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## Postprint Review: Effects of Seed Priming on Salt and Drought Tolerance Traits in Wheat

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### Abstract

Wheat is a crucial grain crop in northern China that is frequently subjected to drought and salt stress in agricultural production, resulting in yield losses. Seed priming is a simple yet effective method that involves treating seeds with natural or synthetic reagents prior to germination to enhance plant stress resistance. Under drought or high-salinity conditions, priming wheat seeds with priming agents advances germination, enhances seedling growth and metabolic activity, improves stress-related physiological indicators, strengthens crop drought and salt tolerance, and ultimately increases yield and quality. This article elaborates on the mechanisms and effects of various priming agents—including water, organic compounds, plant hormones, bioactive substances, biological agents, oxides, and inorganic signaling molecules—on wheat seed priming. It also summarizes the primary mechanisms of seed priming, such as: reducing  $\text{Na}^+$  uptake while increasing  $\text{K}^+$  and  $\text{Ca}^{2+}$  uptake to alleviate salt-induced growth inhibition; promoting the synthesis and accumulation of osmotic adjustment substances such as soluble proteins and soluble sugars to maintain high intracellular osmotic pressure and facilitate root water uptake; inducing increased synthesis and enhanced activity of antioxidant enzymes—including superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase—under stress conditions to effectively scavenge reactive oxygen species and maintain intracellular redox balance; and regulating plant endogenous hormone synthesis and transport to maintain hormone levels in a more stress-adapted equilibrium. Furthermore, it discusses the mutually complementary and promotive relationship between priming agents and plant stress physiology research, and prospects the development and application potential of seed priming in agriculture.

## Full Text

### Preamble

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## Effect of Seed Priming on Drought and Salinity Tolerance of Wheat: An Overview\*

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### Abstract

Wheat is one of the most important crops in northern China, frequently affected by drought and salinity stress that cause yield losses. Seed priming is a simple and effective method to improve plant stress resistance by treating seeds with natural or synthetic compounds before germination. Under drought or high salinity conditions, primed wheat seeds exhibit earlier germination, enhanced seedling growth and metabolism, improved stress-related physiological indices, and ultimately increased yield and quality. This review illustrates the mechanisms and effects of various priming agents, including water, organic compounds, plant hormones, bioactive substances, biological agents, oxides, and inorganic signaling molecules. The main mechanisms of seed priming are summarized as follows: reducing Na<sup>+</sup> uptake while increasing K<sup>+</sup> and Ca<sup>2+</sup> absorption to minimize salt-induced growth inhibition; promoting synthesis and accumulation of osmolytes such as soluble proteins and sugars to maintain high intracellular osmotic pressure for root water uptake; inducing increased synthesis and activity of antioxidant enzymes (superoxide dismutase, peroxidase, catalase, ascorbate peroxidase) to effectively scavenge reactive oxygen species and maintain cellular redox balance; and regulating endogenous hormone synthesis and transport to achieve a more stress-adapted hormonal balance. The complementary and mutually reinforcing relationship between priming agents and plant stress physiology research is discussed, and prospects for agricultural application and development of seed priming are presented.

**Keywords:** Wheat; Seed priming; Priming agents; Drought; Salinity; Tolerance

## Introduction

Wheat (*Triticum aestivum* L.) is a crucial cereal grain that has served as a vital food source for millennia. With continuous population growth and decreasing water resources, ensuring adequate food supply represents one of humanity's greatest challenges. Drought is a primary cause of agricultural yield loss in many global regions, and climate change is exacerbating this problem with increasingly frequent drought events. Simultaneously, soil salinization and secondary salinization are widespread issues worldwide, particularly severe in arid and semi-arid regions. According to incomplete statistics from UNESCO and FAO, global saline-alkali land area reaches approximately 954 million hectares. Both drought and soil salinization have become constraining factors for sustainable agricultural development worldwide.

In China's agricultural production, wheat cultivation is frequently subjected to various biotic and abiotic environmental stresses, with drought and salt stress being the most significant. These stresses substantially affect seed germination and seedling growth. Drought stress impairs water absorption during germination, causing unstable germination, low emergence rates, and in severe cases, complete inhibition of seed germination. It also reduces cell turgor pressure, thereby hindering plant growth. Similarly, soil salinity is a critical factor affecting crop emergence rates. Salt stress induces water deficit and osmotic stress, obstructing water uptake by seeds and affecting germination. The toxic effects of Na<sup>+</sup> and Cl<sup>-</sup> as single ions cause low germination and emergence rates, representing a primary reason for low yields in saline soils. Therefore, improving seed germination and emergence rates is essential for increasing crop production in saline lands.

Under drought and salt stress, crops produce harmful substances that affect growth and metabolism, ultimately leading to yield reduction. Various abiotic stresses cause elevated reactive oxygen species (ROS) levels in plants. Excessive ROS cause peroxidation of lipids, proteins, and nucleic acids, destabilizing membranes and disrupting normal physiological metabolism, even causing cell death. ROS accumulation depends on plant stress tolerance, stress timing, duration, and intensity. Malondialdehyde (MDA), a product of lipid peroxidation, serves as an important indicator of ROS-induced cellular damage.

Plant responses to salt and drought stress share highly similar physiological mechanisms, likely because both stresses result from cellular water loss. Plants respond through physiological, biochemical, and molecular changes that facilitate adaptation. These metabolic adjustments include regulating hormone balance (abscisic acid, salicylic acid, jasmonic acid, ethylene) and accumulating osmolytes such as proline, glycine, and betaine to enhance water uptake and maintain leaf turgor and stomatal opening for continued CO<sub>2</sub> assimilation. Potassium is a crucial mineral element associated with stress resistance; elevated intracellular K<sup>+</sup> concentration can reduce ROS production, while K<sup>+</sup> deficiency impairs CO<sub>2</sub> fixation and photosynthesis. Thus, increasing cellular K<sup>+</sup> content

enhances stress tolerance.

Modern agriculture employs various approaches to improve stress tolerance, including traditional hybridization, screening breeding, and emerging techniques like mutation breeding, polyploid breeding, and genetic engineering. Traditional methods require substantial labor, funding, and time, and due to multigenic complexity, selected varieties may not achieve desired results. While genetic engineering can theoretically introduce specific resistance genes for rapid and precise responses, this technology is expensive, operationally complex, faces biosafety concerns, and has limited agricultural application.

Seed priming, which involves treating seeds with natural or synthetic substances before germination to induce specific physiological responses, was first conceptualized by Heydecker in 1973. The technique involves controlled water absorption to halt seed imbibition at Stage II, allowing pre-germination metabolic activity and repair processes that promote membrane and organelle DNA repair and enzyme activation, preparing seeds for germination while preventing radicle protrusion. Priming enables faster and more robust cellular defense responses when stress occurs, offering a simple, cost-effective, and efficient technology with significant potential for improving crop drought and salt tolerance.

## Inorganic Salt Priming

Numerous studies demonstrate that various media can prime wheat seeds, including water, inorganic salts, and organic compounds, with different effects across wheat varieties.

Water priming is a simple, economical, and safe technique that improves germination and seedling establishment through osmotic adjustment. Seeds are soaked in sterile water at appropriate temperatures for a duration determined by water absorption rate, then air-dried to initial weight. Water-primed seeds exhibit higher water absorption capacity and enhanced seedling growth, even when germination is paused by low osmotic or matric potential in the growth medium. Water priming increases K<sup>+</sup> content in embryos under salt stress, improving salt tolerance. A 12-hour treatment optimally promotes germination, reduces emergence time, enhances growth and tillering, and improves irrigation water use efficiency, increasing wheat yield from 2.28 to 2.42 t · hm<sup>-2</sup> (6% increase).

Halopriming with 50 mmol · L<sup>-1</sup> NaCl for 12 hours enhances wheat salt tolerance. Studies show that priming-induced seedling activity and salt tolerance improvement relate to storage metabolism, increased K<sup>+</sup> and Ca<sup>2+</sup>, and reduced Na<sup>+</sup>. KCl priming significantly decreases Na<sup>+</sup> content in shoots, enhancing salt tolerance. KH<sub>2</sub>PO<sub>4</sub> priming promotes germination, emergence, and growth, with 0.5% K<sub>2</sub>HPO<sub>4</sub> and 0.5% KNO<sub>3</sub> solutions being more effective than higher concentrations. The antioxidant effects of priming are also variety-dependent; KCl and CaCl<sub>2</sub> priming increase activities of CAT, POD, and APX, elevate proline content, and reduce H<sub>2</sub>O<sub>2</sub> concentration, with more pronounced effects in resistant

varieties that also maintain lower leaf Na and higher K /Na ratios.

CaCl priming (50 mmol · L<sup>-1</sup> for 12 hours) shows better salt tolerance enhancement than equivalent NaCl. Compared to ascorbic acid, salicylic acid, and kinetin at the same concentration, CaCl most effectively promotes emergence and increases tillers, grains per spike, thousand-grain weight, total yield, and harvest index while elevating total phenols, soluble proteins, and  $\alpha$ -amylase and protease activities. CaCl priming also improves performance of poor-quality seeds, increasing emergence and final yield. CaSO priming (50 mmol · L<sup>-1</sup> for 12 hours) improves germination under salt stress, increases root length and seedling dry weight, and enhances K content more effectively than equivalent CaCl or NaCl.

Zn<sup>2+</sup> solution priming increases wheat yield. Treatment with 0.3% ZnSO<sub>4</sub> for 10 hours raises seed Zn content from 27 to 470 mg · kg<sup>-1</sup>, significantly increasing shoot dry weight after 15 days and grain yield more than water priming, with a 12% increase in grain Zn content. Water stress reduces grain Se, Fe, P, Zn, and Mg contents, while low Se concentrations positively affect growth and stress resistance. Selenium application accelerates biochemical processes and acts as an osmoprotectant under stress. Low-concentration sodium selenate treatment (25 °C for 1 hour) significantly improves root stress tolerance indices, total seedling biomass, total sugar and free amino acid contents, though soluble protein content decreases, with no effect on root/shoot ratio.

## Organic Priming

Numerous organic substances affect plant growth and development, including plant hormones (auxins, cytokinins, gibberellins, abscisic acid) and bioactive compounds such as ascorbic acid, polyamines, thiols, choline, chitosan, and salicylic acid.

## Plant Hormone Priming

Auxins are important plant hormones closely related to stress responses. Auxin priming promotes wheat seed germination, increases hypocotyl length, seedling dry and fresh weight, and hypocotyl dry weight. Studies by Iqbal and Ashraf show that indoleacetic acid (IAA), indolebutyric acid (IBA), and their precursor tryptophan (Trp) modulate salicylic acid and ion concentration disturbances caused by salt stress, promoting wheat growth. Except for IBA, these priming agents increase final germination rates. Trp-primed seedlings show higher biomass under salt stress, with field trials demonstrating Trp priming is particularly effective for improving yield under saline conditions by reducing Na absorption and transport in roots, increasing Ca<sup>2+</sup>, and regulating ion balance. Further research indicates that salt stress increases endogenous ABA in resistant varieties, while yield correlates positively with net CO<sub>2</sub> assimilation and IAA content but negatively with ABA and free polyamines. All priming treatments reduce salt effects on endogenous ABA, minimizing damage. Trp priming

( $4.89 \times 10^{-4} \text{ mol} \cdot \text{L}^{-1}$ ) most effectively alleviates reductions in net photosynthetic rate and yield loss under salt stress by regulating hormonal balance and enhancing spring wheat salt tolerance.

Synthetic auxins including 2,4-dichlorophenoxyacetic acid (2,4-D), -naphthaleneacetic acid (NAA), and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) have been tested on different wheat varieties. While not improving germination rates, these treatments variably affect  $\text{Na}^+$ ,  $\text{Ca}^{2+}$ , and hormone levels (IAA, IBA, ABA, Put, SA, Spd) in roots and shoots in a variety-specific manner. NAA ( $150 \text{ mg} \cdot \text{L}^{-1}$ ) shows the best priming effect, likely by modulating ion and hormone balance to promote growth and yield. Auxins also induce transient high expression of genes including auxin response factors (ARF), early auxin-responsive genes (Aux/IAA, GH3, SAUR, LBD), many of which are involved in stress responses.

Absciscic acid (ABA), a sesquiterpenoid plant hormone, inhibits seed germination, regulates growth, and promotes senescence. Increasing evidence shows ABA plays crucial roles in plant responses to drought, salinity, and low temperature, earning it the designation “stress hormone.” ABA priming affects endogenous hormone levels (trans-zeatin riboside, IAA, gibberellins) under drought stress, mitigating damage.

Cytokinins (CTK) promote cell division and expansion, induce bud differentiation, release apical dominance, break seed dormancy, and regulate nutrient transport and reproductive development. Under stress, CTK levels decrease, reducing supply from roots to shoots and triggering changes in gene expression and signaling of ABA, ethylene, salicylic acid, and jasmonic acid. CTK antagonizes ABA and interacts with auxins, and CTK priming adapts wheat to salt stress by regulating hormonal balance, significantly improving growth and yield under saline conditions while reducing  $\text{Na}^+$  and  $\text{Cl}^-$  accumulation in shoots.

Iqbal and Ashraf studied two cytokinins—kinetin (Kin) and benzylaminopurine (BAP)—on salt-tolerant and sensitive wheat varieties. Kin priming effectively reduces salt stress impacts on growth and yield by regulating  $\text{Na}^+$  and  $\text{Cl}^-$  content in shoots, primarily through improved water use efficiency and photosynthetic rate, with  $150 \text{ mg} \cdot \text{L}^{-1}$  being most effective. BAP priming, however, does not alleviate growth inhibition under high salinity. The superiority of primed seeds in germination and growth correlates positively with leaf IAA content and negatively with ABA content, suggesting that enhanced salt tolerance may relate to CTK-induced ABA reduction. Kin priming ( $100 \text{ mg} \cdot \text{L}^{-1}$  for non-resistant varieties) and BAP priming ( $150 \text{ mg} \cdot \text{L}^{-1}$  for resistant varieties) significantly increase leaf salicylic acid content under salt stress, with BAP also increasing leaf polyamine content. Kin shows more pronounced effects, though detailed mechanisms remain unclear.

Gibberellins (GAs) regulate various developmental processes including stem elongation, leaf expansion, seed germination, flowering, and fruit development. GA and ABA are antagonistic hormones, with GA promoting and ABA inhibit-

ing these processes. Recent research indicates GA negatively regulates abiotic stress responses, possibly by affecting ABA signaling pathways. Under salt stress, GA priming ( $30 \text{ mg} \cdot \text{L}^{-1}$ ) shortens germination time, increases germination rate, and accelerates seedling growth. At  $150 \text{ mg} \cdot \text{L}^{-1}$ , GA significantly improves salt tolerance in non-resistant varieties by reducing  $\text{Na}^+$  and increasing  $\text{Ca}^{2+}$  and  $\text{K}^+$  concentrations in roots and shoots, elevating salicylic acid, decreasing free putrescine and spermidine, and reducing leaf ABA content without affecting gas exchange or auxin levels. GA enhances salt tolerance and yield under saline conditions by modulating ion uptake, distribution, and hormonal balance.

### Bioactive Substance Priming

Ascorbic acid, a non-enzymatic antioxidant, participates in ROS metabolism, potentially regulates antioxidant enzymes, and serves as a substrate for key enzymes. Together with other antioxidants, it maintains ROS balance, reduces ROS damage, sustains normal cell division and growth, and enhances stress tolerance. Ascorbic acid priming ( $50 \text{ mg} \cdot \text{L}^{-1}$  for 12 hours) increases tillers, grains per spike, thousand-grain weight, total yield, and harvest index in winter wheat while elevating leaf  $\text{K}^+$  content and reducing  $\text{Na}^+$  concentration, total phenols, soluble proteins,  $\alpha$ -amylase, and protease activities. It enhances seedling vigor, increases ascorbic acid content, and boosts CAT and SOD activities, with more pronounced effects in resistant varieties. Ascorbic acid priming improves antioxidant enzyme activity, promotes proline accumulation, maintains membrane stability and cell turgor, and reduces salt stress impacts on seedling growth. Proteomic analysis reveals that salt stress alters 129 proteins in non-primed embryos, primarily related to metabolism, energy, disease resistance, and storage proteins, while ascorbic acid pretreatment mitigates these effects and specifically modifies 35 additional proteins, mostly involved in metabolism, localization, and storage.

Polyamines are regulatory substances whose metabolic changes correlate with plant growth, development, and stress resistance. Priming with putrescine ( $2.5 \text{ mmol} \cdot \text{L}^{-1}$ ), spermidine ( $5.0 \text{ mmol} \cdot \text{L}^{-1}$ ), or spermine ( $2.5 \text{ mmol} \cdot \text{L}^{-1}$ ) improves wheat salt tolerance, promoting shoot growth and yield under salt stress, with spermine showing the most pronounced yield increase. Different polyamines affect ion accumulation ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Cl}^-$ ) and hormone levels (ABA, IAA, SA) differently across varieties, likely through modulation of hormonal balance.

Choline, a phosphatidylcholine precursor and major fungal membrane component, enhances salt tolerance by increasing betaine accumulation. Choline chloride priming ( $5 \text{ mmol} \cdot \text{L}^{-1}$ ) under salt stress significantly improves wheat salt tolerance, increasing seedling  $\text{K}^+$ ,  $\text{Ca}^{2+}$ , and betaine content while reducing  $\text{Na}^+$ ,  $\text{Cl}^-$ , proline content, and plasma membrane peroxidation. A  $400 \text{ mg} \cdot \text{L}^{-1}$  choline chloride seed treatment improves germination rate under salt stress, alleviates chlorophyll degradation, increases soluble sugar content, enhances root activity, reduces plasma membrane permeability, and decreases MDA and proline

accumulation, thereby mitigating water loss and membrane lipid peroxidation damage.

Chitosan, a cationic polysaccharide derived from seafood processing waste, increases germination rate, promotes seedling growth, enhances antioxidant and hydrolytic enzyme activities, elevates soluble protein and sugar content, and increases GA and IAA levels, ultimately improving yield. Chitosan seed coating accelerates germination and enhances stress resistance. Chitosan priming improves germination rate and speed, seedling vigor, and activities of CAT, SOD, and POD under osmotic stress, enhancing drought tolerance by improving free radical scavenging capacity.

Salicylic acid (SA), a key endogenous signaling molecule in plant defense, is a phenolic compound that regulates important metabolic processes including flowering, apical dominance, sex differentiation, seed germination, stomatal closure, membrane permeability, ion absorption, and ethylene synthesis. As a critical signal molecule for biotic and abiotic stress responses, SA induces persistent resistance and activates defense-related enzymes. SA priming increases total soluble sugar content in seedlings of different varieties, alleviating salt stress damage, with resistant varieties showing higher soluble sugar levels that may serve as a drought tolerance indicator.

## Biological and Chemical Priming

### Biological Priming

Biopriming offers safety, high efficiency, and long-lasting effects, attracting increasing attention. Treatment with salt-tolerant *Trichoderma harzianum* improves wheat germination rate, increases root and shoot length, elevates proline and phenol content, and reduces MDA content, mitigating high-salt effects. Drought-tolerant *T. harzianum* biopriming reduces drought impacts on stomatal conductance, photosynthesis, and chlorophyll fluorescence, enhances antioxidant system activity, decreases proline, MDA, and H<sub>2</sub>O<sub>2</sub> accumulation, and increases L-phenylalanine ammonia-lyase activity, thereby improving drought resistance.

### Oxidant Priming

Hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), a stress-responsive signaling molecule, induces resistance-related protein expression. H<sub>2</sub>O<sub>2</sub> priming enhances wheat salt tolerance by advancing germination, reducing seedling H<sub>2</sub>O<sub>2</sub> content (likely through early activation of antioxidant systems), improving photosynthetic capacity, increasing stomatal conductance and leaf water content, maintaining turgor, elevating K<sup>+</sup>, Ca<sup>2+</sup>, NO<sup>-</sup> concentrations and K<sup>+</sup>/Na<sup>+</sup> ratio, and enhancing membrane performance. H<sub>2</sub>O<sub>2</sub> priming also improves drought tolerance by increasing germination rate under water deficit, regulating antioxidant systems, enhancing photosynthetic rate, leaf area, dry weight, water use efficiency, and proline content, while strengthening CAT and APX activities and reducing membrane damage.

### Inorganic Signal Molecule Priming

Nitric oxide (NO), a key regulatory factor in plant growth and development, responds to various biotic and abiotic stresses, playing a central role in coordinating plant-environment interactions. Priming with the NO donor sodium nitroprusside (SNP) significantly reduces salt stress inhibition of germination rate, seed vigor, water absorption, and  $\alpha$ -amylase activity (with minimal effect on  $\beta$ -amylase), while decreasing seedling Na<sup>+</sup> and increasing K<sup>+</sup> content, suggesting that SNP primarily enhances germination under salt stress by improving  $\alpha$ -amylase activity.

Hydrogen sulfide (H<sub>2</sub>S), an important gaseous signal molecule, shows synergistic regulation with NO and participates in plant growth regulation, stress resistance enhancement, and senescence delay. Sodium hydrosulfide (NaHS) priming reduces salt stress inhibition of  $\alpha$ -amylase and esterase activities, enhances CAT, POD, and APX activities, reduces membrane damage, and effectively mitigates salt stress effects on wheat germination and growth.

### Other Priming Agents

Polyethylene glycol (PEG) 6000, a large osmotic regulator that cannot enter cells, enhances wheat seedling salt tolerance by improving antioxidant enzyme activity, osmolyte content, and soluble protein levels when used for seed priming. P O<sub>2</sub> priming shortens germination time and advances flowering under drought conditions while significantly increasing yield. Thiol compounds, particularly thiourea, improve wheat resistance and yield when used for seed treatment.

### Mechanisms of Seed Priming

Drought and salt stress affect plant water uptake, hinder growth and development, cause excessive Na<sup>+</sup> accumulation and toxicity, and disrupt ion homeostasis, osmotic balance, membrane structure, and metabolic processes. Although different wheat varieties perceive and respond to these stresses differently, both drought and salinity delay germination, reduce seedling establishment, impede synthesis, slow growth and metabolism, damage cellular structure and function, and ultimately cause yield loss. Seed priming offers a cost-effective method to mitigate these damages, with potential for large-scale agricultural application. Based on research progress, priming mechanisms can be summarized as follows:

**Regulating ion uptake and transport:** Priming affects ion absorption and transport, influencing ionic balance and metabolic activities. NaCl, KCl, IAA, GA, polyamines, and choline priming reduce root Na<sup>+</sup> uptake and transport to shoots, decrease harmful Na<sup>+</sup> accumulation in leaves, and increase beneficial K<sup>+</sup> and Ca<sup>2+</sup>, promoting growth under salt stress.

**Promoting osmolyte synthesis:** Intracellular osmolyte accumulation helps maintain osmotic pressure for normal physiological activities. CaCl<sub>2</sub>, Na<sub>2</sub>SeO<sub>3</sub>, ascorbic acid, salicylic acid, chitosan, and H<sub>2</sub>O<sub>2</sub> priming promote synthesis of

proline, soluble proteins, and sugars under drought or salt stress, increasing cellular osmotic pressure to facilitate root water uptake and maintain normal metabolism.

**Regulating metabolic and antioxidant enzyme synthesis:** Enzyme synthesis and activity regulation affect physiological reaction rates and plant growth. KCl, CaCl<sub>2</sub>, ascorbic acid, NO, and *T. harzianum* priming promote amylase synthesis, reduce stress effects on enzyme activity, and enhance starch metabolism to promote germination. These agents also induce SOD, POD, CAT, and APX synthesis, strengthening antioxidant reactions to scavenge harmful free radicals and protect membrane stability.

**Modulating hormonal balance:** Plants maintain relative hormonal balance through synergistic and antagonistic interactions. IAA, ABA, CTK, and choline priming affect endogenous hormone synthesis and transport, establishing a hormonal balance suitable for drought or salt stress conditions, thereby reducing stress impacts on growth and development.

Beyond wheat seed priming, various priming agents are applied as foliar sprays during the seedling stage to improve stress resistance. Coumarin treatment enhances wheat salt tolerance, SNP improves growth and photosynthetic efficiency under drought, and thiourea with dithiothreitol increases heat tolerance. Some studies suggest foliar application may be more effective than root drenching or seed treatment, though comprehensive cost-benefit analysis must consider reagent dosage, treatment difficulty, labor, machinery, and chemical costs.

Seed priming technology offers short treatment duration, low labor requirements, simple operation, minimal reagent use, and easy post-treatment management, showing application potential for various crops and vegetables. For example, betaine priming improves rice drought tolerance; water, CaCl<sub>2</sub>, and ABA treatment reduces drought and salt damage in mustard (*Brassica juncea*); ethephon treatment enhances sugarcane (*Saccharum officinarum*) performance under drought; low-concentration chitosan improves salt tolerance in safflower (*Carthamus tinctorius*) and sunflower (*Helianthus annuus*); NaHS priming enhances strawberry (*Fragaria × ananassa*) salt and cold tolerance; and water priming promotes germination and growth of moringa (*Moringa oleifera*) under salt stress.

Plant metabolism is multifactorial, and a single stimulus causes multiple physiological changes. Seed priming applies priming agents as stimuli that target specific metabolic pathways, inducing physiological and biochemical changes that ultimately enhance plant resistance. Identifying effective priming agents reveals critical regulatory points for studying plant metabolism and stress response pathways. Conversely, understanding physiological and biochemical reaction characteristics can guide priming agent selection. Research on priming agents and plant stress physiology are mutually complementary and reinforcing.

## Summary and Outlook

In summary, diverse priming agents—including water, inorganic salts, and organic compounds—effectively improve wheat germination rate, speed, and uniformity. In modern agriculture, seed priming technology increases emergence rates and seedling vigor under adverse conditions, enhances salt and drought tolerance, and reduces yield losses.

Priming effects vary across crops and varieties (resistant vs. sensitive). Some priming agents may be more effective for resistant varieties, while others benefit sensitive varieties. This variation may relate not to inherent resistance but to variety-specific genes that interact with priming agent components. Investigating these gene-component interactions using advanced proteomics and genetic engineering could provide theoretical support for priming agent development.

Practical application should consider crop variety characteristics and priming effects, selecting appropriate agents based on regional environmental conditions, crop type, efficacy, and cost to achieve maximum economic benefit through reduced costs, improved stress resistance, and increased yield.

*Note: Figure translations are in progress. See original paper for figures.*

*Source: ChinaXiv –Machine translation. Verify with original.*