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Beyond Germination: Unravelling the Physiological and Molecular Basis of Seed Priming

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Seed priming is an established seed-enhancement technology in which seeds are partially hydrated under controlled conditions to initiate pre-germinative metabolic events without permitting radicle protrusion. Priming can improve germination rate and synchrony, seedling vigour and tolerance to environmental stresses. Its effects arise from coordinated physiological, biochemical and molecular processes, including membrane repair, mitochondrial activation, reserve mobilization, antioxidant defence, hormonal reprogramming and cellular repair. Increasing evidence indicates that reactive oxygen species (ROS)function not only as damaging molecules but also as signalling components that interact with phytohormones, calcium, nitric oxide and mitogen-activated protein kinase pathways (MAPK) during germination. Recent research further demonstrates close interactions among ROS, abscisic acid (ABA), gibberellins (GA) and epigenetic mechanisms in controlling seed dormancy and germination. At the molecular level, priming modifies gene expression, protein abundance, metabolite profiles and potentially chromatin states. Epigenetic modifications, including DNA methylation and histone modification, have emerged as potential components of priming-induced stress memory. Recent work on chemical priming has also highlighted the importance of salicylic acid, zinc, gibberellic acid and potassium nitrate as frequently investigated priming agents. This review summarizes current knowledge of the physiological and molecular basis of seed priming and discusses its potential for developing resilient crop production systems under environmental stress.

Keywords: Seed priming, Seed germination, Reactive oxygen species, ABA, gibberellin, gene expression, antioxidant defence, stress memory, epigenetics

Introduction

Seed germination represents a critical developmental transition determining successful crop establishment. The process involves rehydration of the dry seed, restoration of cellular metabolism, activation of respiration, synthesis of proteins and nucleic acids, mobilization of storage reserves and eventual radicle protrusion. Germination is regulated by interactions between endogenous physiological status and environmental signals such as water availability, temperature, light, oxygen and nutrients. The molecular regulation of germination is particularly complex because seeds must balance dormancy maintenance with the decision to initiate growth. ABA and GA constitute major hormonal regulators, while ROS, ethylene, auxin, jasmonates, cytokinins and brassinosteroids contribute to the regulatory network. Recent research has emphasized that ROS function as a central signalling hub connecting hormonal, calcium, nitric oxide and MAPK pathways. The concept of priming has developed considerably since early osmotic-priming studies. Modern research views priming as a complex process involving metabolic activation, redox signalling, hormonal regulation, cellular repair, transcriptional reprogramming and potentially epigenetic memory. Recent reviews also emphasize that the response to priming is genotype-dependent and that conventional external priming agents may produce variable responses among cultivars.

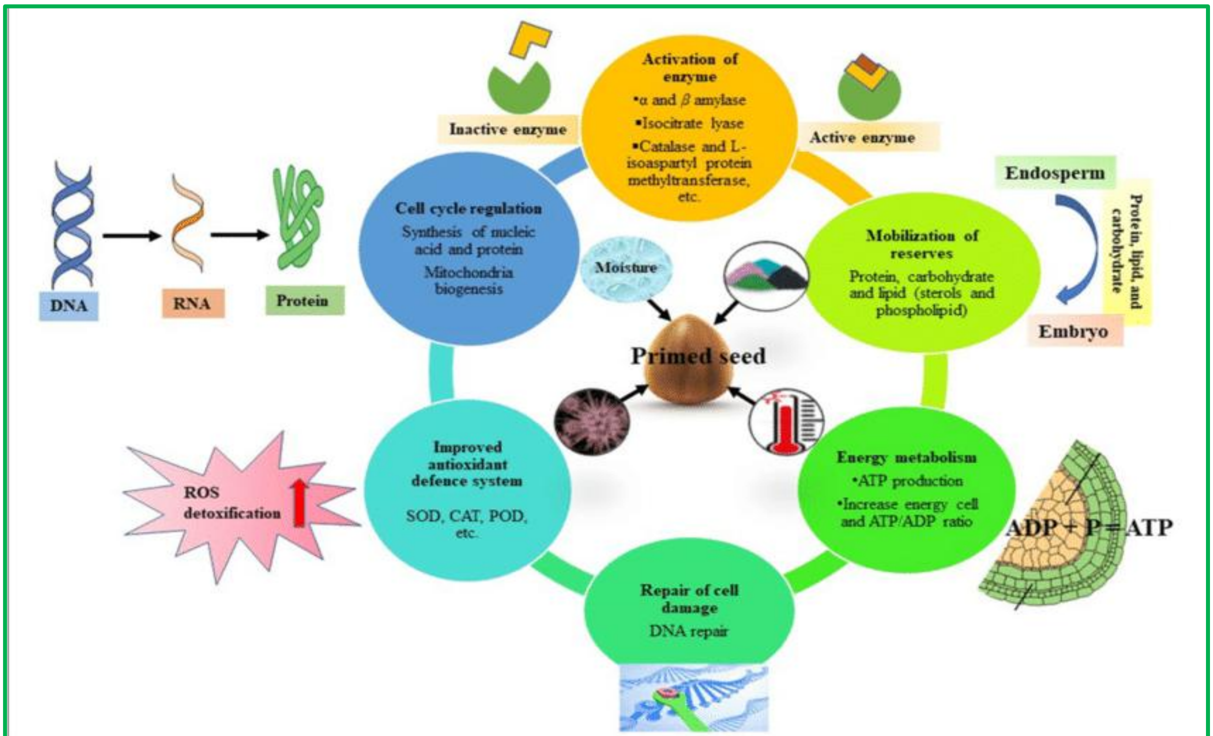
Types of Seed Priming

The major seed-priming approaches include:

Table 1. Major seed-priming approaches and their principal mechanisms

Priming method	Typical agent	Principal mechanism
Hydropriming	Water	Controlled hydration and metabolic activation
Osmopriming	PEG/osmotic solutions	Regulation of water uptake
Halopriming	KNO_3, $CaCl_2$, NaCl etc.	Osmotic adjustment and ion signalling
Hormonal priming	GA, ABA-related compounds, SA, JA	Hormonal reprogramming
Nutripriming	Zn, Fe, P and other nutrients	Improved nutritional status
Biopriming	Beneficial microorganisms	Growth promotion and defence activation
Redox priming	Controlled ROS-generating agents	Redox signalling and antioxidant activation
Nanopriming	Nanoparticles	Enhanced signalling, enzyme activity and stress tolerance
Plasma Priming	Non-thermal plasma containing electrons, ions, ROS, RNS and UV photons	Seed-coat modification → improved wettability and imbibition → ROS/RNS signalling → metabolic and molecular activation

Physiological Basis of Seed Priming



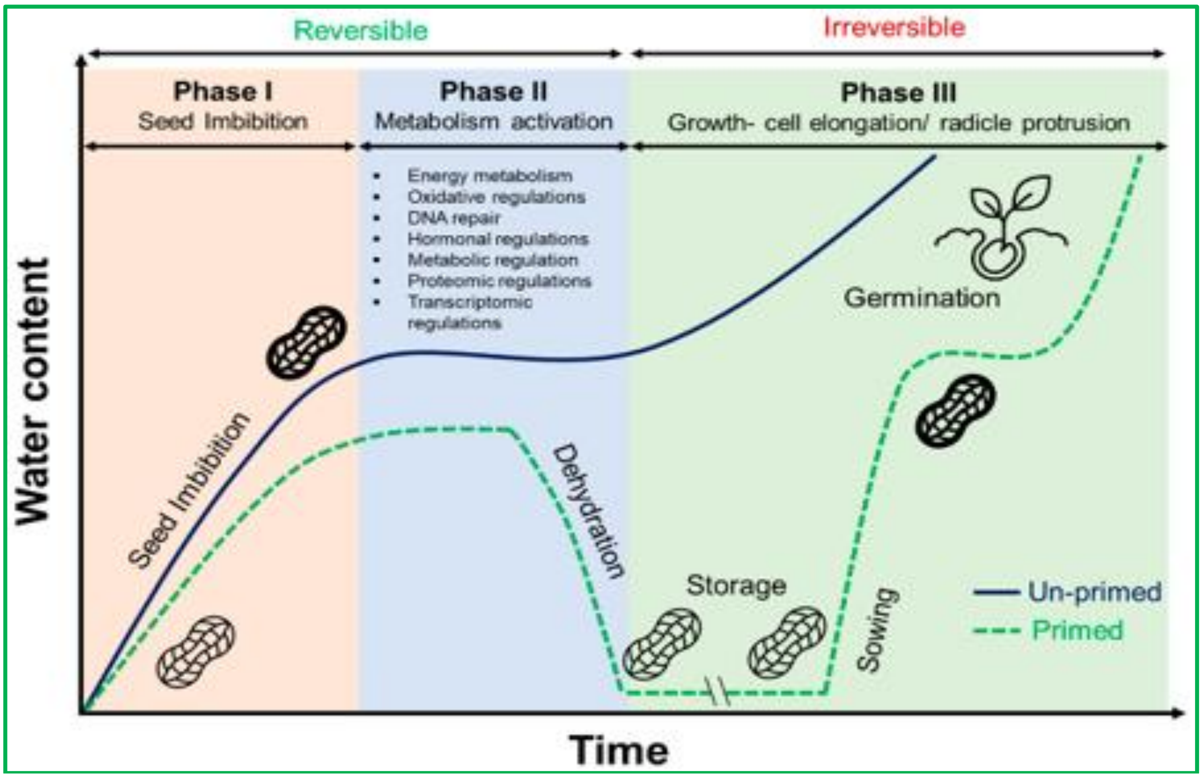
Controlled hydration

Seed hydration can be divided into three general phases:

Phase I — Imbibition

Phase II — Metabolic activation

Phase III — Radicle protrusion



Priming generally maintains seeds in a physiologically active state corresponding largely to Phase II. During this period, cellular hydration increases, membranes reorganize and metabolic pathways are activated without completion of germination.

Membrane repair

Membrane integrity is one of the earliest targets of seed deterioration and imbibitional injury. Controlled hydration allows membrane components to reorganize before the rapid growth phase. Priming therefore contributes to membrane stabilization, reduction of electrolyte leakage, lipid repair, restoration of membrane-associated proteins, and improved cellular compartmentalization. These changes contribute to increased seed vigour.

Metabolic Activation

Mitochondrial activation: Hydration reactivates mitochondrial metabolism and stimulates respiration:

Hydration → mitochondrial activation → electron transport → ATP production

ATP generated during priming supports: protein synthesis, membrane repair, DNA repair, enzyme activation and reserve mobilization. However, enhanced respiratory activity also produces ROS, making redox regulation an essential component of successful priming.

Storage reserve mobilization: Priming can facilitate the mobilization of carbohydrates, proteins and lipids.

In cereal seeds:

GA signalling → aleurone activation → α-amylase production → starch degradation → soluble sugars

These sugars serve as respiratory substrates and carbon sources for embryo growth.

ROS Signalling and Antioxidant Defence

The traditional view of ROS as exclusively damaging molecules has been replaced by a more nuanced understanding. Moderate ROS concentrations participate in germination signalling, whereas excessive ROS cause oxidative damage. Recent reviews describe ROS as a central hub connecting germination with hormonal, calcium, nitric oxide and MAPK signalling.

Major ROS: $O_2^{\bullet-}$, H_2O_2, $\bullet OH$

Major antioxidant enzymes: SOD, CAT/APX/GPX

Priming can therefore establish a favourable redox state in which ROS are maintained at concentrations sufficient for signalling but below levels that cause extensive cellular damage.

Recent evidence demonstrates that controlled ROS generation during priming can function as an acclimation signal. Chen *et al.* (2023) showed that ROS-generating nanoparticles enhanced maize germination and seedling tolerance to drought, salinity and cold stresses. Transcriptomic analysis further revealed activation of plant hormone signal transduction and MAPK signalling pathways, suggesting that ROS-mediated priming involves coordinated signalling rather than simple antioxidant activation.

Hormonal Regulation

ABA–GA antagonism: ABA and GA represent two major hormonal regulators of seed dormancy and germination.

High ABA activity → dormancy

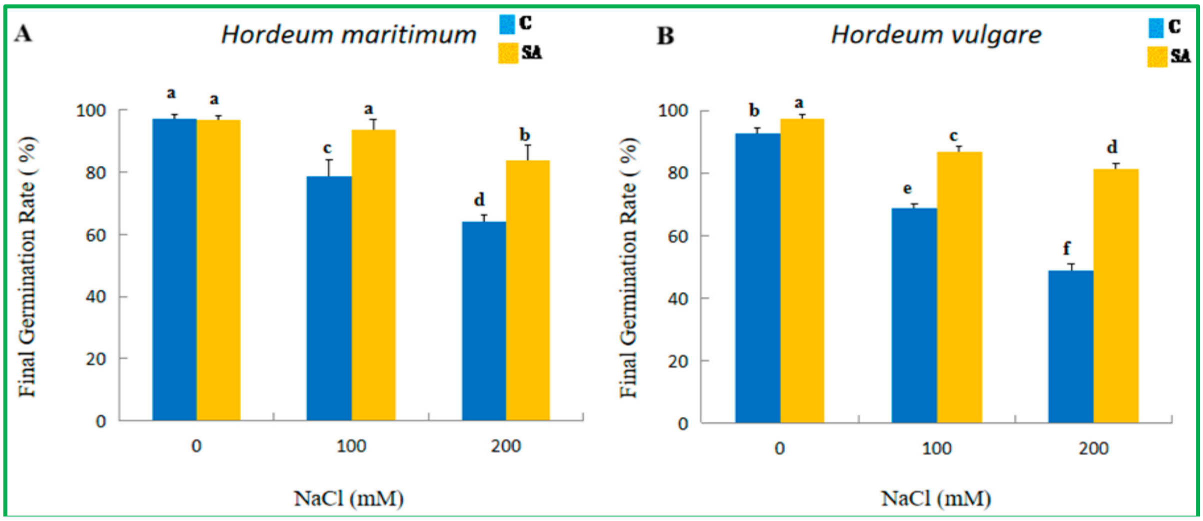
Increased GA activity → germination

Priming can influence ABA metabolism, GA biosynthesis and downstream signalling.

Important molecular components include:

- NCED – ABA biosynthesis
- ABI3/ABI5 – ABA signalling
- GA20ox – GA biosynthesis
- GA3ox – active GA formation
- GA2ox – GA inactivation
- DELLA proteins – negative regulators of GA signalling

Salicylic Acid in Seed Priming: Salicylic acid (SA) acts as an important signalling molecule during seed priming, enhancing germination, antioxidant defense, and stress tolerance. SA modulates the balance of hormones such as abscisic acid (ABA) and gibberellins (GA), promotes ROS signalling, and activates antioxidant enzymes. This hormonal regulation improves seedling establishment under adverse environmental conditions. Salicyclic acid regulate expression of PR-protein (β-1,3-glucanase and chitinase related defense enzymes) and also increase gene expression of IAA27, MPK1, GPX, chitinase and β-1,3-glucanase to protect from biotic stress.(Mahesh *et al*.,2017)



(Effect of Salicyclic acid (SA) seed priming and no pre-treatment(C- control) on germination% of two barley species grown under salinity stress)(Ben *et al*.,2025)

Molecular Reprogramming During Priming

Seed priming induces molecular changes at several levels.

Molecular level	Major changes during priming	Outcome
Transcriptome	Activation/repression of germination, antioxidant and stress-responsive genes	Faster response and germination
Proteome	Activation of metabolic, antioxidant and protective proteins	Improved cellular protection
Metabolome	Accumulation of sugars, amino acids, osmoprotectants and signalling metabolites	Energy supply and stress protection

Redox system	Controlled ROS/RNS production and antioxidant activation	Redox homeostasis
Hormonal system	Modification of ABA–GA and other hormone signalling	Dormancy release and germination
DNA methylation	Locus- or genome-level changes in DNA methylation	Altered expression of stress-responsive genes
Histone modifications	Changes in active/repressive histone marks such as H3K4me3 and H3K27me3	Chromatin accessibility and transcriptional regulation
Small RNAs	Regulation of target transcripts and epigenetic pathways	Fine-tuning of stress responses
Chromatin state	Changes in nucleosome positioning/chromatin accessibility	Maintenance of a primed transcriptional state
Molecular memory	Persistence of selected transcriptional/epigenetic changes	Faster response to subsequent stress

Gene expression

Priming can modify genes involved in antioxidant defence, hormone metabolism, respiration, carbohydrate metabolism, stress responses, DNA repair, cell-wall modification.

- **Antioxidant-related genes:** Superoxide dismutase (SOD), Catalase (CAT), Ascorbate peroxidase (APX/POD) etc maintain ROS homeostasis.
- **Germination-related genes:** genes involved in starch degradation and reserve mobilization, Expression of gene responsible for endosperm cap weakening (SlEXP4, SlGulB, SlMAN2, and SlXTH4)
- **Hormone-related genes**: genes regulating ABA (NCED) and GA metabolism/signalling, (GA20ox1, GA3ox1), SALICYCLIC ACID (expression of PR-protein (β-1,3-glucanase and chitinase) related defense enzymes) Further, an increase gene expression for biotic stress resistance IAA27, MPK1, GPX, chitinase and β-1,3-glucanase
- **Stress-responsive genes:** genes encoding heat-shock proteins (HSP), dehydrins and other protective proteins [Late embryogenesis abundant protein (LEA)]
- **Transcription factors:** ERF/AP2 (ethylene-responsive element binding protein), C2C2-Dof (C2C2-DNA-binding with one finger), and bHLH (basic helix loop helix) families have been implicated in priming-induced stress tolerance in some crops.

Protein metabolism

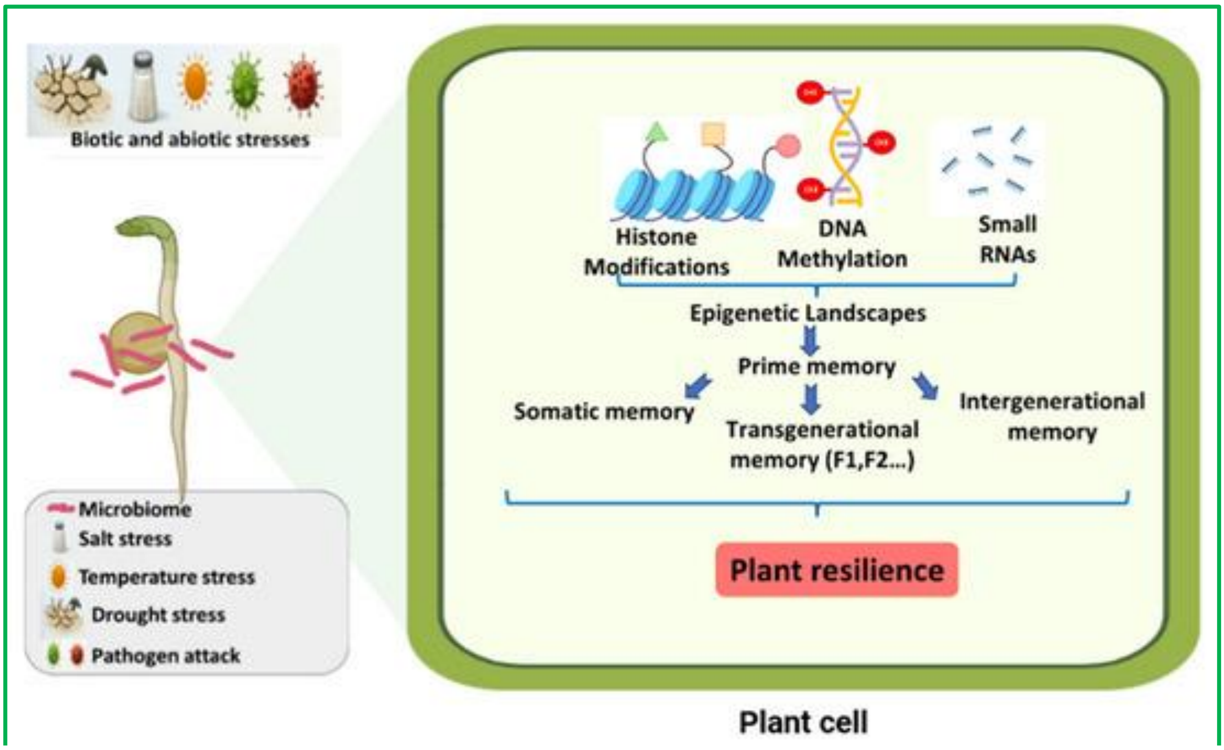
Priming enhances protein synthesis and quality-control processes and may increase protective proteins such as HSPs and LEA proteins.

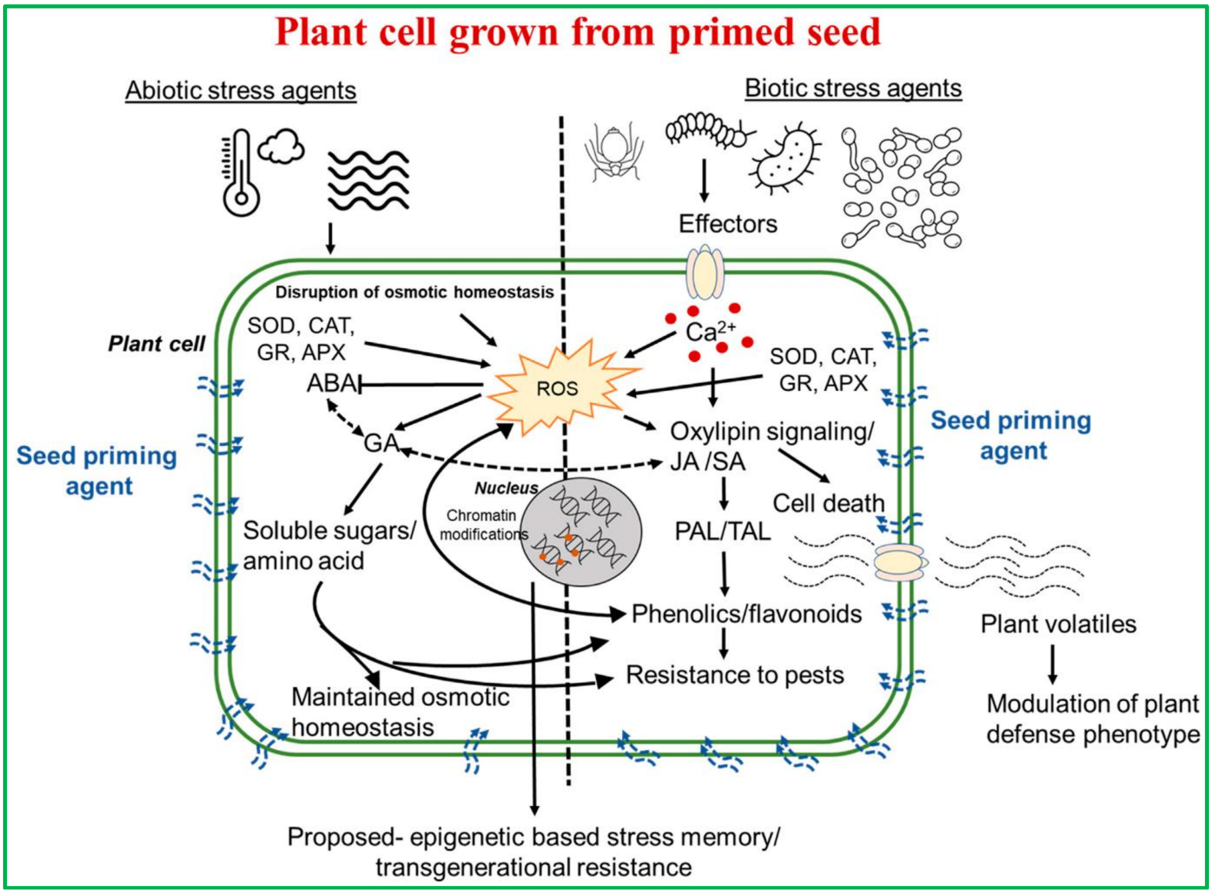
DNA repair

Controlled hydration provides an opportunity for repair of oxidative and replication-associated DNA damage. These molecular changes contribute to the more rapid and coordinated germination of primed seeds.

Epigenetics and Priming-Induced Stress Memory

One of the most important emerging areas is priming-induced molecular memory. Seed priming may induce molecular changes that persist beyond the initial treatment and contribute to stress memory. Proposed mechanisms include DNA methylation, histone modifications, chromosome remodelling, changes in nucleosome positioning and Small-RNA-mediated regulation, Such epigenetic modifications may influence the expression of stress-responsive genes and, under certain conditions, contribute to the persistence of acquired stress tolerance into subsequent generations (Louis *et al.*, 2023). However, the extent and stability of trans-generational inheritance remain dependent on the plant species, stress treatment and experimental context. Yung *et al.* (2026) demonstrates that salt-stress priming in soybean seedlings causes global DNA hypomethylation via reduced DNA methyltransferase activity, which fine-tunes chromatin states and activates stress-response genes.





(Schematic representation of cellular molecular and biochemical mechanisms underlying seed priming-based resistance to biotic and abiotic stress conditions.)(Jatana *et al*.,2024)

Conclusion

Seed priming is a multifaceted biological process that prepares seeds for rapid and coordinated germination. Controlled hydration activates membrane repair, mitochondrial metabolism, respiration and reserve mobilization while stimulating ROS and hormonal signalling networks. The balance between ROS generation and antioxidant defence is particularly important because ROS function both as signalling molecules and potential sources of oxidative damage. At the molecular level, priming modifies gene expression, protein metabolism, hormone signalling and DNA repair. The emerging roles of epigenetic regulation and molecular stress memory suggest that the effects of priming may extend beyond immediate metabolic activation. Recent advances in chemical priming, biopriming and nanopriming further broaden the potential applications of this technology. Future integration of seed physiology, molecular genetics, multi-omics, nanotechnology and computational approaches should enable more precise and sustainable seed-enhancement technologies. Such approaches are particularly relevant for improving crop establishment and resilience under drought, salinity, temperature extremes and other environmental stresses associated with climate change.

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