability within seed lots. This phenomenon is widely present in uncultivated weed species and shows a limited prevalence in crops.

It should be noted that the seeds extracted from their mother plant are generally dormant, where they retain tolerance to desiccation and storage capacity. The combination of development time, through prolonged dry storage or after maturation, and environmental inputs results in the reversal of development fate which leads to the irreversible decision to start germination. This results in a sustained loss of tolerance to desiccation (Bassel, 2016). Variability in dormancy levels is present within seed populations as part of the ecologically beneficial risk coverage strategy used by seeds. In the agricultural context, this dormancy is usually reduced through a controlled period of post-maturation (Holdsworth et al., 2008).

4.2 Other environmental factors affecting seed germination

Environmental factors that influence seed performance include soil fertility, water, temperature, light, and seed position on the plant (Copeland and McDonald, 2000).

Soil Fertility: In general, plants that have been fertilized with the three main elements (N, P and K) produce larger seeds than those that have not been fertilized. The increase in seed size is due to an increased rate of development during the filling period as a result of the increased availability of nutrients. According to Copeland and McDonald (2000), when controlling for the effects of individual nutrients on seed development, nitrogen is the most influencing seed size, germination and vigor.

Water: Water deficits reduce plant metabolism and seed development.

Research has shown a decrease in leaf area, rate of photosynthesis and other effects favorable to flower abortion and the negative influence of assimilation production and translocation on developing seeds; One of the most important effects is the decrease in carbohydrate intake caused by a reduction in the rate of photosynthesis. Prolonged droughts and reduced soil water availability lead to a decrease in seed size, especially when these effects occur during seed filling. If water deficits occur during flowering, its main effect is a reduction in the number of seeds (Copeland and McDonald, 2000).

The moisture content of most seeds is between 5% and 20%, although in some seeds, especially large seeds this content can be considerably higher, sometimes even more than 50%. The moisture content values are largely dependent on the age of the seed, thus, fresh seeds generally have a higher moisture content than older seeds (Bhattacharya and Medlin, 1998).

Temperature: High temperatures during seed development produce smaller seeds, while low temperatures retard seed growth. Germination and seed vigor are also negatively affected by exposure to low temperatures during development. High temperatures are considered to be the main reason for the "forceful maturation" of some plants. This phenomenon is also caused by water deficits or application of desiccant at inappropriate times during ripening. The presence of greenish seeds is undesirable as this anomaly results in reduced germination and seed vigor (Copeland and McDonald, 2000).

Light: The seasonal distribution of solar radiation is a fundamental factor in ensuring adequate plant development. In general, reduced light relative to the mother plant results in smaller seeds (Copeland and McDonald, 2000).

A similar pattern of germination with constant and fluctuating temperature regimes was observed in the 24 hour darkness.

However, by the time the light environment becomes unrestricted for germination, the seeds may have gone dormant.

There is a relationship between the quality of light and the morphological and biochemical parameters of the seed. If the blue LED light is used, the seed germination rate and speed can be improved. By using blue light, it is possible to obtain good quality seedlings with the highest fresh weight, the greatest number of leaves and roots, the highest stomatal frequency as well as a high concentration of pigments and high density. high activity of antioxidant enzymes (Simlat et al., 2016).

Oxygen: Since stimulation of respiration is an essential phase of germination, it is not surprising that partial tensions of oxygen and ear dioxide can affect germination. The oxygen requirements of different seeds vary within fairly wide limits, but most seeds are able to germinate at O₂ tensions below atmospheric concentration.

Increases in partial O₂ tension have been found to promote germination in some grains. Seeds that respond to increased O₂ tensions are likely seeds with a relatively low oxygen permeability layer. However, low O₂ permeability of the coats does not necessarily have to be a limiting factor in seed germination, as removal of fat has been found to significantly increase the respiration rate of embryos from many seeds.

Some seeds are able to germinate in the complete or almost complete absence of O₂. It should be noted, however, that in all of these cases germination under anaerobic conditions does not continue beyond the earliest stages - for example, the plumule will emerge but the root cannot - and that the presence of 'some oxygen is needed for the formation of chlorophyll and for further development.

Thus, the initial release of food stored in seeds at the start of germination occurs mainly through anaerobic respiration. Anaerobic respiration is catalyzed by the activity of enzymes that do not require aerobic conditions such as dehydrogenases.

Dehydrogenase facilitating the transport of electrons from substrates to oxygen by the electron transport chain using nicotinamide adenine dinucleotide (NAD +), nicotinamide adenine dinucleotide phosphate (NADP +) or riboflavin as a cofactor (Robert, 2009). Dehydrogenase activities have been shown to involve those of alcohol dehydrogenase, lactate dehydrogenase, and succinate dehydrogenase (Oaikhena et al., 2015) which induced the conversion of storage lipids and carbohydrates by anaerobic respiration. Succinate dehydrogenase, a complex enzyme closely linked to the inner mitochondrial membrane, oxidizes succinate to fumarate (Devlin, 2011). Lactate dehydrogenase catalyzes the reversible oxidation of lactate to pyruvate using NAD + as a coenzyme.

Anaerobic respiration has been recorded during the resting and germination phases of seeds (Jones et al., 1999). Dehydrogenase reactivity has been shown to cover the first 3 days of cowpea seed germination (Ebukanson and Bassey, 1992).

The increased respiratory rate in germinating seeds is associated with increased glycolytic activity.

Glycolysis intermediates are transferred to the OPPP pathway, which returns its products to glycolysis. The activity of this pathway is therefore also important in determining the flux by glycolysis (Podestá and Plaxton, 1994). During germination, the seeds use sugars and other molecules as a substrate for respiration. Both α -amylase and β -amylase are involved in the breakdown of starch from albumen. The hydrolysis of starch to glucose is catalyzed by the action of α - and β -amylases, the disrupting enzyme and α -glucosidases (maltase) (Andriotis et al., 2016).

Thus, the importance of amylases is related to their ability to provide the growing embryo with respiratory substrates to produce energy and a source of carbon until the established seedling can photosynthesize. In addition, the growth of embryos from the quiescent stage to the active stage depends mainly on the use of stored ATP and the degradation products of stored lipids (Nandi et al., 1995).

Seed germination is a good time to study mitochondria development. Results obtained in previous transcriptome studies have shown a substantial increase in the number of mitochondrial transcripts encoding proteins and their content, accompanied by changes in their functions at the start of 3 hours of seed imbibition (Howell et al., 2007). During the first 48 hours of seed imbibition, 56 differentially expressed proteins were detected, which include the outer membrane channel TOM40 and the inner membrane families TIM17 / 22/23, compared to dry seed.

The interpretation of the suggestion that the capacity of the import pathway is absolutely dependent on the presence of oxygen (aerobic respiration) is related to the significant decrease in the capacity of the general import pathway in the mitochondria under conditions anaerobic versus an aerobic situation. In support of this suggestion, three proteins of the TIM17 / 22/23 family were found to be up-regulated 6 to 14 times under anaerobic conditions (Howell et al., 2007) and a decrease in proteins involving an import apparatus. was detected in the mature mitochondria which could suggest that the accumulation of these imported proteins in the dry

seed could function after two hours of imbibition and then serve as donors of TCA cycle and transport chain components. electrons (Howell et al., 2006).

4.3 Metabolic controls: Chemical composition of seeds: Storage compounds in seeds

4.3.1 Carbohydrates

Starch is the most important insoluble carbohydrate in seeds, although hemicelluloses associated with the cell wall are present in some species as a major carbohydrate store. Oligosaccharides belonging to the raffinose family are also frequently found in the embryo, but in much smaller amounts than polymeric carbohydrates (Black et al., 2006).

Starch is a polymer of glucose composed of long chains of amylose and more and more abundant multibranch chains of amylopectin, the relative amounts of each being determined genetically. Both are synthesized in cell bodies called amyloplasts where starch is formed into discrete granules, the large and small granules becoming denser in the cell. In the endosperms of herbs, they occupy a large part of the cell volume, excluding the living cytosol (Tetlow, 2011).

Low molecular weight sugars are found in the cytosol of many species and represent between 1% in herbs and 16% in some legumes in embryonic dry mass. Raffinose (galactosyl-sucrose) and stachyose (digalactosyl-sucrose), one of the disaccharides in sucrose, are the most common (Horbowicz and Obendorf, 1994). Their importance is as an early source of breathable substrate during germination and early growth of seedlings, before mobilization of major starch or hemicellulose stores begins, but they may also play a role in tolerance to seedling. desiccation of the mature seed.

Ferreira et al. (2009) determined the carbohydrate response to changes in environmental conditions, while highlighting an interesting case in which two populations of an Amazonian species appear to be under different selective pressures, the responses of which are related to the way they use their carbohydrate storage compounds.

4.3.2 Oils (triacylglycerol)

Oils, which are insoluble in water, are esters of three fatty acids (acyl chains) linked to a glycerol backbone (Weiss, 2000).

Fatty acids vary in length and their particular combination in an oil determines its properties. Their distribution in oils is species specific, and while some fatty acids are common to many species, some are found in oils from only one plant family or only a few species.

Seeds rich in oil do not store any of the major carbohydrates in appreciable amounts, and vice versa; oils are alternate forms of stored carbon. Small, wind-dispersed seeds tend to store oils rather than starch, as the former contain more calories per unit weight than the latter. Oils are deposited after their synthesis in discrete subcellular organelles, called oily bodies, in the membrane of which the embedded proteins, oleosin, are found.

These stabilize the membrane and prevent the coalescence of oily bodies during ripening. Seed oils from wild species contain a wide range of unusual fatty acids (Dyer et al., 2008).

4.3.3 Proteins

Proteins are a source of stored carbon, nitrogen and sulfur and are a highly variable and complex group of polymers containing chains of about 20 different amino acids (Shewry & Casey, 1999). They can be composed of a single chain or of several associated chains of similar or different sizes, linked by weak or strong bonds.

Storage proteins are sequestered in protein storage vacuoles (PSVs) during their synthesis; some may contain only one type of reserve protein, while others may have several different types. Some of the minor storage proteins also play a role as a source of nutrients for the growing seedling; coincidentally, they have anti-nutritional properties for humans and pets (Akande et al., 2010).

Albumin, especially those from the lectin (sugar binding) class, are found in seeds which exhibit enzyme inhibitory properties that reduce the effectiveness of food hydrolyzing enzymes in the digestive tract of animals and insects, thus dissuading from preceding the seeds. Some lectins are highly toxic, including ricin D from castor bean and roseate peas (*Abrus precatorius*). Mandelonitrile lyase is a glycoprotein (a sugar molecule bound to specific amino acids) found in black cherry seeds (*Prunus serotina*) and is an enzyme that hydrolyzes the cyanogenic amygdalin disaccharide.

The biosynthesis of other amino acids in seeds involves glycolysis and products of the tricarboxylic acid cycle to produce carboskeletons. Physiological analyzes have shown that phosphoenol pyruvate carboxylase (PEPC) and pyruvate kinase are key regulatory enzymes governing increased anaplerotic carbon flux (Turpin and Weger, 1990).

The chemical content of the seeds can vary. Genetic (variety) and environmental (location of the cultivation area, soil characteristics, exchangeable cations, trace elements, year of cultivation, total rainfall, relative humidity, solarization, temperature) are important (Nikolopoulou et al., 2006).) as well as technological treatments (shelling, cooking, soaking, germination, extrusion) (Wang et al. 2008).

A relatively high number of new pea cultivars is recorded in Poland. Although post-registration tests indicate higher yield and plant proliferation (Coboru, 2008), adverse weather conditions can negatively affect crop yield and protein content of pea seeds (Szwejkowska, 2005). Due to differences in climate, soil, varieties and agronomic practices, field peas may have different chemical components when grown in various parts of the world.

4.3.4 Phytin

Phytin is an insoluble mixed potassium, calcium and magnesium salt of myo-inositol hexaphosphoric acid (phytic acid). Although considered a minor storage element compared to the previous three classes, it is an important source of phosphate and mineral elements, which are released from the compound after germination. Other ions, manganese, iron and copper, may also be associated with phytin in lesser amounts (Lott, 1981). Phytin is often present as discrete dense aggregations in VSPs, but not necessarily in all of them in storage cells. The mineral content of phytin is also not uniform in all regions of the seed; in dicot seeds, calcium is bound to

the molecule in the globoids of the embryonic radicle and hypocotyls, but it is practically absent from those of the cotyledons.

The results indicated that the seeds contained 3.61% moisture, 57.85% fat, 26.39% protein, 10.07% carbohydrate and 2.08% ash. Potassium was the predominant mineral, followed by magnesium and calcium. Essential amino acids were at levels above FAO / WHO / UNU estimated amino acid requirements, with the exception of lysine. The fatty acid composition showed oleic acid to be the main fatty acid, followed by palmitic, linoleic and stearic acids. The physicochemical properties of the seed oil were melting point, 19.67 ° C; refractive index (25 ° C), 1.47; iodine number, 60.72 / 100 g of oil; peroxide number, 0.99meq. 02 / kg of oil; anisidine value, 0.08; total oxidation value (TOTOX), 2.06; Oxidation Stability Index (120 ° C), 52.53 hrs; free fatty acids, 0.39%; acid number, 0.64 mg KOH / g oil; Saponification value, 189.73. The total amount of tocopherols, carotenoids and sterols was 578.60, 4.60 and 929.50 mg / kg of oil, respectively. Ocop-tocopherol (82%), lutein (80%) and β -sitosterol (93%) were the most abundant forms of tocopherols, carotenoids and sterols, respectively.

4.4 The role of hydrolytic enzymes in grain germination

During seed hydration, separate intercellular bodies of carbohydrates, proteins, lipids and phosphates stored in the seeds act as an energy source and carbon skeleton (Bewley and Black, 1982). Seed imbibition triggered many metabolic processes such as activation or recent synthesis of hydrolytic enzymes which resulted in hydrolysis of stored starch, lipids, hemicellulose protein, polyphosphates and others storage materials in a simple form available for the capture of embryos. In addition, the consumption of a high level of oxygen can be induced by the activation / hydration of mitochondrial enzymes, involved in the Krebs cycle and the electron transport chain (Salisbury and Ross, 1992).

4.5 Metabolic controls: Hydrolyses of storage compounds in seeds

4.5.1 Hydrolysis of starch from storage seeds

Numerous studies examining the essential character of α -amylase activity during germination of seeds under drought stress could be summarized as follows: the promotion of germinating seeds

asparagine, aspartate, glutamine and glutamate) and carbon chains necessary for embryonic growth (Quettier and Eastmond, 2009).

The lipid level and lipase activity were studied in various germinating seeds. B-oxidation has been shown to take place 4 days after germination of Castor seeds (Hutton and Stumpf, 1969). The main hydrolytic enzymes involved in lipid metabolism during germination are lipases which catalyze the hydrolysis of ester carboxylate bonds and release fatty acids and organic alcohols (Pereira et al., 2003; Leal, 2002) and reverse reaction (esterification) or even various transesterification reactions (Freire and Castilho, 2008). The ability of lipases to catalyze these reactions with high efficiency, stability and versatility makes these enzymes very attractive from a commercial point of view.

Villeneuve (Villeneuve, 2003) and others have classified the specifics of lipases into three main groups; the 1st group is the specificity of the substrate in which the glycerol esters represent the natural substrates, the 2nd group is called regioselective and includes the subgroups of non-

specific lipases which hydrolyze triacylglycerols to fatty acids and glycerol randomly with the production of mono and diacylglycerols as intermediates; 1.3 specific lipases which catalyze hydrolysis at the level of the C1 and C3 glycerol bonds in triacylglycerols with released fatty acids and unstable intermediates, 2-monoacylglycerols and 1,2 or 2,3-diacylglycerol and fatty acids of specific or selective type which hydrolyze the ester bond of a specific fatty acid or a specific group of fatty acids at any position of triacylglycerol. The third enantioselective group could identify enantiomers in a racemic mixture. The enantiological specificities of lipases depend on the type of substrate (Castro and Anderson, 1995).

4.5.3 Hydrolysis of storage seed proteins

Proteolytic enzymes play the main role in the use of stored proteins in the metabolism of germinating seeds, which go through many stages (Shutov and Vaintraub, 1987). According to Gepstin and Han (Gepstin and Han, 1980), proteolytic activity in the germinating bean increased during the first 7 days, which was partially dependent on the axis of the embryo. Proteases and peptidases were detected in many seeds during germination whereas; plant protease and amylase inhibitors, which are protein in nature, are disappearing (Shivaraj and Pattabiraman, 1980).

It was observed that the antitryptic and antichymotryptic activities were markedly reduced in the endosperm of millet for germination, which could be attributed to the proteolytic activity during the hydrolysis of inhibitory proteins (Veerabhadrapa, 1978). Hydrolysis of stored proteins produces free amino acids, which promote protein synthesis in the endosperm and embryo and thus the germination process (Tully and Beevers, 1978). Schlereth et al. (2000) reported a small initial decrease in free amino acids at the onset of vetch seed imbibition, attributable to axis leakage, but remaining unchanged at the end of the germination stage.

During seed germination, 13S globulin is hydrolyzed by proteolytic enzymes and the products are used by the growing plant. The first step in 13S globulin degradation resulted from limited proteolysis activity of the metalloproteinase with approximately 1.5% cleavage of peptide bonds. This step takes place during the first 3 days of germination. It takes place during the first 3 days of germination (Belozersky and Dunaevsky, 1990). The metalloproteinase activity is controlled by a protein inhibitor (Mr-10 kDa), present in dry buckwheat seeds in a complex with the enzyme which dissociates by divalent cations released from the hydrolysis process of phytin. Phytin is present in buckwheat seeds in sufficient quantity in the form of globoids arranged in protein bodies (Elpidina et al., 1990).

During the second stage of the degradation of 13S globulin; the products of the protein activity of metalloproteinase hydrolyzed into small peptides and amino acids at acidic pH (5.6) by cysteine proteinase and carboxypeptidase which appear in germinating seeds (Dunaevsky and Belozersky, 1989). It was clear that the cysteine proteinase is able to hydrolyze only the modified 13S globulin, but not the native substance. The role of carboxypeptidase is to facilitate the flow of hydrolysis of storage proteins and works in cooperation with cysteine proteinase. In the most recent stage, when the pH becomes more acidic (5.0) in the vacuoles, the aspartic proteinase present in the dry seeds is involved in the evolution of hydrolysis protein bodies.

4.5.4 Hydrolysis of phytic acid during seed germination

Phytic acid (C₆H₁₈O₂₄P₆), also known as inhexol hexophosphate (IP₆) in the seeds of legumes and cereals (Jacela et al., 2010) is the most important form of phosphorus storage (about 50 to 80%). Phytic acid is considered an anti-nutrient because it has the ability to form complexes with proteins and bind to cations (especially Fe, Ca, K, Mn, Mg, Zn) via ionic association to form a mixed salt called phytin or phytate with reduced digestive availability (Lott et al., 1995).

On the other hand, phytate can play an important role as an antioxidant by forming an iron complex that causes decreased generation of free radicals and peroxidation of membranes. It may also act as an anticarcinogen providing protection against colon cancer (Thompson & Zhang, 1991). Considered an antioxidant, anticarcinogen, or vitamin-like substance, it is essential to measure and manipulate the phytate content in food grains such as beans (Coelho et al., 2002; Okazaki and Katayama, 2005).

Thus a high level of stored phytate is not necessary for seed viability and seedling germination or growth. Phytin is mainly stored in protein bodies in seeds called globoids in the aleuron layer and in the scutellum cells of most grains. Phytic acid has a strong ability to chelate multivalent metal ions, especially zinc, calcium, iron, and protein residues. The phytate content of seeds depends mainly on the environmental fertilization of plant phosphorus (Buerkert et al., 1998).

Significant genetic variability in the phytate content of beans has been shown and appears to be a trait controlled by several genes (Santos, 1998). A correlation between phytate and protein content has also been found (Raboy et al., 1991), so that the protein content of cereals can be considered as another factor regulating the phytate content. The phytin present in germinating seeds is hydrolyzed by an acid phosphatase enzyme called phytase (Hubel and Beck, 1996), which releases phosphate, cations and inositol which are used by the seedlings. During refrigeration, it was found that the extractable Pi present in hazelnut seeds showed little change, which could suggest the rapid conversion of Pi to organic form (Mukherji, 1971).

In stressed seeds, many vital processes such as germination, growth, respiration and other related processes are affected, which can consequently have other effects on metabolic activities, in particular the enzymes of the metabolism of the seed. phosphate which play an important role in seed germination and development (Fincher, 1989). Phosphate metabolism is one of the processes negatively affected under various stressful conditions (Mihoub et al., 2005). Under stressful conditions, restriction of growth and availability of phosphorus enhances the activity of phosphatases for the production of Pi by hydrolysis of the insoluble phosphate form modulating the mechanism of free phosphate uptake. In agreement, Olmos and Hellin (1997) reported that acid phosphatase activity increased to maintain the level of Pi, which allowed it to be co-transported with H⁺ on a proton motive force gradient.

5.CONCLUSION

Dormancy is a state of lack of germination in seeds even though favorable conditions are required (temperature, humidity, oxygen and light), it is based on the impermeability of the seed coat or lack of supply and activity of enzymes necessary for germination.

Germination includes the events that begin with uptake of water and end with the lengthening of the embryonic axis. The visible sign that germination is complete is usually the penetration of the

structures surrounding the embryo through the radicle. Subsequent events, including mobilization of major storage reserves, are associated with seedling growth. It should be noted that a dormant seed can achieve virtually all of the metabolic steps necessary to complete germination, but for some unknown reason the embryonic axis (i.e. the radicle) fails to lengthen.

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