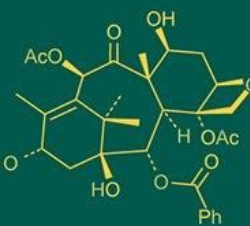
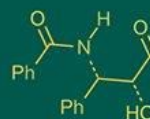


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Pradeep Krishnamurthy
 Division of Plant Physiology,
 Indian Agricultural Research
 Institute, New Delhi, India

Sreehari V Santhosh
 Division of Agricultural
 Statistics, IASRI, New Delhi,
 India

Neethu RS
 Division of Agricultural
 Statistics, IASRI, New Delhi,
 India

Corresponding Author:
Pradeep Krishnamurthy
 Division of Plant Physiology,
 Indian Agricultural Research
 Institute, New Delhi, India

From dormancy to germination: Establishing epigenetic memory and stress tolerance via innovative seed priming technologies

Pradeep Krishnamurthy, Sreehari V Santhosh and Neethu RS

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Abstract

Climate change and its associated anomalies, such as heat and water stress, pose significant risks to seed quality and agricultural productivity. Seed germination and dormancy are critical biological transitions regulated by a complex interplay of genetic, hormonal, and environmental factors to ensure survival in fluctuating environments. This paper explores how the hormonal balance between abscisic acid (ABA) and gibberellic acid (GA) influences the chromatin remodeling and histone modifications, thereby harnessing the key dormancy-related genes like *DOG1*. Moreover, the sensitivity of seed germination often determined by the environmental cues, including light, temperature, salinity, and drought as they persuade oxidative stress and metabolic imbalances. The review highlights what are the advances has been documented through seed priming to mitigate these adverse effects, has emerged as a vital pre-sowing intervention that enhances antioxidant enzyme activity and establishes epigenetic memory for improved stress tolerance in that way improve crop resilience and ensure sustainable productivity under adverse climatic conditions.

Keywords: Early emergence, preharvest sprouting, Abscicic acid (ABA), Gibberellic acid (GA), Delayed of germination 1 (DOG1), REVEILLE1 RVE1, LAFL (LEC1, ABI3, FUS3, LEC2), Phytochrome B PHYB, Histone modifications, histone mono ubiquitination (HUB) chromatin remodelling, seed priming, Nanopriming

Introduction

Climate anomalies at harvest and in the post-harvest period may not necessarily have a significant effect on seed production, but they can lower the morphological, physiological, and biochemical quality, which will ultimately lower the seed yield (Maity *et al.*, 2023) ^[59]. Crop productivity is significantly impacted by significant temperature changes imposed by climate change as they increase the risk factors for plant sustainable growth include heat stress and water stress (Malhi *et al.*, 2021) ^[60]. Due to rapid changes in climatic as they constantly changing external factors can to increases the abiotic stresses include drought stress, high temperature stress, cold stress, light stress and salinity stress that will affect the plant growth and development (Savvides *et al.*, 2016a) ^[74]. Moreover, reduced germination and vigour loss throughout the seed development and maturation phase are also caused by the environmental conditions, which have an impact on field emergence during germination (Akman *et al.*, 2009; Ren *et al.*, 2009) ^[71, 2]. Additionally, when seeds are exposed to high temperatures, a hormonal imbalance is created that results in increased production of abscisic acid (ABA) and decreased synthesis of gibberellic acid, which explains why *Arabidopsis* seeds germinate poorly (Toh *et al.*, 2008) ^[79].

In plant growth phase, germination is a crucial phase which determines the establishment of crop density and uniform maturation, required for the sustainable productivity. Marked environmental instability during the germination phase can impede seedling emergence, resulting in suboptimal crop density and subsequent yield loss (Almansouri *et al.*, 2001; Hampson and Simpson, 1990) ^[40, 5]. According to James *et al.*, 2019, up to 90% of seedlings may die between germination and emergence. Also, it overlaps with the previous study state that the most vulnerable stage is the transition stage between seed germination and the emergence of the seedling (Larson and Funk, 2016) ^[52, 45]. Additionally, early emergence is a significant adaptive factor that may improve the efficacy of reproduction, during resource

competition is intense (Rauf *et al.*, 2007) [70]. Furthermore, under such circumstances, the establishment of reproductive growth was primarily determined by early emergence of the mature seed. Since germination delays may leave crops susceptible to temperature stress at the end of growing seasons or promote uneven maturation of crops (Rauf *et al.*, 2007).

Both germination and dormancy are fated through genetic factors as well as environmental factors to improve the adaptation of habitual diversity. Seed dormancy is an adaptive trait to ensure species survival across fluctuating environments by delaying germination results in an uneven growth of the plant (Graeber *et al.*, 2012) [38]. Furthermore, seed dormancy is also a crucial biological transition that forms the basis of crop fitness and agricultural output, since to avoid pre-harvest sprouting and the ensuing losses in yield and quality, the dormancy threshold requires to be optimized (Simsek *et al.*, 2014) [77]. Although excessively high seed dormancy levels shorten the growing season and delay germination, too low seed dormancy levels might cause germination before a favorable growth season begins, increasing the risk of seedling mortality (Donohue *et al.*, 2010) [29]. Therefore, seed dormancy is also a significant component alongside of germination for plant growth and development (Donohue, 2005; Huang *et al.*, 2010) [42, 28]. Subsequently this review aimed to transcribe a comprehensive research report dwelling on how the uniform and efficient seed germination and establishment of early seedlings can be achieved for the improved agricultural crop production under adverse climatic conditions.

Hormonal regulation on seed germination and seed dormancy

The state of being dormant seed to the state where it can get germinated is the transition phase of seed germination. This transition phase is governed by endogenous bioactive concentration ratio between the abscisic acid (ABA) and Gibberellic acid (GA) (Bentsink and Koornneef, 2008) [10]. During the plant maturity stage, ABA act as key hormone that causes and sustains seed dormancy, as they maintain the quiescent state of seed which are driven by ABA biosynthesis genes, 9-cis-Epoxycarotenoid Dioxygenase 6 (NCED6) and NCED9, by preventing embryo development and preserving the mechanical resilience of surrounding tissues (Cadman *et al.*, 2006; Lefebvre *et al.*, 2006) [53, 17]. The ABA signaling pathway is regulated at the transcriptional and posttranslational levels by a number of regulators in addition to ABA production. For instance, ABA Hypersensitive Germination (AHG), AHG1 and AHG3 genes encode a protein phosphatase 2C PP2C-type phosphatases act as negative regulator of ABA signaling that prevent seed dormancy (Nishimura *et al.*, 2018) [65]. Similarly, SNF1-RELATED PROTEIN KINASES (SnRKs) act as downstream mechanism of ABA signals to promote seed dormancy (Cutler *et al.*, 2010; Hubbard *et al.*, 2010) [43,

25]. The active SnRKs in turns activates the gene expression of ABA insensitive (ABI), ABI3 and ABI4 directly upregulates the several genes involved in regulation of macromolecule metabolites within the seed in order to favors the seed maturity as well as seed dormancy (Mönke *et al.*, 2012; Yang *et al.*, 2011) [61, 87]. In contrast to ABA, GA acts as the primary germination promoter and it is essential to promote the potential embryogenesis leading to triggering the rupture of seed coat protective layers of testa and tegum ultimately breaks the seed dormancy (De Wit *et al.*, 2016) [26]. Moreover, hydrolytic enzymes include α -amylase and endo- β -mannanase, break down store reserves and weaken cell walls to allow the radicle to protrude, are produced by GA (Nonogaki, 2014; Nonogaki *et al.*, 2000; Zhang *et al.*, 2014) [92, 67, 66]. In an instance, DELLA proteins act as repressors of seed germination and dormancy release via GA signalling. And the DELLA proteins are often interacting with other transcription factors to regulate the expression of downstream genes since they lack a DNA binding domain (Liu *et al.*, 2016) [57]. DELLA proteins are essential for preserving seed dormancy by increasing its ability to bind DNA, RGL2 enhances the function of reversal of *cbf* expression 1 (RVE1), subsequently RVE1 stabilizes RGL2 to preserve seed dormancy (Jiang, *et al.*, 2020) [46]. Additionally, by stabilizing RGL2 protein activity and suppressing GA3ox2 transcription, RVE1 keeps seeds dormant (Jiang *et al.*, 2016; L. Yang, Liu, *et al.*, 2020) [86, 85]. On the contrary, while directly increasing the expression of ABI5 through interaction with NF-YC, RGA-LIKE2 (RGL2) prevents the escape of seed dormancy (Figure 1; Liu *et al.* 2016). Similarly, GA INSENSITIVE (GAI) inhibits the transcript of gibberellin 3-oxidase1 (GA3ox1) enzyme which promotes the induction of active GAs by interacting with DOF affecting germination 1 (DAG1) (Boccaccini *et al.*, 2014) [14]. While GA3ox1 and GA3ox2 promote the production of bioactive Gas, gibberellin 2-oxidase2 (GA2ox2) produces inactive Gas (De Wit *et al.*, 2016).

Phytochrome B (PHYB) is downstream of RVE1, and PHYB suppresses RVE1 expression (Jiang *et al.* 2016) [46]. According to Jiang *et al.*, (2016) [46], overexpressing (PHYB) decreases seed dormancy, indicating that the photoreceptor (PHYB) is probably involved in light signaling input during seed development. Thus, by inhibiting RVE1 transcription, (PHYB) functions as a negative regulator of seed dormancy maintenance (Yang *et al.*, 2020) [86, 85]. Likewise, *dog1*'s non-dormant phenotype was inhibited by overexpressing RVE1, and delay of germination (DOG1) controls primary seed dormancy downstream of PHYB (Figure 1, Jiang *et al.*, 2016) [46]. All these research findings elucidate that PHYB acts as a negative regulator of dormancy. Upon activation, it suppresses the expression of RVE1, thereby breaking the RVE1-RGL2 loop and allowing germination to proceed.

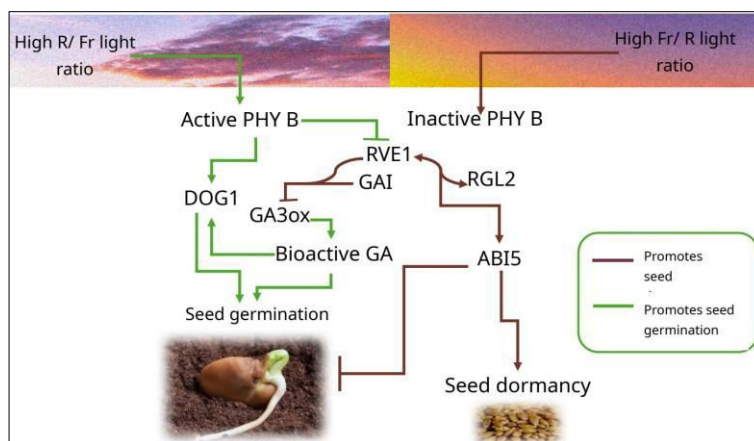


Fig 1: Demonstrates that light-activated PHY B shifts the balance toward GA-mediated growth, while the presence of ABA and its downstream effectors (like RGL and GAI) reinforce seed dormancy by suppressing GA activity.

Emerging Molecular and Epigenetic Regulation

The plant hormone, ABA is responsible for seed dormancy and also inhibit the non-dormancy seed to germinate. Seeds get germinated when testa and endosperm get ruptured due to radicle penetration these were extensive studies from the past research. The underlying molecular response under seed dormancy has reveals that chromatin remodeling regulates the seed dormancy and seed germination through histone mono ubiquitination (HUB) which ubiquitinate the histone H2B protein thereby reducing the seed dormancy suggesting H2B play an important role in seed dormancy (Liu *et al.*, 2007) [58]. Additionally H2B mono ubiquitination indirectly influencing positive methylation at H3ly4 (Sun and Allis, 2002; Wood *et al.*, 2003) and it has been found that H2B mono ubiquitination reduced the expression of seed dormancy related genes DOG1, abscisic acid insensitive (ATS2), NCED9, 1-Cysteine Peroxiredoxin (PER1) and Cytochrome P450, Family 707, Subfamily A, Polypeptide 2 (CYP707A2) (Liu *et al.*, 2007) [58]. In *Arabidopsis* lysine specific demethylase like 1&2 histone demethylase (LDL1, LDL2) repress the seed dormancy through regulating ABA biosynthesis and signal transduction. Additionally, it has been shown that DOG1 transcription level also increased in *ldl1* and *ldl2* mutant plant suggesting LDL1 & LDL2 also controlling the DOG1 expression in *Arabidopsis* plant (Zhao *et al.*, 2015) [93]. Since in *Arabidopsis* it has been found that H3 region has two opposite function on methylation at different position, H3K4 and H3K6 were activate seed maturation gene (Zhang *et al.*, 2009; Mendes *et al.*, 2014) [76, 91, 92] while H3K9 and H3K27 were deactivate the seed maturation gene (Liu *et al.*, 2010; Zhang *et al.*, 2007; Jackson *et al.*, 2004) [44, 56] suggesting that LDL1&LDL2 demethylate at H3K4 AND H3K6 thereby repressing seed maturation gene causing seed germination. Furthermore, ABA hormone involved in chromatin remodeling thereby repressing the histone deacetylation which is responsible for seed germination (Chinnusamy *et al.*, 2008) [21]. Seed maturation and seed dormancy are positively regulated by LAFL regulator network such as Leafy cotyledons1 (LEC1), abscisic inhibitor (AB13), fusca3 (FUS3) and LEC2 (Tsukagoshi *et al.*, 2007) [81]. This LAFL transcriptional factor repressed by high-level expression of sugar inducible gene2 (HSI2) and HSI2-LIKE1 (HSL1) transcription factors. These HSI2 and HSL1 suppress LAFL network by chromatin remodelling complex polycomb repressive complex1 and 2 (PRC1 & PRC2) and pickle (PKL), pickle related 2 proteins (Zhang *et al.*, 2012) [90].

Correspondingly PKL directly blocks the DOG1 gene which is involved in seed dormancy (Dekkers *et al.*, 2016; Footitt, *et al.*, 2020) [35, 27, 26]. Likewise, in polycomb repressive complex1, a crucial factor fertilization independent endosperm (FIE) repressing the ABI3/ABA signalling factor and DOG1 expression thereby reducing seed dormancy (Bouyer *et al.*, 2011) [15]. Furthermore, PKL upregulate the chromodomain helicase DNA binding domain (CHD3) which is evolutionary conserved in plants and animals (Tong *et al.*, 1998) [80]. CHD3 chromatin remodelling protein regulates the nucleosome remodelling histone deacetylase (NuRD) complex which triggers seed germination. Likewise, viviparous1/abi3 like1 (VAL1) and VAL2 B3 are DNA binding protein domain also repressing the LAFL transcriptional network (Suzuki *et al.*, 2007; Tsukagoshi *et al.*, 2007) [78]. In recent research it reveals that PKL recruitment to target loci by VAL1/2 that repress the seed maturation and regulating the PKL for chromatin remodelling (Liang *et al.*, 2022) [55].

Seed Dormancy and Germination in a Changing Climate

Seed dormancy and germination are sophisticated biological processes influenced by a complex interplay of genetic, hormonal, physical, and environmental factors. These factors act as internal and external "sensors" that ensure a plant initiates its life cycle only when conditions are optimal for seedling survival (Graeber *et al.*, 2012) [38]. Several environmental parameters, including temperature, pH, NaCl, water stress, and sowing depth, impact germination and emergence. (Chauhan *et al.*, 2006; Koger *et al.*, 2004; Kołodziejek & Patykowski, 2015) [51, 50, 20]. Amongst abiotic stress, light, temperature, salinity, and drought are considered as the primary factors influencing seed germination in various desert species, *Artemisia tridentata*, *Leymus chinensis*, *Atriplex centralasiatica* and *Desmodium brachypodium* (Bhatt *et al.*, 2019a; Bhatt and Perez-García, 2016; El-Keblawy *et al.*, 2016) [13, 32, 12, 13]. Many biological processes in plants, including seed dormancy and germination, photomorphogenesis, phototropism, shade avoidance, and flowering, are regulated by light, an essential environmental signal (De Wit *et al.* 2016; Jiang *et al.*, 2016) [46, 26]. A minimum of five distinct types of photoreceptors which detect light signals in their environment have evolved in plants such as Phytochromes (PHY) absorbs red and far-red light spectrum (660nm-730nm) and cryptochromes (CRYs) absorb blue/UV-A (320-500 nm) (Cashmore, 2003; Yu *et al.*, 2010) [88, 19]. Usually, red light activates PHYB,

which causes the germination repressor phytochrome interacting factor (PIF1) to degrade vice versa in case of far-red light absorption (Fenner and Thompson, 2005) [33]. The timing and location of seed germination are determined by light with the correlation between light exposure, photoblastism, and germination being positive, negative, or neutral depending on the species (Baskin & Baskin, 2000; Bhatt *et al.*, 2019) [9].

Temperature acts as a primary environmental cue that seeds integrate during both the maturation phase on the mother plant and while residing in the soil seed bank to time their transition to germination. The transcription factors CBF (C-repeat binding factor) and MFT (MOTHER OF FT AND TFL1) are central to this temperature-sensing machinery, acting as molecular bridges between external thermal signals and internal hormonal regulation (Nakamura *et al.*, 2011) [63]. Kendall *et al.*, (2011) [47] demonstrated that the regulation of dormancy driven by low seed-maturation temperatures requires transcription factors of the C-repeat binding factor (CBF) group, while CBFs are strictly required for low-temperature dormancy induction, their own transcript abundances are not temperature-regulated within the seeds themselves suggesting suggests that their activation may depend on post-translational mechanisms (Graeber *et al.*, 2012) [38]. In a transient overexpression and genetic mapping study on the recombinant inbred lines of wheat from *Triticum monococcum* × *T. boeoticum* identified that MFT upregulated after physiological maturity in dormant seeds grown at lower temperatures (13 °C vs. 25 °C). Remarkably, on wheat chromosome 3, MFT is a potential candidate for the gene driving a QTL for pre-harvest sprouting (Nakamura *et al.*, 2011) [63]. It has been reported that the *mft* mutant lines of wheat remains non dormant, indicating that MFT is a germination inhibitor, and variation of MFT underlies variation in seed dormancy (Chono *et al.*, 2015) [23]. Furthermore, the germination-inhibiting hormone 12-oxo-phytodienoic acid (OPDA) significantly increases MFT expression, indicating the role of oxylipin hormones in seed temperature responses (Penfield and MacGregor, 2017) [68]. Also, MFT regulates seed dormancy in a complex gene network that includes hormone metabolism of GA, ABI5, and DELLAs which is not established yet (Zhu *et al.*, 2017) [97].

Similarly, salinity and drought also influence regeneration, growth, and survival in arid and semiarid deserts (Abushamleh *et al.*, 2022; Podda *et al.*, 2017) [69, 1]. Salt stress generally decreases the germination percentage and retards the onset of germination. Overall germination of several species may be influenced more by low osmotic potential than by specific ion effect (Hosseini *et al.*, 2003) [48]. Salinity creates a low external water potential, generating osmotic stress that restricts the seed's ability to imbibe water. Without reaching a minimum water threshold, the metabolic reactions required to trigger germination results dormant seed (Hendawy *et al.*, 2019) [30]. Salt and osmotic stress are among the most challenging environmental factors affecting plant growth and productivity, particularly in arid and semiarid regions (Hameed *et al.*, 2012; Seleiman *et al.*, 2021) [75, 39]. Seed germination represents a critical phase in a plant's life cycle, and the success of seed germination is vital in determining subsequent growth, development, and population persistence. In coastal regions, where salinity and drought are prevalent, understanding the impacts of these stressors

on seed germination is crucial for developing restoration strategies and ensuring the sustainable management and resilience of coastal ecosystems (Alhaddad *et al.*, 2021; Bhatt *et al.*, 2019b; Walsh *et al.*, 2023; Xie *et al.*, 2018) [84, 82, 13, 3, 13]. High concentrations of sodium (Na⁺) and chloride (Cl⁻) ions are directly toxic to seedling tissues. Salinity disrupts ion homeostasis, leading to an imbalance in the ratio that inhibits cellular functions. These conditions trigger the overaccumulation of Reactive Oxygen Species (ROS), such as hydrogen peroxide and superoxide radicals, which damage DNA, proteins, and membranes (Khan *et al.*, 2021) [49].

The Efficacy of Seed Priming as a Pre-Sowing Intervention for Stress Mitigation

Seed germination and young seedling establishment adversely affected through salinity and drought either by lowering the water potential exogenously or by accumulating toxic ions includes Na^+ and Cl^- in the seedling (Hosseini *et al.*, 2003) [48]. While exposing plants towards the toxic chemical in a progressive priming method of hardening shown that the chemically primed plants attain the improved corresponding stress tolerance response (Munns and Tester, 2008) [62]. Multiple investigations have demonstrated that when plants are subjected to different abiotic stresses, root preparation will improve vegetative tissue tolerance. Pretreatment with certain compounds consistently improves systemic tolerance, even if the chemical compound was only applied to one organ (Zandonadi *et al.*, 2010) [89]. The intricate mechanism of action of particular signaling molecules in plant stress tolerance through seed priming has been elucidated in various studies, for instance the frequent utilization of chemical priming induces the production of signaling molecules or transcription factors in an inactive state, thereby leading to a more rapid or robust activation of defense responses upon exposure to stress (Savvides *et al.*, 2016b) [73, 73]. Seed priming facilitates the hyperactivation of stress-responsive transcription factors through the exposure of mild stress thereby establishes the histone modification through DNA methylation and retains this stress induced encounters to respond more effectively under the sequential induction of severe stress in the surroundings (Bruce *et al.*, 2007) [16]. Significant biochemical changes also take place due to priming especially, it increases the enzymatic activity of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), which together assists in the detoxification of reactive oxygen species (ROS) that have accumulated under adverse environments (Khan *et al.*, 2024) [64]. Furthermore, priming increases metabolic respiration rates and promotes the synthesis of adenosine triphosphate (ATP), ensuring the vital metabolic energy required for effective early seedling establishment (Weitbrecht *et al.*, 2011) [83]. Moreover, priming generally triggers Reactive oxygen nitrogen sulfur species (RONSS), such as hydrogen peroxide (H₂O₂), nitric oxide (NO), and hydrogen sulphide (H₂S), act as vital signal transduction molecules during this process (Bae *et al.*, 2005; Baek *et al.*, 2015; Christou *et al.*, 2014; Fotopoulos *et al.*, 2015) [36, 24, 7, 6]. However exogenous pretreatment of chemical agents at higher concentrations will harm the seedling vitality necessitates the development of smart application technologies that enables the application of chemicals most

appropriate concentration (Savvides *et al.*, 2016c) ^[74]. To overcome the toxic effect of chemical priming researcher developed an emerging solution as nanopriming particles smaller than 100 nm, requires less quantity of nanomaterials compared to soil/root or foliar application methods. Therefore, in addition to improving plant salt tolerance, nanopriming ensures the biosafety risks associated with the application of nanotechnology in agriculture through the use of lesser nanoparticle (Cao *et al.*, 2018; Khan *et al.*, 2021; Rossi *et al.*, 2017) ^[72, 18, 49]. Earlier Nano priming investigations was mostly focused on basic metals such as silver (Ag) and zinc oxide (ZnO) to regulate antioxidant systems (Bethke *et al.*, 2006) ^[11]. Recently the nanopriming technology approach was developed into a selenium-doped carbon dots to regulates the free radicals in order to prevent the cellular damage (Chong *et al.*, 2016; Hu *et al.*, 2019) ^[41, 22]. Subsequently, the higher total soluble sugar and protein contents and ATP production were also found in PAA @ Se-CDs nanopriming improved rapeseed salt tolerance. By increasing antioxidant enzyme activities, PAA @ Se-CDs nanopriming also shown improved ROS scavenging capabilities. Additionally, in saline conditions, PAA @ Se-CDs nanopriming improved the K⁺/Na⁺ ratio (Khan *et al.*, 2024). Nevertheless, further study required to understand the mechanisms underlying nanopriming's enhanced salt tolerance during germination and the early stages of seedling growth.

Conclusion

A multifaceted combination of genetic, hormonal, and environmental factors regulates the highly controlled biological process of the transition from seed dormancy to effective germination. The hormonal imbalance between GA and ABA is essential to determines regulation of germination and dormancy which get disturbed by the climatic instability, resulting in an excess of reactive oxygen species (ROS), metabolic imbalance, and increased seedling mortality. To mitigate these adverse effects, seed priming has emerged as a vital pre-sowing intervention. By exposing seeds to mild, controlled stressors, priming establishes an epigenetic memory thereby enhances the activity of antioxidant enzymes to detoxify ROS and boosts ATP production to provide the metabolic energy necessary for uniform seedling establishment. While chemical priming remains effective, emerging technologies like nanopriming gives a more biosafe and efficient approach to improves the crop resilience and sustainable productivity in a changing climate.

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