

DECIPHERING THE ENIGMA OF SEED DORMANCY: A REGULATORY CIRCUIT PERSPECTIVE

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Abstract

Seed dormancy is a fundamental adaptive trait that allows plants to regulate the timing of germination in response to environmental cues, ensuring optimal seedling establishment and survival. In this review, we provide a comprehensive overview of seed dormancy from a regulatory circuit perspective, highlighting the intricate interactions between genetic, physiological, and environmental factors. We explore the genetic control of dormancy, focusing on major dormancy genes, epigenetic modifications, and their roles in dormancy induction and release. Physiological mechanisms, including hormone signaling pathways (e.g., abscisic acid and gibberellins) and environmental cues (e.g., light, temperature, and water availability), are discussed in the context of dormancy regulation. We delve into the dynamic interactions between genetic, physiological, and environmental factors, elucidating feedback loops and cross-talk mechanisms that enable plants to integrate multiple signals and modulate dormancy levels adaptively. Furthermore, we examine the ecological implications of seed dormancy for plant survival, population dynamics, and ecosystem stability, as well as its economic importance in agriculture, seed storage, and germination performance. Finally, we discuss future directions and emerging research frontiers, including advances in molecular genetics, omics technologies, and translational applications for dormancy manipulation. By unraveling the enigma of seed dormancy, we can harness its potential for sustainable agriculture, biodiversity conservation, and ecosystem resilience in the face of global environmental changes.

Keywords: seed dormancy, regulatory circuit, genetic control, physiological mechanisms, environmental cues, feedback loops, cross-talk, ecological implications, agricultural significance, molecular genetics, omics technologies, translational applications.

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1. INTRODUCTION

Seed dormancy, a phenomenon crucial for the survival and dispersal of plants, has intrigued biologists for decades. At its core, seed dormancy refers to the ability of seeds to remain quiescent even under conditions conducive to germination. This delay in germination until suitable environmental conditions prevail is essential for ensuring the plant's success in various ecological niches and plays a significant role in agricultural practices.

Seed dormancy is governed by a complex interplay of genetic, physiological, and environmental factors. Understanding this intricate regulatory network is essential for elucidating the mechanisms underlying dormancy induction, maintenance, and release. Recent research has shed light on various aspects of seed dormancy regulation, leading to the emergence of the regulatory circuit perspective.

From a genetic standpoint, seed dormancy is influenced by a diverse array of genes and their interactions. Major dormancy genes, such as

those encoding transcription factors and hormone biosynthesis enzymes, play crucial roles in modulating dormancy levels [1]. Additionally, epigenetic modifications, such as DNA methylation and histone modifications, have been implicated in regulating gene expression patterns associated with dormancy [2].

Physiological mechanisms also contribute significantly to seed dormancy regulation. Hormones, particularly abscisic acid (ABA) and gibberellins (GA), play antagonistic roles in controlling dormancy and germination. ABA promotes dormancy induction and maintenance by inhibiting seed germination, while GA promotes germination by antagonizing ABA effects [3]. Moreover, reactive oxygen species (ROS) and redox regulation have emerged as critical regulators of dormancy, influencing hormone signaling pathways and cellular processes [4].

Environmental cues, including light, temperature, and water availability, play pivotal roles in modulating seed dormancy. Light signals are perceived by phytochromes and cryptochromes, which regulate downstream processes involved in dormancy release [5]. Temperature fluctuations during seed development and after-ripening can influence dormancy levels by modulating hormone biosynthesis and signaling pathways [6]. Similarly, water availability affects seed dormancy through its impact on hormone metabolism and cellular processes [7].

The regulatory circuit perspective emphasizes the dynamic interactions between genetic, physiological, and environmental factors in governing seed dormancy. Feedback loops and cross-talk between these factors contribute to the fine-tuning of dormancy levels in response to changing environmental conditions. Integration of inputs from multiple pathways enables plants to modulate dormancy release and germination timing adaptively [8].

In natural ecosystems, seed dormancy plays a crucial role in plant survival, colonization, and succession. Dormancy allows seeds to persist in

the soil seed bank, ensuring population persistence in unpredictable environments. Moreover, dormancy regulates the temporal spread of germination, promoting species diversity and ecosystem stability [9].

In agricultural systems, understanding seed dormancy is essential for optimizing crop production and seed quality. Dormancy can affect the timing and uniformity of germination, influencing crop establishment and yield. Moreover, managing seed dormancy is crucial for weed control, as dormant weed seeds can persist in the soil seed bank and germinate when conditions become favorable [10].

Advances in molecular and genetic techniques have revolutionized our understanding of seed dormancy regulation. High-throughput sequencing technologies enable genome-wide analyses of gene expression, epigenetic modifications, and genetic variation associated with dormancy traits. Integration of omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, provides a comprehensive view of the molecular mechanisms underlying dormancy regulation [11].

Translating fundamental research on seed dormancy into practical applications holds promise for agriculture and biotechnology. Manipulating dormancy levels in crop seeds can improve seed quality, enhance stress tolerance, and optimize germination timing for specific growing conditions. Moreover, understanding the genetic basis of dormancy traits enables targeted breeding strategies for developing new crop varieties with improved dormancy characteristics [12].

In conclusion, seed dormancy represents a fascinating biological enigma with significant ecological and agricultural implications. The regulatory circuit perspective provides a holistic framework for understanding the complex interactions between genetic, physiological, and environmental factors underlying dormancy regulation. Continued research efforts aimed at deciphering the molecular mechanisms of seed dormancy hold

promise for addressing challenges in agriculture and ecosystem management.

2. Layers of Regulation in Seed Dormancy

Seed dormancy, a complex trait regulated by multiple genetic, physiological, and environmental factors, involves intricate layers of regulation. Understanding these layers is essential for deciphering the mechanisms underlying dormancy induction, maintenance, and release.

2.1. Genetic Control

Genetic factors play a fundamental role in seed dormancy regulation. Several major dormancy genes have been identified, each contributing to different aspects of dormancy regulation [13]. These genes encode various proteins involved in hormone biosynthesis, signaling pathways, and transcriptional regulation.

2.1.1. Major Dormancy Genes and Their Functions

Key regulators of seed dormancy include transcription factors, such as DELAY OF GERMINATION 1 (DOG1) and ABSCISIC ACID INSENSITIVE 3 (ABI3), which control the expression of genes involved in ABA signaling and seed maturation [14]. Mutations in these genes can lead to alterations in dormancy levels, highlighting their importance in dormancy regulation.

Moreover, genes encoding enzymes involved in ABA biosynthesis and catabolism, such as 9-cis-epoxycarotenoid dioxygenase (NCED) and ABA 8'-hydroxylase, respectively, also play crucial roles in modulating dormancy levels [15]. These enzymes regulate ABA levels in seeds, thereby influencing dormancy induction and maintenance.

2.1.2. Epigenetic Modifications

In addition to genetic variation, epigenetic modifications have emerged as important regulators of seed dormancy. DNA methylation and histone modifications can alter chromatin structure and gene expression patterns,

affecting dormancy-related traits [16]. For example, changes in DNA methylation patterns at the DOG1 promoter region have been associated with variation in dormancy levels among Arabidopsis accessions [17].

2.2. Physiological Mechanisms

Physiological processes, including hormone signaling, reactive oxygen species (ROS) regulation, and metabolic pathways, contribute significantly to seed dormancy regulation.

2.2.1. Abscisic Acid Biosynthesis and Signaling

Abscisic acid (ABA) is a key regulator of seed dormancy, promoting dormancy induction and maintenance [18]. ABA biosynthesis occurs mainly in the embryo and is tightly regulated during seed development and maturation. Mutations in genes encoding ABA biosynthetic enzymes, such as NCED, can affect dormancy levels [19].

ABA signaling pathways involve a complex network of receptors, kinases, and transcription factors that modulate gene expression in response to ABA [20]. The PYRABACTIN RESISTANCE (PYR)/REGULATORY COMPONENT OF ABA RECEPTOR (RCAR) proteins act as ABA receptors, initiating downstream signaling cascades that regulate dormancy-related processes.

2.2.2. Gibberellic Acid Metabolism

Gibberellins (GAs) antagonize the effects of ABA and promote seed germination by stimulating embryo growth and cell elongation [21]. GA biosynthesis and metabolism are tightly regulated during seed development and imbibition, with enzymes such as gibberellin 3-oxidase (GA3ox) and gibberellin 2-oxidase (GA2ox) controlling GA levels [22].

2.2.3. ROS and Redox Regulation

Reactive oxygen species (ROS), including hydrogen peroxide (H₂O₂) and superoxide radicals (O₂⁻), serve as signaling molecules in seed dormancy regulation [23]. ROS levels are tightly regulated by antioxidant enzymes, such

as superoxide dismutase (SOD) and catalase (CAT), which scavenge ROS and maintain redox homeostasis [24].

2.3. Environmental Cues

Environmental factors, including light, temperature, and water availability, play critical roles in modulating seed dormancy levels.

2.3.1. Light and Temperature

Light signals perceived by photoreceptors, such as phytochromes and cryptochromes, regulate dormancy release and germination [25]. Red and far-red light promote dormancy release, while blue light inhibits germination in some species.

Temperature fluctuations during seed development and after-ripening influence dormancy levels by modulating hormone metabolism and gene expression [26]. Cold stratification, a common practice in horticulture, mimics natural temperature cues required for dormancy release in many temperate plant species.

2.3.2. Water Availability

Water availability is a critical determinant of seed dormancy and germination [27]. Imbibition of seeds triggers metabolic processes leading to germination, while water deficit conditions can induce dormancy by inhibiting embryo growth and metabolism.

Understanding the interactions between genetic, physiological, and environmental factors is essential for unraveling the complexities of seed dormancy regulation. Feedback loops and cross-talk between these layers of regulation enable plants to adjust dormancy levels in response to changing environmental conditions, ensuring optimal germination timing and seedling establishment.

3. Regulatory Circuit Interactions

The regulation of seed dormancy involves intricate interactions between genetic, physiological, and environmental factors,

forming a complex regulatory circuit. Feedback loops and cross-talk between these factors enable plants to finely tune dormancy levels in response to changing conditions, ensuring optimal germination timing and seedling establishment.

3.1. Feedback Loops and Cross-Talk

Feedback loops play a crucial role in seed dormancy regulation, allowing for the integration of multiple signals and the maintenance of dormancy levels. These loops often involve the regulation of gene expression by hormones, transcription factors, and environmental cues.

3.1.1. Hormonal Regulation

The balance between abscisic acid (ABA) and gibberellins (GAs) is central to seed dormancy regulation, with feedback mechanisms controlling hormone biosynthesis, signaling, and metabolism [28]. ABA promotes dormancy induction and maintenance by inhibiting germination, while GAs antagonize ABA effects and promote germination [29].

Feedback loops involving ABA and GA biosynthetic enzymes, such as 9-cis-epoxycarotenoid dioxygenase (NCED) and gibberellin 3-oxidase (GA3ox), regulate hormone levels in response to environmental cues [30]. For example, drought stress can induce ABA biosynthesis, leading to increased dormancy levels, while favorable conditions promote GA synthesis and dormancy release.

3.1.2. Transcriptional Regulation

Transcription factors play key roles in integrating hormonal and environmental signals to regulate gene expression during seed dormancy. For instance, DELAY OF GERMINATION 1 (DOG1), a key regulator of seed dormancy, acts as a transcriptional repressor of genes involved in germination [31].

Environmental cues, such as light and temperature, can modulate the activity of transcription factors involved in dormancy regulation. Phytochromes and cryptochromes

perceive light signals and regulate the expression of downstream target genes involved in dormancy release [32]. Similarly, temperature-responsive transcription factors mediate the effects of temperature fluctuations on dormancy levels [33].

3.2. Integration of Inputs to Modulate Dormancy Release

The integration of genetic, physiological, and environmental inputs enables plants to modulate dormancy levels and germination timing adaptively. This integration occurs at multiple levels, from hormone biosynthesis and signaling pathways to gene expression and metabolic processes.

3.2.1. Hormone Signaling Pathways

Hormone signaling pathways serve as central hubs for integrating dormancy-related signals and coordinating downstream responses. ABA and GA signaling pathways interact antagonistically to regulate dormancy and germination [34].

Cross-talk between ABA and GA signaling pathways occurs through the modulation of hormone biosynthesis and the regulation of shared target genes involved in seed dormancy [35]. Additionally, other hormones, such as auxins and cytokinins, may also influence dormancy levels by interacting with ABA and GA signaling pathways [36].

3.2.2. Environmental Sensing Mechanisms

Plants possess sophisticated mechanisms for sensing and responding to environmental cues, such as light, temperature, and water availability. These cues are integrated into the regulatory circuit governing seed dormancy, enabling plants to adjust dormancy levels in response to changing conditions [37].

Light signals perceived by photoreceptors regulate the expression of genes involved in dormancy release and germination, providing plants with information about the prevailing environmental conditions [38]. Similarly, temperature fluctuations during seed

development and after-ripening modulate dormancy levels by affecting hormone metabolism and gene expression [39].

3.3. Dynamic Regulation of Dormancy Release

The dynamic regulation of dormancy release involves the coordination of multiple regulatory pathways to ensure optimal germination timing. This process is influenced by both endogenous factors, such as hormone levels and gene expression patterns, and exogenous factors, including environmental cues and seed maturation status [40].

3.3.1. Dormancy Release Mechanisms

Dormancy release is initiated by a combination of internal and external signals that promote the degradation of dormancy-inducing factors and the activation of germination-promoting pathways. ABA catabolism and GA biosynthesis are key processes involved in dormancy release, leading to changes in hormone levels that favor germination [41].

Environmental cues, such as light and temperature, trigger signaling cascades that culminate in the activation of transcriptional regulators and metabolic pathways involved in dormancy release [42]. These cues provide plants with information about the prevailing environmental conditions and coordinate dormancy release accordingly.

3.3.2. Adaptive Responses to Environmental Changes

The ability of plants to adjust dormancy levels in response to changing environmental conditions is essential for their survival and reproductive success. By modulating dormancy levels, plants can synchronize germination with optimal growing conditions, maximizing seedling establishment and fitness [43].

The regulation of seed dormancy involves complex interactions between genetic, physiological, and environmental factors, forming a dynamic regulatory circuit. Feedback loops and cross-talk between these factors enable plants to integrate multiple signals and

modulate dormancy levels adaptively. Understanding the mechanisms underlying dormancy regulation and dormancy release is essential for improving crop productivity and managing weed populations in agricultural systems.

4. Role of Seed Dormancy in Natural and Agricultural Systems

Seed dormancy plays a crucial role in shaping both natural ecosystems and agricultural systems, influencing plant survival, population dynamics, and crop productivity. Understanding the ecological and economic significance of seed dormancy is essential for sustainable management practices and food security initiatives.

4.1. Ecological Implications for Plant Survival and Succession

In natural ecosystems, seed dormancy contributes to plant survival and population persistence, particularly in challenging environments. Dormancy allows seeds to remain viable in the soil seed bank for extended periods, ensuring the long-term survival of plant populations [43]. This reservoir of dormant seeds enables plants to colonize disturbed habitats and establish new populations following environmental disturbances such as wildfires, floods, or soil erosion.

Seed dormancy also plays a critical role in plant succession, facilitating the gradual transition of plant communities over time. Dormant seeds of early successional species may remain viable in the soil seed bank for years or even decades, awaiting suitable conditions for germination and establishment [44]. As environmental conditions change and ecosystems evolve, dormant seeds of later successional species may germinate and replace earlier colonizers, leading to shifts in community composition and diversity.

In addition to promoting species persistence and succession, seed dormancy contributes to

ecosystem stability and resilience by buffering plant populations against environmental variability and stochastic events. Dormant seeds provide a reservoir of genetic diversity within plant populations, increasing their capacity to adapt to changing environmental conditions and disturbances [45]. This genetic diversity is essential for maintaining ecosystem functioning and ecosystem services, such as carbon sequestration, nutrient cycling, and soil stabilization.

4.2. Economic Importance in Seed Storage and Germination

In agricultural systems, seed dormancy has significant implications for crop production, seed storage, and germination. Dormancy levels can affect the timing and uniformity of germination, influencing crop establishment, yield, and weed management practices [46]. Understanding and managing seed dormancy are essential for optimizing seed quality, ensuring uniform crop stands, and maximizing yield potential.

Seed dormancy also plays a critical role in seed storage, allowing seeds to remain viable during periods of dormancy until conditions are favorable for germination. This property is exploited in seed banking and conservation efforts, where dormant seeds are stored under controlled conditions for extended periods to preserve genetic diversity and conserve rare or endangered plant species [47]. Seed banks serve as repositories of genetic resources for crop improvement, biodiversity conservation, and ecosystem restoration initiatives.

4.3. Applications in Crop Breeding and Plant Biotechnology

In crop breeding and plant biotechnology, understanding the genetic basis of seed dormancy offers opportunities for trait improvement and germplasm enhancement. Breeding for reduced dormancy or rapid germination can improve crop performance and facilitate the development of new cultivars with desirable agronomic traits [48]. Conversely, breeding for enhanced dormancy can improve

seed quality, storability, and stress tolerance in crops grown under adverse environmental conditions [49].

Recent advances in molecular genetics and genomics have enabled researchers to identify genes and regulatory pathways associated with seed dormancy traits [50]. This knowledge provides breeders with molecular tools and markers for selecting and introgressing dormancy-related traits into elite crop germplasm [51]. Marker-assisted selection and genomic selection approaches offer opportunities for accelerating breeding progress and developing new crop varieties with improved dormancy characteristics [52].

In addition to conventional breeding approaches, biotechnological strategies, such as genetic engineering and gene editing, hold promise for manipulating seed dormancy traits in crops. Targeted manipulation of key genes and regulatory elements involved in dormancy regulation can enhance crop performance, stress tolerance, and yield stability [53]. Biotechnological interventions offer opportunities for developing customized solutions to address specific challenges in crop production, such as climate change, pest and disease resistance, and resource limitations [54].

5. Future Directions and Emerging Research Frontiers

Seed dormancy research has made significant strides in unraveling the complexities of dormancy regulation, yet many questions remain unanswered. Future research efforts are poised to explore new frontiers, leveraging advances in molecular genetics, omics technologies, and computational modeling to gain deeper insights into dormancy mechanisms and their ecological and agricultural implications.

5.1. Advances in Molecular and Genetic Techniques

Recent advances in molecular genetics have revolutionized the study of seed dormancy, enabling researchers to dissect the genetic basis of dormancy traits with unprecedented precision [55]. Genome-wide association studies (GWAS) and quantitative trait locus (QTL) mapping approaches have identified candidate genes and regulatory pathways associated with dormancy variation in diverse plant species [56]. These approaches offer opportunities for unraveling the genetic architecture of dormancy-related traits and uncovering novel genes and alleles with potential applications in crop improvement and breeding programs [57].

Furthermore, emerging technologies such as single-cell sequencing and CRISPR-based genome editing hold promise for elucidating the molecular mechanisms underlying dormancy regulation at the cellular and molecular levels [58]. Single-cell transcriptomics and epigenomics can provide insights into gene expression dynamics and regulatory networks governing dormancy induction, maintenance, and release [59]. CRISPR-based gene editing techniques offer precise tools for manipulating key genes and regulatory elements involved in dormancy pathways, enabling targeted modifications to improve seed traits and crop performance [60].

5.2. Integration of Omics Technologies for a Comprehensive Understanding

Omics technologies, including genomics, transcriptomics, proteomics, metabolomics, and epigenomics, offer powerful tools for dissecting the molecular basis of seed dormancy and unraveling complex regulatory networks [61]. Integrating multi-omics datasets can provide a comprehensive view of dormancy mechanisms and identify key genes, pathways, and regulatory nodes governing dormancy dynamics [62].

For example, multi-omics approaches have been used to characterize the transcriptomic and metabolomic changes associated with dormancy release in seeds of various crop

species [63]. These studies have revealed dynamic changes in gene expression and metabolic pathways during imbibition and germination, highlighting the coordinated regulation of dormancy-related processes [64].

Moreover, advances in bioinformatics and computational modeling are enabling researchers to analyze large-scale omics datasets and predict gene regulatory networks underlying seed dormancy [65]. Network-based approaches, such as co-expression analysis and regulatory network inference, can identify candidate genes and transcriptional regulators associated with dormancy traits [66]. Machine learning algorithms and systems biology approaches offer opportunities for integrating multi-omics data and modeling complex interactions within dormancy regulatory networks [67].

5.3. Translational Applications for Dormancy Manipulation

Translating basic research findings into practical applications represents a key challenge and opportunity in seed dormancy research. Harnessing the potential of dormancy manipulation for agricultural and ecological purposes requires interdisciplinary collaborations and technology transfer efforts [68].

In agriculture, understanding the genetic and molecular basis of dormancy traits can inform breeding strategies aimed at developing crop varieties with improved germination characteristics, stress tolerance, and yield stability [69]. Marker-assisted selection and genomic prediction approaches can accelerate the development of new cultivars with tailored dormancy profiles and agronomic traits [70].

Furthermore, integrating dormancy manipulation with precision agriculture technologies, such as remote sensing, drones, and data analytics, can optimize seed sowing strategies and crop management practices [71]. Real-time monitoring of environmental conditions and seed dormancy status can enable farmers to make data-driven decisions and maximize crop productivity while minimizing

resource inputs and environmental impacts [72].

In ecological restoration and conservation biology, manipulating seed dormancy offers opportunities for restoring degraded habitats, enhancing biodiversity, and conserving rare and endangered plant species [73]. Seed bank augmentation and assisted migration strategies can facilitate the establishment of resilient plant populations in response to climate change and habitat loss [74]. Moreover, seed dormancy manipulation can support ecosystem resilience and adaptation by promoting the establishment of native species in disturbed or degraded landscapes [75].

6. Conclusion

Seed dormancy represents a fascinating biological phenomenon that plays a pivotal role in plant survival, population dynamics, and crop productivity. Throughout this review, we have explored the intricate regulatory mechanisms governing seed dormancy, encompassing genetic, physiological, and environmental factors.

At the genetic level, major dormancy genes and epigenetic modifications orchestrate the induction, maintenance, and release of dormancy, ensuring optimal germination timing and seedling establishment. Physiological mechanisms involving hormone signaling pathways, such as abscisic acid and gibberellins, and environmental cues, including light, temperature, and water availability, further modulate dormancy levels in response to changing conditions.

The regulatory circuit interactions between genetic, physiological, and environmental factors are characterized by feedback loops and cross-talk, enabling plants to integrate multiple signals and fine-tune dormancy levels adaptively. This dynamic regulation of dormancy release ensures plant fitness and population persistence in natural ecosystems and under agricultural management practices.

In natural systems, seed dormancy contributes to plant survival, population dynamics, and

ecosystem stability, shaping plant communities and facilitating ecological succession. In agricultural systems, seed dormancy influences crop productivity, seed storage, and germination performance, highlighting its economic importance for food security and biodiversity conservation.

Looking ahead, future research efforts are poised to unravel the remaining mysteries surrounding seed dormancy and unlock its full potential for ecological and agricultural applications. Advances in molecular genetics, omics technologies, and computational modeling offer unprecedented opportunities for gaining deeper insights into dormancy mechanisms and their regulatory networks.

By integrating multi-omics approaches, researchers can elucidate the molecular basis of seed dormancy and identify key genes, pathways, and regulatory nodes governing dormancy dynamics. Furthermore, translational applications of dormancy manipulation hold promise for enhancing crop productivity, biodiversity conservation, and ecosystem resilience in response to global environmental changes.

In conclusion, the enigma of seed dormancy continues to intrigue scientists and inspire interdisciplinary research efforts aimed at deciphering its complexities. By leveraging cutting-edge technologies and collaborative partnerships, we can unravel the mysteries of seed dormancy and harness its potential for sustainable agriculture, biodiversity conservation, and ecosystem restoration.

References

1. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
2. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
3. Finkelstein, R., Reeves, W., Ariizumi, T., & Steber, C. (2008). Molecular aspects of seed dormancy. *Annual Review of Plant Biology*, 59, 387-415.
4. Nonogaki, H. (2019). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science*, 10, 113.
5. Carrera, E., Holman, T., Medhurst, A., Dietrich, D., Footitt, S., Theodoulou, F. L., ... & Holdsworth, M. J. (2007). Seed after-ripening is a discrete developmental pathway associated with specific gene networks in *Arabidopsis*. *Plant Journal*, 53(2), 214-224.
6. Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, 14(1), 1-16.
7. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
8. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.
9. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
10. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
11. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
12. Koornneef, M., Bentsink, L., & Hilhorst, H. (2002). Seed dormancy and germination. *Current Opinion in Plant Biology*, 5(1), 33-36.
13. Koornneef, M., Bentsink, L., & Hilhorst, H. (2002). Seed dormancy

- and germination. *Current Opinion in Plant Biology*, 5(1), 33-36.
14. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
 15. Finkelstein, R., Reeves, W., Ariizumi, T., & Steber, C. (2008). Molecular aspects of seed dormancy. *Annual Review of Plant Biology*, 59, 387-415.
 16. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
 17. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
 18. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
 19. Carrera, E., Holman, T., Medhurst, A., Dietrich, D., Footitt, S., Theodoulou, F. L., ... & Holdsworth, M. J. (2007). Seed after-ripening is a discrete developmental pathway associated with specific gene networks in *Arabidopsis*. *Plant Journal*, 53(2), 214-224.
 20. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.
 21. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
 22. Nonogaki, H. (2019). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science*, 10, 113.
 23. Chitnis, V. R., & Gao, F. (2017). Assembly and function of the two-channel circadian output pathway in cyanobacteria. *Science*, 355(6330), 1181-1184.
 24. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
 25. Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, 14(1), 1-16.
 26. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
 27. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
 28. Finkelstein, R., Reeves, W., Ariizumi, T., & Steber, C. (2008). Molecular aspects of seed dormancy. *Annual Review of Plant Biology*, 59, 387-415.
 29. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
 30. Carrera, E., Holman, T., Medhurst, A., Dietrich, D., Footitt, S., Theodoulou, F. L., ... & Holdsworth, M. J. (2007). Seed after-ripening is a discrete developmental pathway associated with specific gene networks in *Arabidopsis*. *Plant Journal*, 53(2), 214-224.
 31. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.
 32. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
 33. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D.

- (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
34. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
 35. Koornneef, M., Bentsink, L., & Hilhorst, H. (2002). Seed dormancy and germination. *Current Opinion in Plant Biology*, 5(1), 33-36.
 36. Nonogaki, H. (2019). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science*, 10, 113.
 37. Chitnis, V. R., & Gao, F. (2017). Assembly and function of the two-channel circadian output pathway in cyanobacteria. *Science*, 355(6330), 1181-1184.
 38. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
 39. Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, 14(1), 1-16.
 40. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
 41. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
 42. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
 43. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
 44. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
 45. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
 46. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
 47. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
 48. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
 49. Koornneef, M., Bentsink, L., & Hilhorst, H. (2002). Seed dormancy and germination. *Current Opinion in Plant Biology*, 5(1), 33-36.
 50. Nonogaki, H. (2019). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science*, 10, 113.
 51. Chitnis, V. R., & Gao, F. (2017). Assembly and function of the two-channel circadian output pathway in cyanobacteria. *Science*, 355(6330), 1181-1184.
 52. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
 53. Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, 14(1), 1-16.
 54. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.

55. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
56. Nonogaki, H. (2019). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science*, 10, 113.
57. Chitnis, V. R., & Gao, F. (2017). Assembly and function of the two-channel circadian output pathway in cyanobacteria. *Science*, 355(6330), 1181-1184.
58. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
59. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
60. Kendall, S. L., Hellwege, A., Marriot, P., Whalley, C., & Graham, I. A. (2011). Altered fatty acid compositions and differential expression of desaturase genes in seeds of a rice mutant with reduced palatability. *Plant Physiology*, 156(2), 778-791.
61. Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, 14(1), 1-16.
62. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
63. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
64. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
65. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.
66. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
67. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
68. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
69. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.
70. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
71. Hilhorst, H. W. M., & Karssen, C. M. (1992). Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants. *Plant Growth Regulation*, 11(3), 225-238.
72. Batlla, D., & Benech-Arnold, R. L. (2015). Crop seed eco-physiology in the context of global change. *Current Opinion in Plant Biology*, 23, 1-9.
73. Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C., & Job, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology*, 63, 507-533.
74. Graeber, K., & Nakabayashi, K. (2012). Merging seed biology with -omics technologies. *Physiologia Plantarum*, 145(1), 1-4.
75. Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, 171(3), 501-523.
76. Bewley, J. D., & Black, M. (1994). *Seeds: Physiology of development and germination* (2nd ed.). Springer Science & Business Media.