Seed Dormancy and Germination

28

Renu Kathpalia and Satish C Bhatla

Plant life begins with seed formation and is renewed when seed germinates. Seeds are highly dehydrated, quiescent or resting structures, and carriers of the next generation in the life cycle of plants. Seeds have different shapes and sizes, ranging from the smallest orchid seed (10^{-6} g) to the huge seed of the double coconut palm (30 kg). Some seeds are short-lived, e.g., willow seeds are viable for less than 1 week. Mimosa seeds can live up to ~200 years. Seeds of *Canna compacta* have been reported to remain viable up to 600 years, and seeds of lotus can survive up to 1000 years. To accomplish the remarkable feat of next generation, seed contains an embryo with reserve food. During seed germination, the embryo divides and differentiates into shoot-root axis. The tissue containing reserve food material (depending on the species) may persist and get reabsorbed later. Depending on the species, the reserve food material is stored either in the embryo or in the endosperm, and in some cases, it is present in both, embryo and endosperm. The degree of arrest is variable in different species. It may be true sleeping (**dormancy**) or **quiescent stage**, which only requires water for resuming the growth. A viable and nondormant seed is capable of germination after all the necessary environmental conditions are met, but dormant seeds do not germinate even when provided with favorable conditions. Different types of mechanisms impose seed dormancy in diverse climates and habitats. Abscisic acid (ABA) present in seeds induces dormancy, but the intensity of dormancy induction also depends on the genetic makeup of the plant and the environment in which it grows. Temperature, relative humidity, and day length also interact to modulate dormancy, thereby making it a complex phenomenon. Germination in different seeds is not synchronous, and stimuli required to promote germination vary widely. Prior to germination, seeds need to undergo imbibition, i.e., uptake of water by dry seed, followed by reactivation of metabolic activity and redifferentiation of embryonic tissue to mobilize the reserve food material stored in the seed and initiate meristematic activity. The transition from dry seed to seedling is highly sensitive to different environmental conditions, especially light, temperature, and availability of water. This response to

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environmental signals is mediated by one or more hormones whose signaling events lead to activation or de novo synthesis of hydrolytic enzymes. The emergence of radicle is the first visible step and indicates that seed is viable. If germination occurs in the dark, then root growth is slow. On the other hand, shoot growth accelerates. This behavior increases chances of seedling to obtain light so that it can turn green and start photosynthesizing. Once the seedling comes out of the soil, it turns green and starts producing new leaves.

28.1 Seed Morphology and Structure

All seeds are surrounded by a protective layer of dead cells **(testa)** forming seed coat. Sometimes testa is fused with fruit wall or **pericarp** (derived from ovary wall) (Fig. 28.1). In latter case, the "seed" is actually a fruit, e.g., maple, cereal grain, lettuce, and sunflower. The embryo is embedded in the tissue laden with reserve food materials. Most of the eudicot seeds have an embryo with an axis consisting of an embryonic root (the radicle) and an embryonic shoot (the plumule) with a pair of

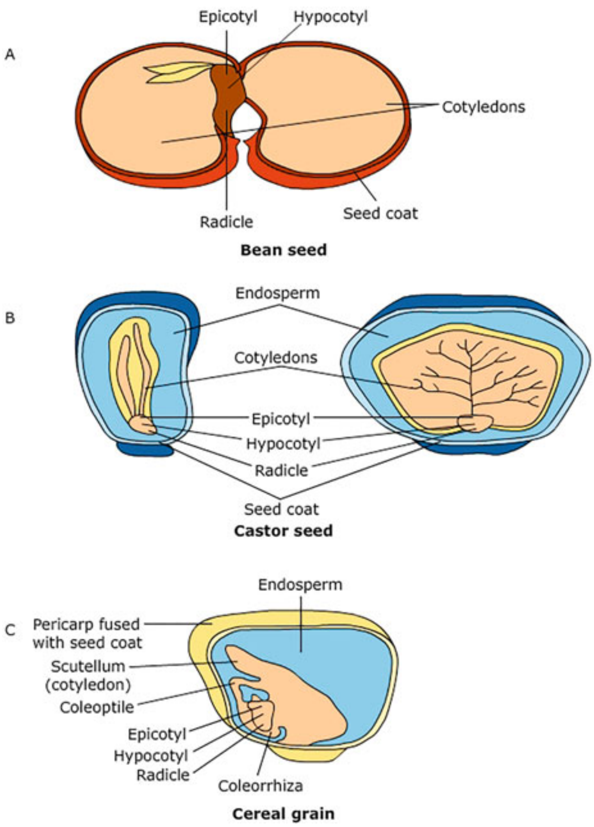

Fig. 28.1 (**a**) Bean seed with two massive cotyledons and an embryonal axis with radicle and plumule. (**b**) Castor seed with thin paper-like cotyledons and embryonal axis embedded in the massive endosperm. (**c**) A cereal grain with fruit wall fused with seed coat, single cotyledon along with embryonal axis having plumule covered by coleoptile and radicle covered by coleorhiza

seedling leaves (the **cotyledons**). Monocot embryos have more variation in their structure with one cotyledon. In grass embryos, the single cotyledon is further modified to form an absorptive organ that lies adjacent to the endosperm. This is known as **scutellum**. In addition, plumule is surrounded by a sheath called as **coleoptile**, and radicle is surrounded by another sheath called as **coleorhiza**. The scutellum is an embryonic tissue and is covered by an epithelial layer, which is similar to aleurone tissue in wall characteristics and nature of reserved food material (Fig. 28.1). Cotyledon is an important part of the embryo within the seed and is formed prior to germination during the process of embryogenesis along with roots and shoots. Angiosperms are divided into two major groups on the basis of number of cotyledons. Plants with only one cotyledon are known as monocots and with two cotyledons are known as dicots. Cotyledons often contain food reserves which are used during the early stages of germination. In most plants, the cotyledons are brought out of the testa and above the ground where they become green and make food by photosynthesis. The cotyledons eventually fall off, usually after the first foliage leaves have been formed. Endosperm is a unique tissue present in angiosperm seeds, and such seeds are called **endospermous seeds**. Stored food in endosperm serves as fuel for the developing embryo. Many seeds, such as those of orchids, are an exception as they lack stored food reserves and their germination requires the participation of symbiotic endomycorrhizal fungi. Endosperm varies from a single layer in *Arabidopsis* to large, oil-storing endosperm of castor bean and starch-storing endosperm in cereals. Some of the eudicots, e.g., beans, which do not have endosperm are called as **non-endospermous seeds**. In non-endospermous seeds, food is stored in the fleshy cotyledons of the embryo. Endosperm is mainly differentiated into two structurally and functionally distinct tissues: the starchy endosperm and the **aleurone** layer (Fig. 28.2). Starchy endosperm contains enzymes but its cells are dead at maturity. The aleurone layer in mature seeds consists of living cells. It is about three to four cell layers thick in rice and barley and single-layered thick in wheat, maize, and oat. The cell wall of aleurone layer is thick and rich in **arabinans** and **arabinoxylans.** The cells of aleurone layer are interconnected with numerous plasmodesmata. Each cell is packed with protein bodies or protein storage vacuoles commonly referred as **aleurone grains**. In addition, aleurone cells also have storage bodies known as **globoids** which are rich in Ca^{2+} and Mg^{2+} salts of

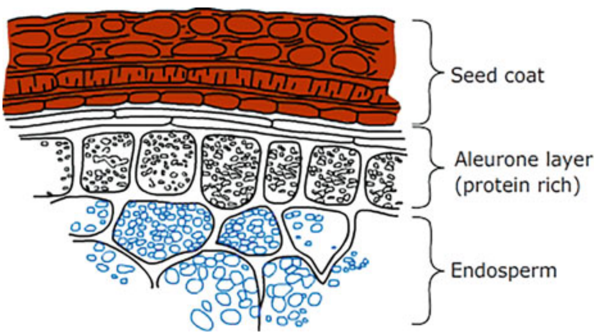

Fig. 28.2 Differentiation of aleurone layer in a seed. The outer most layer of endosperm is rich in proteinaceous aleurone grains and is known as aleurone layer. Inner layers of endosperm are filled with starch

inositol hexaphosphoric acid (phytic acid). When seed germinates, hydrolytic enzymes are activated or synthesized in the presence of gibberellins, and protein bodies lose their reserved proteins. Both aleurone layer and scutellar epithelial cells are secretory tissues. The mature seed consists of protective seed coat layers of dead cells that protect the delicate embryo within. Seed dormancy limits the entry of water and oxygen in the seed. Many legumes and aquatic species have thick seed coat which provides physical barrier and prevents the growth of embryo or imbibition of water. The seed coat often contains phenolic compounds that impart red to brown color to many seeds. These phenolic compounds protect seeds from herbivore and pathogen attacks. In addition, phenolic compounds also protect seeds from harmful effects of short wavelength light and are responsible for imposing dormancy by making seed coat impervious to water and oxygen. Tannins and polyphenols in seed coats are responsible for astringent taste of many fruits and protection from herbivores. The presence of large number of double bonds in polyphenols (such as **proanthocyanidins**) makes these compounds effective in protecting the seeds from the mutagenic effect of short wavelengths of light. Seed coat is also beneficial for human health as a source of dietary fiber. Seed coat contains lignins and polysaccharides, which are largely indigestible and thus allow the passage of food through gut. It is also a rich source of antioxidants, mainly proanthocyanidins.

28.2 Food Reserves in Seeds

Seeds are an important source of food for human and livestock. More than 50% of human caloric intake and 47% of proteins come from consumption of seeds. Ninety percent of world's food is derived from less than 17 plant species. In addition to oils, polysaccharides, and proteins, seeds also store mineral elements. Mineral elements are stored as chelated complexes with inositol hexaphosphate in a compound called **phytate**. Starch grains and cell wall carbohydrates make up the bulk of storage polysaccharides as major food reserves in seeds. However, some of these storage compounds act as anti-nutrients for humans and animals. These include phytate and some storage proteins like lectins, enzyme inhibitors, and thionins. Seeds accumulate these proteins in defense against bacterial and fungal pathogens which also protect them from herbivores and insects. Cereals have two types of proteins in seeds: the water-soluble **globulins** and alcohol-soluble hydrophobic **prolamins**. Globulins are synthesized in rough ER and get accumulated in storage vacuoles, while prolamins assemble into disulfide-linked polymers in ER and form spherical structure known as **protein bodies**.

28.3 Seed Dormancy

Seeds that do not germinate under optimal conditions are considered to be dormant. In other words, seed dormancy refers to inhibition of germination of viable seeds under favorable conditions. This block of germination has evolved differently in different species through adaptation to the environment in which it is growing. Seed dormancy can be due to structural limitations or imbalance of growth substances. On the basis of time of appearance, seed dormancy can be referred as primary or secondary. Freshly harvested mature seeds with capacity of imbibition but unable to germinate are considered to have undergone **primary dormancy**. This type of dormancy is induced during seed development, and such seeds are released from the plant in a dormant state. It is induced due to accumulation of ABA to prevent germination while seeds are still attached to the mother plant. Primary dormancy can be overcome by keeping the seeds in dry state so that embryo gets afterripening period. Alternatively, primary dormancy can be removed by treatment of seeds in the imbibed state. This includes chilling, warm stratification, light, gibberellins, and some other chemical applications. If the conditions are unfavorable for germination at the time of their dispersal, seeds develop physiological dormancy related to seasonal cycles. This type of dormancy due to seasonal changes is referred as **secondary dormancy**. This is induced in mature seeds due to various stress factors mainly temperature after they are released from plants. For example, seeds of *Avena sativa* (oat) become dormant if the temperature at the time of their dispersal is higher than the optimum required for germination, whereas seeds of *Phacelia dubia* (small-flower scorpionweed) become dormant if temperature is below the optimal for germination. Endogenous dormancy prevents seed germination and is mainly due to the physiological status of the seed, while exogenous dormancy is due to seed coat and fruit wall, including endosperm or perisperm, and can be easily overcome. Coat-imposed dormancy is imposed by seed coat and other enclosing tissues, such as endosperm, pericarp, or extrafloral organs. It is associated with long-term viability, e.g., Indian lotus and date palm exhibit high longevity due to highly impermeable seed coat which prevents germination. Embryos of such seeds germinate once the seed coat is removed or damaged artificially or naturally. There are weak points (such as **strophiole** in leguminous seeds) from where damage results in water uptake (Fig. 28.3). Coat-imposed dormancy can be caused by one or more of the following factors: (i) *Prevention of water uptake*: Seed coat is a common cause of seed dormancy in plants found in arid and semiarid regions, especially in legumes. In the seeds of clover (*Trifolium* sp.) and alfalfa (*Medicago* sp.), waxy cuticles, suberized layers, and lignified sclereids combine to restrict water penetration into the seeds. Water impermeability cannot be overcome by **scarification** or passage

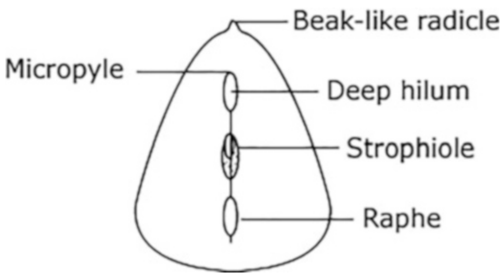

Fig. 28.3 A gram seed showing the presence of strophiole, a small opening from where water enters into the seed during germination

through digestive tract of animals. (ii) *Mechanical constraint*: Seed coat may be too rigid for emergence of radicle, e.g., in nuts which have hard, lignified seed coat. In case of *Arabidopsis*, tomato, and tobacco, endosperm is very hard, and in such seeds the endosperm cell wall needs to be weakened for radicle emergence. (iii) *Interference with gaseous exchange*: Some seed coats are less permeable to gases. As a result, oxygen supply to embryo is reduced, e.g., making a hole in the seed coats of *Xanthium* seeds overcomes dormancy. In some seeds, more oxygen is consumed by the seed coat due to the presence of phenolics in the cell wall, resulting in reduction in oxygen availability to the embryos. (iv) *Retention of inhibitors*: Seed coat may prevent escape of inhibitors from the seeds, or inhibitors may diffuse into the embryo. The inhibitors in seed coat include unsaturated lactones (coumarin), phenolic compounds (ferulic acid), various amino acids, and cyanogenic compounds (i.e., compounds that release cyanide). In case of apple and other members of Rosaceae, seed coat releases cyanogenic compounds (Table 28.1). The *transparent testa (tt)* mutant of *Arabidopsis*, which contains reduced amounts of proanthocyanidins in its seed coat, shows less dormancy and reduced longevity. (iv) *Growth inhibitor production*: In some instances, seed coat and pericarp may contain high concentration of growth inhibitors that can suppress embryo germination. Growth inhibitor production plays important roles in preventing germination in seeds in many fleshy fruits. High concentration of solutes in fruit juices also inhibits seed germination. Besides, ABA has an essential function in preventing in situ germination. Seeds of ABA-deficient tomato mutant show in situ germination. Embryo dormancy is inherent in the embryo and is not due to any influence of the seed coat or other surrounding tissues. In some cases, embryo dormancy can be relieved by amputation of cotyledons, e.g., seeds of peach (*Pyrus* sp.) exhibit slow growth with cotyledons and normal growth without cotyledons. Seeds may also fail to germinate when embryo has not attained maturity, e.g., seeds of celery (*Apium graveolens*) and carrot (*Daucus carota*).

Table 28.1 Inhibitors involved in seed dormancy and their localization in seeds

Inhibitors	Location	Example
Coumaric acid	Seed coat	Legumes
	Glume and hull	*Aegilops*
Ferulic acid	Fruit juice	Tomato
	Embryo	Xanthium
	Endosperm	Iris
	Seed coat	*Cucurbita*
Aflatoxin	Seed	Barley
Amygdalin	Embryo	Rosaceae
Cinnamic acid	Chaff	*Parthenium argentatum (guayule)*

28.4 Hormonal Regulation of Seed Dormancy

Abscisic acid (ABA) plays significant role/s in regulating the onset of seed dormancy and maintaining seeds in dormant state. ABA accumulation is low in developing seeds when storage reserves are being synthesized and its (ABA) level declines as seeds undergo maturation drying. ABA is synthesized in both dormant and nondormant seeds, but generally ABA catabolism is favored in nondormant seeds, while ABA synthesis is favored in dormant seeds, i.e., there is a shift in favor of ABA synthesis accompanying dormancy induction. The absence of ABA during seed development results in the production of viviparous or precocious germination of seeds. In mutants deficient in ABA, precocious germination is not prevented, and seeds exhibit reduced dormancy. ABA-insensitive mutants are programmed to germinate even in the presence of ABA and produce seeds that are intolerant to desiccation. Expression of many genes involved in dormancy can also be enhanced by ABA. Some of the transcripts present in the dormant and ABA-treated embryos encode LEA (late embryogenesis abundant)-type proteins which are synthesized during the later stage of seed development. These proteins are associated with survival during dehydration stress. ABA may also be responsible for the inhibition of radicle elongation during the later stage of seed germination. GA-deficient mutants of tomato and *Arabidopsis* require an exogenous supply of GA to complete germination. According to hormone balance theory, the ratio of ABA and GA is the main determinant of seed dormancy and germination. The tissue concentration of these two hormones is controlled by the rate of their synthesis, degradation and deactivation. Level of ABA decreases at the time of seed germination due to decrease in its biosynthesis and enhanced degradation. The rate-limiting step of ABA biosynthetic pathway involves the activity of 9-*cis*-epoxycarotenoid dioxygenase (NCED). The inactivation of ABA is controlled by ABA-8-′-hydroxylase (CYP707A2 gene). Red light breaks seed dormancy and stimulates seed germination by upregulation of CYP707A2 and downregulation of NCED gene both of which reduce ABA level. For GA, the rate-limiting step in its biosynthetic pathway is cataylzed by GA3-oxidase (GA3ox), and deactivating enzyme is GA2-oxidase (GA2ox), both of which negatively regulate seed germination. At gene level, the two biosynthetic and deactivation pathways are regulated by transcription factors. Promotion of seed germination by GA requires destruction of DELLA proteins. However, if ABA level increases, it promotes ABI—class protein phosphatase—regulated transcription factor and DELLA protein availability. DELLA protein, in turn, suppresses GA biosynthesis, thereby creating a positive feedback loop. The balance between the activities of ABA and gibberellin is controlled by the stage of seed development. During early stages of seed development, gibberellin sensitivity is low and ABA sensitivity is high. However, this gets reversed during seed germination. In addition to environmental conditions, other hormones like ethylene and brassinosteroids reduce the ability of ABA to inhibit seed germination.

Table 28.2 Factors affecting seed dormancy and methods to overcome it

Causes of dormancy	Examples	Methods to overcome dormancy
Rudimentary embryo	*Ginkgo biloba*, barley, wheat, and oat	Afterripening; stratification
Rudimentary endosperm	Tomato, tobacco, pepper, and *Datura*	
Impermeability of seed coat to water	*Chenopodium* and legumes	Scarification with acid
Impermeability of seed coat to gases	Apple, *Xanthium* (cocklebur) Graminaceae	Scarification
Inhibitors	Tomato, *Cucurbita*	Removal of pericarp or testa leach in running water
Hard seed coat	*Lepidium*, *Capsella*, *Acacia* sp., mustard	Scarification, treatment with enzymes and acids

28.5 Mechanisms to Overcome Seed Dormancy

In nature, seeds overcome dormancy by different mechanisms as follows (Table 28.2):

- Microorganisms present in the soil weaken and decompose the hard seed coat.
- Digestive juices present in the alimentary canal of the fruit-eating birds make the seed coat soft.
- Mechanical abrasions weaken the tough and impermeable seed coat.
- Washing away of inhibitors by rain or irrigation water.
- Inactivation of growth inhibitors by high or low temperature.
- Synthesis of growth hormones.
- Maturation of embryo.

28.6 Release from Seed Dormancy

There are mainly two events taking place at the time of germination. *Primary events* are imbibition of water, leading to swelling and hydration. During hydration, dormancy-breaking signals (physical and environmental) are perceived and transduced. This is followed by a series of *secondary events* which overcome dormancy by lowering the level of ABA. The next event is induction of germination which results in the mobilization of reserve food materials in seed. During this phase, level of GA increases, and catabolic reactions increase more than anabolic reactions. There is depletion of tissue surrounding the embryo which is associated with loosening of the cell wall. As a result, radicle shows extension growth. Seed dormancy is under the control of specific genes which get activated or inactivated due to changes in the levels of ABA and GA.

28.6.1 Afterripening

Freshly harvested seeds of many plants do not germinate or show poor germination even under optimal conditions. They require high temperature and dry storage for variable period of time. This phenomenon is known as **afterripening** and is observed in grasses and many dicots. Seeds that require afterripening may show coat-related dormancy, and in such cases, the removal of seed coat induces germination, e.g., in wheat, barley, oat, *Arabidopsis*, and tomato. In embryo-related dormancy, removal of seed coat does not induce germination, and such seeds may require afterripening. This method of breaking dormancy is usually performed in a drying oven. If seeds become too dry (5% or less water content), the effectiveness of afterripening is diminished. The biochemical changes that take place during afterripening are many, and in most cases GAs and ABA both are involved. In the seeds of wild oat, which show embryo-related dormancy, application of GA overcomes dormancy. Similar effect of GA is also observed in tomato and *Arabidopsis*. GA treatment can substitute for afterripening period. A correlation between GA treatment and low temperature is known for many physiological processes. The dormant seeds of many species require afterripening, whereas freshly harvested ones germinate better at low temperature.

28.6.2 Impaction

During seed development, when the seed water content is high, the hilum remains open so that water can evaporate. Once the water content decreases in the seed, then the hilum swells and blocks the entry of water from outside into the seed. In some other seeds, hilum has a plug called **strophiolar plug**, which must be mechanically removed before water and oxygen can enter. This plug also controls seed moisture content and maintains seeds in their dormant state. Impaction involves vigorous shaking of seeds to remove strophiolar plug in leguminous seeds, thereby facilitating their release from dormancy, e.g., sweet clover (*Melilotus alba*).

28.6.3 Scarification

The dormancy induced due to hard seed coat can be removed by mechanically disrupting or removing seed coat. This process is called **scarification**. In nature, scarification can be accomplished by microbial action, fire, leaching of inhibitors, rainfall, or passage of seeds through animal digestive track. Artificially it can be done by rubbing seeds with sandpaper, removing seed coat with knives, or treating them with acid, e.g., in case of some tropical leguminous seeds, cotton, and morning glory, seeds germinate by soaking in concentrated sulfuric acid for up to an hour.

28.6.4 Temperature

Many seeds require diurnal fluctuations in temperature for a season before they can germinate, e.g., *Rumex obtusifolius*. The temperature range over which germination occurs is an indication of the degree of dormancy of the seed. If the temperature range is narrow, then the seed is highly dormant. In many species, secondary dormancy is introduced by exposure to high temperature (20 °C) which causes large seasonal changes in the degree of dormancy. These seasonal changes restrict germination only in spring, which is the beginning of the most suitable season for growth in temperate climates. On the basis of temperature requirement, plants have been divided into summer and winter annuals. Summer annuals produce seeds in autumn and germinate in spring. In such cases, imbibed seeds are exposed to 1–4 months of low temperature (approximately 4 °C) to break dormancy. This process is termed **stratification**. In winter annuals, exposure to relatively high temperatures relieves seeds from dormancy without imbibition. In other words, in winter annuals, low temperature induces dormancy. This causes the seeds to germinate in autumn, which is the favorable condition for many Mediterranean climates.

28.6.5 Light

Seed dormancy is greatly affected by light. Light requirement prevents germination of seeds that are buried deep in soil. Seeds which specifically require light for germination are referred as **photoblastic** seeds**.** Such seeds are common in herbaceous plants which produce large number of seeds with very little reserve food material. Many of the photoblastic seeds require a brief exposure to red light. The photoreceptor involved is phytochrome, and breaking of seed dormancy exhibits red/far-red reversibility. For example, lettuce seeds germinate in response to red light exposure. In lettuce and *Arabidopsis* seeds, red light induces the transcription of gene encoding 3β-hydroxylases which catalyze the conversion of inactive GA into biologically active form. Since far-red light inhibits germination of light-requiring seeds, light-sensitive seeds under a canopy germinate only upon removal of stress by fire or destruction. Under a canopy, the seeds of many herbaceous plants receive only far-red light, as blue, green, and red lights are absorbed by the leaves of the canopy. This light filtering effect of canopies keeps the seeds in dormant state. All light-sensitive seeds exhibit seed coat dormancy, and light enables the radicle to rupture the seed coat by activating some enzymes involved in weakening of the enclosed tissues of the seed coat. Seeds must be in a hydrated state for phytochrome action. This has, for example, been observed in the seeds of lettuce (*Lactuca sativa*) and pepper grass (*Lepidium* sp.).

28.6.6 Light-Temperature Interaction

Seeds of lettuce (*Lactuca sativa*) and pepper grass (*Lepidium virginianum*) remain dormant at high temperature (35 °C) in the presence of light, but they germinate at low temperature (10–15 °C) in light. When temperature is increased, conversion of Pr to Pfr is not affected, but Pfr-triggered reactions are adversely affected, and dark conversion of Pfr to Pr speeds up. However, hydration of seeds is essential for light effect on Pr to Pfr conversion.

28.6.7 Leaching of Inhibitors by Rainfall

Seed coat of many plants has large amount of phenolics (trans-cinnamic acid, coumaric acid, and coumarin) as a defense against predation. Most of these phenolics are water soluble and are washed off during rainfall, thereby facilitating release from dormancy.

28.6.8 Leaching of Chemicals

Different species exhibit variable responses to a variety of chemicals, such as respiratory inhibitors, oxidants, sulfhydryl, and nitrogenous compounds, in facilitating the breaking of dormancy. Nitrate in combination with light is an obligate requirement for release of dormancy of *Sisymbrium officinale* (hedge mustard). Karrikinolide (a compound present in smoke) stimulates germination in many seeds. Nitric oxide (NO), a signaling molecule, can also break dormancy in some plants. The absence of NO reduces germination in *Arabidopsis* mutants, and the effect can be reversed by treating seeds with NO.

28.7 Sequence of Events Breaking Seed Dormancy

I. *Primary events*: The first step in breaking seed dormancy is imbibition leading to hydration of tissues. Seeds perceive dormancy-breaking signals from the environment, and these signals are then passed through different messengers to genes within the nucleus (Fig. 28.4).

II. *Secondary events*: Once the genes sense dormancy-breaking signals, they either trigger the degradation of ABA or enhance synthesis of GA. On the contrary, if the signals repress dormancy-breaking metabolism, then the level of ABA is maintained, and the level of GA is decreased (Fig. 28.5).

III. *Structural changes*: These changes involve weakening of structures surrounding the embryo and facilitate radicle emergence (Fig. 28.6).

IV. *Termination of dormancy.*

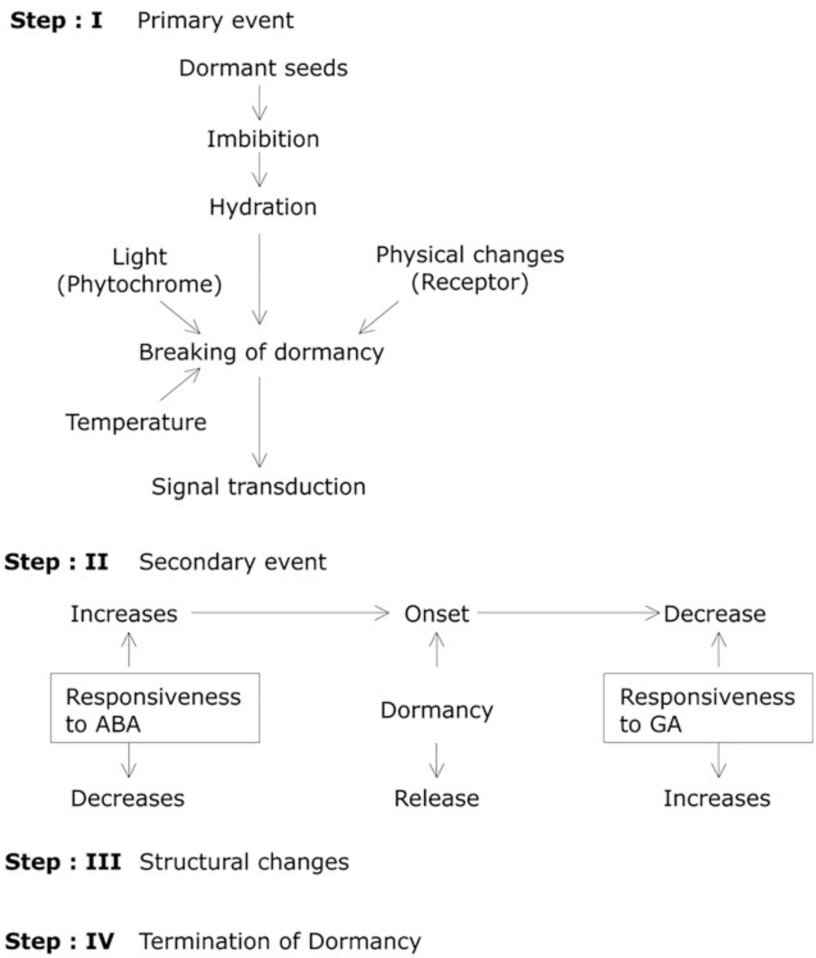

Fig. 28.4 A schematic representation of events involved in breaking seed dormancy

28.8 Significance of Seed Dormancy

28.8.1 Seasonal Synchrony

Seed dormancy ensures survival of a species. It is a kind of defense mechanism against unfavorable growth conditions. It benefits seed survival by synchronizing growth in favorable seasons. Thus, for example, a change in environmental temperature shifts the seeds of some plants in or out of the phase of dormancy, as in *Arabidopsis* and *Ambrosia* sp. (ragweed). Seed dormancy prevents germination in desert plants, which germinate only in rainy season. It helps seeds in sensing

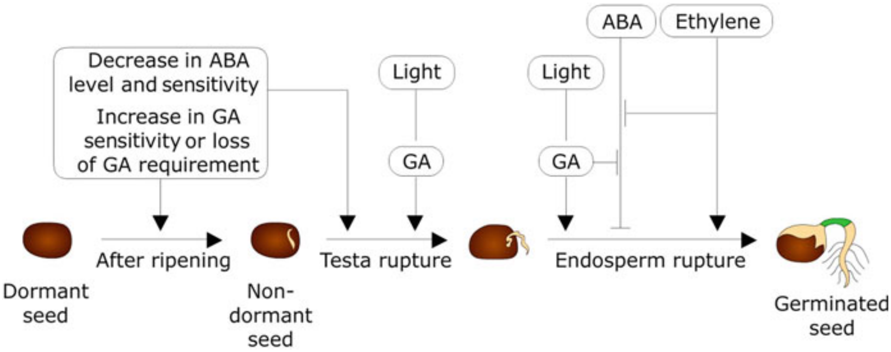

Fig. 28.5 Secondary events in the process of release of seed dormancy. Following imbibition, there is lowering of ABA level and sensitivity. Endosperm and other tissues around the embryo undergo structural changes leading to emergence of radicle

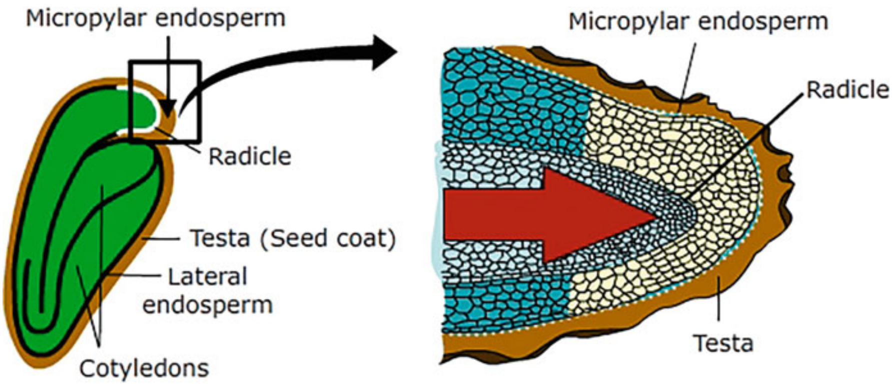

Fig. 28.6 Cellular details showing weakening of endosperm and elongation of radicle

conditions conducive for germination. For example, cypress seeds germinate only in standing water. Seed dormancy also helps in adapting species to the seasonal characteristics of the environment. Thus, peach buds require cold period, so they are distributed only in temperate zone. Photoperiod affects dormancy. Seeds of *Begonia* germinate at photoperiods longer than 12 h. This would synchronize germination in summer.

28.8.2 Geographical Distribution

Seeds of tomato and many other fruits do not germinate until they have been separated from parental fruits. It helps them to achieve distribution/dispersal for their requirement of drying before termination of dormancy.

28.8.3 Spreading Germination Time

Plants develop one of the following mechanisms to spread germination time: (i) *Dormancy dimorphism*: Some weeds produce dimorphic seeds, i.e., seeds are both dormant and nondormant. This phenomenon is common among the members of Asteraceae and Chenopodiaceae. In *Chenopodium album* (fat hen), two kinds of seeds are produced: larger seeds germinate immediately upon release, whereas smaller ones germinate later at varying intervals. (ii) *Sequential dimorphism*: In *Avena fatua* (a grass) and another Compositae member *Asteriscus pygmaeus*, individual seeds along a fruiting axis develop with progressively increasing dormancy. Seeds in the panicle lose dormancy first, and after they are shed, then the next proximal seeds become nondormant. (iii) *Utilizing erratic opportunities to germinate*: *Arabidopsis* seeds are light-sensitive, and they germinate upon exposure to low fluence (2.5 μmolm $^{-2}$) of light, which is equivalent to moon light. Seeds of *Eucalyptus* sp. and *Albizia* sp. have a corky plug in the micropylar region. Fire disrupts this plug leading to penetration of water and oxygen, thereby facilitating germination.

28.8.4 Prevention of Pre-harvest Sprouting

Some degree of dormancy is advantageous, at least during seed development. This is particularly so in cereal crops because it prevents germination of grains while still on the ear of the parent plant. Germination of immature seeds on parent plant is known as **vivipary**. It is a rare phenomenon in angiosperms and is restricted only to mangroves and plants growing in estuaries in the tropics and subtropics.

28.9 Seed Germination

A seed is said to have germinated when the embryonic root emerges from the seed coat or, in other words, embryo growth resumes depending on environmental factors (Fig. 28.7). Seeds of some plants, such as rubber tree, sugar maple, and the willow, are viable for only a week or so, whereas many other seeds appear to retain their viability for several hundred years. The latter category includes seeds of *Mimosa glomerata* which, when kept in dry storage in a herbarium for 220 years, have been reported to germinate after being soaked in water. Similarly, seeds of *Albizia julibrissin* have been reported to germinate after 147 years. Seed germination in parasitic plants is dependent on host-plant signals. Obligate parasites, such as witchweed (*Striga*), must attach to a host within a few days of germination for their survival. Witchweed seeds germinate in response to hydroquinones released from the roots of its host (maize or sorghum). For some seeds, light is a major regulator of germination. Some of the other factors which affect seed germination include water for tissue hydration, oxygen to support aerobic respiration, and suitable physiological temperature. A delicate balance among the levels of various hormones is not only evident during early, mid, and late stages of seed development. Seed germination also exhibits modulation by IAA and GA (Fig. 28.8). Process of seed germination can be considered under five steps:

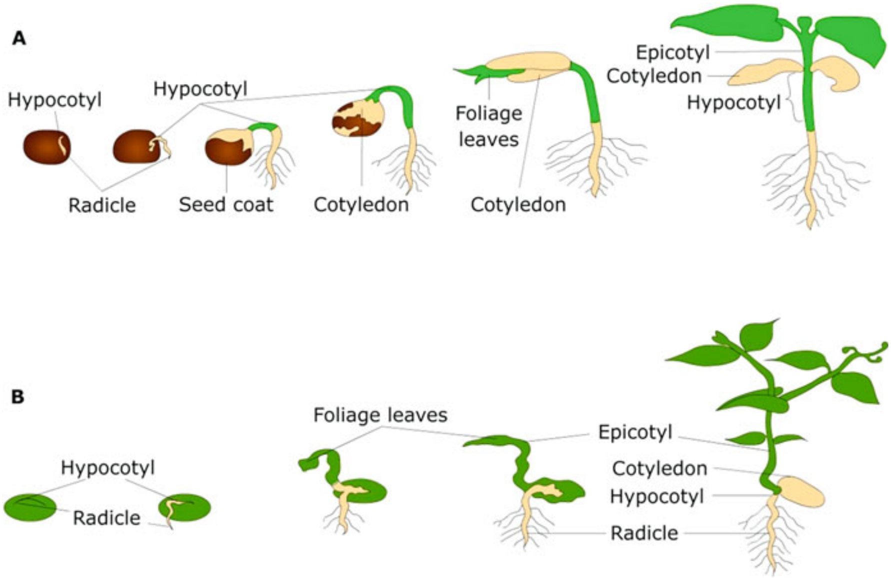

Fig. 28.7 Stages of seed germination in dicots. (**a**) Epigeal type of germination in bean seed where hypocotyl elongates and pushes the cotyledonary leaves above the ground. (**b**) Hypogeal type of germination in pea seed where elongation of epicotyl leads to emergence of first foliage leaves above the soil

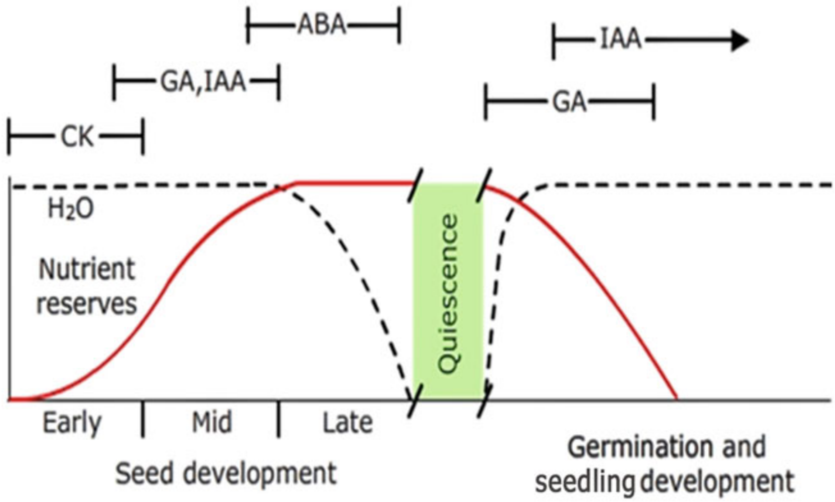

Fig. 28.8 A graphical representation of the changes involving plant growth regulators, water, and nutrients, during seed development, germination, and seedling development. *ABA* abscisic acid, *CK* cytokinin, *GA* gibberellic acid, and *IAA* indole acetic acid

28.9.1 Imbibition

"Dry" seeds usually contain less than 20% water, and many seeds have a water content of less than 5% in dry storage. Quite a few seeds turn nonviable if their water content falls below 30%. They are usually dislodged from the parent plant on to the moist soil and germinate. Mangrove seeds are known to germinate on the mother plant, producing primary roots which grow 10 cm before the seeds are released from the parent plant. Upon falling on the ground, roots penetrate into the mud for seeds to begin their independent existence. Imbibition is a physical process and takes place in both living and dead seeds because of hydration of seed storage polymers. It is the first step in seed germination. Irrespective of dormant or nondormant state, all seeds exhibit imbibition. Dry seeds initially exhibit rapid uptake of water. Water uptake by seeds can be considered under three phases: *Phase I*: Matric potential (ψ_m) is very high in dry seeds. This results in lowering of their water potential creating steep gradient and causing water influx into the seed. Initial rapid uptake of water occurs due to hydration of large biomolecules and electrostatic attraction between water, molecules, and the cell wall constituents, proteins and various other hydrophilic biomolecules. *Phase II:* Water uptake by imbibition gradually declines as all the binding sites for water get saturated, and matric potential (ψ_m) of seed becomes less negative. This phase is considered as "**lag phase**" during which the solute potential (ψ_s) of the embryo becomes more negative due to breakdown of reserve food materials into osmotically active solutes (OAS), and metabolic processes, including transcription and translation, are initiated. *Phase III*: Uptake of water resumes after lag phase due to decrease in water potential in the seed. It causes rapid cell wall loosening and cell expansion in this phase. Uniform uptake of water by seeds under limited water availability condition is at times facilitated by the presence of a mucilage layer on the surface of seed coat. The mucilage hydrates very quickly (within seconds) and generates a pressure of 10–20 MPa (100–200 Atm) which is, at times, sufficient even to break rocks. This pressure is referred as **imbibition pressure**. During this process, swelling of seeds takes place with great force rupturing the seed coat (testa and pericarp) and enabling the radicle to emerge as primary root.

28.9.2 Respiration

Tissue of mature dry seeds contains poorly differentiated mitochondria. However, they contain sufficient enzyme of Krebs cycle and oxidases to generate required amount of ATP to support metabolism for several hours after imbibition during seed germination. In starch-storing seeds (e.g., cereals), repair and activation of preexisting organelles predominate. However, oil-storing seeds produce new mitochondria. Imbibition triggers the activity of respiratory enzymes which are conserved in the dehydrated state of the seeds. After an initial steep rise, a decline in respiration rate is observed until radicle penetrates the soil. Using preexisting mRNA transcript and ribosomes, protein synthesis also begins. This is followed by the release of hydrolytic enzymes and renewed cell division and cell elongation in the embryonic axis. The hydrolytic enzymes digest and mobilize stored food reserves. Glycolytic and citric acid pathways operate, and ATP is produced along with carbon skeleton required for the growth of developing embryo. Although initially seeds may respire anaerobically, but as soon as oxygen is available, they start respiring aerobically. Plowing aerates the soil and facilitates seed germination. Seeds implanted deep in soil may not germinate due to insufficient oxygen. Another reason may be the absence of light in case of photoblastic seeds.

28.9.3 Light Requirement

Light sensitivity of seeds for the release of dormancy and germination has been discussed in Sect. 28.6.5.

28.9.4 Mobilization of Reserves and Growth Regulators

Depending upon the type of seeds, the food reserves may either be stored in the endosperm or in the cotyledons. Regardless of site of storage, the food reserves of the seeds consist of starch, triglycerides, or storage proteins, all of them being insoluble in water. These molecules must be broken down into respective smaller subunits that are soluble in water and can be easily absorbed and transported to growing embryo. In cereal grains, the starch reserves are mobilized from the endosperm to embryo via a shield-like cotyledon (scutellum). The outermost layer of endosperm has specialized cells forming an aleurone layer. The cells of aleurone layer secrete hydrolyzing enzymes, such as α-amylases and proteases, which facilitate the breakdown of stored starch and proteins in the endosperm. Sugars and amino acids so formed are transported to newly formed epicotyl, hypocotyl, radicle, and plumule of the embryo through scutellum. The initiation of the biosynthesis of hydrolytic enzymes is promoted by gibberellic acid released from embryo (Fig. 28.9). The proteases released during seed germination are categorized into four categories depending on their site of action on the polypeptide chain of enzyme: 1. Endopeptidases: These enzymes cleave peptide bonds to yield smaller peptides. 2. Aminopeptidases: They cleave terminal amino acid end of the polypeptide chain. 3. Carboxypeptidases: Amino acids are cleaved by these proteases from the carboxyl end of the chain. 4. Peptidases: They degrade small peptide fragments into amino acids.

Thioredoxin, a regulatory disulfide protein, regulates mobilization of both protein and carbohydrate reserves in developing seedlings. In cereal endosperm, NADPH and a flavin enzyme NADP-thioredoxin reductase reduce thioredoxin, which then reduces disulfide (S-S) groups of many stored enzyme proteins, thereby increasing their solubility which leads to their rapid proteolysis. Thioredoxin also regulates the activity of selected enzymes in cereal grains and legume seeds. Transgenic seeds with altered thioredoxin activity clearly manifest its role in seed germination. Cereal grains with higher activity of thioredoxin have been found to germinate faster, and

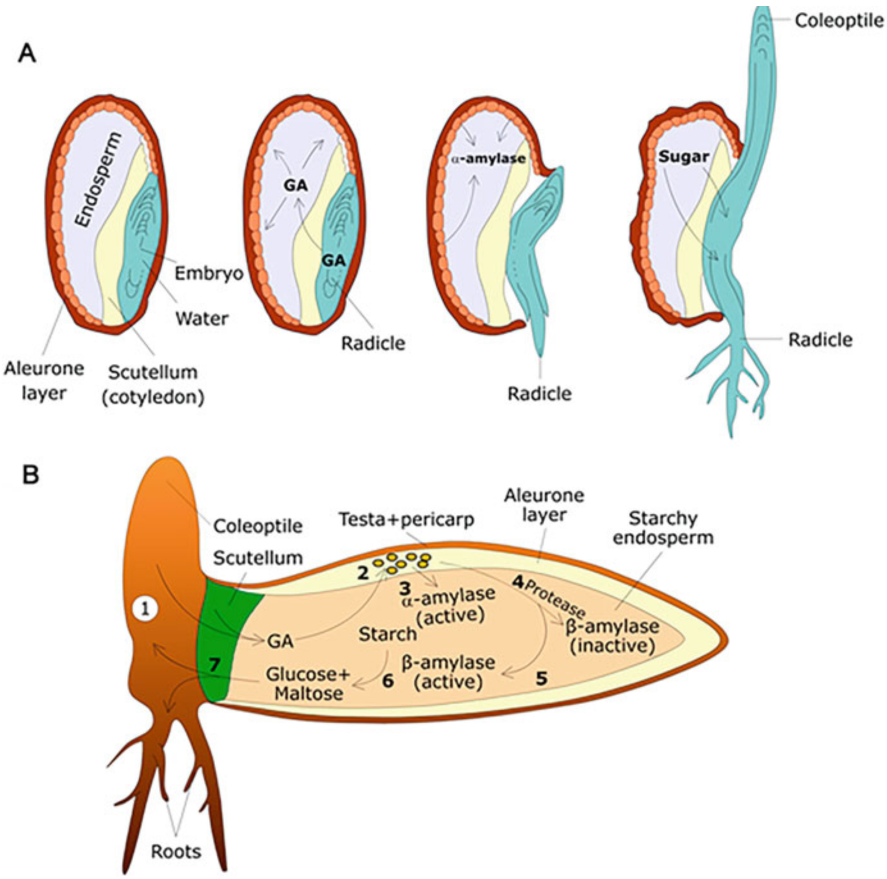

Fig. 28.9 (**a**) Mobilization of reserves and release of growth regulators (GA) during seed germination in cereals. (**b**) The biochemical changes during seed germination in cereal seeds where GA induces release of amylase and other proteases from aleurone layer

downregulation of its activity slows down germination. Some of the proteases are synthesized de novo, while others may be present in the dehydrated seeds in inactive form. In cereals, acid hydrolases (hydrolytic enzymes active at pH between 4 and 5) are synthesized in the aleurone layer. Starch is a major carbohydrate reserve in most plants, consisting of amylose and amylopectin. It is cleaved by two types of enzymes: phosphorolytic enzymes that use Pi to break glycosidic bonds and hydrolytic enzymes that use water to break these bonds. Their actions have been discussed in Chap. 9.

The stored lipids in seeds, triacylglycerols (TAGs), are degraded and converted into glucose as plants are not able to transport fats to other tissues. It involves three organelles: (i) the oleosomes (the oil bodies), where triacylglycerols (TAGs) stored

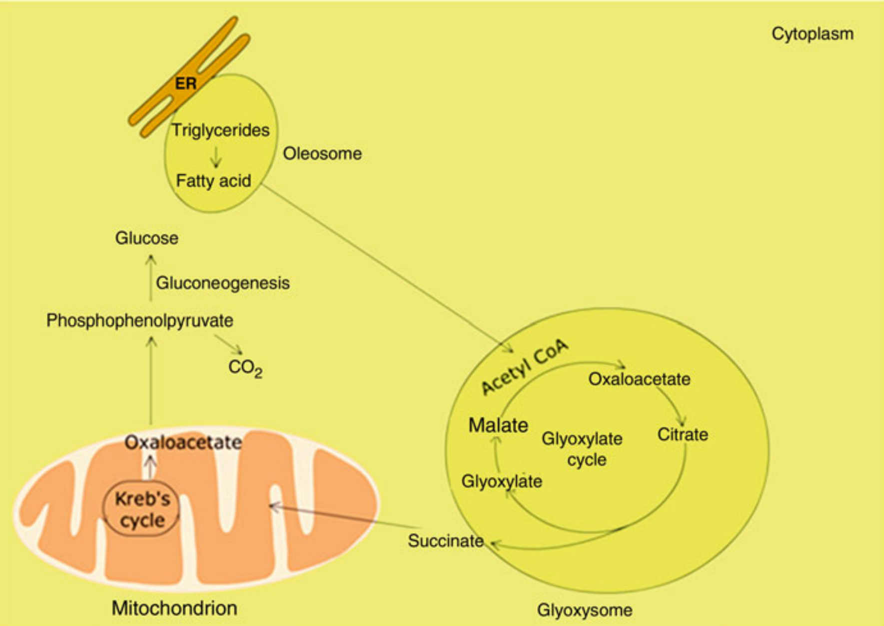

Fig. 28.10 The conversion of lipids into glucose involving oleosome, glyoxysome, and mitochondria during germination in oil seeds

in oil bodies are converted into fatty acids and glycerol; (ii) glyoxysomes (specialized peroxisome), where fatty acids are converted into acetyl-coenzyme A (CoA) by β-oxidation and then to succinate by the glyoxylate cycle; and (iii) mitochondrion, where succinate is either respired or converted to malate which is transported to cytosol for further conversion to hexoses by gluconeogenesis (Fig. 28.10). Mineral elements stored in seeds as complex with phytic acid, namely, myo-inositol hexaphosphoric acid (IP_6), are hydrolyzed by enzyme phytase (a phosphatase that releases phosphate and chelated cations). During seed germination, phytase level increases, making phosphate and other minerals available to help embryo growth and development. The presence of phytates makes the seedling growth independent of external supply of essential elements for few days after germination.

28.9.5 Development of Embryonic Axis into Seedling

Radicle extension is the last event in seed germination. Two distinct phases of DNA synthesis occur in the radicle cells after imbibition. Immediately after imbibition, repair of damaged DNA (formed during dehydration) and synthesis of mitochondrial DNA take place. In the second phase, DNA synthesis associated with cell division occurs. Elongation of radicle is a turgor-driven process after translocation of food has occurred during germination. Breaking of dormancy of many seeds is stimulated by the presence of nitrate in the growth medium. When the parent plant grows in nitrogen-rich soil, seeds accumulate nitrate which is adequate for germination.

Summary

- The plant life begins with seed formation and is renewed when seeds germinate. Seeds are highly dehydrated and quiescent or resting structures and have different shapes and sizes. A seed has a meristematic axis associated with a storage tissue and is enclosed by a seed coat. High amounts of auxin, cytokinins, and gibberellins are present in seeds during early embryonal growth and seed development.
- Embryo is embedded in the tissue laden with reserve food materials which protects it from adverse conditions for long period of time. Seed coat is made up of layers of dead cells that protect the delicate embryo and has a significant role in dormancy of seed. It limits the entry of water and oxygen in the seed. Cotyledons often contain food reserves which are used during the early stages of germination. In most plants, the cotyledons come out of the testa and above the ground where they become green and make food by photosynthesis. The cotyledons eventually fall off, usually after the first foliage leaves have been formed. Almost all seeds contain stored food in endosperm. When seed germinates, hydrolytic enzymes present in the endosperm are activated or synthesized by GA action, resulting in breakdown of reserve food.
- Seed dormancy can be due to structural limitations or imbalance of growth substances. Primary dormancy is induced during seed development, and such seeds are released from the plant in a dormant state. On the other hand, secondary dormancy is induced in mature seeds after release from plants due to various stress factors. Seed dormancy can be coat or embryo-induced. Seed dormancy is affected by light, temperature, internal hormone level, and physiological status of the seed. The first step in breaking the dormancy is imbibition and hydration of tissues. The seed perceives dormancy-breaking signals from environment, and the signals are then passed through different messengers to genes in the nucleus, and seeds overcome dormancy.
- A seed is said to have germinated when the embryonic root emerges from the seed coat or, in other words, resumption of embryo growth is evident in response to different environmental factors. Imbibition is the first step of seed germination. It is a physical process and takes place in both living and dead seeds due to hydration of seed storage polymers. Subsequently, insoluble starch and proteins must be broken down chemically into smaller subunits that are soluble in water and can be easily absorbed and transported to the growing embryo. Radicle emergence is the last event in seed germination.

Multiple-Choice Questions

1. The aleurone layer is specialized outer layer of endosperm, and it is rich in:
   (a) Arabinans and arabinoxylans
   (b) Cellulose and hemicellulose
   (c) Cellulose and pectin
   (d) Arabinans and cellulose
2. Phytates are major storage compound and mainly consist of:
   (a) Sulfur
   (b) Phosphorus
   (c) Iron
   (d) Copper
3. Absence of ABA in seeds leads to:
   (a) Seed dormancy
   (b) Nonviable seeds
   (c) Vivipary
   (d) Delayed germination
4. Photoblastic seeds are usually________ in size:
   (a) Very small
   (b) Large
   (c) Medium
   (d) Variable
5. Strophiole, a special structure present in legumes, plays an important role in:
   (a) Uptake of water during imbibition
   (b) Gas exchange
   (c) Emergence of radicle
   (d) Blocking the entry of water so that seed does germinate precociously
6. Which of the following statement is true for seed?
   (a) Seed has high matric potential and low water potential.
   (b) There is no difference in water and matric potential in a seed.
   (c) Seed coat has low water potential and high matric potential.
   (d) Dry seed has high matric potential and low water potential.
7. The rate of respiration is _________ in germinating seeds:
   (a) Low
   (b) Average
   (c) High
   (d) Not affected
8. Which of the following seeds are non-endospermic?
   (a) Custard apple
   (b) Orchids
   (c) Wheat
   (d) Mango

9. Stratification of seeds is done to:
   (a) Stimulate natural winter conditions
   (b) Prolong shelf life of seed
   (c) Induce dormancy
   (d) Induce imbibition
10. Which of the following is not correct?
   (a) Scarification is the process of removing hard seed coat.
   (b) In nature, scarification can be accomplished by microbial action, fire, and leaching of inhibitors.
   (c) Scarification can also be done by treating the seeds at low temperature.
   (d) Scarification treatment is given to the seeds having seed coat-imposed dormancy.

Answers

1. a 2. b 3. c 4. a 5.a 6.d 7.c
8. b 9. a 10. c

Suggested Further Readings

Baskin JM, Baskin CC (2004) A classification system for seed dormancy. Seed Sci Res 14:1–16
Miransari M, Smith DL (2014) Plant hormones and seed germination. Environ Exp Bot 99:110–114
Roberts J, Downs S, Parker P (2002) Plant growth and development. In: Ridge I (ed) Plants. Oxford University Press, New York, pp 221–274