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Seed Dormancy and After-ripening Mechanisms in Seed Germination: A Comprehensive Review

R.Jeya Chandra [a], P.Masilamani [a*], B.Suthakar [b], P.Rajkumar [a], S.D.Sivakumar [c] and V.Manonmani [d]

[a] Agricultural Engineering College and Research Institute, TNAU, Kumulur-621 712, Tiruchirappalli, Tamil Nadu, India.
[b] Agricultural Engineering College and Research Institute, TNAU, Coimbatore-641003, Tamil Nadu, India.
[c] Institute of Agriculture, TNAU, Kumulur-621 712, Tiruchirappalli, Tamil Nadu, India.
[d] Department of Seed Science and Technology, TNAU, Coimbatore-641003, Tamil Nadu, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

A review on seed dormancy and after-ripening mechanism on seed germination was conducted. After-ripening is an important post-harvest phase in seeds that causes physiological and biochemical changes that reduce dormancy and promote germination. It is a time based and environment regulated process that occurs in dried seeds and determines germination potential. This post-harvest period is characterized by a series of biochemical and molecular changes that modify the seeds internal environment, ultimately breaking dormancy and enabling germination.

**Corresponding author: E-mail: masil_mahesh@yahoo.com;*

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The process of after ripening is mediated by several key mechanisms, including hormonal balances, particularly the reduction of abscisic acid levels and the increase in gibberellins and reactive oxygen species serve a dual function in both signalling and oxidative damage repair, contribute to dormancy associated barriers. Unlike other dormancy breaking methods, such as stratification, which requires external factors like light or temperature fluctuations, after-ripening primarily occurs under dry storage conditions. Molecular studies have shown that after-ripening involves gene expression with transcriptional regulation of dormancy related genes and activation of germination promoting genes are observed. Epigenetic modifications, such as DNA methylation and histone modifications also contribute to the regulation of these genes during after-ripening. Understanding the after-ripening mechanism is very important for improving seed storage, enhancing germination rates and optimizing crop yields and helps in management of seed banks, minimizing unwanted in-situ germination before harvest and also elucidates the complication of seed dormancy and germination, providing valuable information for both basic plant biology and applied agricultural sciences. Hence, understanding the interaction of external factors, internal seed biology, and after-ripening conditions are critical for optimizing seed germination rates and crop productivity.

Keywords: Seed dormancy; after ripening; abscisic acid; gibberellin; germination.

1. INTRODUCTION

Seed germination is a process by which a seed develops into a new plant [1]. Seeds are unable to germinate due to the phenomenon of dormancy [2]. Seed dormancy is defined as the inability of the viable seeds to germinate under conditions that are typically conducive to growth [3]. Physiological dormancy, which is the most widespread form of seed, refers to an inherent barrier that is present in either the embryo dormancy or the surrounding tissues (endosperm/testa, coat enhanced dormancy) dormancy [4]. Non-deep physiological dormancy which is prevalent with seeds of most weeds, vegetables, and many garden flowers [5], and is typically disrupted by short periods of cold stratification or dry seed storage at room temperature [4,5,6].

Dormancy is regulated by a complex mechanism of plant hormone interactions, the balance between two hormones, abscisic acid (dormancy induction) and gibberellins (dormancy release) [7]. It is also determined by environmental factors like temperature, moisture and other genetic factors [8]. The seed dormancy can be broken and germination potential can be acquired during a prolonged period of dry storage called **"**after ripening" [9]. After ripening, which often occurs after several months of dry storage at room temperature of freshly harvested and mature seeds, is a frequent strategy used to break dormancy and promote germination [10]. The seeds of many plants are dormant and unable to germinate at maturity, but gain the ability to germinate through after ripening during dry storage [11]. After-ripening (AR) is a process that takes place in the dry seed and is influenced by both time and environmental factors, determines the potential of the seed to germinate [12]. Additionally, dry storage and after-ripening treatments show positive effects on the release of dormancy and germination for many plant seeds [13]. It is a physiological process that involves the germination of mature seeds that have left the parent plant and undergone a series of physiological, biochemical and molecular changes like hormone levels, particularly the decrease in abscisic acid (ABA) and the increase in gibberellins, as well as shifts in gene expression and epigenetic modifications [14]. During after-ripening, seeds undergo metabolic and hormonal adjustments, including changes in abscisic acid and gibberellin levels, although decline in ABA content and increase in GA signalling, which helps towards on germination [15]. This review describe the importance and environmental factors influences the after ripening, difference between dormancy and after ripening, transcriptional changes and regulatory mechanism in after ripening, various crops with their unique mechanism in after ripening and its impact on agriculture.

2. CHARACTERISTICS OF SEEDS AFTER RIPENING

Seeds that have undergone after-ripening can be characterized by the following:

Expansion of the temperature range for germination: After-ripening widens the temperature range within which seeds can successfully germinate [16].

Reduction in ABA levels and sensitivity: There is a decrease in abscisic acid levels and sensitivity, along with an increase in gibberellin sensitivity or a loss of the GA requirement [17].

Elimination of light requirements for germination: Seeds that initially do not germinate in darkness may lose their light requirement during after-ripening [16].

Increased sensitivity to light: Seeds that do not germinate even with light may exhibit heightened sensitivity to light after-ripening [18,19].

- **Loss of nitrate requirement:** The need for nitrate to initiate germination is often lost during after-ripening [16].
- **Acceleration of germination velocity:** After-ripening can accelerate the germination process, as seen in tobacco seeds, Arabidopsis where it promotes testa and endosperm rupture [17,20].

The review focus on the adaptation mechanisms of after ripening of seeds to inbuilt from seed dormancy and germination, of their potential implications in various adaptations.

3. IMPORTANCE OF AFTER RIPENING

The after-ripening mechanism in seeds is important for the proper regulation of seed dormancy, germination and growth (Fig. 1).

Breaking dormancy: After-ripening is crucial for breaking seed dormancy, a survival strategy that prevents seeds from germinating under unfavourable conditions. By undergoing after-ripening, seeds synchronize their germination with optimal environmental conditions, enhancing their chances of successful seedling establishment.

Hormonal changes: During after-ripening, there are significant changes in the levels of plant hormones, particularly abscisic acid and gibberellins. ABA increase which inhibits germination, while GA increases which promotes germination. This hormonal shift is essential for the germination [4].

Metabolic adjustments: Seeds undergo metabolic changes during after-ripening, including the activation of enzymes that degrade stored reserves and provide energy for the growing embryo. These metabolic adjustments are critical for the resumption of growth and development, once dormancy is broken [6].

Genetic and epigenetic regulation: After-ripening involves changes at the genetic and epigenetic levels, including the expression of specific genes associated with dormancy and germination. Epigenetic modifications, such as DNA methylation, also play a role in regulating seed dormancy and after-ripening [21].

Adaptation and evolution: After-ripening is an adaptive trait that enhances the fitness of plant species in various ecological niches. It allows seeds to remain dormant during adverse conditions and germinate when the environment is conducive to growth, contributing to the evolutionary success of plants [5].

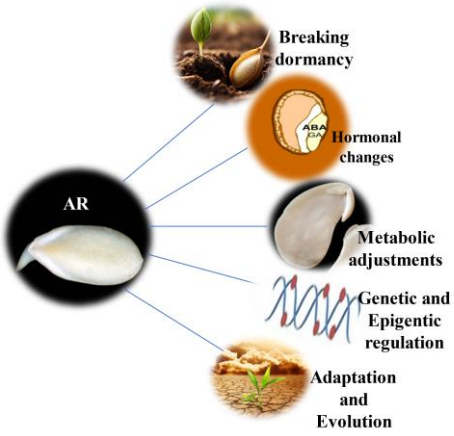


Fig. 1. After-ripening mechanism in seeds [4,5,6,21]

4. DIFFERENCE BETWEEN DORMANCY AND AFTER RIPENING

Dormancy and after-ripening are distinct but related concepts in seed biology, each playing a life threatening role in regulating when a seed can successfully germinate [4]. Dormancy is a complex trait that prevents germination from favourable conditions [22]. The seeds do not germinate until conditions are optimal for seedling establishment. Dormancy is regulated by various mechanisms, including high levels of the hormone abscisic acid, low levels of gibberellins, physical barriers like seed coats, and sometimes the presence of chemical inhibitors [7]. In contrast, after ripening is a post harvest process that seeds undergo to break dormancy and become capable of germination [11]. During after-ripening, physiological and biochemical changes occur, such as a reduction in ABA levels, an increase in GA, alterations in gene expression, and the degradation of dormancy associated proteins, which favours seed germination [11].

The primary difference between dormancy and after-ripening lies in exist way (Tables 1a & 1b). Dormancy prevents seeds from germinating prematurely, while after ripening is the process that overcomes dormancy, allowing seeds to germinate. Dormancy can last for varying periods, from days to years, depending on the species and environmental conditions, whereas after-ripening typically occurs over weeks to months [10,14]. Environmental factors like temperature and humidity can influence both processes, but in different ways dormancy is maintained or induced by certain environmental signs, while after ripening is accelerated or hindered by them [23,24]. For example, many tree and flower species exhibit dormancy to avoid germination during unfavourable seasons. In contrast, after-ripening is common in seeds like cereal grains, preparing them for uniform germination in the next growing season.

5. ENVIRONMENTAL FACTORS AND CHANGES REQUIRED DURING AFTER-RIPENING

After-ripening primarily causes a widening of the environmental conditions (temperature, light, oxygen) that allow germination, as well as an increase in germination speed process [4].

Effect of Temperature with light: Temperature plays a vital role by modulating the enzymatic and metabolic activities within the seed, although specific range of temperatures is often required to facilitate after ripening, with both low and alternating temperatures being common triggers for dormancy release (Table 2a & 2b) [5,19]. For example, chilling temperatures can break dormancy in some species, while warm temperatures promote after-ripening in others by accelerating the metabolic processes that lead to dormancy loss.

Light also has a significant impact especially in photoblastic seeds, which require specific light conditions for dormancy release and germination (Tables 2a & 2b) [27]. Red light is known to stimulate germination by converting phytochrome to its active form, promoting the breakdown of dormancy. In contrast, far-red light or darkness can maintain dormancy in some species. The interaction between light and temperature is also essential, as light can enhance or inhibit the effects of temperature on after-ripening, depending on the species and ecological context [4,28].

Moisture: Moisture is essential for seed germination, which alters the rate of dormancy alleviation during dry storage [19], it provides hydration and enhance permeable to the seed coating (Table 3). This mechanism ensures that seeds remain dormant during periods of high moisture, like in wet seasons, and only germinate once the dry after ripening phase is complete, aligning germination with more suitable conditions [4]. The physiological changes occur in the seed coat and embryo affecting their ability to regulate water uptake and ensures that seeds do not germinate prematurely [5].

Oxygen: The Oxygen is essential for the metabolic processes that occur during after-ripening. Where, adequate oxygen levels are necessary for cellular respiration, which provides the energy required for the biochemical changes that break seed dormancy. In conditions where oxygen availability is low, the after-ripening process may be delayed or inhibited. Seeds may remain dormant longer if they do not receive enough oxygen, as key metabolic activities are suppressed [43]. It is also used for aerobic respiration, which generates ATP, the energy currency of the cell. This energy is used for the synthesis of proteins and other molecules that are involved in breaking dormancy.

Table 1a. Difference between dormancy and after ripening

Aspect	Dormancy	After-ripening
Definition	A state of inhibited germination despite favorable conditions.	A process during dry storage that enables seeds to overcome dormancy and become capable of germination.
Nature	Inhibition mechanism	Enabling process
Occurrence	Immediately after seed maturation and dispersal	During a period of dry storage post-dispersal
Types	Physical, Physiological, Combinational, Morphological and Morphophysiological	Time-dependent process
Hormonal regulation	High levels of ABA maintain dormancy.	Decreased ABA levels and increased GA levels promote germination.
Environmental influence	Induced or maintained by environmental factors like light, temperature, and moisture.	Influenced by temperature and moisture content during storage.
Genetic and molecular changes	Specific gene expression patterns that inhibit germination.	Changes in gene expression, including the degradation of dormancy related mRNAs.

Table 1b. Difference between dormancy and after ripening

Aspect	Dormancy	After-ripening
Physiological state	Seeds in dormancy have low metabolic activity and are insensitive to germination signals.	Seeds remain metabolically inactive but gradually become responsive to germination signals upon imbibition.
Duration	Dormancy can last from a few days to several years depending on species and environmental conditions	The duration of after-ripening varies, it can take weeks to months depending on the species and storage conditions.
Practical implications	Dormancy helps in seed dispersal and survival during unfavorable conditions.	Ensures synchronized germination under optimal conditions, enhancing seedling survival and establishment
Purpose	Ensures seed germination occurs under optimal conditions	Prepares seed for germination by breaking dormancy
Timing	Immediate post maturation	Over a period of dry storage
Image		
Reference	[25,26]	

Table 2a. Effect of temperature with light on after ripening of seeds

Agricultural and Horticultural crops	Optimal temperature for dormancy release	Light	Reference
Wheat (*Triticum* spp.)	15-20°C	Light plays a minor role in dormancy release, but it can contribute to germination under suitable conditions.	[4]
Rice (*Oryza sativa*)	20-25°C	Light is generally not required for dormancy release but can improve germination in some varieties.	[28]
Barley (*Hordeum vulgare*)	15-20°C	Light has a limited role, but in some cases, it can enhance dormancy release when seeds are near the soil surface.	[6]
Sunflower (*Helianthus annuus*)	20-25°C	Light exposure can help release dormancy, especially under optimal temperature conditions.	[4,19,29]
Tomato (*Solanum lycopersicum*)	20-25°C	Light promotes germination after dormancy release, particularly under warm conditions.	[4]
Carrot (*Daucus carota*)	15-20°C	Light is not a primary factor, but certain conditions can enhance germination post after-ripening.	[28]
Lettuce (*Lactuca sativa*)	15-20°C	Light is essential for breaking dormancy in many varieties, especially when exposed to red light.	[6]
Arabidopsis (*Arabidopsis thaliana*)	20-25°C	Light, particularly red light, enhances dormancy release in combination with after-ripening.	[6]
Sorghum (*Sorghum bicolor*)	25-30°C	Light generally has a minor role in dormancy release but can affect germination rates depending on environmental conditions.	[4]
Pea (*Pisum sativum*)	15-20°C	Light is not typically required for dormancy release; germination occurs under optimal moisture and temperature conditions.	[28]
Annual ryegrass (*Lolium rigidum*)	9-50°C	-	[30]

Table 2b. Effect of temperature with light on after ripening of seeds

Tree crops	Role of temperature	Role of Light	Reference
Apple (*Malus domestica*)	Low temperatures (0-10°C) are crucial for dormancy release; prolonged chilling is necessary.	Light has minimal impact; dormancy release primarily depends on chilling requirements.	[31,32]
Peach (*Prunus persica*)	Chilling temperatures (5-12°C) required for dormancy release; inadequate chilling delays blooming.	Light exposure is not critical; focus is on meeting chilling requirements.	[33]
Cherry (*Prunus avium*)	Chilling temperatures (5-10°C) needed; sufficient chilling leads to uniform bud break.	Light does not significantly affect dormancy release; temperature is key.	[34]
Grape (*Vitis vinifera*)	Dormancy is broken by exposure to moderate temperatures (10-15°C) after chilling.	Light can enhance bud break post-dormancy but is not essential.	[35]
Pomegranate (*Punica granatum*)	Dormancy release occurs at moderate temperatures (10-15°C); cold exposure is less critical.	Light exposure can promote uniform bud break, particularly after chilling.	[36]
Rose (*Rosa* spp.)	Moderate temperatures (10-20°C) facilitate dormancy release; essential for continuous blooming.	Light exposure can promote flowering and bud break in some varieties.	[37]
Lilac (*Syringa vulgaris*)	Low temperatures (0-10°C) are necessary for dormancy release; chilling is crucial.	Light exposure can enhance flowering after dormancy release.	[38]
Magnolia (*Magnolia* spp.)	Chilling temperatures (5-10°C) required for breaking dormancy and uniform bud break.	Light exposure has a minor role; chilling is the primary factor.	[39]
Azalea (*Rhododendron* spp.)	Moderate temperatures (10-15°C) are effective in dormancy release; requires adequate chilling.	Light can enhance bud break and flowering, especially in controlled environments.	[40]
Maple (*Acer* spp.)	Low temperatures (0-5°C) are essential for dormancy release; extended chilling is required.	Light exposure is not a major factor; temperature controls dormancy release.	[41]
Teak (*Tectona grandis)*	Moderate temperature (25-30^{o}C) storage for 12 to 24 months for releasing dormancy	Light has minimal impact on dormancy release; temperature is the primary factor. However, light can enhance germination once dormancy is broken.	[42]

Table 3. Effect of moisture on after ripening of seed

Crop	Optimal moisture content for dormancy release	Reference
Wheat (*Triticum* spp.)	10-12%	[4]
Rice (*Oryza sativa*)	11-13%	[28]
Barley (*Hordeum vulgare*)	8-10%	[6]
Sunflower (*Helianthus annuus*)	6-8%	[4]
Tomato (*Solanum lycopersicum*)	8-10%	[4]
Carrot (*Daucus carota*)	7-9%	[28]
Lettuce (*Lactuca sativa*)	6-8%	[6]
Arabidopsis (*Arabidopsis thaliana*)	5-7%	[4]
Sorghum (*Sorghum bicolor*)	8-10%	[4]
Pea (*Pisum sativum*)	10-12%	[28]
Annual ryegrass (*Lolium rigidum*)	Below 9%	[30]

The reactive oxygen species, which are by-products of oxygen metabolism, play a vital role in signalling pathways that regulate seed dormancy and germination. It helps to breakdown the dormancy by modulating hormone levels, such as reducing abscisic acid and increasing gibberellin activity.

Table 4. Effect of light on after ripening of seed

Crop	Role of light in dormancy release	Light condition	Reference
Lettuce (*Lactuca sativa*)	Light is essential for breaking dormancy, particularly red light exposure.	Red light (660 nm), often continuous light	[44]
Tomato (*Solanum lycopersicum*)	Light promotes germination after dormancy release, particularly under warm and light-exposed conditions.	White light (400-700 nm), photoperiod of 12-16 hours	[4]
Apple (*Malus domestica*)	Light has minimal impact; dormancy release primarily depends on chilling requirements.	Light is generally not required	[31]
Cherry (*Prunus avium*)	Light exposure can enhance bud break post-dormancy but is not essential.	Indirect sunlight, diffuse light exposure	[34]
Grape (*Vitis vinifera*)	Light can enhance bud break post-dormancy but primarily depends on temperature.	Diffuse sunlight, shade conditions	[35]
Pomegranate (*Punica granatum*)	Light exposure can promote uniform bud break, particularly after chilling.	Full sunlight, 12-14 hours of photoperiod	[36]
Rose (*Rosa* spp.)	Light exposure can promote flowering and bud break in some varieties.	Full sunlight or high light intensity	[37]
Sunflower (*Helianthus annuus*)	Light exposure is necessary for germination post-dormancy release.	Full sunlight, photoperiod of 12-14 hours	[4]
Peach (*Prunus persica*)	Light generally has a minor role, with chilling being more critical for dormancy release.	Light is generally not required	[33]
Lilac (*Syringa vulgaris*)	Light exposure can enhance flowering after dormancy release.	Indirect sunlight, morning light preferred	[38]

Light: The after ripening mechanism in seeds in relation to light plays an important role in regulating dormancy and seeds germination under optimal light conditions (Table 4) [4]. After ripening changes the action of phytochromes, which are light-sensitive proteins that regulate seed responses to red and far-red light. It became more receptive to red light, indicating that they have been exposed to sunlight rather than shade. This technique prevents seeds from germinating in darkened, potentially less suitable settings [6].

6. VARIOUS MECHANISMS ON ARABIDOPSIS DURING AFTER RIPENING

In *Arabidopsis thaliana*, after ripening is a process that breaks seed dormancy and allows germination under favourable conditions. This involves several interconnected mechanisms that control gene expression, hormonal regulation and environmental responses. Some of the key mechanisms and their roles in mediating after ripening are in (Table 5) [4].

7. EXAMPLES OF AFTER-RIPENING IN VARIOUS CROPS WITH UNIQUE MECHANISMS

After ripening ensures releasing seed dormancy in various crops and different species exhibit unique mechanisms that regulate this process (Tables 6a, 6b, 6c & 6d).

8. AFTER RIPENING AND ITS IMPACT

After-ripening is a process in seeds that improves germination by breaking dormancy and allowing the seed to mature under optimal environmental conditions (Table 7).

9. AFTER RIPENING INDUCES TRANSCRIPTIONAL CHANGES AND REGULATORY MECHANISM IN SEEDS

Seed dormancy increases during seed maturation and reaches maximum in harvest ripened seeds [68]. The term "after ripening" refers to the process by which seeds undergo physiological changes during a time of dormancy before germination allowing seed embryos to overcome hibernation during development [11]. This process occurs during a period of dry storage of freshly harvested mature seeds [4,12]. The dormancy formation during seed development is governed by networks of transcription factors with distinct roles. The environmental factors following after ripening and stratification are being studied at the molecular level processes underlying dormancy and germination [68].

Table 5. Gene expression, hormonal regulation, environmental responses and their role in mediating after ripening

Mechanism	Genes involved	Role played	Interaction and effects	Reference
Hormonal changes	ABA	Maintains dormancy	Reduction in ABA levels during after-ripening helps break dormancy.	[45]
	GA	Promotes germination	Increase in GA levels promote seed germination after dormancy is broken.	[45]
Reactive oxygen species (ROS)	ROS-producing genes (e.g., RBOH)	Signaling molecules in dormancy breaking	ROS levels increase during after-ripening, acting as signals to break dormancy.	[46,47]
Gene expression	DOG1	Regulates seed dormancy	Expression decreases during after ripening, allowing germination.	[43]
	ABI3	Mediates ABA response	Expression decreases, reducing ABA signaling and dormancy.	[48]
	GA3ox1 and GA3ox2	GA biosynthesis	Increased expression promotes GA biosynthesis, aiding germination.	[49]
	ABI5 (ABA Insensitive 5)	Mediates ABA response	Decreased expression reduces ABA signaling, aiding dormancy break.	[50]
	Atsd4l	Mediates DOG 1 and GA response	Aiding dormancy break and germination	[51]
	AtPER1	suppress ABA catabolism and GA biosynthesis	Seed germination	[52]
	MKK3-MPK7	Phosphorylates ERF4	Reduction of ABA leads germination	[53]
	WRKY36 and AFP2	Suppress DOG 1	Promotes germination	[31]
	GID1b (GA Insensitive DWARF1b)	-	Promotes germination	[11]
	WOX	Regulate PHYB	Generate germination	[54]

Table 6a. After ripening in various crops with unique mechanism

Plant Species	After ripening duration	Description of after ripening effects	Unique mechanisms or characteristics	Reference
Wheat (*Triticum aestivum*) 	Several weeks to months	Germination inhibitors are degraded, allowing seeds to germinate more readily.	Degradation of abscisic acid (ABA) and activation of gibberellins (GA) signaling pathways.	[55]
Rice (*Oryza sativa*) 	1-3 months	Increased seed vigor and germination rates.	Reactive oxygen species (ROS) involvement in breaking seed dormancy.	[56]
Barley (*Hordeum vulgare*) 	Several weeks to months	Dormancy decreases, leading to increased germination rates.	Changes in hormonal balance, particularly the reduction in ABA levels.	[57]
Corn (*Zea mays*) 	1-2 months	Breaking of physiological dormancy, enhancing germination capability.	Modulation of ABA and GA levels, activation of metabolic processes.	[58]

Table 6b. After ripening in various crops with unique mechanism

Plant Species	After ripening duration	Description of after ripening effects	Unique mechanisms or characteristics	Reference
Soybean (*Glycine max*) 	2-4 weeks	Overcoming of seed dormancy, promoting uniform germination.	Seed coat permeability changes, allowing water uptake and gas exchange.	[59]
Sorghum (*Sorghum bicolor*) 	Several weeks to months	Overcoming of seed dormancy and promotion of seedling vigor.	Involvement of ROS and hormonal changes, specifically reductions in ABA.	[60]
Sunflower (*Helianthus annuus*) 	1-2 months	Breaking of physiological dormancy, enhancing germination capability.	Changes in hormonal balance and activation of metabolic processes.	[61]
Tomato (*Solanum lycopersicum*) 	1-2 months	Enhancement in germination speed and uniformity.	Modulation of ABA and GA levels, and changes in seed coat properties.	[62]
Pea (*Pisum sativum*) 	1-2 months	Dormancy reduction, leading to improved germination rates.	Seed coat permeability and changes in hormonal balance.	[4]

Table 6c. After ripening in various crops with unique mechanism

Plant Species	After ripening duration	Description of after ripening effects	Unique mechanisms or characteristics	Reference
Lettuce (*Lactuca sativa*) 	2-4 weeks	Overcoming of seed dormancy, promoting uniform germination.	Sensitivity to light and temperature, changes in ABA and GA levels.	[63]
Arabidopsis thaliana 	1-2 months	Dormancy alleviation and promotion of germination	Changes in hormonal balance (reduction in ABA and increase in GA), involvement of reactive oxygen species (ROS), and alteration in gene expression.	[64]
Oak (*Quercus* spp.) 	2-6 months	Ensures spring germination	Cold stratification; breakdown of inhibitors, hormone changes	[5]
Maple (*Acer* spp.) 	1-3 months	Synchronizes with favorable conditions	Cold stratification; hormonal changes, seed coat breakdown	[4]
Apple (*Malus domestica*) 	2-4 months	Prevents germination inside the fruit	Cold stratification; reduction of ABA, increase in gibberellins	[6]

Table 6d. After ripening in various crops with unique mechanism

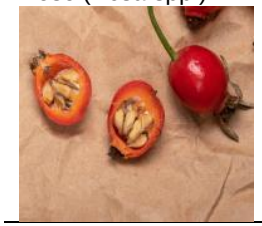
Plant Species	After ripening duration	Description of after ripening effects	Unique mechanisms or characteristics	Reference
Peach (*Prunus persica*) 	1-3 months	Promotes spring germination	Warm and cold stratification; enzymatic changes	[33]
Primrose (*Primula* spp.) 	2-6 months	Avoids winter germination	Cold stratification; changes in seed coat permeability, hormonal balance	[65]
Lupine (*Lupinus* spp.) 	1-3 months	Ensures optimal germination conditions	Scarification; changes in seed coat and internal biochemistry	[4]
Rose (*Rosa* spp.) 	2-3 months	Promotes synchronized germination in spring	Cold stratification; reduction of ABA, increase in gibberellins, enzymatic changes	[5,6]

Table 7. Advantages of after ripening

Aspect	Benefits	Practical applications	Reference
Improved germination rates	Enhanced and uniform germination of seeds	Seed treatments to break dormancy, improving sowing success rates	[55]
Seed storage optimization	Better prediction of seed viability over time	Optimized storage conditions to maintain seed viability	[56]
Synchronized germination	More uniform crop emergence	Timing sowing to ensure synchronized germination, leading to uniform crop growth	[57]
Reduction of preharvest sprouting	Minimizing unwanted germination before harvest	Breeding and selecting varieties with desirable after ripening characteristics	[66]
Enhanced seedling vigour	Increased seedling growth and establishment	Use of after-ripening techniques to produce robust seedlings	[67]
Control of weed seed bank	Managing weed seed dormancy and germination cycles	Application of after ripening knowledge to reduce weed seed bank in fields	[28]

Table 8. Percentage germination of dormant and after ripened seeds of wheat cv. AC domain imbibed in water and ABA solution

Sample	24 HAI	36 HAI	48 HAI
D	0	0	0
AR	99%±1.0	100%±0.0	100%±0.0
AR±ABA	4%±2.0	96%±2.4	100%±0.0

After ripening: Dormancy release and enhancing germination: In tobacco seed Havana 425 possess photodormancy under dark germination, which can be released during after ripening period with addition of GA and has the ability to germinate under dark germination enhances rupturing testa and endosperm, as well as subsequent stimulation of ABA degradation, inhibition of ABA biosynthesis, and b-1,3-glucanase accumulation in the micropylar endosperm [69]. The findings, which were similar to Arabidopsis testa mutants, demonstrated that reduced seed coat imposed dormancy is correlated with increased sensitivity to GA and suggest that GA requirement for seed germination is regulated by the testa restrictions and ABA [64].

In *Arabidopsis thaliana* found that gas plasma activated water (GPAW) which released the physiological dormancy by after ripening storage. The freshly harvested (FH) seeds of Col-0 and C24 seed populations were treated with control, GPAW, KNO_3, He/O_2 GPAW, H_2O_2were practiced and showed dormancy which release by GPAW attain 80% germination is due to weakening of endosperm is inhibited by ABA, promoted by GA and ROS, while He/O2-GPAW also released dormancy 40% by trigger the hormonal regulation like ABA degradation with 8'-hydroxlase encoded by the *CYP707A2* gene enhancing the seed germination [20]. In *Nicotiana tabacum* seeds also showed the dormancy due to hard texture of seed coat, it may also release by after ripening with rupturing of testa and endosperm, associated with transient ß-1,3 glucanase [70].

In wheat seed dormancy examined with dormant (D) and after ripening (AR) on germination of 24 and 36 hours after imbibition (HAI) (Table 8). The after ripened water imbibition poses germination after 24 h, whereas delaying of germination with ABA treatment, although seminal roots were observed in water imbibed after ripened seeds and no roots were observed during ABA treated after ripened seeds [71].

In rice variety, Jiucaiqing (*Oryza sativa* L. subsp. *japonica*) seeds were evaluated with dormancy release by using different after ripening times 1, 2 and 3 months on germination and seedling emergence, which showed that 1 month of after-ripening within 10 days of imbibition recorded 95% of germination and 85% of seedling emergence were detected compared to freshly harvested seeds with less than 45% of germination and 20% of seedling emergence. The dormancy was released in three months after ripening which was accompanied with a decrease in ABA content and an increase in IAA content during imbibition [72].

The apple seed varieties of 'Gold Milenium', 'Ligol' and 'Szampion' dormancy were released

through stratification at 3 °C for 90 days in darkness using distilled water or aqueous solutions of 500 mM salicylic acid (SA), 10^{-3}M jasmonic acid (JA), gibberellin A3 (GA_3) and 6-benzylaminopurine (BAP) at 250 mg·dm^{-3} and 100 mg·dm^{-3}, respectively. The results indicated that 'Szampion' seeds exhibited the highest germination percentage ranging from 88–100%, 'Ligol' seeds with lower germination rates, while 'Gold Milenium' seeds show lowest germination percentage (30 to 60%). This reduced germinability of 'Gold Milenium' seeds may be partially attributed to the negative influence of germination inhibitors present in apple fruit extracts such as abscisic acids and chlorogenic acids. Conversely, the lower germination percentage of 'Ligol' seeds may be attributed to insufficient maturity. Notably, the differences in germinability may also be influenced by cultivar specific properties. The application of growth regulators generally enhanced seed germinability, suggesting their involvement in the dormancy release. The most significant results were observed by following GA_3 treatment, which increased 'Ligol' seed germination by 100% compared to the control [73,74] also demonstrated the involvement of gibberellins in the cold-mediated removal of dormancy in apple seeds.

The germination enhanced by after ripening or stratification, release of dormancy is regulated by ABA and gibberellins, along with other phytohormones such as jasmonic acid (JA), brasenosteiod (BR) and ethylene inhibited the ABA accumulation and enhanced the dormancy release, which positively regulates seed dormancy by modulating the WRKY genes, along with gibberellin and abscisic acid regulated MYB (GAMYB) GA response factors are played intermediated to transition dormancy to germination [75].

The role of *Arabidopsis thaliana* seed dormancy 4-like (AtSdr4L) as a novel specific regulator for seed dormancy and germination. The study demonstrated that AtSdr4L inhibits dormancy and promotes germination by regulating the GA pathway downstream of the function of delay of germination (DOG1), assessed through germination of wild type (WT) and mutants of Atsdr4l-1 and Atsdr4l-2. The results indicated that only 1% of freshly harvested Atsdr4l mutant seeds germinated compared to 10% for the WT. Furthermore, after 1 month of dry storage WT seeds achieved 80% germination, while mutant seeds remained at approximately 10%. The dormancy of Atsdr4l seeds stored for 1 month could be completely broken by stratification for 3 d at 4 °C to release dormancy. The complete dormancy release was observed after 50 d for WT seeds and after 80 d for the mutant seeds [51].

In Arabidopsis showed dormancy induction, whereas mRNAs converted to monosomes rather than polysomes which contain 10,000 mRNAs, helps to avoid premature germination, whereas after ripening oxidation of 8-oxo-guanine aids in dormancy release and that long-term storage allows for oxidative damage, which damages germination. While imbibition of germination, mRNA triggers redox regulation, energy regulation and protein synthesis thus proteins that promote dormancy have lower translational fidelity, which accelerates the transition to germination [76].

In Peanut, variety Luhua No.14 with deep dormancy was experimented with three different developmental stages such as freshly harvested seed (FS), after ripening seed (DS) and newly germinated seed (GS) were assessed. The freshly harvested seeds can germinate at four days after imbibition (DAI) reach germination of 75% at 10 DAI, whereas after ripening seeds started to germinate at two days imbibition and germination increased at 4 DAI and reached 100% of germination at 6 DAI. This could be due to mobilization of reserves and energy production, oxidative phosphorylation, carbohydrate metabolism and glutathione metabolism, cell wall modifications and some of the genes which responsible for germination like expansin and xyloglucan endotransglycosylase were expressed [77].

The seeds of *Eucommia ulmoides* on germination showed that freshly harvested seeds at 13.3±0.7%, but 25.2±1.3%, 23.3±1.1%, 21.7±1.2%, and 20.0±0.8% after 30, 60, 90 and 120 days of after-ripening showed increased germination and further decreased due to short period availability of after ripening. In *Silybum marianum* were tested under fresh and after ripened seeds like fresh, 2- and 7-months storage of germination with (5, 10, 15, 20, 25, 30, 35^{0}C) and six alternating (5/15, 10/20, 15/25, 15/30, 20/30 and 25/30^{0}C) temperatures in continuous darkness and in light (12/12 h light/dark) [13]. The findings indicated that milk thistle seeds are both photoblastic and photodormant, with varying germination responses under darkness among distinct populations [78].

The solanum species of *cv. Oforiwa* and *cv. Kpando* were assessed with maturity stages like 30, 40, 50, 60 and 70 days after anthesis and four various after ripening periods such as 0, 5, 10 and 15 days on germination of fruits harvested at 40 days after anthesis (DAA) failed to germinate, while 50 DAA fruits exhibited not more than 50% germination in both cultivars. However, when seeds extracted from these fruits underwent a 15-day ripening period in storage, the germination percentage increased significantly by 63 to 72% and the seeds extracted from fruits harvested on 60 or 70 DAA achieved maximum germination, ranging from 93 to 94% (cv. Oforiwa) and 78 to 96% (cv. Kpando), independent of after-ripening treatment [79]. It is concluded that after-ripening is inconsequential and unnecessary when seeds are harvested at physiological maturity (60-70 DAA)

The ageing on *in vitro* true seed and *in vivo* drupe germination as well as the dormancy mechanism in teak were studied. Fresh, one year and two year stored drupes were used to represent various stages of ageing. Under in vivo conditions, two year old treated drupes recorded the highest germination of 32%, followed by two year old control drupes at 17 % and fresh drupes with both control and treated drupes recorded minimum germination of 2 % and 3 % respectively (Table 9). This indicated that the germination rate in teak drupes increased as the storage period were increased. When true seeds isolated from fresh drupes and grown under in vitro conditions showed a 58.3% increase in germination rate. The SEM analysis also helps to forecast the difference and nursery studies show that one and two year old drupes have the highest germination [80]. This result is confirmed with several authors in teak seed [81,42,82,83,84,85]. The germination capacity of teak drupes was retained for more than 7 years also reported [86].

The brinjal variety of kemer 27 cultivar undergo with different maturing harvest stages like (55-60-70-80-90 DAA) in two subsequent conditions with drying methods of Control (C), after ripening AR, second drying method (SDM), SDM with AR, first drying method (FDM), FDM with AR on germination and seedling emergence were practiced. The highest germination rates were recorded in the 1st year; 51% in 55th day seeds, 75.5% in 60th day and 98% in 90th day in AR group, 91% in 70th day from FDM with AR, and in 80th day harvest 87% in AR and SDM with AR were determined. In the second year, seeds harvested on the 70th and 90th days, the highest values were obtained from AR and SDM with AR applications. This shows the reductions in germination performance of 90 DAA seeds in certain drying and AR application conditions can be attributed to the inability to regulate the available moisture in seeds that were not harvested at the optimal maturity stage [87].

Table 9. Effect of fresh, one-year and two-year stored drupes on *In vivo* germination of teak

Treatments	Germination (%)	Number of seedlings/100 drupes	Root length (cm)	Shoot length (cm)	Dry matter production (mg/10 seedlings)	Vigour index
T_1-Fresh-drupes	2.0 (8.13)	3.0	2.0	3.5	40	9
T_2-Fresh drupes - S-D for 6 days	3.0 (9.97)	4.0	2.2	3.4	42	12
T_3- One year-old drupes	6.0 (14.17)	10.0	2.5	1.8	36	13
T_4- One year-old drupes -S-D for 6 days	14.0 (21.97)	24.0	3.0	3.4	38	50
T_5-Two year-old drupes	17.0 (24.35)	30.0	2.7	3.5	36	62
T_6-Two year-old drupes -S-D for 6 days	32.0 (34.45)	38.0	2.9	4.0	37	130
Mean	12.3 (20.26)	18.1	2.5	3.2	38.1	46.0
Sed	0.119	0.464	0.075	0.069	1.099	1.294
CD (P=0.05)	0.255	0.990	0.168	0.154	2.450	2.884

Table 10. Germination percentage (GP), vigour index (VI), speed of germination, maximum growth potential (MGP), dormancy intensity (DI) and seed viability (TZ) of cucumber CU-1047 and CU-1051 seeds following various dormancy-breaking treatments.

Treatment	GP (%)	VI (%)	SG (etmal)	MGP (%)	DI (%)	TZ (%)
P0: Control	1	0	0.8	1	99	97
P1: Dry heat at 36°C, 3 days	18	10	3.0	18	82	92
P2: Dry heat at 36°C, 5 days	8	3	1.6	8	92	92
P3: Dry heat at 36°C, 7 days	14	5	2.6	14	86	92
P4: Dry heat at 36°C, 9 days	24	10	4.6	24	74	97
P5: Dry heat at 50°C, 24 hours	8	4	1.0	8	93	94
P6: Dry heat at 50°C, 72 hours	15	5	1.0	15	86	95
P7: Dry heat at 50°C, 120 hours	20	5	3.0	20	81	96
P8: Dry heat at 80°C, 6 hours	17	5	3.0	18	82	98
P9: Dry heat at 80°C, 12 hours	40	23	9.5	41	60	98
P10: Dry heat at 80°C, 24 hours	62	22	16.7	66	34	94
P11: DHT chamber	59	26	10.4	60	40	97
P12: Distilled water	2	1	0.4	2	98	95
P13: Distilled water + drying	0	0	0.2	1	100	98
P14: 1000 ppm GA_3	2	1	0.1	2	98	96
P15: 1000 ppm GA_3 + drying	2	1	0.4	2	98	95
P16: 2000 ppm GA_3	5	5	0.7	5	94	98
P17: 2000 ppm GA_3 + drying	24	8	5.1	24	76	94
P18: 1% KNO_3	23	17	6.3	23	77	95
P19: 1% KNO_3 + drying	55	31	12.6	55	45	97
P20: 2% KNO_3	19	11	4.7	20	80	97
P21: 2% KNO_3 + drying	22	11	4.9	22	78	92
CV	25.17	36.40	23.76	25.04	6.39	1.93

Table 11. Synchrony pattern of dormant and non dormant seeds

Species	Mature seed-dormant seed		After ripening-non dormant	
	Asynchrony	Synchrony	Asynchrony	Synchrony
Experiment 1				
Brassica napus	3.14±0.016	0.089±0.002	2.57±0.042	0.116±0.007
Sinapsis arvensis	2.40±0.014	0.054±0.001	2.84±0.072	0.132±0.002
Experiment 2				
Brassica napus	2.75±0.022	0.023±0.002	1.95±0.062	0.115±0.002
Sinapsis arvensis	2.25±0.012	0.038±0.004	2.00±0.009	0.140±0.0029

Mitogen-activated protein kinase 3 (MKK3)-MPK7 ethylene response factor (ERF4) - expansin (EXPA) interaction used for breaking the dormancy in arabidopsis. The ERF4 binds to the GCC boxes in the exons of some EXPA and inhibits their transcription and maintain their dormant state. The signal molecule H_2O_2, which activates the MKK3- MPK7 module, it activated

module phosphorylates ERF4, leads to its degradation, and relieves suppressive effect on expression of the EXPAs, it helps promote cell expansion in the radicle protrusion and suitable for seed germination [88].

The WRKY36 is a novel negative regulator of primary seed dormancy that binds to the DOG1 promoter to suppress their effect. The effect of higher amount of WRKY36 depends on ABA-insensitive five-binding protein 2 (AFP2), leads histone deacetylation thereby suppressing delay of germination (DOG1) expression and promote germination [88]. In *Avena fatua* seed showed dormancy in caryopsis can release by after ripening thus enables reduction in ABA content in embryos increase with GA before the germination completed, along with that nitric oxide (NO) also plays mediate role in reduction of dormancy [89].

In *Panax notoginseng* seeds during after ripening helps the loss of dormancy through CHH 698 hyper-methylation. The high levels of DNA methyltransferases, including PnCMT2 in the embryo and PnDRM2 in the endosperm, cause hyper-methylation and alter the transcriptional status of genes associated with hyper-DMRs. Transcriptional repression is one of the factors that contribute to seed dormancy and after-ripening. Meanwhile, DNA hypermethylation stimulates gene expression in resistant seeds during after-ripening. This activation changes the hormone mediated signaling pathway and energy metabolism, hence significantly contributing to embryo development and after-ripening processes. DNA methylation plays a crucial part in the after-ripening phase of refractory seeds, offering a comprehensive understanding of the epigenetic regulation of MPD-typed seed dormancy in plants [90].

The cucumber varieties of CU 1047 and CU 1051 imposed dormancy released by using dry heat treatments (DHT) at 36, 50 or 80°C. The result showed that dry heat at 80°C for 24 hours recorded highest germination 62%, followed further by DHT chamber a 59% compared with control 1% (Table 10). An alternative method was used soaking the seeds in 1% KNO_3 enhancing 55% germination [91].

The two species of *brassica* such as *Sinapis arvensis* and *B. napus* shows physiological dormancy, can be broken by after ripening and stratification methods. The seeds show inverse relationship between the germination, *Sinapis arvensis* resulted with three months after ripened have more synchronous germination than mature seeds. The most synchronous and asynchronous germination was observed for seeds stratified for 5 days and mature seeds of *B. napus.* The germination synchrony directly corresponded with the level of dormancy, the germination asynchrony was different between two species ranging from 3.14 in *B. napus* to 2.25 in *S. arvensis* (Table 11). Since application of stratification and after ripening enabled seeds to germinate in synchronous manner [92].

The use of exogenous application of GA and ABA on *Panax notoginseng* resulted that GA with 50, 250 and 500 mg L^{-1} with control (CK) shows that 250 mg L^{-1} on 0, 15, 35 and 45 days after ripening (DAR) of embryo/endosperm (Em/En) revealed that 0 DAR resulted that embryo enclosed by the endosperm, while 30 DAR shows more than half of the embryo length. The germination rate of 30 days after treatment, GA_3 treatment significantly shows control was raised by 10.0% and 27.0% at 45 DAR and 60 DAR, respectively, while the increase in the 50 mg L^{-1} GA_3 treated seeds were 30.0% and 53.0% respectively (Ge et al., 2023a). The ABA treatment with CK, 1 mg L^{-1} and 10 mg L^{-1} resulted that 53.64% and 52.34%, respectively, which were lower than CK 61.98% at 30 DAR on Em/En [93].

Investigated the effects of 0, 28 and 56 days after ripening (DAR) on germination and seedling emergence in rice varieties such as *Japonica Nipponbare* (NPB), Nanjing 9108 (NJ 9108), Wuyunjing 7 (WYJ 7), Zhendao 88 (ZD 88), and indica 9311. The germination percentage (GP), seedling percentage (SP), and germination index (GI) of NPB seeds improved considerably after 10 days of imbibition, reaching 92%, 67% and 4.0, respectively, indicating that seed dormancy levels had been partially discharged. The GP, SP, and GI of NPB seeds at 56 DAR were 98%, 98% and 5.2 after 10 days of imbibition, respectively. The results showed that the complete seed dormancy release of NPB seeds was mostly at 56 DAR [94]. The two processes are closely interrelated and regulated the seed dormancy, 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 [95,96,97]

10. CONCLUSION

After-ripening is a complex mechanism that helps in seed transition from dormancy to active germination. This period is mainly influenced during storage conditions and the duration can influence through various environmental factors such as temperature and moisture. Additionally, biochemical and hormonal changes that enable the seeds to overcome dormancy and enhance seedling germination are documented. Hence, understanding the interaction of external factors, internal seed biology, and after-ripening conditions are critical for optimizing seed germination rates and crop productivity.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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