



Seed Dormancy and Regulation of Germination

P. C. Nautiyal, K. Sivasubramaniam, and Malavika Dadlani

Abstract

Seed germination and dormancy are vital components of seed quality; hence, understanding these processes is essential for a sound seed production system. The two processes are closely interrelated and regulated, both by genetic as well as environmental factors. While dormancy provides an inherent mechanism aimed at the survival of the plant species to withstand adverse external conditions by restricting the mature seed from germinating, the ability of the dehydrated seed to remain viable and produce a vigorous seedling upon hydration under favourable conditions is the key to the survival and perpetuation of the plant species. In addition, quality seed is expected to result in timely and uniform germination under favourable field conditions after sowing to establish a healthy crop stand. Therefore, in seed technology, dormancy is not considered a desirable trait in the seed lots used for sowing. Thus, to achieve the highest germination percentage, understanding the factors controlling these two interlinked and contrasting processes is vital. In seed testing and seed trade, knowledge of seed germination and dormancy is needed for a reliable assessment of seed quality and its planting value, and to make right decisions. Though much is yet to be understood, the present status of knowledge on these aspects has made significant advances, especially in genetic control, molecular mechanism, and physiological and environmental factors influencing germination and dormancy. The

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information compiled in this chapter may help the seed technologists in developing new methods for breaking dormancy and testing germination,

Keywords

Types of dormancy · Regulation of dormancy · Release of dormancy · Types of germination · Hormonal regulation · GA and germination · ABA and dormancy · Induction of dormancy

1 Introduction

Both inductions of seed dormancy and onset of germination are crucial physiological states of seed which determine the success of field establishment after sowing in several crop plants. Seed dormancy and germination are mainly regulated through several physiological processes and environmental factors. Though contrasting in their expression, both processes are equally important for the management and planning of crop cultivation. A low degree of dormancy is seen to be of vital advantage in preventing in situ germination in various crop species, for example, Spanish-type groundnut (Nautiyal et al. 1993, 2001), wheat (Mares 1983), maize (Neill et al. 1987), and rice (Sohn et al. 2021). On the other hand, a deep dormancy would prevent normal germination even under favourable conditions, resulting in poor crop stand. There are reports that interaction between environmental factors (i.e., light, temperature, water status) and growth hormones (i.e., abscisic acid, gibberellic acid and ethylene) play an essential role in dormancy vs. germination. Germination may be seen as a chain of processes transforming a quiescent embryo into a metabolically active one and developing well-differentiated tissues (viz., apical meristems, root and shoot), which are essential for establishing a healthy seedling. The germination process starts with the imbibition of water, followed by a metabolically active phase, during which a series of biochemical reactions take place providing energy and supporting the cellular processes leading to radicle emergence and seedling growth. The metabolically active phase begins with enzyme activation, hydrolysis and mobilisation of stored food reserves. After mobilisation of reserve food material, embryo growth is initiated followed by the weakening and rupture of the seed coat to make way for radicle emergence. These are crucial steps directly related to the seedling establishment and, thus, crop productivity. This chapter discusses fundamental processes underlying regulation of seed dormancy and germination, including the external environmental and internal hormonal factors.

2 Seed Dormancy

2.1 Definition

Seed dormancy has been defined differently by different researchers. Several workers have broadly described it as a state of temporary suspension of the ability of a viable seed to initiate germination, even under favourable environmental conditions (Bewley 1997; Baskin and Baskin 2004; Hiroyuki et al. 2018). On the other hand, a non-dormant and viable seed would germinate when favourable environmental conditions are given (Baskin and Baskin 1998). Thus it is presumed that a dormant seed is unable to germinate due to some inadequacies or possessing some inherent blocks that must be overcome and released to initiate germination (Bewley and Black 1994). The state of dormancy may be differentiated from quiescence—a term commonly used for the phenomenon, where a non-hydrated seed remains non-germinated because of not being provided with adequate conditions like water, temperature or air that are essential for germination. This characteristic is the basis of prolonged storability (also termed longevity) of desiccation-tolerant ‘orthodox’ seeds. Further, it is clear that dormancy is a mechanism that organises the distribution of germination in time or space and having immense ecological significance. It is evident from the fact that seed of several plant species shows variability in the degree of dormancy, which exhibits sporadic release from dormancy resulting in irregular germination. Hence, the significance of temporal dispersal is clearly to help in enhancing spread and survival of the species. The temporal dispersal thus enhances the spread and survival of the species and is more evident in monocarpic than polycarpic species. In nature, seasonal environmental changes (particularly light and temperature), depth of burial in the soil or light penetration through the canopy above ground, and interventions of birds and animals are some of the factors determining seed dormancy and germination processes. Induction of dormancy during the late stage of maturation also renders the seed protection against pre-harvest sprouting which is a desirable feature in many cereal species. It is a well-established fact that environmental temperature regulates both dormancy and germination, while light germination alone (Vleeshouwers et al. 1995; Batlla et al. 2004). Moreover, the role of light in the induction of dormancy is a debatable issue (Bewley and Black 1994; Baskin and Baskin 2004).

2.2 Classification of Seed Dormancy

Different classification systems have been proposed by seed ecologists for different forms of dormancy, whereas seed technologists need an internationally acceptable hierarchical system of and the underlying mechanisms to develop suitable treatments for breaking seed dormancy. Baskin and Baskin (2004) have suggested a modified version of the scheme of the Russian seed physiologist Marianna G. Nikolaeva for classifying seed dormancy. The modified system includes three hierarchical layers, i.e., class, level and type and includes five classes of dormancy: physiological

dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY) and combinational dormancy (PY + PD). The most extensive classification schemes are for PD, which includes three levels and five types of dormancy in the nondeep level, whereas MPD includes eight levels but no difference in their types. PD (non-deep level) is the most common kind of dormancy that occurs in gymnosperms (Coniferales, Gnetales) and in all major clades of angiosperms. Recently, the diversity in kind of seed dormancy and its classification has been reviewed by Ordóñez-Parra King (2022) and Baskin and Baskin (2021).

2.2.1 Morphological Dormancy

Seeds with morphological dormancy (MD) are often characterised by small and underdeveloped embryos, but well differentiated into cotyledon(s) and hypocotyl-radicle (Baskin and Baskin 1998). Embryos in seeds with MD are not physiologically dormant and do not require a dormancy-breaking pre-treatment in order to germinate, these simply need time to complete the development of embryo to grow to full size and then germinate. The period of dormancy in such seeds (that is the time between incubation of fresh seeds and radicle emergence) may extend from a period of a few days to 1–2 weeks, and germination would complete in about 30 days. In addition, the following features are also commonly seen in seeds with morphological dormancy: (a) physical factors such as impermeability of seed coat or pericarp to water and oxygen; (b) chemical factors such as chemical inhibitors (phenols) in pericarp or in seed coat; and (c) mechanical factors (i.e., mechanical resistance of pericarp, seed coat or endosperm to embryo growth). Such seeds also show light sensitivity, at times.

2.2.2 Physiological Dormancy

Most of the species with physiological dormancy (PD) exhibit non-deep dormancy. Further, based on the responses to temperature in breaking dormancy, five types of non-deep PD are recognised. Physiological dormancy is best explained in terms of hormonal balance, in which ABA acts as an inhibitor and GA as a promoter. These hormones simultaneously and antagonistically regulate the onset, maintenance and termination of dormancy (Amen 1968; Wareing and Saunders 1971). Hilhorst et al. (2010) proposed a model for onset of germination and release of dormancy following ABA and GA interaction in response to environment. In this model GA and ABA do not interact directly. While ABA produced by the embryo induces dormancy during seed development, GA promotes germination of non-dormant seeds. Further, the amount of GA required for germination of ripe seeds is determined by ABA concentrations during seed development. Thus, seeds with a low level of ABA produced during their development exhibit low dormancy and require low concentrations of GA to promote germination, whereas those with a high concentration of ABA exhibit deep dormancy, and require higher concentrations of GA. Experimental results on tomato (Groot and Karssen 1992), sunflower (Le Page-Degivry and Garelo 1992) and wild oat (Fennimore and Foley 1998) support this model. Evidences have been presented for the involvement of both ABA and GA in dormancy break in seeds of potato (Alvarado et al. 2000), groundnut

(Nautiyal et al. 2001) and other crops. In addition to ABA and GA, ethylene, a third plant hormone, is also involved in the regulation of seed dormancy and germination in some species (Nautiyal et al. 1993; Kepczynski and Kepczynska 1997; Matilla 2000), possibly by decreasing the responsiveness of the seed to endogenous ABA. Thus, ethylene may promote germination by interfering with the action of ABA (Beaudoin et al. 2000). Studies on wild oats have shown that ABA-responsive genes specific to mRNAs and heat-stable proteins are upregulated, synthesised, and maintained in embryos of imbibed dormant seeds, and decline in non-dormant or after-ripened seeds as a result of GA synthesis and signalling and disappear during seed germination (Li and Foley 1994; Holdsworth et al. 1999; Hilhorst et al. 2010).

2.2.3 Physical Dormancy

Physical dormancy (PY) is mainly referred to the state in which seeds are dormant because of some physical barriers that do not allow imbibition of water into the seed which is the primary requirement of germination. It is mainly due to the water-impermeability of the seed or fruit coat (Jayasuriya et al. 2009). Physical dormancy is reported to be caused by one or more water-impermeable layers of palisade cells in the seed or fruit coat (Baskin Jerry et al. 2000). Typically, PY dormancy breaks both under natural environmental conditions (ambient), or by subjecting to some physical or chemical treatments that helps in the formation of an opening (water gap) or a specialised anatomical structure on the seed (or fruit) coat such as strophiole, through which water moves to the embryo (Baskin Jerry et al. 2000). Similarly in some taxa of Fabaceae, dormancy is reported to be broken by heating which weakens the seed coat in region(s) other than the strophiole (lens), making it water permeable (Morrison et al. 1998). Thus, mechanical or chemical scarification are often effective and simple methods for releasing non-deep physiological dormancy and promote germination.

2.2.4 Combinational Dormancy

In this type of dormancy, two factors are involved to impart dormancy such as seeds with physiological and physical dormancy which can be represented as PY + PD; or morpho-physiological dormancy. This type of dormancy is a combination of impermeability of the seed coat for water uptake, and physiologically dormant embryo. Morpho-physiological dormancy is mostly the result of underdeveloped embryos, combined with physiological inadequacy during embryo development (Baskin and Baskin 2004). Such seeds, therefore, require a combination of dormancy-breaking treatments, for example, a combination of warm and/or cold stratification, followed by GA application for dormancy release.

The physiological component of such dormancy appears to be of non-deep level, for example, freshly matured seeds of some winter annuals, *Geranium* (Geraniaceae) and *Trifolium* (Fabaceae) have some conditional dormancy, which can be broken by after-ripening in dry storage or in the field within a few weeks after maturity, even while the seed coat remains impermeable to water (Baskin and Baskin 1998). Embryos in *Cercis* (Fabaceae) and *Ceanothus* (Rhamnaceae) are more dormant (but non-deep) and require a few weeks of cold stratification, after the PY is broken

and seeds imbibe water before they can germinate. Seshu and Dadlani (1991) observed that dormancy in rice (*Oryza sativa* L.) seed is a result of certain physical and chemical factors associated with both the hull and the pericarp, a type of combinational dormancy. They also reported the role of nonanoic acid, a short chain (C 9) fatty acid, in imposing dormancy and its release by dry heat treatment, a common practice in releasing low dormancy in rice. The relative significance of these substances in cultivars of tropical and temperate origins and their implications in terms of ecogeographic adaptability were suggested. Embryos in *Cercis* (Fabaceae) and *Ceanothus* (Rhamnaceae) are more dormant (but non-deep) and require a few weeks of cold stratification, after PY is broken and seeds imbibe water before they germinate.

2.3 Types of Seed Dormancy in Legumes and Cereals

The contrasting germination and seed dormancy patterns have extensively been reported in chickpea (*Cicer arietinum*) by Sedlakova et al. (2021). In groundnut seed dormancy, which causes huge economic losses due to in situ sprouting at times in Spanish-type varieties (Fig. 1a), is directly associated with the duration of crop maturity, i.e., longer the duration, prolonged is the seed dormancy and vice versa (Nautiyal et al. 2001; Bandyopadhyay et al. 1999). The long-duration varieties of Virginia type showed dormancy for longer duration (63 days), than the Spanish and Valencia types, which showed no dormancy or exhibit it for a shorter period (maximum of 30 days). It was also seen that while in Spanish groundnut varieties,



Fig. 1 (a) Pre-harvest sprouting (in situ seed/pod germination) in groundnut due to unseasonal rain before or during harvest. (b) Pre-harvest sprouting (in situ germination) in sorghum millet due to rain before harvest or during harvest

dormancy is mainly controlled by testa (or seed coat), in Virginia types the seed coat, cotyledons and embryonic axis all contribute to it. The term fresh seed dormancy (FSD) was used for seed germination at high moisture content (>22%) seeds before or during harvest under field condition (Nautiyal et al. 2001).

Pre-harvest sprouting in wheat, barley, maize, rice, sorghum (Fig. 1b), rye and triticale poses a serious problem in crop cultivation (Gualano et al. 2014) due to environmental factors such as temperature, rains and light quality. It seems that a certain degree of dormancy is essential to prevent yield losses in several crop species (Rodriguez Maria et al. 2015). As in seeds of many other species, the antagonism between the plant hormones abscisic acid and gibberellins is instrumental for the inception, expression, release and re-induction of dormancy. Thus, resistance to pre-harvest sprouting could be associated with a number of physiological, developmental, and morphological features of the grains on the spike, including pericarp colour, transparency, hairiness, waxiness, permeability of water, α -amylase activity, and levels of growth substances such as ethylene, ABA, and GA in the embryo (Sohn et al. 2021).

The seed dormancy and pre-harvest sprouting in cereals are important issues in crop production. Pre-harvest sprouting is a matter of serious concern as it results in total loss of seed viability as the seed loses its desiccation tolerance in several cereals such as wheat, barley, maize, rice, sorghum, rye and triticale (Gualano et al. 2014) (Fig. 1b). These cereals mainly originated from both temperate and tropical regions and developed diverse responses to environmental factors such as temperature, rains and light quality. Hence, a short period of dormancy is a desirable agronomic trait to prevent pre-harvest sprouting in cereals (Rodriguez Maria et al. 2015). As in seeds of many other species, the antagonism between the plant hormones abscisic acid and gibberellins is instrumental in cereal grains for the inception, expression, release and re-induction of dormancy, though its induction and regulatory mechanism varies in each species. In oat (*Avena sativa* L.) freshly harvested seeds are dormant at relatively high temperatures (>20–25 °C), which results partly from the structures surrounding or adjacent to the embryo (pericarp, testa and endosperm) and partly due to the embryo itself.

In rice, the pre-harvest sprouting is regulated both by genetic and environmental factors, as well as interactions between these. Further, pre-harvest sprouting resistance could be associated with a number of physiological, developmental and morphological features of the grains on the spike, including pericarp colour transparency, hairiness, waxiness, permeability of water, α -amylase activity and levels of growth substances such as ethylene, ABA and GA in the embryo, all of which play a role in the resistance against pre-harvest sprouting (Sohn et al. 2021).

2.4 Induction of Dormancy

Though dormancy is genetically predisposed, its induction is controlled by various environmental factors, such as temperature, humidity and light during seed development, which significantly influence the onset and release of seed dormancy. This

underlines the need to understand the effect of changing environmental conditions on seed germination under field conditions. Integrating research techniques from different disciplines of biology, i.e., transcriptomics, proteomics and epigenetics, could help in understanding the mechanisms of the processes controlling seed germination, and induction of dormancy in developing seed (Kluczyńska and Pawłowski 2021). Seed dormancy is influenced by both short- and long-term effects of climate. Long-term effects may result in inheritable dormancy differences through species, ecotype and clonal variation (Montague et al. 2008), whereas short-term effects are specific to weather conditions during seed maturation (Huang et al. 2015), or germination. Dormancy, that is observed early in the seed development process or induced by the mother plant, is known as primary dormancy, while secondary dormancy is imposed by the harsh environmental conditions unfavourable for seed germination (Nadella and Foley 2003).

2.4.1 Primary Dormancy

Several workers have shown that ABA synthesis in the embryonic axis during seed maturation and its continued synthesis *de novo* is an essential requirement for the induction and persistence of dormancy (Ketring and Morgan 1969). It is also reported that ABA controls the expression of specific ABA-responsive genes, such as a set of late embryo abundant proteins (LEAs), which control dormancy in the developing seed, as seen in many cereal crops with some degree of primary dormancy that do not germinate to escape unfavourable conditions (Hilhorst 2007; Hilhorst et al. 2010).

2.4.2 Secondary Dormancy

There are several reports mentioning that secondary dormancy may be induced by environmental conditions, such as high temperature and hypoxia (Grahl 1965; Leymarie et al. 2008; Corbineau and Come 2003). The experiments conducted with barley and oat found that induction of thermodormancy was apparent after 3–8 h of incubation at 30 °C, and was maximum after 1–3 days (Leymarie et al. 2008). In addition, induction of thermodormancy requires a critical moisture content in the embryo (approx. 40–50% dry weight basis) (Hoang et al. 2012) and develops concomitant with activation of the cell cycle (Gendreau et al. 2008). Secondary dormancy can also be imposed during imbibition at low temperatures (10–15 °C), combined with low oxygen tensions in seeds having primary dormancy (Hoang et al. 2014).

2.5 Phytochrome and Seed Dormancy vs. Germination

Photoperiod sensitivity in plants, a quantitatively inherited trait which has many biologically important consequences, is regulated through the phytochromes—receptor of the light stimulus. Hence phytochromes, members of a duplicated-gene family of photoreceptors, are the most important environmental sensors in plants. Phytochromes exist in two forms. Synthesised in dark, phytochrome remains in a

biologically inactive (Pr) form, which upon exposure to the light get converted into biologically active form (Pfr). This process of photo conversion to the far-red light-absorbing (Pfr) form is optimised at red wavelengths. Photo conversion of Pfr, back to the biologically inactive Pr form is optimised at far red wavelengths, resulting in a dynamic photo equilibrium of Pr and Pfr in natural light conditions. The basic mechanism of phytochrome signalling involves a physical interaction of the photo-receptor with the PHYTOCHROME INTERACTING FACTORS (PIFs)—a sub-family of bHLH (basic Helix Loop Helix) transcription factors (Ngoc et al. 2018). This system is reported to enable plants to alter gene expression rapidly in response to fluctuations in the light environment. In addition, five phytochrome genes (PHY, A-E) are considered to be mainly associated with seed dormancy (Goosey et al. 1997; Tomoko 1997).

The enabling role of gibberellins (GAs) in seed germination is well documented (Yamauchi et al. 2007), and the effect of light on GA signalling proteins is also suggested. The GA-deficient mutants were unable to germinate without exogenous GA application, whereas GA signalling mutants produced defective phenotypes (Steber et al. 1998; Bassel et al. 2004). Yamaguchi et al. (1998) reported that one of the two 3- β -hydroxylase enzymes (encoded by the GA4H gene) is induced by the phytochrome in germinating seeds. Crucial in this process are the DELLA proteins which repress GA action. Among various DELLA proteins, RGL2 (repressor of GA1-3 like 2) plays the major role in regulating seed germination. During dormancy release and seed germination, the change in the GA content and its expression is gene-regulated (Yamauchi et al. 2007). An important signal transduction component of light-induced germination is the bHLH transcription factor PIF1 (Phytochrome Interacting Factor 1), also known as PIL5 (Phytochrome-Interacting factor 3-Like 5) (Castillon et al. 2007), which binds to Pfr and causes proteasome degradation. Similarly, alteration in GA level is also brought about by the repression of GA biosynthesis genes, activation of GA2ox gene, and genes encoding DELLA proteins. Somnus (SOM) which encodes a nucleus-localised CCCH-type zinc finger protein, is another gene acting downstream of PIL5 (Kim et al. 2008), suggesting that PIL5 regulates genes regulating ABA and GA metabolism partly through SOM.

Molecular control of seed dormancy and germination has been reviewed extensively at the gene action level by Garello et al. (2000), Finch-Savage William and Leubner-Metzger (2006), Matilla Angel (2020) and Faiza et al. (2021), which indicate a major role of the DELAY OF GERMINATION (DOG) genes in the regulation of germination and dormancy. Available information also suggests that binding of DOG1 to Protein Phosphatase 2C ABSCISIC ACID (PP2C ABA) Hypersensitive Germination (AHG1) and heme are independent processes, but both are essential for DOG1's function in vivo. AHG1 and DOG1 constitute a regulatory system for dormancy and germination.

2.6 Methods to Release Dormancy

The above discussion elaborated the significance of seed dormancy, its regulation and release in nature. However, from the seed technological perspectives, germinability remains the most crucial factor in crop establishment ensuring uniform emergence and for maintaining optimum plant population, for which knowledge of dormancy behaviour in different species, and methods to release these are vital. Various physical, chemical or physiological treatments may be applied to release different levels of dormancy.

2.6.1 Scarification

Scarification is the most common method of breaking seed dormancy in hard seed coat type. This literally mean creating a scar on the seed coat so that water gets its entry into the seed and hydrates the embryo. Seeds can be scarified following any of the means such as physical and chemical treatment. In chemical treatment, seeds can be treated with commercial-grade (95%) H_2SO_4 @ 100 mL/kg or a strong alkali, i.e., NaOH (20%) for 2–3 min followed by washing in running water to remove the traces of acid or alkali. The duration of treatment may vary depending on the degree and proportion of hardness of the seed coat. Acid scarification is employed in legumes (blackgram, green gram), rose, tamarind, and *Acacia* spp., etc., whereas alkali treatment is effective in scarifying cashew drupes. Physical methods using heat or mechanical abrasion are also employed to release hard seededness. Also, exposing seeds to high temperatures ruptures the seed coat, whereas puncturing or clipping the abaxial end of the seed coat helps imbibition. Seeds of chickpea, *Acacia* spp. hedge lucerne respond well to soaking in hot water for 10–15 min to soften the seed coat. Exposure to high temperature (~50 °C) also enables dry seeds to overcome dormancy in many cereals. Dry heat treatment for 7–14 days removes dormancy of rice seeds. In some tree species (i.e., Teak) the heat generated by natural or created fire scorches the pericarp of the seed making the seed coat permeable, and resulting in germination. Besides, compounds produced by the charring of plant materials are also reported to have a stimulating effect on dormancy release in many woody species (Keeley and Fotheringham 2000; Baskin et al. 2002).

2.6.2 Stratification

The seeds having morpho-physiological dormancy may be treated following stratification. In this process, seeds are treated with GA_3 or thiourea to counter the influence of ABA. Cold stratification is another way to remove dormancy and it involves placing the seed in stratified layers of wet sand/soil/sawdust/absorbent cotton wool in 1:4 ratio, and exposing them to temperatures of 3–5 °C for 2–3 days to several months, depending on the type of seed. This treatment is common to overcome seed dormancy in seeds requiring after-ripening period. In this case seed is shed with underdeveloped embryos. In some species, seeds are fully soaked in cold water, i.e., 3–5 °C for 48 h. After draining the water, seeds are mixed with moist sand (1:4 ratios at 20–25 °C) or alternating temperatures of 20–30 °C for a period of 2–6 weeks, depending on the species to overcome the morphological dormancy (i.e., oil palm).

2.6.3 Leaching of Metabolites (Inhibitors)

Leaching simply is a washing off the inhibitors present in seed or fruit coat by soaking or placing under running water. It mainly, involves soaking seeds in water for some time (i.e., 2–4 h to 3 days). In prolonged soaking change of water once in 12 h is a must to avoid fermentation or decay. Seeds soaked in running water for a day to leach out the inhibitors such as cyanides and phenolic compounds as reported in sugar beet (Kumar and Goel 2019).

2.6.4 Treating Seed with Chemical Activators and Growth Hormones

Seed dormancy when present mainly due to the presence of inhibitors (mainly ABA) may be subjected to prolonged washing. Also, such dormancy may be released by application of GA and kinetin (100–1000 ppm). In addition, GA₃ and KNO₃ are used as light substituting chemicals and exhibited germination in tomato seed that require light for germination. Thiourea can be used for seeds that require both light and chilling treatment in lettuce (see chapter “Testing Seed for Quality”).

3 Seed Germination

Germination could be defined in the physiological terms as the metabolic activation of seed upon hydration, culmination with ‘chitting’ or protrusion of the radicle through the seed coat. However, a seed technologist may define it as ‘the emergence and development of seedling from embryo, having the essential functional structures indicative of the ability to produce a normal seedling under favourable conditions’ (Lawrence and Miller 2001; Parihar et al. 2014). Under field conditions a seed is considered as germinated when it emerges completely out of the soil which is referred as ‘field emergence’. Thus, seed germination is not only the first crucial step in the life cycle of plants, it also determines the crop stand for obtaining an optimum plant population, and hence is crucial in agricultural production.

However, even for agronomic success, a basic understanding of the process of germination could be useful. Nature has evolved an intrinsic mechanism of regulation of germination and dormancy that has many ecological advantages, a knowledge of which could be applied by the seed technologists for practical use. This includes a number of mechanisms evolved by the mother plant, such as the hard outer tissues of seeds; the seed coat which is derived from the ovule integuments, or the pericarp, which is the maternal fruit tissue; which regulates the physiological behaviour of the progeny seeds. In addition, physiological and biochemical changes, responses of seeds to environmental cues that can trigger germination, and morphological changes during germination, all of which can impart a direct or an indirect influence on the survival and growth of seeds and seedlings and vegetative growth which consequently affect yield and quality. There are several reviews on physiological aspects of seed germination including dormancy, plant-water-relations, environmental factors and hormonal control (Finch-Savage William and Leubner-Metzger 2006; Holdsworth et al. 2008; Karin et al. 2011; Gerardo et al. 2020). Similarly, the speed of germination is an important parameter to measure seed

vigour and models have been developed for calculating this (Jardim et al. 2021; Chao et al. 2021), which could provide a more accurate assessment of the planting value of the seed.

Several intrinsic factors including genetic control, regulation by hormones and chemical stimulants, and cellular repair processes (Loic et al. 2012) have been examined to fully understand the process of germination. The current advances through the post-genomics approaches have drawn special attention to three main aspects: (a) the translational control of germination and the role of stored components, (b) the importance of metabolic transitions in germination, and (c) the search for biomarkers of seed vigour.

3.1 Morphology of Seed Germination

Irrespective of the number and structure of the cotyledons, two types of seed germination are seen in nature based on their fate upon germination. It is basically of two types as could be seen in bean and pea seeds (Fig. 2). Although these seeds are similar in structure and are from the same taxonomic family. These two forms of seed germination and seedling emergence are commonly known as epigeal and hypogeal. As literary meaning of epigeal is defined as germination above ground, is a characteristic feature of bean seed and is considered more primitive than the hypogeal germination, which is below into the soil (King Keith 2003). Further, it could be elaborated that in epigeal germination the cotyledons are raised above the ground where they continue to provide nutritive support to the growing points. On the other hand, in hypogeal germination, as in pea seeds, cotyledons or comparable storage organs remain under the soil while the plumule pushes upward and emerges

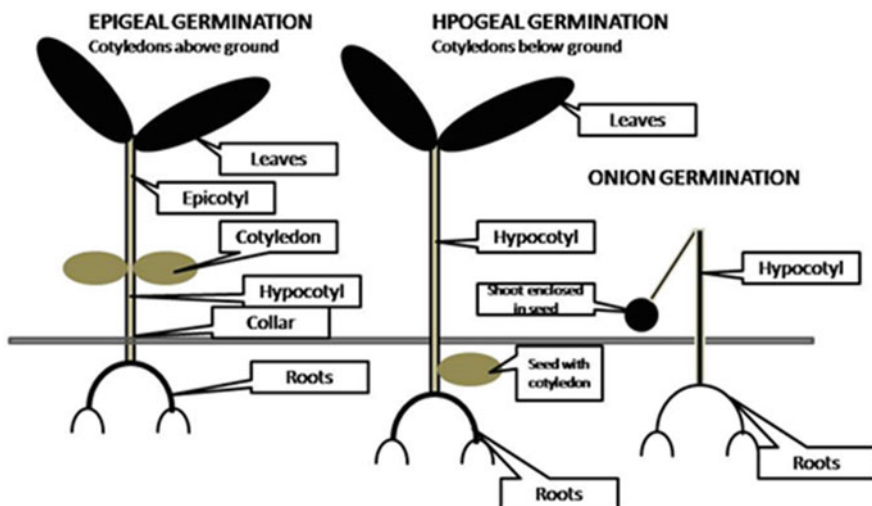


Fig. 2 Types of germination

above the ground. Understanding the type of germination is useful during preparation of beds, sowing, planning, as well as evaluating the field emergence (i.e., counted based on germinated and healthy seedlings).

3.2 Metabolic Processes During Seed Germination

Seed germination is the result of a series of physiological, biochemical and morphological changes which are responsible for germination, seedling survival and vegetative growth of various plant parts that influence both field emergence and stand establishment. Dry seeds are usually at very low water potential, in the range of -350 to -50 MPa. The metabolic activation of a quiescent seed starts with the absorption of water, which is majorly determined by the tissues surrounding the radicle. In soft-coated seeds (meaning water-permeable seed coat) water imbibition initially is almost entirely a physical phenomenon up to the start of a steady phase II.

The weakening of these tissues by enzymatic action is a key event regulating the timing of radicle emergence. And it is suggested that endo- β -mannanase is involved in the weakening of tissues in this process. It is still speculated that it may not be the only determinantal factor for radicle emergence (Loic et al. 2012) as several other factors are also influencing the radicle emergence under natural conditions.

The process of seed germination, thus, may be categorised into three major phases: phase I, characterised by rapid water imbibition; phase II, characterised by reactivation of metabolism, cell elongation and chitting; and phase III, characterised by rapid cell division and coinciding with radicle growth. The phase II is most crucial during which physiological and biochemical processes such as hydrolysis of food reserves, macromolecular biosynthesis, respiration, reorganisation of subcellular structures, and cell elongation are reactivated that play a key role in the onset of germination (Bonsager et al. 2010). In addition, phase II is also critical in invigoration of seed after a period of drying (see chapter “Seed Vigour and Invigoration” for more). After the onset of germination, stored and de novo synthesised messenger RNAs (mRNAs) play important roles, as germination relies both on the quality and specificity of the transcription and translational apparatus and on posttranslational modifications such as carbonylation, phosphorylation and ubiquitination (Loic et al. 2012).

3.2.1 Hydrolytic Enzymes and Seed Germination

Various metabolic processes, including activation or synthesis of hydrolytic enzymes for breaking down of stored starch, protein, lipid, hemicellulose, polyphosphates and other reserve food materials into simple carbohydrates, get activated in a fully imbibed seed. There is an elevation of oxygen requirement, with the rise in the activities of mitochondrial enzymes involved in the Krebs cycle and electron transport chain (Mayer and Poljakoff-Mayber 1989). The hydrolysed food material is the source of energy that provides the carbon skeleton for growth and development of juvenile seedling.

Such metabolic processes during seed germination in several crop species have been reviewed from time to time by several workers (Loic et al. 2012; Renu 2018).

3.2.2 Hydrolysis of Starch

In monocot seed carbohydrates represent the primary storage reserve. It is well documented that α -amylase in the aleurone layers of the monocot seeds plays an important role in hydrolysing the endosperm starch into sugars, which provide the energy for the growth of roots and shoots. Starch, stored in the endosperm is reported to be hydrolysed rapidly during germination, in *Oryza sativa* (Palmiano and Juliano 1972), *Sorghum bicolor* (Elmaki et al. 1999) and *Avena sativa* (Xu et al. 2011) seeds. In these seeds, most hydrolytic enzymes are produced in the aleurone or scutellum in response to germination signals. Kaneko et al. (2002) using mutants defective in shoot formation, and epithelium cell development reported that synthesis of active GA in the epithelium is important for α -amylase expression in the endosperm. In addition, the role of calcium might be expected to involve amylase stability, and to have a much more complex involvement in regulating enzyme activities. The amylase activity is regulated by the concentration of reducing sugars in vivo in both cotyledons and axes which increases gradually, while the starch decreases (Wang et al. 2011). Though starch, protein and fat reserves in dry seeds were not found significantly correlated with germination percentage or speed of germination, soluble sugars and soluble protein contents at different germination stages are reported to be positively correlated with germination rate in some grassland species (Zhao et al. 2018).

3.2.3 Hydrolysis of Proteins

During seed germination and seedling development, hydrolysis of proteins from reserve food material generates free amino acids, these are used as the building blocks for protein synthesis in endosperm and embryo (Tully and Beevers 1978). In addition, carboxypeptidase in combination with cysteine proteinase facilitates the flow of protein hydrolysis. The other key enzymes catalysing protein hydrolysis and biosynthesis in germinating seed are proteinases, proteases, legumin-like proteinase (LLP), metalloproteinase and aminopeptidases.

3.2.4 Hydrolysis of Lipids

During the process of germination in the oil-rich seeds, simple sugars are the end products of the lipid breakdown, which in growing tissues acts as an important regulatory agent. In developing legume seeds a strong negative association is commonly seen between accumulation of storage proteins and storage lipids. Lipids are stored in the form of triacylglycerols in oleosomes and may comprise 35–40% of seed dry weight in oil-rich seeds (Graham 2008). As the germination progresses, triacylglycerols are hydrolysed to free fatty acids and glycerol molecules. The glycerol, thus released, is further metabolised to the glycolytic intermediate dihydroxyacetone phosphate (DHAP) for the synthesis of sugars, amino acids (mainly asparagine, aspartate, glutamine and glutamate) and carbon chains required for other macromolecules for sustaining the embryonic growth (Quettier and Eastmond

2009). The flow of lipid-derived carbon skeletons to amino acids was illustrated in lupin seeds, and at least four alternative or mutually complementary pathways of carbon flow from the breakdown of storage lipids to newly synthesised amino acids have been suggested (Sławomir et al. 2015). Thus, lipases are the most important group of hydrolytic enzymes associated with the lipid metabolism during germination which catalyse the hydrolysis of ester carboxylate bonds releasing fatty acids and organic alcohols (Perreira et al. 2003). There are reports of a sugar-dependent lipase in *Arabidopsis* (Quettier and Eastmond 2009), activity of which may be regulated by the available sugars. However, the activities of the key enzymes in glycolysis, pentose phosphate pathway (PPP), the tricarboxylic acid cycle (TCA cycle), and amino acid metabolism investigated during germination in several species, reveal that glyoxylate cycle predominated over the TCA-cycle pathway in seed mitochondria.

The glyoxylate cycle (GC) plays a crucial role in breaking down the lipids in germinating seeds. The beta-oxidation of fatty acids releases acetyl CoA, which is metabolised to produce 4- and 6-C compounds. Thus, besides providing NADPH for biosynthetic reactions in germinating seeds (Perino and Come 1991), in the process of GC, the stored lipids are converted to glucose (gluconeogenesis), the main respiratory substrate utilised during germination and seedling establishment (Muscolo et al. 2007). The activity of the key enzymes of glyoxylate-cycle, i.e., isocitrate lyase and malate synthetase found to be remarkably high during seed germination after the emergence of radicle and reaching a maximum at 8 days in a sesame an oil-rich seed (Hyun-Jae et al. 1964). The action of the two glyoxylate cycle enzymes isocitratelase (ICL) and malate synthase (MS) is essential in the process of germination oilseeds in bypassing the decarboxylation steps of the TCA cycle. In this reaction, 2 mol of acetyl-CoA are introduced with each turn of the cycle, resulting in the synthesis of 1 mol of the four-carbon compound succinate that is transported from the glyoxysome into the mitochondrion and converted into malate via TCA cycle. The malate, thus formed, is exported to cytosol in exchange for succinate and is converted to oxaloacetate. In addition, phosphoenol pyruvate carboxykinase (PEP-CK) catalyses the conversion of oxaloacetate to phosphoenol-pyruvate which fuels the synthesis of soluble carbohydrates necessary for germination (Muscolo et al. 2007).

3.2.5 Hydrolysis of Phytic Acid

The phytic acid (inositol hexaphosphate or IP6) is the principal form of storage of total phosphorus (P) in legumes and cereal seeds (Jacela et al. 2010). Phytin is mainly stored in protein bodies in the aleurone layer and scutellum cells of most seeds. In germinating seeds phytin is hydrolysed by phytase, an acid phosphatase enzyme (Raboy et al. 1991) releasing phosphate, cations and inositol which are utilised by the developing seedling. In addition, IP6-related compounds such as pyrophosphate containing inositol phosphates (PP-IP) play a vital role in providing Pi for ATP synthesis during the early stages of germination. Phosphate metabolism is one of the negatively affected processes under various stressful environments. Under stressed conditions, the restriction of growth and phosphorus availability

result in enhancement of the activity of phosphatases to produce Pi by hydrolysis that modulate mechanism of free phosphate uptake.

The hydrolysis of major seed reserves during germination can be broadly classified as:

Stored seed reserve	Key enzymes	Primary products
Starch	Amylases, glucosidases	Glucose
Proteins	Proteinases	Amino acids
Fats	Lipases	Fatty acids and glycerol
Phytin	Phytase	Inositol, PO_4^{2-} , Ca^{2+} , Mg^{2+}

In addition, complex carbohydrates such as hemicelluloses, mannans and galactomannans, which are primarily structural components of the cell wall, and play an important role in seed germination, are also known to undergo hydrolysis and provide respiratory substrate to the germinating seeds in some species (Fincher 1989; Pandey et al. 2009).

3.3 ROS Function

Oxygen, the basic life support system for respiration during germination, also generates reactive oxygen species (ROS), such as singlet oxygen ($^1\text{O}_2$), superoxide ($\text{O}_2^{\bullet-}$) or hydroxyl ($\cdot\text{OH}$) radicals, and hydrogen peroxide (H_2O_2). These are considered as the main ROS involved in cellular signalling (Petrov and Van Breusegem 2012). The ROS is accumulated in seed during dry storage also, but much of these are quenched during the initial water imbibition phase. The controlled generation of ROS plays an important role in the perception and transduction of environmental conditions that control germination. When these conditions are permissive for germination, ROS levels are maintained at a level which triggers cellular events associated with germination, such as hormone signalling. It has also been reported that the spatiotemporal regulation of ROS production, in combination with hormone signalling, influences cellular events involved in cell expansion during germination (Christophe 2019). Accumulation of H_2O_2 on the other hand, in association with the oxidative damages to the antioxidant machinery, is regarded as the source of stress that may suppress germination (Chmielowska-Bkak et al. 2015). Matilla (2020) suggested a link between the homeostasis of the reactive oxygen species (ROS) and seed after-ripening (AR) process, wherein the oxidation of a portion of seed long-lived (SLL) mRNAs appears to be related to dormancy release.

3.4 Nitrogenous Compounds and Seed Germination

Promotion of seed germination by the exogenous application of nitrates is known in a wide range of plant species. The effect of nitrate compounds on promotion of seed germination is best realised in combination with other optimising factors such as

temperature or light (Eremrena and Mensah 2016). Among all such compounds potassium nitrate (KNO_3) is the most widely used chemical for releasing seed dormancy and promoting germination. For this purpose, the Association of Official Seed Analysts (AOSA) and the International Seed Testing Association (ISTA) recommend solutions of 0.1–0.2% KNO_3 for optimising germination tests of many species, which show low/shallow dormancy patterns (see chapter “Testing Seed for Quality”). The detrimental effect of salts on seed germination, seedling growth, mitotic activity and chromosomal aberrations were found significantly reduced by the application of KNO_3 (Kursat et al. 2017). Similarly, KNO_3 solutions are among the most commonly applied priming chemicals for enhancing seed germination by improving uniformity and speed of germination (Shin et al. 2009; Thongtip et al. 2022).

3.5 Mobilisation of Reserve Food Material

Once the seed storage reserves are hydrolysed into usable metabolites, mobilisation of these from storage tissues to growing points is a critical step ensuring supply of nutrients for the growth of the developing seedling until it becomes autotrophic. This process determines early vigour in developing seedling for crop establishment under field conditions. The first step in the mobilisation of food reserve is hydrolysis of sugar and to provide it to the germinating seed embryo. In addition to the hydrolysis of carbohydrates in the endosperm or cotyledons, it is also released from the catabolism of lipids. Similarly, a part of the complex carbohydrates are mobilised and utilised by the seed to support early seedling development (Bewley et al. 2013). Similarly, sucrose constitutes a significant reserve in the scutellum which is efficiently consumed by the growing embryonic axis, as seen in maize seed, where a net flow of sucrose takes place from the scutellum to the growing embryo axis during germination. Sucrose and hexose transporters, as well as H^+ -ATPase, become fundamental in the transport of nutrients during radicle elongation, required for successful germination (Sanchez-Linares et al. 2012). In cereals, where starch is the major food reserve, starch—the primary source of nutrients stored in the endosperm—are broken down by enzymes synthesised and secreted by the aleurone and scutellar tissues, and transported to the endosperm. The sugars are transported back to nourish the growing embryo. However, often the increase in soluble sugars in the embryo is not concomitant with a decrease in starch in the endosperm, suggesting that sugars originated mostly from the catabolism of lipids.

In oil-rich seeds such as sunflower in which soluble sugars and starch constitute only about 2.2% of the cotyledon dry mass, lipids are the main seed reserves mobilised during germination, while proteins are the second most utilised reserves (Alencar et al. 2012). In groundnut seeds lower seed-weight was found associated with insufficient supply of reserve food materials resulting into poor vigour of seedlings (Nautiyal 2009; Nautiyal and Yadav 2019). In addition, the hormonal metabolism and signalling leads the seed to germinate. Germination essentially depends on the resumption of cell cycle after a period of quiescence. Hence, entry

into G1 and progression from G1 to S states may represent an important control of the cellular events in early seedling development (Maria et al. 2005). Based on the expression analysis of cell cycle genes with mRNA in situ localisation, β -glucuronidase assays, and semi-quantitative reverse transcription-polymerase chain reaction (RT-PCR), Maria et al. (2005) showed that transcription of most cell cycle genes was detected only after completion of germination. They, however, suggested spatial and temporal expression profiles of cell cycle control genes of importance in germinating seeds of *Arabidopsis* and white cabbage (*Brassica oleracea*).

3.6 Hormone Metabolism and Signalling

To understand the molecular mechanisms underlying the process of after-ripening (seed dry storage) in triggering hormone-related changes and dormancy decay in wheat, temporal expression patterns of genes related to abscisic acid (ABA), gibberellin (GA), jasmonate and indole acetic acid (IAA), their role in signalling and levels of the respective hormones were established in dormant and after-ripened seeds in both dry and imbibed states (Liu et al. 2013; Wang et al. 2020).

To unravel the complex interplay of plant hormones and novel signalling molecules that regulate germination, and to determine the mechanisms of signal transduction are the major aims of seed biology studies. Studies on the involvement of plant hormones have revealed the novel aspects of seed physiology and the complex metabolic balance between multiple hormones during germination and development (Preston et al. 2009; Kanno et al. 2010). Of various plant hormones, ABA and GA unquestionably play the most critical roles in regulating the processes of dormancy and germination. ABA induces the expression of LEA proteins, which become abundant during the late stage of seed maturation, which is characterised by rapid dehydration. Hence, LEA proteins are suggested to act as chaperones to protect macromolecular structures against desiccation injury (Nautiyal and Shono 2010). In addition, it also exerts an inhibitory effect on the metabolic processes triggering precocious germination of developing seeds on the mother plant (pre-harvest sprouting) thereby allowing the maturation process to be completed and maintaining the economic value as well as quality of seeds at harvest maturity. However, to germinate successfully a non-dormant seed must undergo certain changes counteracting the inhibitory effects of ABA and synthesise tetracyclic diterpenes, the gibberellins (GAs), which are essential to activate germination (Loic et al. 2012), decrease the sensitivity and biosynthesis inhibition to reduce the active level of ABA (Faiza et al. 2021). In addition, synthesise tetracyclic diterpenes, the gibberellins (GAs), which are essential germination activators (Loic et al. 2012). High levels of bioactive ABA found in imbibed dormant seeds of *Arabidopsis thaliana* (Ali-Rachedi et al. 2004) further confirmed the idea that the ABA/GA ratio regulates the metabolic transition required for germination.

Production of GA in the embryos of the germinating wheat seed, on the other hand, was found to diffuse to aleurone layer initiating a signalling cascade in the

cellular system. This result in the synthesis of α -amylases and other hydrolytic enzymes which are then transported to the endosperm to hydrolyse the food reserves. A variety of cellular processes in plants are under the control of phytohormones which play key roles and coordinate various signal transduction pathways under abiotic stress, as well as regulating germination. During the early phase of seed germination in *Arabidopsis*, a decrease in the contents of germination inhibitors jasmonic acid (JA) and salicylic acid (SA) and an increase in the levels of auxins were recorded (Ali-Rachedi et al. 2004), suggesting that both JA and SA act as negative regulators of germination. Auxins are considered to be regulating the process of germination via a crosstalk with GAs, ABA and ethylene (ET). Similarly, the brassinosteroid signals could stimulate germination by decreasing the sensitivity to ABA. Molecular and genetic bases of hormonal interactions or crosstalk regulating seed germination have recently been reviewed by Gerardo et al. (2020).

Further, there are reports suggesting epigenomic modulation of the expression of genes regulating or influencing dormancy, maturation and germination. For example, specific chromatin modifiers and re-modellers have been reported to promote seed dormancy or germination by enhancing or repressing the expressions of specific gene subsets, respectively (Rajjou et al. 2004; Loic et al. 2012; Wang et al. 2013; Matilla 2020). Also, dry seeds are shown to accumulate RNAs whose abundance change towards a “germination-friendly” transcriptome (Nakabayashi et al. 2005). Similarly, Karrikins, a group of plant growth regulators found in the smoke of burning plant material is reported to stimulate seed germination in *Arabidopsis* spp. by enhancing light response (Nelson et al. 2010), mimicking a signalling hormone.

3.7 Ethylene and Other Growth Regulators

Ethylene (ET), the smallest gaseous hormone, plays an important role via crosstalk with other hormones in various activities of plants such as seed germination, seed dormancy, plant growth and developmental processes. It can stimulate seed germination and overcome dormancy in many species. For instance, the inhibitory effects of high temperature on seed germination of lettuce can be overcome by exogenous ethylene. Significant progress has been made in unveiling ET crosstalk with other hormones and environmental signals, such as light (Matilla 2007; Jalal et al. 2020; Loic et al. 2012). Similarly, several other plant hormones, i.e., brassinosteroids, salicylic acid, cytokinin, auxin, jasmonic acid and oxylipins are also known to influence seed germination process in different ways. These hormones may form an interlocked signalling network interacting with one another and influencing seed germination directly or indirectly. Their response is particularly significant in response to environmental stresses.

3.8 Environmental Factors Influencing Seed Germination

Regulation of germination (and dormancy) by environmental factors is considered to be an adaptive mechanism of evolutionary significance, and has assumed a greater significance in the present scenario of climate change. The response to any type of stress is related to the application of an external factor that exercises a detrimental influence on the metabolism of the plant tissue, causing injury, disease or physiological abnormalities (Jaleel et al. 2009). Hence, abiotic and biotic stresses can significantly influence seed germination, seedling growth and crop stand leading to a decline in biological and economic yields.

Under field conditions, optimum soil moisture is a prerequisite for satisfactory seed germination. Upon sowing in the field seeds start absorbing water to prepare for germination. The amount of water absorbed by the seed will depend on the water-energy status of the seed and the soil water potential (Bradford 1995). The condition of deficit water during seed germination may delay primary root protrusion, reduce the percentage of seeds that complete the process, or completely inhibit germination (Lei et al. 2017). At low soil moisture levels, thus, the initial stages of germination may initiate, but may not be sufficient to complete the process of germination. On the other hand, excessive moisture level inhibits germination by creating anoxia (i.e., depletion of oxygen in the soil). Similarly, the reduced germination caused by soil salinity results from the combined action of two types of stress: the water deficit created by the osmotic effect of the salt in the soil, also known as 'osmotic drought', and the toxicity as a result of the excessive influx of ions, such as Cl^- and Na^+ into the tissues (Munns et al. 1995; Zhu 2003). In addition, under saline conditions, osmotic and ionic stress leads to the excessive production of reactive oxygen species (ROS) in chloroplasts, mitochondria and the apoplasmic space (Nazar et al. 2011). As the sensitivity to salinity is more pronounced at the seedling stage, it can be used in some crops as a reliable criterion for the selection of genotypes with better tolerance to salinity stress.

Large thermal variations that occur during the day, when the air or the soil surface temperatures reach 40 °C or more at mid-day, can considerably reduce the germination of hydrated seeds (Boero et al. 2000). Every crop species exhibit specific requirement of the optimum, maximum, minimum and base temperatures for germination. Hence, the base temperature for crops cultivated during winter season is lower than that for summer/rainy season. The effects of temperature on the rate of germination and the total germination have been explained exhaustively by Mayer and Poljakoff-Mayber (1989), which are also applied in standardisation of germination test procedures. The combined effects of water stress and temperature may vary among species (Benech-Arnold Roberto and Augusto 2017). Besides, germination is greatly affected by the interactions between temperature, water potential, and water flow within the soil and by variations in the Q_{10} factors (i.e., temperature coefficient—a method of comparing effective seed biological activity rates).

Further, the aeration regimes (i.e., rates of gaseous exchange) in the soil affect the biological activity of the microflora and enhance the competition for oxygen with germinating seeds. As oxygen is required in germination as a terminal electron

receptor in respiration and other oxidative processes of a regulatory nature, low oxygen availability can reduce or even prevent germination in many crop species (Bradford et al. 2007). Mayer and Poljakoff-Mayber (1989) reported that there is a sharp rise in oxygen requirement for metabolic activities at an early stage of germination. It is followed by a second peak that marks the beginning of the growth stage and radicle emergence. Also, oxygen supply is greatly influenced by the thickness of the water film covering the germinating seed, and of the hydrated seed coat, especially in seeds that have a swollen mucilaginous cover with very low diffusivity to oxygen. In seeds rich in fatty or starchy storage substances, germination is inhibited if the oxygen level falls below 2%. Oxygen requirements also increase with the rise in soil temperature and under light and/or water stress. Therefore, good aeration and gaseous exchange attained in well-structured, aggregated soil beds support healthy growth of germinating seeds, while soil crusting and compaction may have deleterious effects on gaseous exchange and, in turn, on seed germination, besides exerting mechanical pressure by the germinating seeds.

Germination testing protocols, a vital component of seed quality assurance, are therefore, standardised taking into account the type of germination (epigeal or hypogeal) and root morphology (adventitious/fibrous and tap root systems) to identify the most suitable substratum; optimum temperature regimes; requirement of light or other triggers; dormancy behaviour (deep or shallow; coat imposed or embryo dormancy; hard seededness; requirement of after-ripening or stratification based on morpho-physiological behaviour, etc.); speed of germination, and time to complete seedling development to derive at the days of first and final counting days (see chapter “Testing Seed for Quality” for more details).

4 Conclusions and Future Thrust Areas

Dormancy is the mechanism that supports seed to escape unfavourable environmental conditions for germination and seedling establishment, and favours survival and distribution over time and space. However, for successful crop cultivation, it is important to understand various processes of seed dormancy that are regulating the germination. Moreover, to mitigate the serious threats of climate change, a low degree of seed dormancy with subsequent rapid germination could be an important strategy for crops grown in arid and semi-arid regions. On the other hand, by adopting ways and means to manipulate dormancy through external treatments, it could be possible to maintain seeds in quiescent state for as long as the growing conditions are not favourable. It is well established that during and after germination, early seedling growth is supported by the catabolism of stored reserves (proteins, lipids, or starch) accumulated during seed maturation, which requires necessary attention of seed technologists and agronomists to ensure satisfactory conditions during grain filling stage, especially in seed multiplication plots. The molecular pathways, recognised by omics and molecular biology analyses, may elucidate more about the effects of plant hormones on seed germination and dormancy. In addition,

the role of soil bacteria interacting with plant hormones, and hence promoting seed germination, also needs to be explored for better use as an effective tool to enhance seed germination under field conditions.

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