

## (2) Seed Dormancy

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### 1. Definition

Despite the importance of the subject, there is no clear and unique definition for seed dormancy. This lack of consensus may be due to dissimilar perspectives from different disciplines about this phenomenon. For example, what a seed physiologist considers to be a dormant seed may be different from what an ecologist or seed technologist considers a dormant seed. Additionally, as we will see later in this presentation, there are many different types of seed dormancy mechanisms and treatments to overcome these dormancies, which even further complicate a universal consensus on the definition.

(4) These are some common definitions for seed dormancy:

- "... a mechanism that prevents germination of a seed at an inappropriate time" (Vivrette, SCST Seed Technologist Training Manual, Chap. 9, 2002)
- "...the absence of germination of an intact, viable seed under germination favoring conditions within a specific time lapse". (Hilhorst, 1995)

(5) Something that remains vague in these definitions is what "inappropriate time" is or what "germination favoring conditions" are. If the germination favoring conditions for a particular species are optimal conditions used for the standard germination test for that species, (6) this implies that after the standard germination test, any viable seed that fails to germinate would be considered dormant, and those that germinate (normal or abnormal) are non-dormant. In this case, a seed lot of may have different levels of dormancy, from 0% if all the seeds germinate to 100%, if all the seeds are viable but do not germinate. Using this definition, however, each seed does not have a level of dormancy, it is simply dormant or non-dormant. In reality, this is not the case.

(7) Seed dormancy also has been defined as: "*an innate seed property that defines the environmental conditions in which the seed is able to germinate*" (Finch-Savage and Leubner-Metzger, 2006).

According to this definition, dormancy is not only associated with the absence of germination, but it is a seed characteristic that determines the conditions required for germination. This definition better fits the results of many studies in seed germination and dormancy. Many of these deal with seeds possessing different levels of non-deep dormancy and dormancy is evaluated according to the ability of the seed to germinate under different conditions, for instance: light or dark, different temperatures, different water potentials or different external ABA concentrations. This is the definition that we will use during this presentation.

(8)

**2. Significance of Dormancy**

(9) From an ecological perspective, dormancy is an important survival mechanism that favors propagation and dissemination of seeds to establish plant populations.

Because specific conditions are required to break dormancy, it may favor germination and seedling emergence under more favorable conditions. For example:

- (10) seeds that require cold stratification to break dormancy may avoid germinating in winter.
- (11) seeds that require light for germination may avoid germinating when they are too deep in the soil or under plant shadows that would compete with the seedling, giving it little or no chance to survive.

(12) Additionally, because individual seeds in a seed population usually have different levels of dormancy, they spread their germination over time, thereby avoiding unfavorable environmental events such as a drought that would eliminate the population if all the seeds germinated at one time. This is the reason why weeds are difficult to eliminate in a field because the seed banks provide a vast array of seeds with differing levels of dormancy. In the case of weed seeds, the “unfavorable event” may be an herbicide application or soil cultivation, but because not all weed seeds germinated at the same time, these control practices fail to totally eliminate the entire weed population.

Dormancy may also distribute seed germination in the soil over years, so weeds continue to emerge in the field even after years of rigorous weed control.

(13) In some cases, dormancy favors the spatial distribution of plant populations. For instance, when ingested by animals or birds, seeds with hard seed coats are abraded during digestion and, when expelled from the animal, are scarified and able to germinate in a location far from the mother plant.

(14) Despite all the benefits of dormancy for natural plant populations, this is an undesirable trait for most crops because it makes rapid and uniform germination during crop establishment difficult. (15) In most economically important species, deep dormancy has been eliminated by breeding. For example, in maize, soybean, and brassicas, most commercial cultivars have seeds that germinate rapidly and uniformly over a broad range of environmental conditions. (16) However, in less domesticated genotypes in which breeding has not been a focus, dormancy issues may still arise and be a problem. This occurs most commonly in less domesticated species such as ornamental, medicinal and vegetable crops of recent introduction. (17) In commercial seeds, dormancy is not only a problem for plant establishment, but also during seed quality evaluation. Because the objective of the standard seed germination test is to report germination percentage under optimal conditions, seed analysts must identify treatments to overcome dormancy and favor germination when dormancy exists in a seed lot.

(18) Although deep seed dormancy would be a problem in agricultural species, some level of dormancy is desirable to prevent sprouting or precocious seed germination before harvest to maintain seed quality. This is particularly important in winter cereal species.

(19) Another aspect of seed dormancy that is beneficial for natural plant populations, crop producers and germplasm banks is the positive relationship between

seed dormancy and longevity or storability. Dormant seeds have the potential to remain viable for longer periods in the soil or during storage. However, even though this beneficial relationship between seed dormancy and longevity has been implied in varying studies, it has also been questioned in others.

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### 3. Dormancy Classification

Similar to the lack of consensus in seed dormancy definitions, differing ways have been identified to classify seed dormancy. (21) However, most authors agree in the basic classification scheme that provides a distinction between *primary* and *secondary* dormancy.

(22) **Primary dormancy** is induced during seed development resulting in seeds that are dormant when dispersed from the mother plant.

(23) **Secondary dormancy** is induced by unfavorable environmental conditions following shedding of mature seeds from the parent plant. Secondary dormancy can be induced by conditions unfavorable for germination, such as adverse temperatures, illumination or oxygen. Types of secondary dormancy include:

(24) **Thermodormancy**, which is caused by prolonged exposure of imbibed seeds to temperatures unfavorable for germination, generally high temperatures.

**Skotodormancy**, which is induced in seeds that require light for germination when they are imbibed in the dark for extended periods of time, and

**Photodormancy**, which occurs in seeds that are inhibited by light when they are exposed to an excess of light.

Note, that secondary dormancy is not only induced in non-dormant seeds, but also in seeds that already have some form of primary dormancy. For example, a lettuce seed that requires light to germinate is said to be *photosensitive* and, when imbibed in the dark, it will not germinate until light is provided. However, if dark imbibition is extended for a period of time, skotodormancy can be induced and the seed will not germinate even if it is placed under optimum light conditions.

(25) There is a great variety of types of primary and secondary dormancy distinguished by the physical, morphological, or physiological mechanism(s) imposing dormancy, the method(s) that break the dormancy, and how “deep” is the dormancy, in other words, how easy is it to overcome the dormancy imposing mechanism. Additionally, dormancy may be imposed by multiple mechanisms and more than one dormancy alleviating treatment may be necessary. These factors collectively make it difficult to reach a consensus on how to classify different dormancy types. This presentation will use the classification system proposed by Nikolaeva (1977) and modified by Baskin and Baskin (2004). (26) Five classes of seed dormancy are included in this system:

1. Physiological dormancy
2. Morphological dormancy
3. Morphophysiological dormancy
4. Physical dormancy
5. Combinational dormancy

(27) This is a hierarchical system in which each class may be divided into levels and each level into different types.

(28) 1. *Physiological Dormancy*

This is the most abundant form of seed dormancy in angiosperm plants. As we will see later in this presentation, this is also the most prevalent form of seed dormancy in “model” species commonly used for the study of seed dormancy, such as *Arabidopsis thaliana*, tobacco (*Nicotiana* spp.), sunflower (*Helianthus annuus*), tomato (*Lycopersicon esculentum*), *Avena fatua*, and many cereal species.

Physiological dormancy is divided into three levels: deep, intermediate, and non-deep.

(29) In deep physiological dormancy:

- The excised embryo produces an abnormal seedling
- GA does not promote germination
- Seeds require 3 to 4 months of cold stratification to germinate.

(30) In intermediate physiological dormancy:

- The excised embryo produces a normal seedling
- GA promotes germination in some species
- Seeds require 2 to 3 months of cold stratification to germinate
- Dry storage can shorten the cold stratification period.

(31) In non-deep physiological dormancy:

- The excised embryo produces a normal seedling
- GA promotes germination
- Depending on the species, cold (0-10°C) or warm ( $\geq 15^\circ\text{C}$ ) stratification breaks dormancy
- Seeds may after-ripen in dry storage
- Scarification may promote germination

(32) Non-deep physiological dormancy is the most common dormancy type and is present in the majority of angiosperm species. This level is divided into types 1 to 5 represented in this figure. (33) In each graph, the x-axis represents the progression of dormancy release, from (34) 1.0 which is the fully dormant condition, to (35) 0.0 which represents dormancy break or a non-dormant condition. The y-axis represents the temperature at which the seeds can germinate. Note, that in types 1, 2 and 3, during the progression from fully dormant (x-value = 1.0) to non-dormant (x-value = 0.0), the range of temperatures at which the seeds germinate gradually increases. (36) For example, seeds with type 1, non-deep physiological dormancy do not germinate or germinate at a very narrow range of low temperatures when fully dormant (x-value close to 1); (37) when middle dormant (x-value = 5), seeds would germinate over a range of temperatures from cold to medium; and (38) when non-dormant (x-value = 0) would germinate over a wide range of temperatures from cold to hot. In types 1, 2, and 3, during the progression

from dormant to non-dormant, sensitivity to other factors such as light (phytochrome) and plant growth regulators increases. (39) In types 4 and 5, seeds do not progress from dormant to non-dormant and only germinate in a very narrow range of temperatures; hot in type 4 and cold in type 5. (40) Most seeds with non-deep physiological dormancy belong to types 1 or 2.

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#### 2. Morphological dormancy

This class of seed dormancy refers to seeds with underdeveloped and differentiated embryos, this includes embryos in which the cotyledon(s) and hypocotyl-radicle axis are differentiated, but small in size. These embryos do not have physiological dormancy and only require additional time to grow and germinate. (42) Commonly, under favorable conditions, embryos in such seeds begin growth (elongate) within a period from a few days to several weeks, and seeds germinate within 30 days. Celery (*Apium graveolens*) seed is an example of morphological dormancy. Other examples are presented in this table.

(43)

#### 3. Morphophysiological dormancy

In this class, seeds have embryos that are underdeveloped and differentiated as well as a physiological component to their dormancy. Thus, to germinate, these seeds require time for embryo growth and a dormancy-breaking treatment. Morphophysiological dormancy can be divided into eight levels with possible dormancy-breaking treatments as shown in this table.

(44)

#### 4. Physical dormancy

This class of seed dormancy is caused by one or more water-impermeable layers of palisade cells in the seed coat (testa or pericarp) that impede germination because the seed cannot complete imbibition. Chemical or physical abrasion (scarification) of these water impermeable layers can break physical seed dormancy. Seeds with physical dormancy are commonly called hard seeds, and this class of dormancy is typically found in species from the families Fabaceae, Malvaceae, Chenopodiaceae, and Liliaceae.

(45)

#### 5. Combinational dormancy

This class groups seeds with simultaneous physiological and physical dormancy. In this case, physiological dormancy is generally characterized as non-deep. A cold stratification treatment of seeds after scarification to permit imbibition is a common dormancy-breaking treatment in this class of seeds.

(46)

### 4. Factors that Control Dormancy Induction

(47) Induction of dormancy is controlled both genetically and by the environment. Additionally, genetic control may be associated with embryo genotypes or the mother plant. According to Baskin and Baskin (2004) "seed dormancy is a typical quantitative

genetic trait, involving many genes, influenced substantially by the environment during seed development, and exhibiting continuous (non-discrete) phenotypic variation”.

As mentioned previously, under natural conditions, seed dormancy can be beneficial for propagation and dissemination of plant populations. On the other hand, in agronomic systems, dormancy is a problem for seed evaluation and seedling establishment. Thus, genetic control of dormancy is understandable when the prevalence of seed dormancy between domesticated and non-domesticated species is compared.

(48) Additionally, even within the same species, variation in the class or intensity of seed dormancy can be observed. For example, in this Table (Sung et al., 1998), the germination percentage of five lettuce genotypes produced under similar conditions at 5 temperatures and 2 light conditions is shown. Note, that both photosensitivity and thermoinhibition are different for the different genotypes. For instance, when germinated at 30°C, seed germination under light for Dark Green Boston is 3.3%, while Everglades germination is 100%. Similarly, at 30°C under dark conditions, germination for Dark Green Boston and Everglades seeds is 0 and 100%, respectively.

(49) Seeds from the same genotype may also have different dormancy levels or intensities depending on the environment under which the seed developed. (50) This “environment” includes not only the conditions under which the mother plant grew, but also the “micro-environment” for each seed. For instance, seeds that develop in different parts of an inflorescence on the same plant may be exposed to different water and nutrient supply, light, temperature, relative humidity, etc. based on their location in the inflorescence, and all these factors affect dormancy induction of each seed. (51) This Table shows how the position of celery seeds in the umbel affects seed weight and germination percentage. Note that similar response patterns were observed in the three celery cultivars.

(52) Some environmental factors affecting seed dormancy include: temperature, water availability, light quality, photoperiod, altitude, and mineral nutrition. Although the response to each factor will be influenced by the kind of seed dormancy, some trends have (53) been observed. For example, high temperature, drought and short days during seed development are usually associated with higher germinability or lower seed dormancy intensity.

Given differences in the nature of physical, morphological or physiological mechanisms causing dormancy among species, it is expected that the same environmental factor(s) may have different effects on dormancy intensity depending on the species. (54) Even with these differences, generalizations about the mechanisms involved in dormancy imposition have been suggested. For example, high temperatures during seed development are generally associated with lower physiological dormancy, which may be caused by reduced synthesis of inhibitory compounds (e.g., abscisic acid) at high temperatures, or greater synthesis of promoting substances (e.g., gibberellins). (55) However, there are also examples of species in which dormancy increases with higher temperatures during seed development; for instance, high temperatures caused the development of thicker soybean seed coats resulting in more dormant seeds. In this case, the same factor (temperature) is affecting dormancy differently depending on the dormancy mechanism (physiological vs. physical). (56)

In the case of water availability, the type of response to drought conditions during seed development is also influenced by the kind of dormancy. When dormancy is imposed mechanically by a thick seed coat, drought usually increases its thickness, thereby contributing to reduced germinability. On the other hand, drought typically causes a reduction in seed dormancy when it is imposed biochemically, possibly by interfering with the synthesis of inhibitors or promoters of germination. (57) With respect to the light environment of the maternal plant, day-length and light quality (wavelength composition) influence germinability during seed development. (58) Day-length has been more studied and, in most cases, longer days cause decreased germinability and higher dormancy, although exceptions have been noted. This table shows the example of *Polypogon mospeliensis*. Seeds from this species had higher germination when produced under longer days compared to shorter days. (59) When light quality has been studied, seeds developed under light environments with lower red to far-red ratios have lower germination in the dark compared to seeds developed under environments rich in red light. (60) For instance, this figure shows the dark germination of lettuce seeds produced under a red- or far-red-rich light treatment. At any of the four temperatures under which dark germination was evaluated, seeds from the far-red-rich treatment produced more dormant seeds. (61) In addition, when germination was evaluated under light at different temperatures, seeds from the red-rich treatment germinated at higher percentages and faster rates under a wider range of temperatures.

(62)

### 5. Mechanisms of Dormancy

At this point of this presentation, after reviewing dormancy classification, it is clear that there are a great diversity of mechanisms governing seed dormancy. To be consistent with the dormancy classification system presented earlier, the mechanisms of dormancy will be classified into physical, morphological, and physiological categories.

(63)

#### *Physical causes*

As mentioned earlier when dormancy classification was discussed, a class of seed dormancy is caused by impermeability of the seed coat (testa and/or pericarp) to water uptake. Physical dormancy is present in species of at least 15 angiosperm families, including Fabaceae, Malvaceae, Convolvulaceae, Chenopodiaceae, Cannaceae, and Liliaceae. In some of these species, seed coat impermeability may delay germination for several years.

(64) In general, seed coat impermeability is caused by one or more layers of sclereid cells with thick lignified cell walls. In addition to lignin, sclereid cells possess other water-repellent compounds such as cutin, suberin, waxes, phenolics, and callose. This figure shows a section of the impermeable seed coat from *Melilotus alba* in the Fabaceae family. Note that, in this case, in addition to sclereid cells, there is a waxy cuticle contributing to testa impermeability. Similar testa structures are present in other legumes and experimental data suggest that osteoclereids are the primary barrier (65) for water uptake. This figure shows the effect on seed imbibition of puncturing the testa of *Coronilla varia* seeds to different depths. Perforating the cuticle and sub-cuticle layers

had practically no effect on increasing seed imbibition and more imbibed seeds were found after perforating the osteocleroid layer.

In addition to the overall impermeability of the seed coat; in some cases, there are specialized structures that regulate water movement to and from inside the seed. These structures are associated with natural openings in the seed coats such as the micropyle (66) and hilum in Fabaceae seeds. For example, in *Trifolium repens*, *T. pratense*, and *Lupinus arboreus*, the hilum functions as a hygroscopically activated valve regulating water movement through the impermeable testa. At low relative humidity, the fissure in the hilum opened and the seed lost water; at high relative humidity, the fissure closed and water uptake was impeded. This graph shows the changes in seed water content in white clover (*Trifolium repens*) hard and scarified seeds transferred to chambers at different relative humidities. Note that hard seeds, which have their seed coat intact, lose water when moved to lower relative humidity, but do not increase water content when moved to higher relative humidity. In the case of scarified seeds, seed coat permeability has been altered, and seed water content increases or decreases depending on the external relative humidity.

Physical dormancy is alleviated when the seed coat becomes permeable due to unplugging of natural openings or surface cracking of the seed coat. Under natural conditions, this typically occurs by exposure of the seed to extreme temperatures or temperature fluctuations. Passage of the seed through animal digestive tracts is another approach to breaking physical dormancy, although data supporting this mechanism are few.

Some seed coats extrude a mucilage layer that impedes germination under less than optimum water conditions. When there is too much water, the mucilage layer is impermeable to oxygen and, when there is too little water, the mucilage layer becomes hydrated, but not the embryo.

(67)

#### *Morphological causes*

Although the morphological dormancy classification system proposed by Baskin and Baskin (2004) refers only to differentiated - underdeveloped embryos, we will include both differentiated and undifferentiated embryos in this discussion.

(68) Some families, such as Orchidaceae and Orobanchaceae, have species that disperse seeds with underdeveloped and undifferentiated embryos. These seeds are usually very small and contain embryos consisting of only 2 to 100 cells where development appears to be arrested before histodifferentiation occurs. Because these seeds do not contain sufficient reserves for embryo growth, external nutritional sources are required to complete embryo development that include the ability to parasitize or utilize nutritional resources from other organisms with which they interact.

(69) In other species, the embryo is underdeveloped, but differentiated, i.e., it has completed histodifferentiation. In these seeds, the small embryo is typically embedded in a relatively large endosperm. After seed dispersal and before germination occurs, the embryo uses the endosperm reserves to complete development. This picture (Jacobsen 1979) of celery seeds shows the small embryo embedded in the endosperm. (70) After 5 days of imbibition, the embryo continued growth at the expense of the endosperm and had the ability to germinate.

Usually, these seeds only require additional time to complete germination. As a result, the classification of dormant may be questionable. However, they continue to be referred to as morphologically dormant.

(71)

*Physiological causes*

Physiological dormancy is the most common dormancy class found in seeds and is generally (72) believed to be regulated by the existence of growth inhibitors, promoters or the balance between them. In the past two decades, many studies have been conducted that led to a better understanding of the growth compounds associated with seed dormancy establishment and alleviation. Among the compounds that act to induce seed dormancy is (73) abscisic acid (ABA) which appears to play an important role, both by its presence in the seed or by sensitivity of the embryo to its action. The use of ABA-deficient mutants and inhibitors of ABA synthesis has been helpful in demonstrating the importance of ABA in dormancy induction of several crops. One of the first studies was conducted on *Arabidopsis* by Karssen and co-workers (1983). This study established that the onset of dormancy correlated with the presence of ABA produced by the embryo during seed development. (74) In sunflower, Le Page-Degivry et al. (1990) found that endogenous ABA levels, which increased sharply in the first half of the seed development period, fell at precisely the same moment when embryo dormancy was established. This information is presented in this graph and table. The “a” line in the graph shows the peak of ABA at 15 days after pollination, which is about halfway to seed physiological maturity. The table shows germination values at different times of embryo development. (75) In this study, blocking the synthesis of ABA by the use of fluridone was effective in reducing the embryo ABA content, which is shown in the “b” line of the graph. (76) This table shows that fluridone prevented embryo dormancy when applied before ABA content was maximum, but not when applied later. It was concluded that dormancy must be induced by ABA during seed maturation. Peaks in ABA concentration about halfway during seed development have been reported in other species such as sorghum, maize, and lettuce.

(77) In studies of tomato, seeds from an ABA-deficient line did not have dormancy, had higher rates of germination, and germinated under more negative water potentials compared to seeds from the wild-type genotype. (78) This picture shows viviparous germination of ABA-deficient seeds in over-ripe tomato fruits, a phenomenon that did not occur in the wild-type genotype. (79) In the graph on the right is the percentage of vivipary in seeds homozygous for the ABA-deficient mutation, curve 1, and homozygous for the wild type gene, curve 3. Curve 2 represents seeds from the self-pollination of a plant heterozygous for the gene, therefore around 25% of that seed should be homozygous for the mutated allele. Maturation is defined as the moment when the fruits turn red. (80) This graph demonstrates that germination rates were also affected. (81) These are the germination curves for tomato seeds in water, note that the ABA-deficient mutants germinated faster than the wild-type. (82) When germination was evaluated in a -0.5 MPa osmotic solution, not only was germination rate affected, but also the final germination percentage: ABA-deficient seeds germinated faster and at a higher percentage than seeds from the wild-type.

Evidence also shows that ABA is not only induces dormancy but also is responsible for dormancy maintenance. (83) During seed imbibition, *de novo* ABA biosynthesis occurs in dormant, but not non-dormant seeds of species such as *Arabidopsis thaliana*, lettuce, *Nicotiana plumbaginifolia*, and sunflower. This figure shows ABA content during imbibition in dark of lettuce seed from two cultivars: Ritsa and Strada. Accumulation of ABA is observed in Ritsa, a cultivar that requires light to germinate, but not in Strada, a genotype that germinates in dark. Interestingly, when light was applied to Ritsa seed during the first two hours of imbibition, the amount of ABA accumulated in the seed was lower. (84) This graphs shows that in dark imbibition of Ritsa seed, the application of Zoria, an inhibitor of ABA synthesis, has a similar effect as light in reducing ABA accumulation. (85) This table shows that the application of the ABA-synthesis inhibitor was effective in increasing the percentage dark germination in Ritsa seed; however, this effect was reversed by the application of external ABA.

(86) While existing evidence suggests that ABA is the hormone responsible for the induction and maintenance of seed dormancy, other studies suggest that gibberellins (GA) are the hormone responsible for seed germination. This has been observed, for instance, in GA-deficient lines of *Arabidopsis* and tomato that are not able to germinate without the addition of external GA. Similar findings has been observed with the use of GA-synthesis inhibitors such as paclobutrazol. (87) For example, this figure shows the cumulative germination of GA-deficient mutant tomato seeds under different conditions. (88) In A, germination under different external GA concentrations is presented and shown that without the application of external GA, seeds do not germinate. Germination rates and final percentages increased with higher external GA concentrations. (89) In B and C, germination at different water potential and two GA concentrations is presented. At higher GA concentration, seeds germinated faster and at higher percentage under decreasing osmotic potentials.

(90) Our current knowledge of hormonal regulation of seed germination suggests that seed dormancy is controlled by the ABA:GA ratio rather than the absolute hormone content. Thus, induction of seed dormancy would depend on:

- ABA metabolism
- GA metabolism
- ABA sensitivity
- GA sensitivity

(90) And, when we refer to ABA and GA metabolism, this includes any process that changes the amount of the active form of the hormone such as synthesis, degradation, activation or deactivation (e.g., by conjugation with other molecules).

So, the events that induce dormancy are ABA synthesis or activation, GA degradation or deactivation, increase of ABA sensitivity, and decrease of GA sensitivity. The opposite events will lead to dormancy alleviation and germination.

(92) Until now, this presentation has focused on two hormones to explain the mechanisms governing physiological dormancy, which may be a convenient simplification of the process. Although abundant evidence shows that ABA and GA are

the most important regulators of seed dormancy, it must be understood that there are other compounds that may be involved in dormancy induction or breaking. (93) For instance, this figure shows a model for the hormonal interactions during seed dormancy regulation of *Nicotiana* sp. As can be observed, in addition to ABA and GA, there are others phytohormones playing a role in breaking dormancy and promoting germination. (94) In this case, ethylene and brassinosteroids promote germination directly or by interfering with ABA action (highlight this in the figure). Cytokinins and auxins are two other hormones implicated in promoting seed germination in some species.

(95) This model also can be used to introduce the two topics which will finish this presentation. One is the discussion of the mechanisms by which ABA and GA promote and reduce dormancy, respectively. (96) The other refers to mechanisms and factors that break dormancy, such as afterripening and light in this model.

(97) In this figure,  $\beta$ Glu I stands for class I  $\beta$ -1,3-glucanase genes. According to this model, ABA inhibits endosperm rupture by inhibiting the expression of the class I  $\beta$ -1,3-glucanase genes. On the other hand, GA, ethylene and brassinosteroids promote endosperm rupture and counteract the inhibitory effects of ABA, in part by inducing  $\beta$ -1,3-glucanase gene expression in the micropylar endosperm at the site of radicle emergence.

(98) This figure presents a model explaining the regulation of dormancy and germination in tomato seeds. Similar to the *Nicotiana* sp. Example, this model suggests that ABA and GA interact in determining the ability of the embryo to rupture the endosperm and germinate. (99) The model represents two antagonistic forces: one is the embryo growth potential, and the other is the endosperm yield threshold or mechanical resistance of the endosperm to radicle growth. (100) When the embryo growth potential is greater than the endosperm yield threshold, germination occurs. (101) Note that, according to this model, ABA inhibits germination by decreasing embryo growth potential and possibly increasing endosperm yield threshold via the inhibition of cell wall hydrolases. (102) GA plays the opposite role, it increases embryo growth potential and decreases the endosperm yield threshold by inducing the action of cell wall hydrolases.

(103)

## 6. Methods to Overcome Dormancy

(104) The methods to overcome dormancy are better understood once the mechanisms of dormancy are known. For instance, if the cause of dormancy is an impermeable seed coat that impedes seed water uptake, removing the seed coat or reducing its permeability should break dormancy. When dormancy is caused by an underdeveloped embryo, additional time for embryo growth should overcome dormancy. Finally, when dormancy is imposed by a physiological mechanism, actions that decrease the amount of or sensitivity to dormancy-inducing compounds (e.g., ABA), along with actions that increase the amount of or sensitivity to dormancy-breaking compounds (e.g., GA) should break dormancy. This table shows effective methods in overcoming dormancy of different species.

(105) Here are common methods to overcome dormancy:

- Scarification
- Afterripening
- Stratification (chilling)
- Use of chemical compounds
- Light
- Leaching
- Alternating temperatures
- Priming

(106) **Scarification** is a treatment that removes or abrades the seed coat, allowing water uptake into the seed and promoting germination. There are two types of scarification treatments: mechanical and chemical.

(107) - *Mechanical scarification* includes a diversity of treatments that alter seed coat impermeability by mechanical means, such as grinding seeds with abrasives or sand, use of sand paper, piercing the coat with a needle, brief immersion in boiling water, heating, cooling, drastic temperature shifts, etc.

- *Chemical scarification* involves the use of a chemical compound to degrade the seed coat. The most common compound used for chemical scarification is sulfuric acid. Other alternatives are sodium hypochlorite and hydrogen peroxide.

It must be noted that, despite dormancy breaking and enhancement of germination, scarification treatments create damage to the seed due to the disruption of essential cells, favoring fungal invasion and mechanical injury. Precautions should be taken to minimize damage while maximizing dormancy relief. (108) For instance, optimal times for chemical scarification with sulfuric acid should be determined for each species. Longer periods will damage the seed, while shorter periods will be ineffective in dormancy breaking. In this example, 90 minutes in sulfuric acid were effective to overcome physical seed dormancy in *Acacia caven*. Note the improvement in seed germination of treated- versus non-treated seeds. (109) In this picture is the difference in volume of treated versus untreated seeds, showing the lack of water uptake in non-treated seeds.

(110) While 90 minutes of scarification in sulfuric acid are required to overcome *Acacia caven* seed dormancy, in the case of *Prosopis chilensis* only 10 minutes was required. In this species more time would result in severe seed damage, while 10 minutes in *Acacia caven* would be ineffective in dormancy breaking.

(111) **Afterripening** is defined as the progressive loss of dormancy in mature dry seeds. Afterripening rates may increase in response to environmental factors such as increased oxygen and temperatures and decrease with increasing seed water contents. (112) In this figure, the effects of afterripening in reducing seed dormancy of *Phleum arenarium* are presented. After 6 and 13 months of dry afterripening, the seeds achieved higher germination percentages under a wider range of temperatures.

Although the mechanisms explaining afterripening remain unknown, some possibilities exist. For example, in seeds with morphological dormancy, afterripening may explain the progressive growth of the embryo during dry storage. (113) Afterripening in seeds with physiological dormancy could be associated with a reduction in the concentration of an inhibitory compound or a lower sensitivity to it. For example, this table shows how the seed ABA content from two tomato genotypes decreased after one year of dry storage.

(114) **Stratification** is the exposure of the imbibed seed to low or warm temperatures. Because the most common approach is to expose seeds to cold temperatures, stratification is often used as a synonym for chilling or prechilling treatments. Use of warm stratification has been usually associated with release of morphological dormancy, while cold stratification has proven effective in overcoming physiological dormancy.

The temperature used for cold stratification usually ranges from 3 to 10°C, and the times of treatments vary depending on the species. While cold stratification is an absolute requirement for germination for some species; in others, it may only improve germination rates or uniformity. For some species, cold stratification may increase the range of temperatures under which germination occurs, or increase light sensitivity in species that require light for germination. (115) Effects of cold stratification in seeds with physiological dormancy are probably the result of changes in the balance of endogenous promoters and inhibitors.

For instance, this figure shows the changes in ABA and GA concentrations in plum seeds during stratification. A drastic reduction in the ABA concentration and increase in GA concentration occurred that would explain dormancy breaking in this species after stratification.

(116) In this example, germination rates of liquidambar seeds were improved by a stratification treatment of 15 days at 0°C, and this effect was similar to seed imbibition in a GA solution. Note that final germination percentage was similar in both treated and untreated seeds.

(117) **Chemical compounds.** Imbibition of dormant seeds in a solution containing a compound that induces germination is another alternative to breaking physiological dormancy. An obvious and effective choice is imbibition of seeds in a GA solution. Other compounds that have been used to break dormancy are potassium nitrate, ethrel, butenolide (the active ingredient from smoke), hydrogen peroxide, and anaesthetic compounds (e.g., acetone, ethanol)

(118) **Light.** Light quantity and quality can provide information about a seed's relative position in the soil or surrounding vegetation. Many seeds, especially small seeds, require light for germination. One of the most common and best studied examples is lettuce. This figure compares germination of lettuce seeds from a photosensitive genotype in dark vs. light. In lettuce and other species, the light mediated induction of germination in seeds is governed by phytochrome, which implies that red light induces germination and far-red light inhibits it. It has been determined that *Pfr*, the far-red absorbing or activated form of phytochrome, induces germination by promoting GA synthesis.

In some species, continuous light may inhibit germination. Onion and leek are examples of species where seed germination has been reported to be inhibited by continuous light. In these cases, seeds must be germinated in the dark.

(120) **Leaching.** Physiological dormancy may be overcome by modifying the balance of compounds that inhibit and promote germination in the seed. In some cases such as beet seeds, dormancy may be alleviated by exposing seeds to running water that dilutes or removes the inhibitory compounds from the seeds. This treatment is known as *leaching*.

(121) **Alternating temperatures.** In addition to light, temperature fluctuation is another signal for a seed regarding its relative position in the soil or surrounding vegetation. Deep in the soil and in the middle of abundant vegetation, temperature fluctuations during the day and night are lower than near the soil surface or in a gap without surrounding vegetation. This variation may explain, in part, why seed germination in some species is favored by alternating temperatures compared to a constant temperature; e.g., 30/20°C day/night versus a constant 25°C. Changes in hormone sensitivity have been suggested as a possible mechanism mediating induction of germination by alternating temperatures.

(122) **Priming** treatments enhance germination percentage, uniformity and rate in several species. Additionally, in some species such as lettuce, priming treatments alleviate thermoinhibition and the light requirement for germination. This picture shows the positive effect of priming on seed germination at relatively high temperatures and in the dark for a lettuce genotype sensitive to both the lack of light and high temperatures.

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