Dormancy in Plants

Advanced article

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Article Contents

doi: 10.1002/9780470015902.a0002045

Dormancy is a strategy of higher plants to survive adverse conditions. Seed dormancy is controlled by a hormone balance of gibberellins and abscisic acid. Physiological and genetic analysis is revealing the interplay between both hormone signalling pathways.

Introduction

The term 'dormancy' refers to a state of a plant or plant organ that is characterized by the virtual absence of metabolic activity and/or a lack of further development and growth. Dormancy occurs in seeds, bulbs, tubers, buds and whole plants. It is an adaptive trait that has evolved by selection for the capacity to survive prolonged unfavourable environmental conditions, such as heat, cold and drought. The evolutionary origin of dormancy may be associated with the climatic changes during the Earth's history. The number of plant species that may acquire dormancy appears to increase with the geographical distance from the equator and, thus, with the occurrence of seasons (Baskin and Baskin, 1998). There is no doubt that the phenomenon of dormancy has significantly contributed to the development of new species and the successful dispersion of those already present.

Ecology of Dormancy

To survive, plant species will adjust their phases of activity and rest to climate changes. Evidently, the terms 'favourable' and 'unfavourable' will vary with the climatic zones. For example, in the Mediterranean region the hot dry summer may be the unfavourable period, whereas the wet temperate winter conditions may provide sufficient opportunities for successful growth and reproduction. However, in the more temperate regions, the summer season is generally the favourable period for growth. (see **Figure 1**)

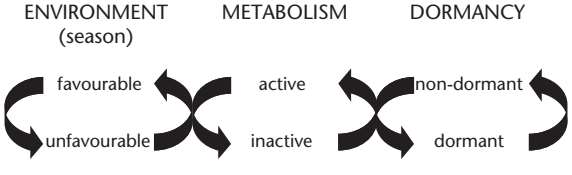

Figure 1 Synchronization of plant metabolic activity and dormancy with the seasons.

Plant species possess diverse strategies to protect themselves against extreme conditions. For example, many species form flower or leaf buds prior to the unfavourable season which are well protected against adverse conditions while they remain attached to a plant with low metabolic activity. Other species may survive as a whole plant, with or without buds, displaying low metabolic activity with the roots as major suppliers of nutrients. However, seeds embody the ultimate survival strategy of many higher plants. Seeds can withstand the most extreme of conditions, often in the dry state and for extended periods of time. In addition, seeds that are dispersed in the soil seedbank have the remarkable ability to sense the environment. This allows for a very accurate adjustment of their active and inactive phases to the changing of the seasons. This behaviour is usually called 'dormancy cycling'.

Dormancy cycling

Seeds in the soil seedbank not only sense the actual field temperature, but are also able to accumulate long-term temperature information. For example, seeds from many temperate species require several months of cold (winter) temperatures to break most of their dormancy. Thus, the seeds may become nondormant just prior to the growth season. However, local conditions other than the temperature, may not be favourable for successful establishment of a new plant. Therefore, seeds are also equipped to sense some essential growth factors, such as light and nitrogenous components in the soil. Competitors will change the intensity and quality of the incident light and locally deplete the soil from nutrients. These environmental signals then prevent the seed from germinating and establishing a seedling. Subsequently, the seeds will become dormant again to await a new opportunity in the following year. Thus, seeds may pass through many successive cycles of dormancy before the field conditions are optimal for germination and growth (see **Figure 2**).

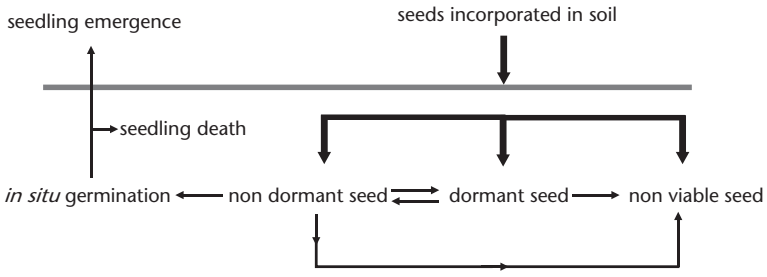

Figure 2 Events occurring in the soil seedbank between seed dispersal and seedling emergence. The transition from the dormant to the nondormant state is reversible and forms the basis of dormancy cycling.

Categories of Seed Dormancy

Since germination (radicle protrusion) is the net result of opposing forces exerted by the thrust of the embryo against the mechanical restraint of the surrounding tissues, it is clear that dormancy may be located in both the embryo and the enveloping tissues. Seeds from some species have a fully differentiated embryo that does not enter the maturation phase, i.e. they do not expand and accumulate food reserves. Seeds of this type usually contain relatively large amounts of endosperm tissue, often entirely embedding the small embryo. These embryos have to grow inside the dispersed seed prior to germination, e.g. in coffee and celery seeds. In such species, the surrounding endosperm is digested during embryo growth and radicle protrusion does not occur until the embryo has attained a pre-defined length and the micropylar endosperm has been sufficiently digested. Many seeds possess a seed coat that poses a mechanical restraint to embryonic growth. However, seed coats may also contain chemical inhibitors, such as phenolic compounds, or they may be impermeable to oxygen or water (mechanical and chemical dormancy). Physiological dormancy, which is imposed by the fully developed and matured embryo, represents a reversible block to germination. In contrast, coat-imposed dormancy is irreversible: it can be released but not induced again. The reversible nature of physiological dormancy allows the occurrence of repeated dormancy cycles in seeds in the soil. So far, most studies have predominantly focused on physiological dormancy.

The Acquisition and Loss of Seed Dormancy

The plant hormone abscisic acid (ABA) shows a transient presence during seed development. ABA levels commonly increase during the first half of seed development and decline during late maturation, concomitantly with the decrease in seed water content. ABA has been detected in all seed tissues and has been related to such developmental processes as storage protein synthesis, suppression of precocious germination, dormancy and induction of desiccation tolerance. In addition, ABA commonly inhibits seed germination. The gibberellins (GAs), a large group of plant hormones, have long been associated with dormancy release and germination. Inhibition of GA-biosynthesis by chemical means blocks germination, and environmental factors that break dormancy, such as light, may be substituted by the addition of GAs. These results have led to the formulation of the 'hormone balance theory' in which the occurrence of dormancy or germination depends on the dominance of either of these hormones. However, this theory was largely based on correlative evidence. Only with the aid of genetic methods it is possible to find causal relationships.

The genetics of seed dormancy

Genetics is an important tool to find and understand the function of genes that regulate a trait such as seed dormancy. This is based on the fact that when genes affecting such a trait are mutated this should have an effect on the expression of the trait. Genetic variation within a species is the basis for any genetic study. In the case of dormancy, this variation can not only be induced by mutagenic treatments but it can also be present between varieties or ecotypes of a specific species. For seed dormancy where environmental factors, but also the duration and conditions of seed storage, play an important role, genetic variation can only be studied when genotypes are physiologically similar. This means that seeds should have developed, and have been stored and tested under strictly identical conditions. Because of the environmental effects, mutant screens based on seed germination and dormancy have been limited, although obvious phenotypes such as vivipary have been detected in general mutant screens. In cases where nongerminating mutants were identified in *Arabidopsis thaliana* and tomato, most of them appeared to be deficient in GAs. These mutants also show defects in other GA-controlled traits such as elongation growth. Mutants have been used predominantly in model plants such as *Arabidopsis* and rice to clone the respective genes

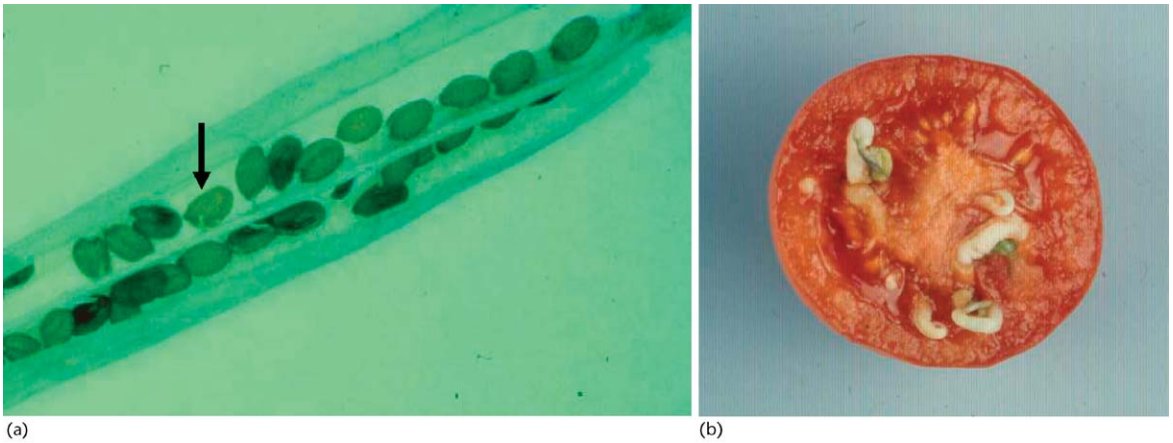

Figure 3 Vivipary (a) The ABA-insensitive *abi-3* mutant of *Arabidopsis*; (b) The ABA-deficient *sitiens* mutant of tomato. Arrow indicates germinated seeds while still in the silique.

(see **Figure 3**). **See also**: *Arabidopsis Thaliana* as an Experimental Organism

Detailed physiological and molecular studies have demonstrated the importance of this hormone in germination *sensu stricto* where the weakening of the cell layers surrounding the embryo plays an important role. The isolation of mutants in which GAs are not required any more for germination has led to the isolation of ABA-deficient and ABA-insensitive mutants. This provided evidence that GAs are required to overcome ABA-induced dormancy, which corroborated the hormone balance theory. ABA-insensitive mutants (*abi*) could also be isolated on the reduced growth inhibition by ABA of these mutants. ABA mutants display the so-called pleiotropic effects, such as reduced control of stomatal closure by drought. Thus, tomato mutants selected for increased wilting were shown to be less dormant.

In *Arabidopsis*, mutants are known to have a very abnormal seed maturation phase. These mutants are also nondormant, indicating that dormancy is a developmental event and requires a normal maturation process. In a similar way, the role of the testa in the regulation of dormancy, using testa colour and testa structure mutants, was demonstrated (Debeaujon and Koornneef, 2000). Mutants that have been isolated only on the basis of reduced dormancy are for instance the *rdo* mutants in *Arabidopsis* which are not related to hormonal defects (Peeters *et al*., 2002).

Another important source of genetic variation is the difference between varieties, land races, etc. This so-called natural variation is mostly studied with quantitative trait loci (QTL) analysis, which detects where on the chromosomes are genes located that differ between the parents and that affect the trait under study. QTL studies for seed dormancy have not only been performed extensively in cereals such as barley, rice and wheat but also in *Arabidopsis* (Alonso-Blanco *et al*., 2003). In the latter species many accessions appeared to have a stronger dormancy than the commonly used laboratory strains in which selection for nondormant mutants was troublesome. These more dormant accessions such as Cvi (originating from the Cape Verde Islands) are evidently more attractive for physiological (Ali-Rachedi *et al*., 2004) and genomic (Cadman *et al*., 2006) studies of dormancy. QTL analysis of the progeny of crosses of such dormant accessions and the nondormant laboratory strain Landsberg (Ler) has identified a large number of QTLs which are now being cloned on the basis of their map position. In contrast to the hormone mutants, lines that differ in natural variation often show no pleiotropic phenotypes and may be specific for seed dormancy and germination.

Transcription profiling using whole genome DNA microarrays is now shedding new light on genes and their regulation involved in dormancy. The current consensus is that several hundreds of genes are committed to the regulation of dormancy in *Arabidopsis*. Many of these genes contain the so-called ABA responsive elements (ABREs) in their promoter regions. These ABREs function as binding sites for transcription factors that promote transcription. These transcription factors are controlled by ABA. The number and type of ABREs in a given gene may render the fine adjustment of the seed's responses to conditions that alter its dormancy status.

In this rapidly developing research field, studies are in progress to unravel the 'cross talk' among the steadily increasing numbers of genes that control seed dormancy and germination. Important questions can now be addressed: Which genes affect which other genes, and how is the activity of multiple genes coordinated? What is the biochemical function of the gene products and how do these modify the physiology of the seeds? Perhaps one of the most intriguing questions is how seeds perceive environmental signals and how these are translated into endogenous signalling pathways.

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