Pak. J. Bot., 55(6): 2295-2301, 2023. DOI: http://dx.doi.org/10.30848/PJB2023-6(30)

SEED DORMANCY AND GERMINATION MECHANISM OF RARE AND ENDANGERED PLANTS

MEI-YING QIN[1, 2, 3#], HAN ZHAO[3#], SHU-LIN ZHANG[2, 3], XIN-YUE SHAN[3], YING HAN[3], LU-YING FENG[3], TA-NA WUYUN[3], FANG-DONG LI[3], WEI-YI LIU[1*] AND GAO-PU ZHU[1, 2, 3*]

[1]*Forestry college of Southwest Forestry University, and Engineering Research Center of Sympodial Bamboo of National Forestry and Grassland Administration, Kunming 650224, P. R. China*
[2]*School of Biology and Food Engineering, Anyang Institute of Technology, Anyang, 45000, P.R. China*
[3]*Research Institute of Non-timber Forestry, Chinese Academy of Forestry, Kernel-Apricot Engineering and Technology Research Center of National Forestry and Grassland Administration, and Key Laboratory of Non-timber Forest Germplasm Enhancement & Utilization of National Forestry and Grassland Administration, Zhengzhou 450003, P. R. China*
**Corresponding author's email: poog502@hotmail.com*

Abstract

Rare and endangered plants not only provide mankind with scarce chemical, pharmaceutical, and living materials but also witness geological changes, plant evolution, and phylogeny. They are also one of the indispensable life-forms for maintaining the biodiversity on the earth. However, difficulties with dormancy and germination are the major reasons for their near extinction. By understanding the causes of seed dormancy for rare and endangered plants, artificial regulation of seed dormancy can achieve the purpose of lifting their endangered status. This paper reviews the external and internal causes of seed dormancy in rare and endangered plants in recent years. By focusing on the key genes, miRNAs, and transcription, the factors causing seed dormancy have been gradually revealed. This provides the foundation for the molecular regulation of seeds. The paper also reviews the methods of dormancy release on both physical and chemical levels. It discusses the critical directions for future research to provide a scientific basis for renewing rare and endangered plant populations and the establishing engineered breeding technology systems for them.

Key words: Rare and endangered plants; Seed dormancy; Seed germination; Mechanism.

Introduction

Rare or endangered plants have played a significant part in the evolution of the environment and human culture. They are the cornerstone of biodiversity and supply precious medical, chemical, and domestic raw resources for human social development (Hu *et al*., 2021). they also serve as witnesses to geological changes, plant evolution, and phylogeny. Biodiversity is the material foundation for human survival and development; it is of great significance to the long-term development of humans socially and economically, as well as a shared future for mankind. However, due to seed dormancy, human intervention, and natural disasters, certain plants are scarce or only exist in limited habitats. If no conservation measures are undertaken, they risk extinction at any moment, which profoundly and detrimentally influences the entire ecosystem.

Usually, adequate water, a suitable temperature, and sufficient oxygen are the essential external conditions for seed germination, but the seeds of some plants are dormant and cannot germinate even in a suitable external environment. This is one of the leading causes limiting the expansion of their populations, eventually making them endangered or even extinct (Sun *et al*., 2019). the extinction of rare and endangered plants may result in the destruction of entire ecosystems, which in turn threatens human survival and development. In recent years, biodiversity has been disappearing at an unprecedented rate due to the intensification of human activity. China is the one of the most biodiverse countries in the world, is also one whose biodiversity is most seriously threatened (Huang, 2020), in the past 50 years, about 200 species of plants have been extinct (Zhong *et al*., 2022). Many perils endanger plants, among which seed dormancy is very significant. Therefore, researching the physiological mechanisms for breaking seed dormancy in rare and endangered plants is urgent.

This paper reviews the causes of seed dormancy in rare and endangered plants, the results from recent representative research on dormancy, and discusses future directions. It provides a scientific basis for the renewal of rare and endangered plant populations. It also outlines engineering breeding technologies for other plant seedlings whose dormancy is difficult to break for germination.

Causes of seed dormancy in rare and endangered plants: The different classes of seed dormancy among plant species result from a combination of exogenous and endogenous factors. They include physical dormancy, physiological dormancy, morphological dormancy, combinational dormancy and morphophysiological dormancy. Most external causes involve physical dormancy caused by limitations of the seed coat and unsuitable environmental factors. Endogenous factors are a combination of a seed’s structure and characteristics, such as its maturity, endogenous inhibitors, amylase activity, endogenous regulatory factors (Guo, 2016), etc.

Exogenousl factors: A hard testa (Pericarp) is the major extrinsic factor in seed dormancy. Its degree of impact varies depending on the species of plant. *Taxus maire* and *Taxus chinensis* (Pilger) Rehd., For example, have keratinized testa. The poor water and oxygen permeability of these endangered plants derive from the mechanical binding of the tough pericarp or testa, which prevents water and air exchange and causes the seeds to enter a dormant state. Pericarpal toughness in *Davidia involucrata* Baill (Luo, 2002). and *Sinojackia xylocarpa* Hu severely hampers the entry of external water and air into the seed embryo (Jiang *et al*., 2021). The episperm of *Rosa praelucens* Byhouwer comprises multilayered thick-walled cells, and its endopleura has hard, dense palisade tissue. These create a huge barrier to imbibition, making *Rosa praelucens* Byhouwer difficult to germinate even under suitable conditions (Pan *et al*., 2019).

Temperature, moisture, and light are the environmental factors affecting seed dormancy, of which temperature is often considered to be the most significant. It primarily affects the formation of dormancy inducers during seed maturation. During seed development, high temperatures result in low or no seed dormancy, while low temperatures increase dormancy. For example, the seeds of *Primula mallophylla* Balf.f. are non-deep physiological dormant but need 60d of cold stratification at 5°C to break dormancy (Tang, 2016). Moisture plays a decisive role in regulating dormancy and germination, too. For instance, prolonged dry or water storage is detrimental to the development of embryos of *Cycas revoluta* Thunb. and makes them difficult to germinate (Tian *et al*., 2016). Light also affects seed dormancy and germination, with germination usually induced by red light, whereas far-red light inhibits it (Zhao *et al*., 2022; Yang *et al*., 2020). *Pinus koraiensis* seeds treated with red/far-red light may boost germination. Germination of *Emmenopterys henryi* Oliv. is inhibited under far-red light, and blue light inhibits the germination of *Cunninghamia lanceolata* seeds (Li, 2021). The germination of *Dracaena cambodiana* seeds is highly dependent on the micro-environment, such as temperature and light intensity. Micro-environment alteration may be one of the principal reasons for its endangered status.

Endogenous factors

Seed maturity: A complete embryo consists of a germ, an embryonic axis, radicles, and a cotyledon. Some seeds are morphologically mature, though the embryo is not fully developed. These seeds usually require a long period of low-temperature lamination or a certain amount of high temperature and humidity to complete the differentiation of the embryo cells before germination. This is called embryonic dormancy. The embryos of *Meconopsis punicea* Maxim. are immature mostly in the spherical or heart-shaped embryo period during the developmental period (Chen *et al*., 2021). The endosperm of *Magnolia wilsonii* seeds is abundant at the phenotypic maturity period. However, the embryo only accounts for about a fifth of the seed volume. The embryo needs to grow inside and requires prolonged cold lamination and GA_3 to break dormancy (Han & Long, 2010). Although the seeds of *Paeonia delavayi*, *Ginkgo biloba* and *Manglietia grandis* are mature at the time of harvest, their embryos are not differentiated and need to complete organ differentiation under suitable conditions (Zhang *et al*., 2021).

Endogenous inhibitors: The endogenous inhibitors of testa and endosperm are significant influencing factors in dormancy and are mostly endogenous hormones, terpenoids, phenols, organic acids, fatty acids, etc (Zou *et al*., 2018). Highly conserved mechanisms for seed dormancy and germination may be regulated by endogenous hormones (Wang *et al*., 2021). Abscisic acid (ABA) and gibberellin (GA) are the major factors regulating seed germination and dormancy, with ABA promoting dormancy and GA promoting germination, each of which are antagonistic to the other (Ali *et al*., 2021). Ethylene also has a role in promoting seed germination (Farooq *et al*., 2022). The endogenous inhibitors in the episperm of *Magnolia sieboldii* K. Koch crucially inhibit cotyledon development, and inhibitors in endosperm produce inhibit radicel (Mei, 2020). The endosperm of *Tilia amurensis* greatly restricts its seed germination, and the germination rate can reach 100% after the endosperm is removed (Wang *et al*., 2022). Terpenoids and alkaloids metabolites cause the seeds of *Paeonia ludlowii* to root but not germinate in the year of sowing and also interfere in the natural renewal of *Nyssa yunnanensis* W. C. Yin seeds (Lu, 2021).

Amylase activity: Amylase is the general term for the enzymes that hydrolyze starch and glycogen. During seed germination, amylase catalyzes the hydrolysis of starch into soluble sugars, providing a source of energy. Amylase activity is influenced by environmental conditions, such as temperature, humidity, light, exogenous hormones or self-conditions. GA stimulates multiple codes hydrolyticα-Amylase gene expression, α- Amylase can provide energy for seed germination and growth (Yang *et al*., 2022; He *et al*., 2022). Generally, seeds with high α-Amylase activity have a higher germination rate (Zhang *et al*., 2013). In *Torreya grandis* Fort. et Lindl. seeds, α-Amylase plays a role in the breakdown of starch during the lamination process, allowing the seed embryo to achieve physiological maturation and germination. This α-Amylase activity is generally higher than for β-Amylase (Li & Dai, 2015), suggesting the starch in seeds are mostly amylocellulose, and faster degradation to the predominant nutrient for seed development such as *Torreya grandis* Fort. et Lindl.

Endogenous regulatory factors: In the present era, seed dormancy research has evolved from cellular and organelle levels to the molecular level. Many endogenous factors associated with dormancy have been identified and demonstrated in model plants. The genes associated with seed dormancy and their corresponding encoded proteins are summarized in (Fig. 1).

These genes can be broadly classified into three major categories: hormone regulation-related, dormancy release-related and other dormancy-related genes. The genes related to hormone regulation and dormancy regulate seed dormancy essentially by regulating ABA and GA sensitivity or synthesis and accumulation. *DOG1*, the major dormancy gene specifically expressed in seeds, and is the signature gene for dormancy (Niu *et al*., 2017; Zhao *et al*., 2022; Nakabayashi *et al*., 2012). Its protein level determines the level of dormancy, but the function of the protein encoded by this gene is currently unknown (Yang *et al*., 2020; Song *et al*., 2020; Wu *et al*., 2021; Huo *et al*., 2016; Nonogaki *et al*., 2019; Sall *et al*., 2019). Both *DEP* and *ATHB20* regulate dormancy by regulating ABA sensitivity. *DEP* encodes a C3HC4 ring finger protein that may play a major role during seed development by promoting dormancy through up-regulated expression (Huang *et al*., 2016). Mutations in the *DEP* gene can result in complete loss of dormancy. *ATHB20* is involved in the regulation of ABA sensitivity by light induction. When *ATHB20* is over-expressed, the production site exhibits ABA insensitivity, but for mutation, it shows hypersensitivity (Barrero *et al*., 2010). The *Sdr4* gene is seed-specific and is one of the crucial genes controlling the germination of rice ear (Han, 2021). Temperature-dependent dormancy regulation of *qSD7-1/qPC7/Rc/TT8, MFT, FLC qSD7-1/qPC7/Rc/TT8* acts on the *bHLHTF* protein to control dormancy probably by regulating ABA and flavonoid biosynthetic pathways. Heat treatment eliminates dormancy (Gu *et al*., 2011). *MFT* responds to ABA and GA signaling pathways (Li *et al*., 2014). Up-regulation of *MFT* expression bolsters seed dormancy (Zuo & Xu, 2021; Li *et al*., 2022; Chen *et al*., 2018). The developmental process of *Triticum aestivum* L. and low-temperature regulation of promoter mutations lead to up-regulation of *MFT* expression and enhance seed dormancy. High *FLC* expression may encourage germination by reducing the endogenous ABA content (Chiang *et al*., 2009).

Seed dormancy requires the interaction of specific miRNAs and target hormones involved in seed dormancy and germination. In *Oryza sativa* L., *IPA1* is the target gene of *miR156*, regulating several genes in the GA pathway; mutations in *miR156* suppress GA and enhance seed dormancy (Miao *et al*., 2019). While in *Ginkgo biloba* seeds, *miR156* is involved in regulating *SPL13*, up-regulation of *miR156* suppresses germination and causes dormancy (Jia *et al*., 2021), *miR159* stimulates GA synthesis and accumulation by repressing the target gene *GAMYB* and promoting *Ginkgo biloba* germination. In *Arabidopsis thaliana*, *miR163* inhibits the accumulation of its target gene *PXMT1* under light conditions and improves seed germination (Chung *et al*., 2016). *miR160* targets *ARF10* (AUXIN RESPONSE FACTOR10) to alter hormone sensitivity when its over-expression reduces ABA sensitivity and inhibits germination (Liu *et al*., 2007). Exogenous GA in *Zea mays* down-regulates *miRl60b* and assists germination (Liu *et al*., 2020). *miR159, miRl66a, miRl66b, miR171b*, and *miR396a* play a crucial role in regulating the balance of GA and ABA hormones in *Cunninghamia lanceolata* seeds. Cool and moist conditions result in predominantly GA-related gene expression, leading to dormancy release (Cao *et al*., 2016). These findings suggest that the dynamic balance of ABA/GA concentration and sensitivity plays a critical role in the dormancy and germination of various seeds; and that the degradation and synthesis of miRNAs affect the expression levels of several critical genes in ABA and GA metabolism and signaling processes.

Transcription factors are also involved in the seed dormancy. *ABI3, ABI4*, and *ABI5* are vital genes in the ABA signaling pathway, and ARF10 is a transcription factor downstream from the growth hormone signaling pathway. Over-expression of *ARF10* in *Arabidopsis thaliana* can up-regulate the expression of *ABI3, ABI4*, and *ABI5*. It increases ABA sensitivity in seeds and enhances seed dormancy (Sano & Marion-Poll, 2021; Li *et al*., 2018). It has been shown that the associated transcription factors of seed dormancy can be regulated in certain plant genes and that regulation can lead to alterations in the transcription factors. The helix-loop-helix transcriptional factor SPT and PIL5 play an essential role in the regulation of seed dormancy by cold lamination, which makes SPT lose its inhibitory effect on seed germination, including seed germination in the dark. Dormancy can be released by transferring the seeds to room temperature after lamination (Huo *et al*., 2016). The change from wet and cold conditions to germination conditions reduces ABA-signaling transcription factors and sensitivity to ABA in *Picea gluca* and improves seed germination (Liu *et al*., 2015). In GA biosynthesis genes of *Ginkgo biloba*, the cold lamination up-regulates the expression of *GA200X1* and *GA200X2* and promotes the release of *Ginkgo biloba* embryo dormancy (Jia *et al*., 2021). It is assumed that cold lamination increases the normal germination of some seeds with dormant characteristics; possibly, the low temperature is conducive to the regulation of ABA, GA, and other related biosynthetic genes towards dormancy release and germination, and its temperature depends on seeds characteristics.

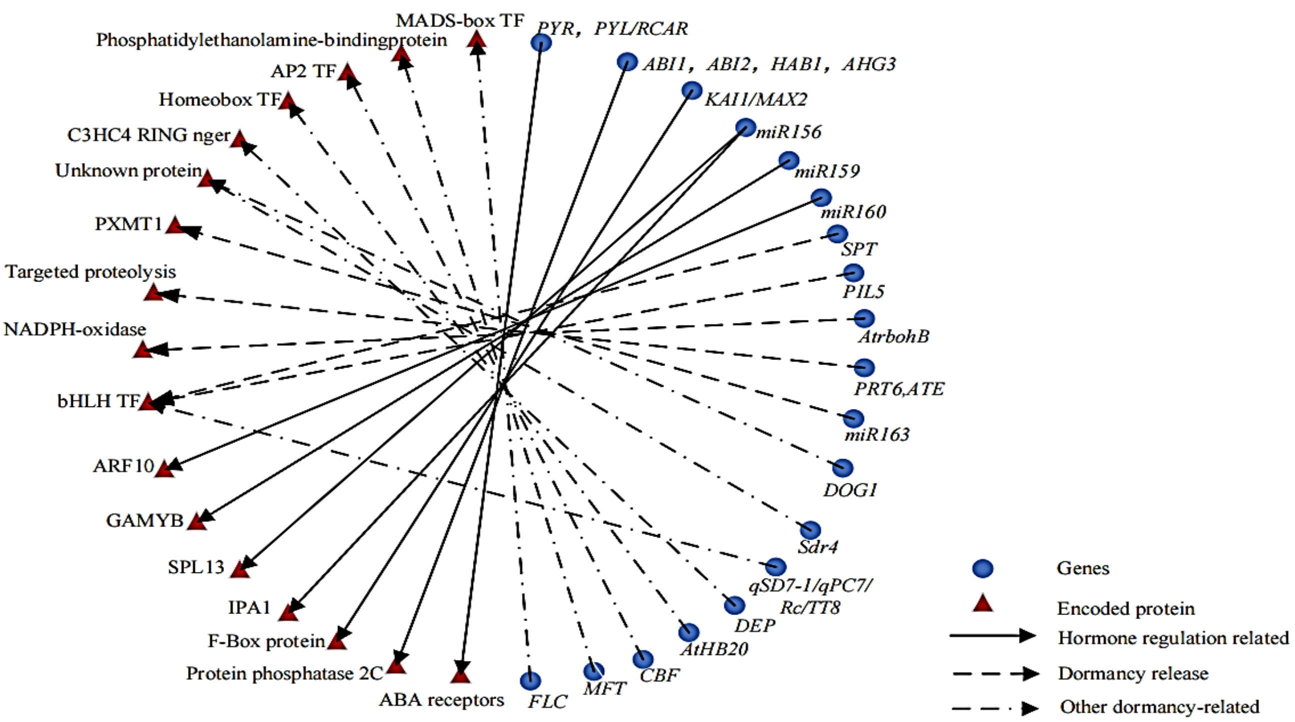

Fig. 1. Genes relevant to dormancy regulation.

Seed dormancy relieving method of rare and endangered plants: The dormancy of seeds of rare and endangered plants relates closely to their dormancy characteristics, endogenous phytohormones, alkaloids, and changes in the content of their endogenous substances. Both physical and chemical regulation techniques can release dormancy (Fig. 2).

Physical regulation technology

Temperature control: As a suitable temperature is necessary for seed germination, the temperature can affect the activity of enzymes in seeds (Chen *et al*., 2022; Tang *et al*., 2022). Too low or too high temperature can inhibit seed germination and even cause death. Lamination allows the seed embryo to gradually complete morphological maturation. Conversion of macromolecular storage substances into small molecules such as soluble sugars and soluble proteins under the action of related enzymes provides energy for the embryo during metabolism and growth. Variable temperature lamination is an effective way to break seed dormancy by softening the testa, enhancing seed permeability, increasing respiration rate, reducing the ABA content, and increasing the GA content. For example, the variable-temperature lamination of *Taxus cuspidata* Sieb. & Zucc. seeds can shorten the dormancy time. Warm temperatures in the early stages of lamination accelerate the development of embryos, while low temperatures in the later stages are necessary for germination into seedlings. In addition, low temperatures reduce the seed germination inhibitors' content and facilitate changes in the structure of micropyle, promoting seed germination (Zheng *et al*., 2017). Suitable temperature stratification can provide a good developmental environment for seeds and promote the release of dormancy. Suitable stratification temperature and time should be selected according to the characteristics of seeds.

Light management: Light is primarily a signaling stimulus for seed germination. Most higher plants normally germinate in light or dark conditions, but some seeds are light-sensitive and require specific conditions to germinate normally. *Emmenopterys henryi* Oliv. has extreme requirements for light intensity for seed germination, and unsuitable light in the physical environment makes germination difficult (Guo *et al*., 2021); *Cathaya argyrophoylla* can only germinate and develop under well-lit conditions. Neither continuous light nor a 14/10 photoperiod improved seed germination of *Parashorea chinensis* Wang Hsie; its germination under four layers of black nylon mesh shade was better than under full natural light (Yan & Cao, 2007). Therefore, light management should be dictated by the seed characteristics.

Other physical control technology: With the development of technology, methods of treating dormant seeds can be more specialized and advanced than the previous techniques. Electrical radiation, ultrasound, infrared, and laser can all enable seed germination in some way. In addition, the way seeds are planted influences germination. *Kmeria septentrionalis* seeds have a low germination rate in their natural state, but a substrate of river sand can result in better germination (Lai *et al*., 2007). This may be related to the better permeability of river sand and the low resistance of the seeds to top soil.

Chemical regulation techniques: Chemical conditioning techniques, including chemical and hormonal treatments, are the most common methods used in production today. Some chemicals increase permeability by promoting the softening or breaking of the episperm. Commonly used chemicals are concentrated sulfuric acid, sodium hydroxide (NaOH) and hydrogen peroxide (H_2O_2) also have the same effect. Physical dormancy of *Firmiana danxiaensis* seeds can be effectively broken by etching with 98% concentrated sulfuric acid for 20min (Zhang *et al*., 2018). The peel of *Tilia amurensis* Rupr. also has well-developed palisade tissue that blocks the entry of moisture and gas, treatment with 30% NaOH for 1.5 h can improve the air permeability of seeds to a certain extent. In addition to improving water permeability, it also promotes the reaction speed of endogenous hormones in seeds and promotes dormancy release (Zheng *et al*., 2014; Zhu *et al*., 2020). Mature *Cinnamomum camphora* seeds with poorly permeable episperm can be treated with hydrogen peroxide to increase germination (He *et al*., 2012).

Plant hormones play a decisive role in the release of seed dormancy. Available studies demonstrate that GA relieves seed dormancy while ABA upgrades seed dormancy. ABA and GA antagonize each other to regulate seed dormancy and germination. During seed dormancy release in *Garcinia paucinervis*, the genes related to GA synthesis and ABA decomposition were up-regulated, and the genes related to ABA synthesis and GA decomposition were down-regulated, which cooperated with the regulatory network of transcription factors to break dormancy (Zhang *et al.*, 2021). After treatment with 100 or 200mg/L GA_3, the seed germination potential of *Physocarpus amurensis* was significantly increased (Wei *et al*., 2013). *Gentiana tibetica* King ex Hook.f., and *Acer yangjuechi*, *Paris polyphylla* were treated with GA_3 to improve seed germination (Lu *et al*., 2018; Liu *et al*., 2019). Ethylene interfered with ABA signaling and counteracted the inhibitory effect of ABA on seed germination (Ali *et al*., 2021). The germination rate of *Bletilla striata* (Thunb.) Reichb.f., and *Camellia nitidissima* was increased after 6-BA treatment. NAA (naphthalene acetic acid) encourages cell division and rooting. The germination time and rate for *Urophysa rockii* Ulbr. seeds were significantly better after being treated with 100mg/L NAA. In addition, the external application of melatonin boosted germination and protected the internal lipids from oxidation during seed germination (Chen *et al*., 2020). These show that different hormones play different roles in acting as seed dormancy regulators.

Some gaseous signaling molecules impact seed germination. Nitrate is the primary source of nitrogen for many plants. With it, plants can synthesize nitric oxide (NO), which regulates plant growth (Zhang, 2020). NO can alter different genes involved in ABA and GA metabolism (Grainge *et al*., 2022). Rapid accumulation of NO in *Arabidopsis thaliana* can induce a reduction in ABA and lessen seed dormancy (Liu *et al*., 2009). Exogenous hydrogen sulfide (H_2S) is antagonistic to ABA and IAA. Low concentrations of H_2S improve germination, and high concentrations inhibit regulating the expression of related genes may influence endogenous hormone synthesis and metabolic processes, thus affecting seed germination (Banerjee *et al*., 2018; Wang, 2021).

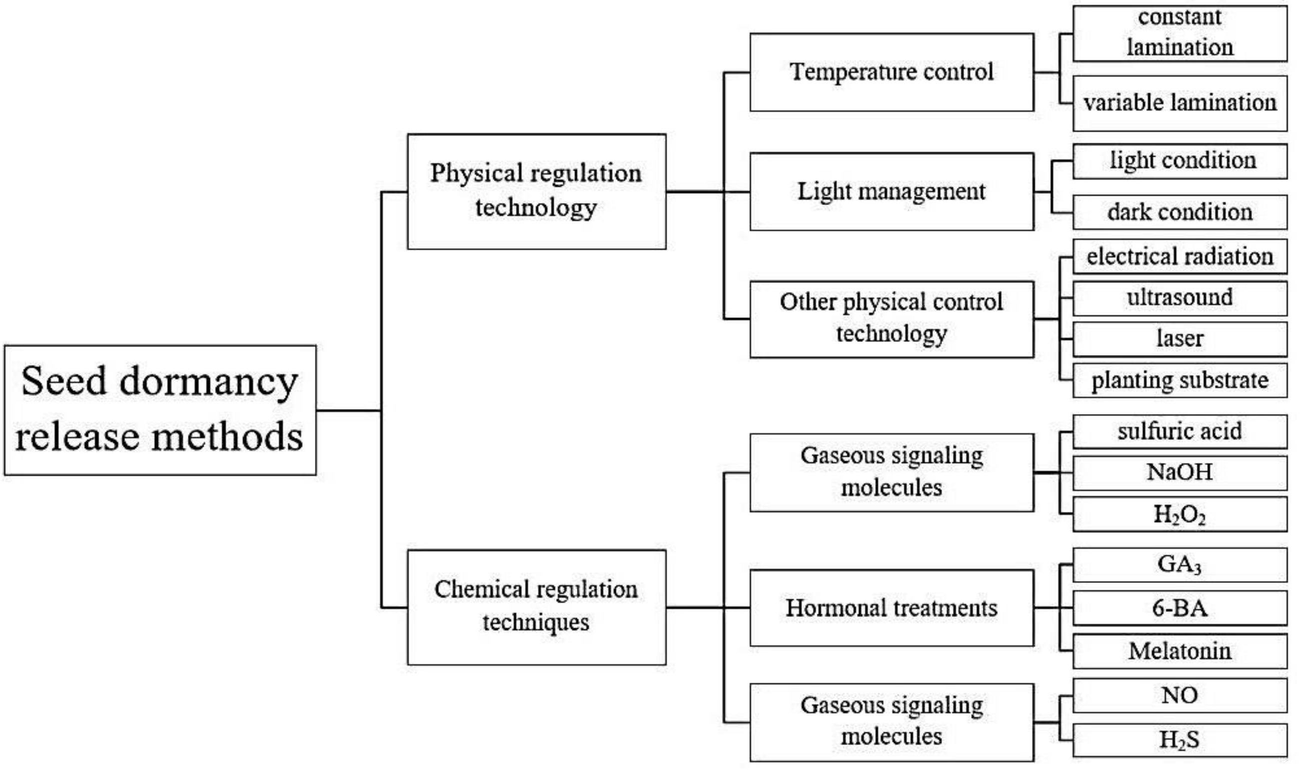

Fig. 2. Seed dormancy release methods of rare and endangered plants.

Discussion

The dormancy of endangered plant seeds is a complex process. In order to break the dormancy, we should comprehensively analyze the dormancy type and dormancy depth, and take corresponding measures to relieve the dormancy according to the dormancy characteristics. The balance between the ratio and sensitivity of ABA and GA significantly regulates seeds' dormant and germinating states. Exogenous hormones are applied to achieve rapid germination for a standard method of regulating seeds' internal hormonal state in production (Li *et al*., 2019). In addition, changes in the external environment, such as temperature and light, can profoundly affect the levels of these two hormones during germination and regulate seed dormancy (Tognacca *et al*., 2021). The critical genes, miRNAs, and transcription factors associated with seed germination are also closely related to their hormonal levels. In the future, these factors can be molecularly regulated by genetic engineering to achieve the desired state of real-time regulation.

The extinction of one species can cause a chain reaction throughout its ecosystem, leaving other species vulnerable to the same fate. Rare and endangered plants not only play an active role in maintaining nature's ecological balance, but also play a vital role in the development of human society by providing valuable forest products such as medicinal herbs. However, in general, seeds of rare and endangered woody plants are dormant from more than one type of dormancy, especially when they are not in environmental conditions suited to achieving all the conditions required for seed germination. As a result, the study of seed dormancy in rare and endangered plants needs to consider both the internal and external causes. In particular, seeds of plants with incomplete seed development, such as *Trillium tschonoskii* Maxim. require two years of cold lamination to produce seeds even with low germination rates (Liu *et al*., 2014). Their seeds need to be artificially regulated to achieve seed germination by means of tissue regeneration or molecular design to transcend the physiological defects in the development of the seeds themselves. This study finds that the earth is in the midst of its sixth mass extinction process. This one differs from the previous five extinction events caused by natural phenomena such as planetary impacts and climate crises in that humans are responsible for it. Due to the conscious selection of species that are beneficial to humans (Ceballos *et al*., 2020), it is hoped that more scholars will join the study of rare and endangered plants so that endangered plants will not become extinct.

Acknowledgments

This work was supported by the National Key R&D Program of China (2019YFD1001200).

References

Ali F., G. Qanmber, F. Li and Z. Wang. 2021. Updated role of ABA in seed maturation, dormancy, and germination. *J. Adv. Res.*, 35: 199-214.

Banerjee, A., D.K. Tripathi and A. Roychoudhury. 2018. Hydrogen sulphide trapeze: Environmental stress amelioration and phytohormone crosstalk. *Plant Physiol. Biochem.*, 132: 46-53.

Barrero, J.M., A.M, Anthony, J. Griffiths, T. Czechowski, W.R. Scheible, M. Udvardi, J.B. Reid, J.J. Ross, J.V. Jacobsen and F. Gubler. 2010. Gene expression profiling identifies two regulatory genes controlling dormancy and ABA sensitivity in *Arabidopsis* seeds. *Plant J.*, 61(4): 611-622.

Cao, D.C., H.M. Xu, Y.Y. Zhao, X. Deng, Y.X Liu, W.J.J. Soppe and J.X. Lin. 2016. Transcriptome and degradome sequencing reveals dormancy mechanisms of *Cunninghamia lanceolata* seeds. *Plant Physiol.*, 172(4): 2347-2362.

Ceballos, G., P.R. Ehrlich and P.H. Raven. 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc. Nat. Acad. Sci. USA*, 117(24): 13596-13602.

Chen, H.G., W.L. Zhao, L. Jin, Y. Li, Z.H. Liu and T. Du. 2021. Study on dormancy and breaking methods of *Meconopsis punice*a Maxim. *Acta. Agrestia. Sinica.*, 29(02): 402-406.

Chen, J.Z., X.L. Huang, X.F. Xiao, J.M. Liu, X.F. Liao, Q.W. Sun, L. Peng and L. Zhang. 2022. Seed dormancy release and germination requirements of *Cinnamomum migao*, an endangered and rare woody plant in southwest China. *Front. Plant Sci*., 13: 770940.

Chen, X., Y. Yang and F.Q. Liu. 2020. Research progress of plant melatonin. *Jiangsu Agri. Sci.*, 48(24): 17-24.

Chen, Y.K, X.P. Xu, X.H. Chen, Y. Chen, Z.H. Zhang, X. Xuhan, Y.L. Lin and Z.X. Lai. 2018. Seed-specific gene mother of FT and TFL1 (MFT) involved in embryogenesis, hormones and stress responses in *Dimocarpus longan* Lour. *Int. J. Mol. Sci.*, 19(8): 2403.

Chiang, G.C., D. Barua, E.M. Kramer, R.M. Amasino and K. Donohue. 2009. Major flowering time gene, flowering locus C, regulates seed germination in *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. USA*, 14; 106(28): 11661-11666.

Chung, P.J., B.S. Park, H. Wang, J. Liu, I.C. Jang and N.H. Chua. 2016. Light-inducible miR163 targets PXMT1 transcripts to promote seed germination and primary root elongation in *Arabidopsis*. *Plant Physiol.*, 170(3): 1772-1782.

Farooq, M.A., W. M, S.X.S. and A. Gu. 2022. Underlying biochemical and molecular mechanisms for seed germination. *Int. J. Mol. Sci*., 23(15): 8502.

Grainge, G., K. Nakabayashi, T. Steinbrecher, S. Kennedy, J. Ren, F. Iza and G. Leubner-Metzger. 2022. Molecular mechanisms of seed dormancy release by gas plasma-activated water technology. *J. Exp. Bot.*, 73(12): 4065-4078.

Gu, X.Y., M.E. Foley, D.P. Horvath, J.V. Anderson, J.H. Feng, L.H. Zhang, C.R. Mowry, H. Ye, J.C. Suttle, K. Kadowaki and Z.X. Chen. 2011. Association between seed dormancy and pericarp color is controlled by a pleiotropic gene that regulates abscisic acid and flavonoid synthesis in weedy red rice. *Genetics*, 189(4): 1515-1524.

Guo, L.J., Z.P. Xiao, C.M. Yin, Y.R. Wu, J.P. Hu, Y.Y. Liu and Y.C. Zhong. 2021. The research on characteristics of seed germination of endangered plant *Emmenopterys henryi*. *Ecol. Sci.*, 40(04): 13-18.

Guo, L.P. 2016. Study on dormancy and dormancy breaking of tree peony seeds. Master Degree Thesis of Northwest A&F University, China.

Han, C.Y. and C.L. Long. 2010. Seed dormancy, germination and storage behavior of *Magnolia wilsonii* (magnoliaceae), an endangered plant in China. *Acta. Bot. Yunnanica*, 32(01): 47-52.

Han, P.P. 2021. Function analysis of quinoa PEBP family gene and seed dormancy related genes. Master Degree Thesis of Shandong Normal University, China.

He, L., L. Zeng, Y.K. Gu and F. Li. 2022. Study on ulra-cryopreservation of *Dracaena cambodiana* seeds. *Seed*, 41(09): 84-90.

He, L.P., L.G. Li and J.S. Qian. 2012. Germination of *Psammoilene tunieoides* seeds with treatments of different chemicals. *J. Yunnan Agr. Univ. (Nat. Sci.*, 27(03): 340-345.

Hu, D., Y. Cui and J. Zhang. 2021. Nervonic acid amends motor disorder in a mouse model of Parkinson's disease. *Transl. Neurosc.*, 12(1): 237-246.

Huang, L.L, D.F. Zhang and T. Xia. 2016. Research progress of molecular regulation mechanism of seed dormancy. *Agri. Sci. Technol.*, 17(04): 786-791.

Huang, Z.H. 2020. The research progress of endangered causes and protection strategy of rare and endangered plants in China. *J. Univ. S. Chin.* (*Sci. and Technol.*), 34(03): 42-50.

Huo, H.Q., S.H. Wei and K.J. Bradford. 2016. Delay of Germination 1 (*DOG1*) regulates both seed dormancy and flowering time through microRNA pathways. *Proc. Nat. Acad. Sci.*, 113(15): E2199-E2206.

Jia, Z.C., B.B. Zhao, S. Liu, Z.G. Lu, B. Chang, H.R. Jiang, H. Cui, Q.S. He, W.X. Li, B. Jin and L. Wang. 2021. Embryo transcriptome and miRNA analyses reveal the regulatory network of seed dormancy in *Ginkgo biloba*. *Tree Physiol.*, 41(4): 571-588.

Jiang, Q., X. Zheng, K. Zhang, Y. Zhan and L.Z. Tang. 2021. Basic characteristic and dormancy mechanism of *Sinojackia xylocarpa* fruit and seed. *J. Southwest For. Univ. (Nat. Sci.)*, 41(02): 145-150.

Lai, J.Y., K.X. Huang, C.L. Pan, W.G. Qin, H.M. Shi and J.B. Liu. 2007. Study on the seed storage and germination of *Kmeria septentrionalis*. *Guangxi For. Sci.*, (01): 19-21.

Li Q., C. Fan, X.M. Zhang, X. Wang, F.Q. Wu, R.B. Hu and Y.F. Fu. 2014. Identification of a soybean MOTHER OF FT AND TFL1 homolog involved in regulation of seed germination. *PLoS One*, 9(6): e99642.

Li Y.G., H. Ren, Y.J. Zhang, R.N. Li, H. Ai and X.Z. Huang. 2022. Analysis of the molecular evolution of the PEBP gene family in cruciferous plants. *Biodiv. Sci.*, 30(06): 164-174.

Li, F.D., T.N. Wuyun and G.P. Zhu. 2019. *Cultivation operative technology of kernel-apricot.*Vol: 1.China Forestry Publishing House, China.

Li, J.X. and W.S. Dai. 2015. Storage substance content and their enzyme activity during stratification of *Torreya grandis* seed. *J. Zhejiang For. Sci. Technol.*, 35(05): 37-40.

Li, J.Y., P.H. Dai, J. Yang and X.D. Liu. 2018. Functional verification of transcription factor based on ARF10 and its effect on dormancy and germination of *Arabidopsis thaliana* seeds. *J. Xinjiang Agric. Univ.*, 41(02): 109-116.

Li, Q.Y. 2021. Effect of different light and temperature treatment on seed germination of *Cunninghamia lanceolata*. *J. Jiangsu For. Sci. & Technol.*, 48(01): 33-36.

Liu, J., X. Guo, T. Zhai, A. Shu, L. Zhao, Z. Liu and S. Zhang. 2020. Genome - wide identification and characterization of microRNAs responding to ABA and GA in maize embryos during seed germination. *Plant Biol.*, 22(5): 949-957.

Liu, J.Y., C. Shao and H. Zhang. 2014. Investigated the biological characteristics of the endangered species *T.kamtschaticum Pal1*., *Ginseng Res.*, 26(01): 36-37.

Liu, P.P., T.A. Montgomery, N. Fahlgren, K.D. Kasschau, H. Nonogaki and J.C. Carrington. 2007. Repression of AUXIN RESPONSE FACTOR10 by microRNA160 is critical for seed germination and post-germination stages. *Plant J.*, 52(1): 133-146.

Liu, Y., K. Müller, Y.A. El-kassaby and A.R. Kermode. 2015. Changes in hormone flux and signaling in white spruce (*Picea glauca*) seeds during the transition from dormancy to germination in response to temperature cues. *BMC Plant Biol.*, 15(1): 292.

Liu, Y.G., L. Shi, N.H. Ye, R. Liu, W.S. Jia and J.H. Zhang. 2009. Nitric oxide- induced rapid decrease of abscisic acid concentration is required in breaking seed dormancy in *Arabidopsis*. *New Phytol.*, 183(4): 1030-1042.

Liu, Z.H., S.S. Xie, B.R. Rao, D.H. Liu and S.Z. Huang. 2019. Factors affecting the seed germination rate of *Paris polyphylla*. *Chin. J. Trop. Agri.*, 39(02): 25-28.

Lu, Y.Z. 2021. Ecological adaptability and endangered mechanism of *Paeonia Ludlowi*i. Doctor degree Thesis of Tibet University, China.

Lu, Y.Z., Y.B. Wang, Y. Zhao, E.H. Zhang and X.Y. 2018. Study on germination characteristics of *Gentiana tibetica* King ex Hook.f. seeds in endangered medicinal plants. *Seed*, 37(05): 94-98.

Luo, S.J. 2002. Study on the anatomic structure of seed of *Davidia involucrata*. *J. Hubei Inst. For. Nationalities*, (04): 18-19.

Mei, M. 2020. Functions and mechanisms of *MsARF5* in embryo development of *Magnolia sieboldii* K.Koch during the seed after-ripening. Doctor degree Thesis of Shenyang Agricultural University, China.

Miao, C.B., Z. Wang, L. Zhang, J.J. Yao, K. Hua, X. Liu, H.Z. Shi and J.K. Zhu. 2019. The grain yield modulator miR156 regulates seed dormancy through the gibberellin pathway in rice. *Nat. Comm.*, 10(1): 3822.

Nakabayashi, K., M. Bartsch, Y. Xiang, E. Miatton, S. Pellengahr, R. Yano, M. Seo and W.J.J. Soppe. 2012. The time required for dormancy release in *Arabidopsis* is determined by delay of germination1 protein levels in freshly harvested seeds. *Plant Cell*, 24(7): 2826-2838.

Niu, Y.Q., H.B. Xu, Y.X. Zhang, L. Lian and J.H. Jiang. 2017. Studies on molecular mechanism of plant seed dormancy. *Fujian J. Agric. Sci.*, 32(10): 1156-1164.

Nonogaki, H. 2019. Seed germination and dormancy: The classic story, new puzzles, and evolution. *J. Integr. Plant Biol.*, 61(5): 541-563.

Pan, L.J., W.L. Guan and Y.H. Li. 2019. Seed dormancy mechanism and its ecological significance of endangered species *Rosa praelucens*. *Subtropst Plant Sci.*, 48(01): 21-25.

Sall, K., B.J.W. Dekkers, M. Nonogaki, Y. Katsuragawa, R. Koyari, D. Hendrix, L.A.J. Willems, L. Bentsink and H. Nonogaki. 2019. DELAY OF GERMINATION1-LIKE4 acts as an inducer of seed reserve accumulation. *Plant J.*, 100(1): 7-19.

Sano, N. and A. Marion-Poll. 2021. ABA metabolism and homeostasis in seed dormancy and germination. *Int. J. Mol. Sci.*, 22(10): 5069.

Song, S.Q., J. Liu, H.H. Xu, X. Liu and H. Huang. 2020. ABA metabolism and signaling and their molecular mechanism regulating seed dormancy and germination. *Sci. Agr. Sinica.*, 53(05): 857-873.

Sun, Y.Q., L. Yang, Z.J. Chen, C.L. Wang and M.L. Wei. 2019. Postripeness physiological characteristics of *Panax stipuleanatus* seeds II: endogenous inhibitory substances extraction and bioactivity determination from stratified seeds. *Swest Chin. J. Agric. Sci.*, 32(01): 75-80.

Tang, A.J. 2016. Dormancy/germination physiology and seedling emergence patterns of endangered *Primula mallophylla* (Primulaceae). *Plant Physiol. J.*, 52(09): 1421-1428.

Tang, Z.Y., J.M. Liu, X.L. Huang, J.Z. Chen, D. Wang and B.L. Tong. 2022. Storage substance content and corresponding enzyme activity during the stratification of *Cinnamomum migao* seeds. *Mol. Plant Breed*., 20(04): 1317-1324.

Tian, M.H., Z.W. Zhao and A.J. Tang. 2016. Desiccation sensitivity and effects of temperature and moisture content of the substrate during storage on after-ripening in seeds of *Cycas revoluta*. *Plant Physiol. J.*, 52(02): 225-233.

Tognacca, R.S. and J.F. Botto. 2021. Post-transcriptional regulation of seed dormancy and germination: current understanding and future directions. *Plant Comm.*, 2(4): 100169.

Wang J.C. 2021. Study on the Mechanism of hydrogen sulfide and phytohormones crosstalk in regulating seed germination. Master Degree Thesis of Huazhong Agricultural University, China.

Wang Y.H, Y.G. Kong, Q.H. Li, D.J. Wu, L.P. Yan, T. Xu, Y.Z. Lu and G.F Zhai. 2022. Study on germination characteristics and dormancy breaking methods of *Tilia amurensis* seeds. *Chin. Agri. Sci. Bull*., 38(29): 80-85.

Wang, Y.M., X.X. Zhang, X.Z. Zhu, Z.H. Zhang and Z. L. 2021. Research progress on dormancy and germination mechanism of forest seeds. *Sci. Silvae Sinicae*, 57(10): 128-144.

Wei, X.H., D.S. Yin and H.L. Shen. 2013. Technique of accelerating germination of *Physocarpus amurensis* seed. *Bull. Bot. Res.*, 33(06): 709-712.

Wu, Y., Y.J. Zhou, H. Hu and Y.B. Shen. 2021. Advances in molecular mechanisms of seed dormancy and release. *Seed*, 40(05): 63-70.

Yan, X.F. and M. Cao. 2007. Effects of light intensity on seed germination and seedling early growth of *Shorea wantianshuea*. *Chin. J. Appl. Ecol.*, (01): 23-29.

Yang N., Y.C. Cao, B.Q. Wei and L.H. Wang. 2022. Research progress on seed germination and dormancy of monocot and dicot plants. *J. Plant Genet. Resour*., 23(05): 1249-1257.

Yang, L.W., S.R. Liu and R.C. Lin. 2020. The role of light in regulating seed dormancy and germination. *J. Integr. Plant Biol.*, 62(9): 1310-1326.

Zhang, J., Z.C. Lin, L.Y. Cao and X.H. Shen. 2013. Genetic research progress on pre-harvest sprouting and dormancy rice. *J. Nucl. Agric. Sci.*, 27(08): 1136-1142.

Zhang, J.J,. L.Y. Zhang, K. Xia, M. Jiang and X. Wei. 2021. Transcriptomic analysis of the seed of Garcinia paucinervis, a rare and endangered plant species, during dormancy releasing. *Forest. Res*., 34(01): 35-46.

Zhang, W. 2020. Study on dormancy releasing mechanism of *Tulipa thianschanica* Regel seeds. Doctor degree Thesis of Shenyang Agricultural University, China.

Zhang, W., Y.T. Huang, P.S. Zhong, X.Y. He and H.F. Chen. 2018. Study on the characteristics of seed germination of the endangered plant *Firmiana danxiaensis*. *For. Environ. Sci.*, 34(06): 51-55.

Zhang, Z.L., F.W. Xing, X.G. Hou, F.G. Wang and Q.Q. 2021. Research progress of peony reproductive biology chinese wild plant resources. *Chin. Wild Plant Resour.*, 40(08): 41-47.

Zhao, B., H. Zhang, T.X. Chen, L. Ding, L.Y. Zhang, X.L. Ding, J. Zhang, Q.Q and Y. Xiang. 2022. Sdr4 dominates pre-harvest sprouting and facilitates adaptation to local climatic condition in Asia cultivated rice. *J. Integr. Plant Biol*., 64(6): 1246-1263.

Zhao, H.Y., Y.M. Zhang and Y. Zheng. 2022. Integration of ABA, GA, and light signaling in seed germination through the regulation of ABI5. *Front. Plant Sci*., 13: 1000803.

Zheng J.H., S.J. Lin, Y.M. Zhang, Y.J. Wang, Y.H. Lin, F.W. Cui, Z.H. Jiang, B.F. Xu, Y.J. Wang and H.Y. Liang. 2014. Effects of NaOH treatment on breaking dormancy and physiological and chemistry characteristic of *Tilia amurensis* Rupr. seeds. *Chin. Agri. Sci. Bull*., 30(16): 35-40.

Zheng, D.J., L.R. Yang, Y. Yun, J.L. Chen and X. C. 2017. Seed dormancy mechanism and its ecological significance of endangered species *Dracaena cambodiana*. *Guihaia.*, 37(12): 1551-1559.

Zhong, Q.F., T. Zhu, W.H. Zhu, W.C. Zhong, L.W. Jiang, Y.C. Dong, H.F. Chen and F.G. Wang. 2022. Investigation and protection of rare and endangered plants in Longmen Nankunshan, Guangdong. *Guangxi Forest. Sci.*, 51(05): 709-715.

Zhu, H.B., J.Y. Yang, Z.M. Wang, T.B Gou and S.J. Lin. 2020. Effects of NaOH on endogenous hormone of overcoming dormancy in *Tilia amurensis* seeds during germination. *Prot. Forest. Sci. Technol*., (11): 19-20.

Zou, Y.T., L. Chen, X.J. Fan and X.S. Li. 2018. Preliminary identification of endogenous inhibitors in *Crataegus viridis* seeds. *Seed*, 37(12): 23-28.

Zuo, Y. and Y.H. Xu. 2021. Research Progress on the Mechanism of GA and ABA during seed germination. *Mol. Plant Breed.*, 19(18): 6221-6226.

(Received for publication 2 August 2022)