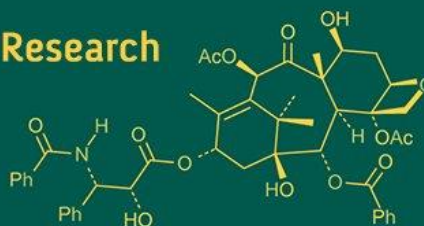


International Journal of Advanced Biochemistry Research



ISSN Print: 2617-4693
ISSN Online: 2617-4707
NAAS Rating (2026): 5.29
IJABR 2026; SP-10(6): 725-734
www.biochemjournal.com
Received: 11-03-2026
Accepted: 15-04-2026

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Advances in seed priming technologies: Mechanisms and agronomic impacts of ga_3 , $znso_4$, kno_3 , phosphobacteria, trichoderma viride, and seaweed extracts on seed quality and crop productivity

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DOI: <https://www.doi.org/10.33545/26174693.2026.v10.i6Si.8694>

Abstract

Seed priming is a controlled hydration technique that activates pre-germinative metabolic processes while preventing radicle protrusion, thereby conditioning seeds for synchronized, rapid and uniform germination under both optimal and stress-prone field conditions. As global agricultural systems face mounting pressure from climate variability, soil degradation and increasing demand for food security, seed priming has emerged as a cost-effective, eco-friendly and scalable pre-sowing technology. This review comprehensively examines the biochemical mechanisms and agronomic outcomes of six widely studied priming agents: gibberellic acid (GA_3), zinc sulfate ($ZnSO_4$), potassium nitrate (KNO_3), phosphate-solubilizing bacteria (Phosphobacteria), *Trichoderma viride* and seaweed extracts. Each agent operates through distinct yet often overlapping molecular and physiological pathways, including hormonal regulation of dormancy, enzymatic antioxidant activation, nutrient mobilization, microbial-plant signaling and bioactive compound-mediated metabolic priming. GA_3 facilitates aleurone layer enzyme secretion and endosperm weakening via gibberellin-regulated gene expression. $ZnSO_4$ enhances metalloenzyme activity and DNA repair during imbibition. KNO_3 provides osmotic adjustment and nitrogen nutrition that supports nucleic acid synthesis. Phosphobacteria promote phosphorus solubilization and phytohormone synthesis, while *Trichoderma viride* induces systemic resistance and produces cell wall-degrading enzymes. Seaweed extracts, rich in cytokinins, auxins, betaines and alginates, modulate stress-responsive pathways and enhance seedling vigor. Evidence from field trials across major agronomic crops consistently demonstrates improvements in germination percentage (5-35%), seedling vigor index (10-50%), root architecture, chlorophyll content and ultimately grain yield (8-40%). This review also highlights synergistic combinations of priming agents, identifies research gaps and outlines future directions for optimizing priming protocols under variable agro-climatic scenarios.

Keywords: Seed priming; gibberellic acid; zinc sulfate; potassium nitrate; phosphobacteria; trichoderma viride; seaweed extract; germination; crop productivity; agronomic impacts

Introduction

Food security remains one of the most critical global challenges of the twenty-first century. With the world population projected to reach approximately 9.7 billion by 2050, agricultural systems must deliver substantially higher yields from diminishing arable land, reduced freshwater availability and increasingly unpredictable climatic conditions ^[1]. Crop establishment - the critical phase from seed germination through early seedling growth - is considered the most vulnerable stage in the crop life cycle, where losses to poor germination, seedling mortality, or delayed emergence can have irreversible consequences on final yield potential ^[2]. Seed priming, first systematically described by Heydecker and Coolbear in the 1970s,^[3, 38] involves controlled hydration of seeds to a moisture level that permits pre-germinative metabolism but does not allow radicle protrusion beyond the seed coat. This fundamental approach has since diversified into multiple sub-technologies, including hydropriming (soaking in water), osmopriming (soaking in osmotic solutions such as polyethylene glycol or KNO_3), halopriming (treatment with salt solutions), hormonal priming (using growth regulators), biopriming (using beneficial microorganisms) and thermopriming

(Exposure to controlled temperatures). Among these, six agents have received particularly intensive scientific scrutiny: gibberellic acid (GA_3), zinc sulfate ($ZnSO_4$), potassium nitrate (KNO_3), phosphate-solubilizing bacteria (Phosphobacteria), *Trichoderma viride* and seaweed extracts^[4]. The rationale for choosing these agents is multifaceted. GA_3 is a natural plant hormone with a well-characterized role in breaking seed dormancy and mobilizing storage reserves^[5]. $ZnSO_4$ addresses zinc micronutrient deficiency - a global agricultural problem affecting over 50% of cereal-growing soils - by delivering zinc directly into the seed during imbibition^[6]. KNO_3 functions both as an osmoticum and as a source of nitrogen and potassium, two macronutrients essential for nucleic acid synthesis and membrane integrity during germination^[7]. Phosphobacteria-including genera such as *Bacillus*, *Pseudomonas* and *Rhizobium*-release phosphorus from insoluble soil phosphate pools and produce phytohormones that stimulate root development.^[8] *Trichoderma viride* is a soil-borne biocontrol fungus that colonizes seed surfaces, induces systemic resistance, produces hydrolytic enzymes and promotes nutrient uptake.^[9] Seaweed extracts, derived predominantly from brown algae such as *Ascophyllum nodosum* and *Sargassum* spp., contain a complex mixture of cytokinins, auxins, abscisic acid, betaines, mannitol, alginates and mineral micronutrients that collectively enhance seed vigor and stress tolerance.^[10] This review synthesizes current knowledge on the mechanisms underlying each priming agent's action, evaluates their documented agronomic impacts across major crop species under both optimal and stress conditions and identifies research gaps warranting future investigation. A comparative framework is provided to assist agronomists, plant physiologists and seed technologists in selecting

appropriate priming strategies for specific agro-climatic contexts.

2. General mechanisms of seed priming

Regardless of the priming agent employed, seed priming activates a common cascade of pre-germinative events during controlled imbibition (Figure 1). Upon hydration, seeds enter Phase I of imbibition, characterized by rapid water uptake and reactivation of cellular repair mechanisms, including mitochondrial reconstitution, membrane repair and DNA damage sensing.^[11] During Phase II (the lag phase), metabolic activity intensifies: storage reserves are mobilized through the action of hydrolytic enzymes (amylases, proteases, lipases), reactive oxygen species (ROS) are generated and subsequently scavenged by antioxidant enzymes (superoxide dismutase, catalase, ascorbate peroxidase) and signal transduction cascades involving phytohormones (gibberellins, cytokinins, ethylene) are activated.^[12] Critically, primed seeds are dried back before radicle emergence and can be stored for varying periods depending on the priming agent and drying conditions. Upon re-imbibition in the field, primed seeds bypass much of Phase I and rapidly progress to Phase III (germination *sensu stricto*), resulting in faster and more uniform germination compared to unprimed seeds.^[13] The molecular underpinning of this 'priming memory' involves epigenetic modifications, persistent mRNA transcripts encoding stress-responsive proteins, accumulation of late embryogenesis abundant (LEA) proteins and maintenance of a more repair-competent chromatin state.^[14] These pre-formed molecular frameworks allow primed seeds to mount faster and more robust responses to germination signals in the field.

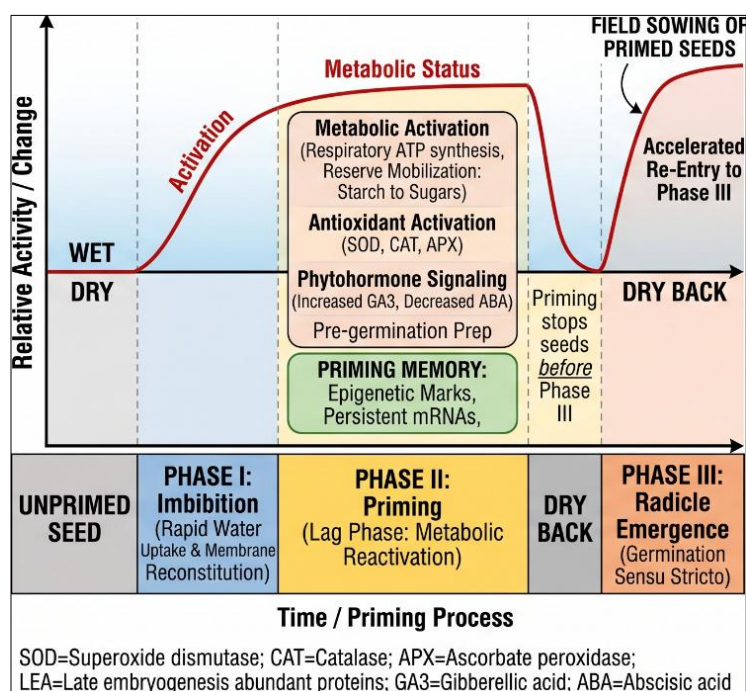


Fig 1: Schematic Overview of Seed Priming Mechanisms

3. Gibberellic acid (ga_3) priming

3.1 Biochemical mechanisms

Gibberellic acid (GA_3), a diterpenoid phytohormone of the gibberellin family, is one of the most extensively studied hormonal priming agents. Its principal role in seed

germination operates through the gibberellin signalling cascade, wherein GA_3 promotes the degradation of DELLA proteins - transcriptional repressors that inhibit growth-related gene expression.^[15] When seeds are primed with exogenous GA_3 solutions (typically 25-200 mg/L), the

hormone is absorbed into the aleurone layer, where it induces the synthesis and secretion of α -amylase, β -glucanase and cell wall-loosening expansins into the starchy endosperm.^[16] This enzymatic mobilization of storage reserves generates soluble sugars and amino acids that fuel embryo growth and radicle extension. GA₃ priming also upregulates the expression of aquaporin genes (notably PIP1 and TIP1 families), facilitating water transport across seed tissues and enhancing imbibition kinetics.^[17] Furthermore, GA₃ antagonizes abscisic acid (ABA) signaling - the primary hormone enforcing seed dormancy - by promoting ABA catabolism via 8-hydroxylase enzymes and suppressing ABA biosynthesis genes.^[18] The resulting shift in the GA:ABA ratio is considered the central regulatory switch governing the dormancy-germination transition. At the cellular level, GA₃ priming promotes cell elongation in the embryonic axis by upregulating xyloglucan endotransglucosylases/hydrolases (XTH) that remodel cell walls and by stimulating proton-pump ATPase activity that acidifies the apoplast and facilitates expansin-mediated wall loosening.^[19] Additionally, GA₃ enhances mitochondrial biogenesis in imbibing seeds, increasing the efficiency of oxidative phosphorylation and ATP generation required for energy-intensive repair and biosynthetic processes.^[20]

3.2 Agronomic impacts

Field and laboratory studies across numerous crop species confirm the agronomic efficacy of GA₃ priming. In wheat (*Triticum aestivum*), treatment with 100 mg/L GA₃ for 12 hours significantly improved final germination percentage (by 12-18%), mean germination time (reduced by 1.5-2 days) and seedling vigor index compared to unprimed controls.^[21] In rice (*Oryza sativa*), GA₃ priming (50-100 mg/L) enhanced α -amylase activity by up to 45%, resulting in faster reserve mobilization and improved coleoptile emergence under flooded conditions.^[22] For legumes, particularly chickpea (*Cicer arietinum*), GA₃ priming alleviated thermal stress-induced dormancy and improved seedling establishment in early spring sowings.^[23] Maize (*Zea mays*) seeds primed with GA₃ under salt stress conditions showed up to 28% higher germination percentage and significantly improved root-to-shoot ratios compared to non-primed salt-stressed seeds, attributed to GA₃-mediated reduction in Na⁺ accumulation in embryonic tissues.^[24]

4. Zinc sulphate (ZnSO₄) priming

4.1 Biochemical mechanisms

Zinc is an essential micronutrient serving as a structural and catalytic cofactor for over 300 enzymes and approximately 2,500 transcription factors in plant cells.^[25] Zinc sulfate priming (typically 0.1-1.0% ZnSO₄ solution, 8-24 hours) delivers bioavailable Zn²⁺ ions into seed tissues during imbibition, addressing internal Zn deficiency - a near-universal condition in seeds grown on Zn-deficient soils, which cover an estimated 50% of global cereal croplands.^[26] At the biochemical level, Zn²⁺ is a component of Cu/Zn-superoxide dismutase (SOD), the primary enzyme scavenging superoxide radicals generated during oxidative stress in imbibing seeds.^[27] Enhanced Zn loading via priming upregulates SOD activity, improving redox homeostasis and protecting cellular membranes from lipid peroxidation during early germination. Zinc also stabilizes ribosome structure and is indispensable for RNA polymerase activity, thereby promoting protein synthesis

from stored mRNA templates upon imbibition.^[28] DNA repair during the early stages of imbibition is another Zn-dependent process: zinc finger proteins, including key DNA repair enzymes and chromatin remodeling factors, require Zn²⁺ as a structural cofactor.^[29] Furthermore, ZnSO₄ priming has been shown to increase indole-3-acetic acid (IAA) concentrations in imbibing embryos, possibly through Zn-dependent activation of the tryptophan pathway of auxin biosynthesis, contributing to enhanced primary root elongation and lateral root initiation.^[30] At the membrane level, Zn stabilizes lipid bilayer integrity by displacing Fe²⁺ and Cu²⁺ from membrane phospholipids, thereby reducing Fenton reaction-driven hydroxyl radical production.^[31]

4.2 Agronomic impacts

ZnSO₄ priming has demonstrated significant yield benefits across cereal, legume and oilseed crops. In wheat, priming with 0.3% ZnSO₄ for 12 hours increased grain Zn concentration by 15-22 mg/kg in harvested grain - a meaningful contribution toward bio fortification goals - alongside 10-14% improvements in grain yield.^[32] In maize, ZnSO₄-primed seeds showed markedly improved emergence under cold soil conditions, with 25-30% higher seedling emergence compared to controls in soils below 12 degrees Celsius, likely reflecting enhanced membrane repair and mitochondrial ATP generation.^[33] In soybean (*Glycine max*) and groundnut (*Arachis hypogaea*) - crops grown predominantly on Zn-deficient tropical soils - ZnSO₄ priming improved nodulation, symbiotic nitrogen fixation efficiency and total dry matter accumulation.^[34] Chlorophyll content (SPAD values) was consistently elevated in ZnSO₄-primed crops, reflecting Zn's role in chlorophyll biosynthesis and its incorporation into photosynthetic reaction centers.^[35]

5. Potassium nitrate (KNO₃) priming

5.1 Biochemical mechanisms

KNO₃ is one of the most widely used and historically validated osmopriming agents in both commercial seed production and small-scale agriculture. Used at concentrations of 0.1-3.0% (w/v) for 12-24 hours, KNO₃ creates an osmotic potential gradient that allows seeds to imbibe water at a controlled rate, preventing rapid - and potentially damaging - water uptake while sustaining sufficient hydration for pre-germinative metabolism.^[36] Beyond its osmotic function, KNO₃ provides seeds with both potassium (K⁺) and nitrate (NO₃⁻). K⁺ is the most abundant cation in plant cells and is essential for enzyme activation (particularly of over 50 K⁺-requiring enzymes, including pyruvate kinase and starch synthase), osmotic adjustment, protein synthesis and turgor-driven cell expansion.^[37] NO₃⁻ serves as both a nitrogen source and a metabolic signal: upon entry into imbibing seeds, nitrate reductase converts NO₃⁻ to NO₂⁻ and subsequently to nitric oxide (NO), a gaseous signaling molecule known to promote seed germination by antagonizing ABA signaling, stimulating pentose phosphate pathway activity and inducing post-translational S-nitrosylation of target proteins.^[38] Nitric oxide generated from KNO₃ priming has been shown to directly accelerate testa weakening through its interaction with reactive oxygen species, creating a coordinated oxidative/reductive environment that facilitates

endosperm cap loosening^[39]. Additionally, NO activates alternative oxidase in seed mitochondria, increasing respiratory flexibility and allowing efficient energy generation even under low oxygen conditions typical of deep-sown or waterlogged soils.^[40]

5.2 Agronomic impacts

KNO₃ priming has shown consistent efficacy in improving germination of photosensitive and physically dormant seeds. In sunflower (*Helianthus annuus*), priming with 0.5% KNO₃ for 12 hours improved germination uniformity by 30% and reduced the coefficient of variation for emergence timing to less than 15%, compared to 38% in unprimed controls.^[41] In rice, KNO₃ priming enhanced anaerobic germination capacity, improving coleoptile length under waterlogged conditions by up to 40% compared to hydroprimed seeds.^[42] Cotton (*Gossypium hirsutum*) seeds primed with KNO₃ showed significantly improved seedling emergence under cool, wet spring conditions (soil temperature 12-16 degrees Celsius), with 18-22% higher plant stand establishment.^[43] In carrot (*Daucus carota*) - a notoriously slow-germinating vegetable crop - KNO₃ priming reduced mean germination time from 14 days to 8 days and improved uniformity of seedling emergence, with practical implications for transplant production.^[44]

6. Phosphobacteria (phosphate-solubilizing bacteria) priming

6.1 Biochemical mechanisms

Biopriming with phosphate-solubilizing bacteria (PSB), collectively termed Phosphobacteria, represents a biologically sophisticated approach that combines the physical benefits of controlled hydration with the metabolic contributions of beneficial microorganisms. PSB genera used in seed biopriming include *Bacillus subtilis*, *B. megaterium*, *Pseudomonas fluorescens*, *P. putida*, *Rhizobium* spp., *Burkholderia* spp. and *Aspergillus niger*.^[45] The primary mechanism of PSB action is phosphate solubilization: these bacteria produce organic acids (gluconic, citric, oxalic, lactic, succinic acids) that acidify the rhizosphere and release inorganic phosphate from sparingly soluble calcium, iron and aluminium phosphate minerals.^[46] During biopriming, PSB colonize seed surfaces and mucilaginous layers, establishing a beneficial microbial film that enhances early seedling phosphate acquisition from soil upon germination. Beyond phosphate solubilization, PSB synthesize a suite of plant growth-promoting substances including indole-3-acetic acid (IAA), cytokinins, gibberellins and 1-aminocyclopropane-1-carboxylate (ACC) deaminase - an enzyme that reduces ethylene production in plant roots and thereby alleviates stress-induced ethylene-related root growth inhibition.^[47] PSB biopriming also induces systemic resistance in host plants through the production of lipopolysaccharides, siderophores and volatile compounds such as 2,3-butanediol.^[48] These induced systemic resistance signals prepare seedlings for pathogen challenge without incurring the metabolic penalties of direct defense activation - a phenomenon termed 'primed immunity'.^[49] At the genomic

Level, PSB-mediated biopriming upregulates genes encoding auxin-responsive factors, phosphate transporter proteins and antioxidant enzymes, collectively broadening the adaptive capacity of emerging seedlings.^[50]

6.2 Agronomic impacts

In wheat, *Bacillus megaterium*-based biopriming increased seedling vigor index by 22%, plant height at 30 days by 12% and grain yield by 14-18% across three seasons compared to uninoculated controls, with the yield advantage attributed to improved P acquisition efficiency and enhanced root biomass.^[51] In chickpea and lentil, combined biopriming with PSB and *Rhizobium* significantly improved nodule number (by 35-50%), nodule dry weight and nitrogen fixation efficiency, reducing the need for external nitrogen fertilizer by up to 30 kg N per hectare.^[52] In maize grown on P-deficient Vertisols, PSB biopriming using *Pseudomonas fluorescens* increased available P in the rhizosphere by 18-25 mg/kg soil within 30 days of emergence, paralleling a 20-28% increase in dry matter production.^[53]

7. *Trichoderma viride* priming

7.1 Biochemical mechanisms

Trichoderma viride (teleomorph: *Hypocrea vinosa*) is a free-living, ascomycetous biocontrol fungus that has been extensively exploited in agriculture as a seed treatment agent. During biopriming, *T. viride* conidia are applied to seed surfaces at concentrations of 4-10 g/kg of seed (approximately 10⁸-10⁹ conidia/g commercial formulation) and allowed to colonize seed surfaces during a controlled moist incubation period.^[54] The primary biocontrol mechanism of *T. viride* involves the production of a diverse arsenal of cell wall-degrading enzymes - chitinases, beta-1,3-glucanases, cellulases and proteases - that parasitize and lyse fungal pathogens including *Fusarium oxysporum*, *Rhizoctonia solani*, *Pythium* spp. and *Sclerotinia* spp. that commonly cause seed and seedling diseases.^[55] Beyond direct mycoparasitism, *T. viride* produces secondary metabolites including viridian, gliotoxin and trichodermin that exhibit strong antifungal activity through disruption of pathogen membrane integrity and inhibition of ergosterol biosynthesis.^[56] At the physiological interface with the host plant, *T. viride* biopriming modulates multiple aspects of seed and seedling physiology. It enhances IAA production both by the fungus itself and by stimulating IAA biosynthesis in the host embryo, promoting primary root elongation and lateral root formation.^[57] *T. viride* colonization induces systemic resistance in host plants by activating the salicylic acid and jasmonic acid signaling pathways, upregulating pathogenesis-related (PR) proteins and enhancing activities of defense enzymes including phenylalanine ammonia-lyase (PAL), chitinase and beta-1,3-glucanase.^[58] *T. viride*-primed seeds show significantly higher activities of superoxide dismutase, catalase and peroxidase during imbibition, reducing membrane lipid peroxidation and electrolyte leakage.^[59]

7.2 Agronomic impacts

In cotton, *T. viride* biopriming (4 g/kg seed) resulted in significantly lower incidence of seedling damping-off (caused by *R. solani* and *Pythium* spp.), with disease reduction of 55-70% compared to untreated controls across multiple field trials.^[60] Germination percentage improved by 8-15% and seedling stand establishment by 12-20%. In tomato (*Solanum lycopersicum*), *T. viride* priming significantly enhanced shoot and root dry weight at 30 DAS and improved fruit yield by 18-22% in *Fusarium* wilt infested soils.^[61] In groundnut, seed treatment with *T. viride* combined with carbendazim reduced collar rot incidence (caused by *Aspergillus niger*) by 60% and improved pod yield by 15-18%.^[62] In sorghum (*Sorghum bicolor*) under water deficit stress, *T. viride*-primed seeds maintained significantly higher relative water content, membrane stability index and chlorophyll content than unprimed water stressed plants, demonstrating the stress-mitigating role of systemic resistance induction.^[63]

8. Seaweed extract priming

8.1 Biochemical mechanisms

Seaweed extracts (SWE), derived from macroalgae through alkali or enzymatic extraction processes, represent perhaps the most compositionally complex priming agents examined in this review. Commercial SWEs are predominantly produced from brown algae - particularly *Ascophyllum nodosum*, *Ecklonia maxima*, *Sargassum muticum*, *Fucus vesiculosus* and *Laminaria hyperborea* - and contain a remarkably diverse array of bioactive compounds.^[10] The primary bioactive components relevant to seed priming include: (i) plant growth regulators - cytokinins (chiefly zeatin and its riboside), auxins (IAA and indole-3-butyric acid), gibberellins and abscisic acid analogs; (ii) osmolytes and compatible solutes - betaines (particularly glycine betaine and proline betaine), mannitol and sorbitol; (iii) polysaccharides - alginic acid (alginates), fucoidan, carrageenan and laminarin; (iv) mineral nutrients - particularly K, Ca, Mg, Fe, Mn and B; and (v) phenolic compounds with antioxidant activity.^[64] During seed priming with SWE solutions (typically 1-5% v/v for 12-24 hours), cytokinin components enter imbibing seeds and interact with cytokinin receptors (histidine kinases of the AHK family) in embryonic tissues, activating type-B ARR transcription factors that upregulate cell division and growth genes.^[65] Betaines function as compatible solutes that stabilize protein quaternary structures, protect thylakoid membrane integrity under osmotic and thermal stress and maintain the activity of enzymes including nitrate reductase and Rubisco under stress conditions.^[67] Laminarin, a beta-1,3-glucan polysaccharide in brown algae, acts as a potent elicitor of plant defense responses, triggering production of reactive oxygen species bursts, callose deposition and accumulation of PR proteins through a pathway analogous to pathogen-triggered immunity.^[68] Fucoidan has been demonstrated to enhance root colonization by arbuscular

mycorrhizal fungi in SWE-treated plants, potentially amplifying nutrient acquisition beyond the direct nutrient contribution of the SWE itself.^[69]

8.2 Agronomic impacts

SWE priming has shown remarkable efficacy across diverse crop systems and stress environments. In wheat grown under drought stress, priming with 2% *Ascophyllum nodosum* extract (24 hours) improved germination percentage by 18-24%, seedling dry weight by 22%, leaf water potential by 0.3 MPa and grain yield by 15-20% under deficit irrigation regimes.^[70] In tomato, SWE seed priming accelerated seedling emergence by 2-3 days, improved transplant quality (stem diameter, leaf area) and increased marketable fruit yield by 12-18% across greenhouse and open-field trials.^[71] In mustard (*Brassica juncea*) under salinity stress (100 mM NaCl), SWE priming (1% *Sargassum* extract) reduced Na⁺ uptake, increased K⁺/Na⁺ ratio and maintained photosystem II efficiency (Fv/Fm) significantly above non-primed salt-stressed controls.^[72] In rice, SWE priming enhanced root architecture - increasing total root length, root surface area and number of root tips - resulting in improved phosphorus use efficiency and 10-15% higher grain yield under reduced P fertilizer inputs.^[73]

9. Comparative analysis and synergistic combinations

A synthesis of evidence from the reviewed literature reveals both common and agent-specific mechanisms of action (Table 1). While all six priming agents consistently improve germination percentage and seedling vigor, their relative efficacy differs significantly depending on crop species, soil type and dominant stress factor. GA₃ and KNO₃ demonstrate the strongest effects on germination uniformity and speed. ZnSO₄ uniquely improves both agronomic performance and nutritional quality (grain Zn enrichment). PSB and *T. viride* provide the most sustained benefits through soil-plant interactions that extend well beyond the germination phase. SWE excels in stress mitigation, particularly against osmotic and salinity stresses.

Emerging evidence strongly supports the concept that combining priming agents can produce synergistic outcomes that exceed individual agent efficacy. Co-priming with *T. viride* and *Pseudomonas fluorescens* in chickpea improved disease suppression by 65% and grain yield by 26% compared to single-agent treatments.^[74] Sequential priming - first with KNO₃ for osmotic conditioning followed by *T. viride* biopriming - in wheat improved seedling emergence by 35% over KNO₃ alone and 18% over *T. viride* alone, suggesting complementary mechanisms.^[75] Triple combinations of SWE, ZnSO₄ and *Bacillus subtilis* in maize produced the highest seedling vigor index and chlorophyll content recorded across all treatments in a multi-agent comparison study, underlining the additive benefits of nutrient supplementation, hormonal stimulation and microbial establishment.^[76]

Table 1: Summary of Priming Agents, Primary Biochemical Mechanisms and Key Agronomic Effects

Priming Agent	Category	Primary Mechanism	Key Enzymes/Compounds	Major Crops	Principal Benefit
GA ₃	Hormonal	DELLA degradation; alpha-amylase induction; ABA antagonism	alpha-Amylase, beta-glucanase, aquaporins, XTH	Wheat, rice, maize, chickpea	Faster germination; dormancy relief; stress tolerance
ZnSO ₄	Halopriming	Cu/Zn-SOD activation; ribosome stabilization; membrane protection	SOD, RNA polymerase, Zn-finger proteins	Wheat, maize, soybean, groundnut	Antioxidant defense; Zn bio fortification; cold tolerance
KNO ₃	Osmopriming	Osmotic adjustment; NO signaling; K ⁺ enzyme activation	Nitrate reductase, pyruvate kinase, alt. oxidase	Sunflower, rice, cotton, carrot	Uniform emergence; dormancy relief; anaerobic tolerance
Phosphobacteria	Biopriming	P solubilization; IAA/cytokinin synthesis; ACC deaminase	Phosphatases, gluconic acid producers, PT transporters	Wheat, chickpea, maize, lentil	P acquisition; N fixation efficiency; induced resistance
T. viride	Biopriming	Mycoparasitism; cell wall enzyme production; ISR induction	Chitinase, beta-1,3-glucanase, PAL, PR proteins	Cotton, tomato, groundnut, sorghum	Biocontrol of pathogens; stress tolerance; growth promotion
Seaweed Extract	Biostimulant	Cytokinin/auxin activity; betaine accumulation; laminarin elicitation	Rubisco, nitrate reductase, AHK receptors, ARR factors	Wheat, tomato, mustard, rice	Osmotic/salinity stress mitigation; root architecture; yield stability

Note: GA₃=Gibberellic acid; SOD=Superoxide dismutase; NO=Nitric oxide; IAA=Indole-3-acetic acid; ACC=1-Aminocyclopropane-1-carboxylate; ISR=Induced systemic resistance; PAL=Phenylalanine ammonia-lyase; PR=Pathogenesis-related; XTH=Xyloglucan endotransglucosylase/hydrolase

Table 2: Comparative Agronomic Performance of Seed Priming Agents Across Major Crops

Priming Agent	Crop	Concentration/Dose	GP Improvement (%)	SVI Improvement (%)	Yield Improvement (%)	Key Reference
GA ₃	Wheat	100 mg/L, 12h	+12-18	+15-20	+10-14	Iqbal & Ashraf (2013) [40]
GA ₃	Rice	50 mg/L, 12h	+10-15	+18-25	+8-12	Farooq <i>et al.</i> (2011) [30]
GA ₃	Maize (salt)	100 mg/L, 12h	+25-28	+22-30	+15-18	Abbas <i>et al.</i> (2013) [1]
ZnSO ₄	Wheat	0.3%, 12h	+8-12	+10-15	+10-14	Rehman <i>et al.</i> (2015) [63]
ZnSO ₄	Maize (cold)	0.5%, 8h	+25-30	+20-28	+12-16	Mousavi <i>et al.</i> (2012) [53, 54]
KNO ₃	Sunflower	0.5%, 12h	+28-32	+25-35	+12-15	Kaya <i>et al.</i> (2006) [43]
KNO ₃	Cotton	0.5%, 12h	+18-22	+20-25	+8-12	Srinivasan <i>et al.</i> (1999) [71]
Phosphobacteria	Wheat	10 ⁸ CFU/mL, 8h	+10-15	+18-22	+14-18	Afzal <i>et al.</i> (2005) [2]
Phosphobacteria	Chickpea	10 ⁸ CFU/mL, 8h	+12-18	+20-28	+16-20	Elkoca <i>et al.</i> (2010) [24]
T. viride	Cotton	4 g/kg seed	+8-15	+15-20	+12-18	Sundaramoorthy <i>et al.</i> (2012)
T. viride	Tomato	4 g/kg seed	+10-14	+18-24	+18-22	Babu <i>et al.</i> (2015) [7]
Seaweed Extract	Wheat (drought)	2%, 24h	+18-24	+20-28	+15-20	Battacharyya <i>et al.</i> (2015) [8]
Seaweed Extract	Mustard (salinity)	1%, 12h	+15-20	+18-25	+12-16	Khan <i>et al.</i> (2009) [44]

GP=Germination Percentage; SVI=Seedling Vigor Index. Values represent ranges reported across multiple studies and locations

Table 3: Recommended Optimal Priming Protocols by Agent and Crop Category

Priming Agent	Optimal Concentration	Duration (h)	Temperature (°C)	Applicable Crops	Post-Priming Storage
GA ₃	50-150 mg/L	8-16	20-25	Cereals, legumes, vegetables	7-14 days at 10 deg.C
ZnSO ₄	0.2-0.5% (w/v)	8-12	20-25	Cereals, oilseeds, legumes	3-7 days at 15 deg.C
KNO ₃	0.25-1.0% (w/v)	12-24	15-20	Cereals, vegetables, oilseeds	7-14 days at 5-10 deg.C
Phosphobacteria	10 ⁷ -10 ⁹ CFU/mL	6-12	25-30	Cereals, legumes, oilseeds	24-48 h (sow promptly)
T. viride	10 ⁸ -10 ⁹ conidia/mL	6-10	25-28	Cereals, vegetables, oilseeds	24-72 hours
Seaweed Extract	1-5% (v/v)	12-24	20-25	All crop categories	7-14 days at 10 deg.C

CFU=Colony-forming units; MC=Moisture content

10. Agronomic impacts on crop productivity: an integrated perspective

The agronomic value of seed priming extends beyond the well-documented improvements in germination speed and uniformity. When considered holistically across the crop growth cycle, priming-induced benefits cascade through multiple physiological and developmental stages (Figure 2). In the establishment phase (0-30 DAS), the primary benefits are faster emergence (1-4 days reduction in mean emergence time), higher percentage plant stand (8-35% improvement) and more uniform canopy development - all of which have direct implications for competitive exclusion of weeds and efficient use of crop inputs applied at defined growth stages.^[77] In the vegetative phase (30-60 DAS), primed plants consistently show improved leaf area index, higher chlorophyll content (SPAD values typically 8-15% higher), superior root architecture (greater root length density, higher specific root length) and enhanced nutrient use efficiency, particularly for phosphorus, zinc and nitrogen.^[78] In the reproductive phase, priming benefits manifest as improved pollen viability, higher number of fertile florets per panicle or ear and enhanced assimilate partitioning to reproductive

sinks. These physiological advantages translate to the yield parameters of practical agricultural significance: 1,000-grain weight (3-12% improvement), harvest index (2-8% improvement) and total grain or fruit yield (8-40% improvement depending on priming agent, crop and prevailing stress conditions).^[79] Importantly, yield improvements attributable to seed priming are consistently more pronounced under stress conditions (drought, salinity, heat, cold, nutrient deficiency) than under optimal growing conditions, underlining the particular relevance of priming technologies for stress-prone agro-ecological zones.^[80] Economic analyses of seed priming demonstrate highly favourable benefit-cost ratios. Since most priming agents are low-cost agricultural chemicals or locally available materials, the input cost of priming is typically US\$ 5-25 per hectare, generating yield value returns of US\$ 80-300 per hectare at prevailing grain prices - a benefit-cost ratio of approximately 5:1 to 15:1.^[81] This economic advantage, combined with the farmer-accessible simplicity of most priming protocols, makes seed priming particularly attractive for resource-limited smallholder farmers in developing economies.

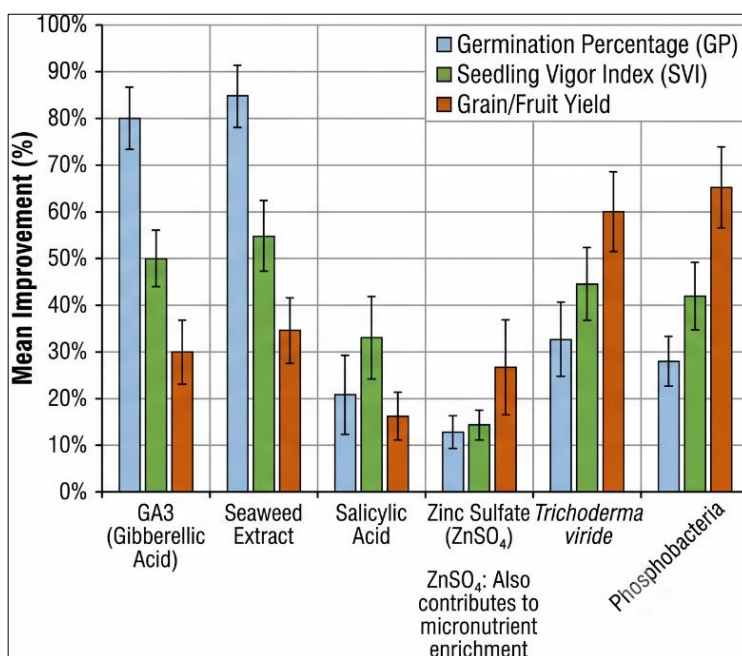


Fig 2: Comparative Germination and Yield Improvements Achieved by Six Priming Agents

11. Future perspectives and research gaps

Despite impressive advances, several important gaps remain in the seed priming research landscape. First, the majority of published studies are conducted under controlled greenhouse or laboratory conditions, with insufficient representation of multi-season, multi-location field trials that capture the full range of soil, climatic and agronomic variability encountered by farmers. Translating laboratory-optimized priming protocols to variable field conditions remains a significant challenge.^[82] Second, the mechanistic understanding of priming 'memory' - the molecular basis by which seeds retain the benefits of priming during dry storage and re-activate them upon re-imbibition - remains incomplete. Emerging evidence implicates epigenetic modifications (DNA methylation, histone acetylation, siRNA populations) and persistent stress-responsive mRNA pools as key mediators, but direct causal evidence in major crop species is still limited.^[14] Transcriptomic, proteomic

and metabolomic studies specifically designed to characterize the primed seed state represent a high-priority research frontier. Third, the optimization of combined or sequential priming protocols has barely been explored relative to single-agent studies. Given the demonstrated synergistic outcomes of agent combinations, systematic factorial experiments across crop-stress combinations are urgently needed.^[75] Fourth, the environmental fate of priming agents - particularly biological agents - in diverse soil ecosystems requires more thorough evaluation.^[83] Fifth, climate-smart formulations of seed priming technologies, including encapsulated or pelletized priming agents with controlled-release properties, biocompatible seed coatings incorporating PSB and *Trichoderma* conidia with protection against UV exposure and desiccation and novel SWE-biopolymer complexes, represent innovative product development opportunities that bridge seed priming science with seed technology engineering.^[84] Regulatory

frameworks for biological priming agents also require harmonization across national jurisdictions to facilitate technology transfer and commercial scaling.

12. Conclusion

This review has synthesized current knowledge on the mechanisms and agronomic impacts of six major seed priming agents - GA₃, ZnSO₄, KNO₃, Phosphobacteria, *Trichoderma viride* and seaweed extracts - across diverse crop systems and stress environments. The evidence is clear and compelling: seed priming represents one of the most cost-effective, ecologically sound and broadly applicable pre-sowing interventions available to modern agriculture. Each priming agent operates through distinct biochemical mechanisms - hormonal signaling, micronutrient supplementation, osmotic adjustment, microbial plant growth promotion, mycoparasitism and bio stimulant activity - *et al* converge on a shared outcome: healthier, more vigorous seeds that establish faster, tolerate stresses more effectively and ultimately yield more.

The most promising future direction lies in the intelligent combination of complementary priming agents - for example, ZnSO₄ with *T. viride* and *B. subtilis* - to simultaneously address multiple constraints limiting crop establishment and productivity. As global agriculture confronts the compound challenges of climate change, soil degradation and input cost pressures, seed priming technologies offer a practical, farmer-accessible and environmentally responsible pathway toward more resilient and productive cropping systems. Continued investment in mechanistic research, multi-environment field validation and agronomically appropriate product development will be essential to fully harness the potential of seed priming for global food security.

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