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Review

Mapping mechanistic pathways of seed priming in maize (*Zea mays* L.): A systematic review

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Abstract. Seed priming is recognised as an effective approach to enhance stress resilience and crop performance in maize (*Zea mays* L.), however, the underlying mechanistic relationships remain insufficiently integrated. This review systematically synthesises the literature from 2020 to 2025, analysing how various priming agents, stress types, and maize genotypes are linked on the core biochemical and physiological pathways. The results reveal that all effective seed priming strategies converge on the rapid induction of antioxidant enzymes, superoxide dismutase, catalase, and peroxidases, which form the primary defence against oxidative stress during early development. The specific priming agent determines the recruitment of auxiliary pathways, including hormone crosstalk, osmoregulation, ion homeostasis, and reserve mobilisation, which are engaged according to the prevailing stress condition. The genotype background modulates the extent, but not the direction, of physiological benefits, with tolerant lines consistently displaying superior outcomes. To encapsulate these multidimensional relationships, a Sankey diagram is presented, mapping the flow from the priming type through activated mechanisms to physiological responses and genotype outcomes. This integrative visual framework clarifies the hierarchical and context-dependent nature of seed priming in maize, serving as a practical tool for designing targeted, genotype-tailored interventions.

Keywords: mechanistic pathways, physiological responses, genotype-stress interactions, Maize (*Zea mays* L.)

1. INTRODUCTION

Maize (*Zea mays* L.) is a globally essential cereal crop that supports food, feed, and industrial economies, but its productivity is increasingly being threatened by diverse abiotic and biotic stresses, including drought, salinity, extreme temperatures, and soil-borne pathogens (Nawaz H. *et al.*, 2020; Rehman *et al.*, 2024). These challenges are expected to intensify under climate change scenarios, highlighting the urgency to enhance stress resilience and ensure yield stability in maize-growing regions. Seed priming, including hydro, osmo, bio, chemical, and physical interventions, has emerged as a promising and pragmatic strategy to improve seed germination, seedling establishment, and ultimate crop performance under adverse conditions (Mir *et al.*, 2021; Nawaz M. *et al.*, 2021; Afrouz *et al.*, 2023).

Over the past five years, a surge of mechanistic and physiological studies has unravelled how priming agents modulate multiple defence and adaptation pathways, including the rapid induction of antioxidant enzyme networks, hormone crosstalk, osmoregulation, and reserve mobilisation (Hussain *et al.*, 2023; Gnawali and Subedi, 2021; Saeed *et al.*, 2023). Nonetheless, major gaps persist in translating these mechanistic insights into integrative

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frameworks that predict physiological and agronomic outcomes across diverse stress scenarios and maize genotypes (Khaliq *et al.*, 2024; Rehman *et al.*, 2024; Sezer *et al.*, 2021).

However, a comprehensive, functionally orientated synthesis is still needed that links priming type, activated mechanism, physiological response, and genotype dependence using systematically curated evidence and multidimensional analysis. Particularly lacking are syntheses that resolve (i) how priming-induced mechanisms (antioxidant, hormonal, osmoregulatory, reserve mobilisation, gene modulation) interact to drive physiological resilience, (ii) whether certain secondary pathways are consistently linked to specific classes of priming agents or stress contexts, and (iii) to what extent genotype background modulates the magnitude or direction of priming benefit.

To address these gaps, this review conducts a systematic literature analysis of seed priming studies in maize published between 2020 and 2025, integrating mechanistic, physiological, and agronomic data across stress types and maize varieties. By classifying each study by priming agent, activated mechanism, physiological response, stress type, and genotype, and employing a multidimensional evidence synthesis, we aim to answer the following central research question:

- *How do distinct seed priming strategies in maize map onto core mechanistic pathways and physiological responses under varying stress conditions?*

In this review, we systematically classify and synthesise the recent progress in maize seed priming, categorising evidence from 2020 to 2025 into nine principal mechanistic classes: antioxidant/redox defence, hormone crosstalk, osmoregulation and water relations, photosynthetic protection, reserve mobilisation, gene/signal modulation, growth and primary metabolism, defence and immunity, and stress memory/root development. By mapping these mechanisms across priming types, stress conditions, and physiological responses, we clarify the hierarchical and context-dependent pathways that underpin maize resilience. These interconnections are encapsulated in a multidimensional Sankey diagram, offering an integrative framework to inform genotype and environment-specific seed priming strategies.

2. METHODOLOGY

A systematic literature review was undertaken to synthesise mechanistic and physiological insights into seed priming strategies in maize. The review methodology combined comprehensive database querying with rigorous evidence extraction to ensure balanced coverage of both experimental and functional dimensions.

Relevant articles were identified in the Scopus database using the search string:

- (“corn” OR “maize”) AND seed AND priming.

This initial search retrieved 398 documents. To focus the review on plant-based physiological studies, exclusion criteria were applied using Boolean filters to remove articles concerning animal studies, drug effects, nanoparticles, and genetics (specifically: animal OR animals, drug AND effect, nanoparticles OR nanoparticle, and genetics OR genetic OR gene). This reduced the dataset to 273 records.

Then, further inclusion criteria were applied as follows:

- Only peer-reviewed journal articles published in English were retained, yielding 245 records.
- To ensure relevance to current mechanistic advances, only articles published between 2020 and 2025 were considered.

Studies were excluded if they did not report, in sequence: stress type, activated mechanism, and physiological response. This final screening produced a set of 72 articles.

2.1. Data extraction and mechanistic synthesis

For each eligible study (2020-2025), detailed data extraction was performed to enable mechanistic, physiological, and agronomic comparisons. The following fields were systematically extracted: author(s), type of seed priming, activated mechanism, physiological response, type of stress, and genotype or variety.

The data extracted were tabulated to facilitate comparative mechanistic analysis in nine classes: (i) antioxidant/redox defence, (ii) hormone crosstalk, (iii) osmoregulation and water relations, (iv) photosynthetic protection, (v) reserve mobilisation, (vi) gene/signal modulation, (vii) growth and primary metabolism, (viii) defence and immunity, and (ix) stress memory/root development.

Subsequently, a standardised classification was applied to the type of seed priming, stress type, activated mechanism, and physiological response. These classifications comprised:

- Priming Type: The original descriptors in each paper (*e.g.*, “hydropriming,” “melatonin soaking,” “zinc sulphate treatment,” “PEG-induced osmopriming,” “laser exposure”) were mapped to a controlled vocabulary. This mapping used regular expression rules targeting common priming strategies: Hydropriming, Osmopriming, Halopriming, Nutrient Priming, Hormonal Priming, Biostimulant Priming, Biopriming, Antioxidant/Redox Priming, Chemical Priming, Physical Priming, Combination/On-Farm Priming, Stress-Induced Priming, and others.
  - ◦ Example: “Water soaking” and “hydropriming” are both mapped to “Hydropriming”; “PEG-6000” and “osmopriming” to “Osmopriming.”
- Stress Type: Reported stressors or test conditions (*e.g.*, “salinity stress,” “drought,” “heat shock,” “oxidative stress,” “cadmium exposure,” “biotic infection”) were similarly categorised via rules: Drought/Water Deficit, Salinity/Alkalinity, Temperature Stress, Oxidative

Stress, Biotic Stress, Heavy-Metal Toxicity, Chemical Stress, Abiotic Stress, *etc*.
  - Example: "PEG-6000 induced stress" becomes "Drought/Water Deficit"; "NaCl" becomes "Salinity/Alkalinity."
- Activated Mechanism: Mechanistic descriptors (often diverse and idiosyncratic in the literature) were harmonised to a smaller set of canonical mechanisms. The rules captured both direct mentions (*e.g*., "CAT activity ↑") and indirect indicators (*e.g*., "reduced MDA" mapped to redox, "shoot length ↑" to growth activation):
  - Antioxidant/Redox Defence (e.g., SOD, CAT, POD, APX induction, ROS scavenging)
  - Hormone Crosstalk (*e.g*., gibberellin, ABA, melatonin, SA signalling)
  - Osmoregulation and Water Relations (proline, glycine-betaine, osmotic adjustment)
  - Reserve Mobilisation (amylase, starch breakdown, endosperm weakening)
  - Photosynthetic Protection (chlorophyll content, photoprotection, Rubisco)
  - Gene/Signal Modulation, Growth and Primary Metabolism, Defence and Immunity, Stress Memory/Root Development, etc.
- Physiological Response: Outcomes were also standardised: Germination and Seedling Vigour, Growth and Biomass, Biochemical Markers, Seedling Photosynthetic Capacity, Yield Attributes, Morphological Traits, Water-Relation Response, Vigour Indices, Photochemical Efficiency, Respiration and Enzyme Activity, *etc*. Both explicit and implied metrics were mapped (*e.g*., "PI ↑" and "seedling emergence" both to "Germination and Seedling Vigour").

After all entries were mapped, a multi-stage Sankey diagram was generated and depicted, connecting each study's priming type → stress context → activated mechanism → physiological response. Categories such as "Other" or "Not reported" were grouped at the end and do not feature in the visualised flows.

The images were created in Adobe Illustrator and PowerPoint and the Sankey diagram in Python.

3. RESULTS

In the following sections, we build on these trends by synthesising the mechanistic, physiological, and agronomic evidence for the major classes of seed priming agents and interventions.

3.1. Antioxidant/redox defence mechanism

In antioxidant-centred redox defence, maize seedlings have different physiological responses. The physiological responses to germination and seedling vigour directly report on the ability of superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD/APX) to neutralise imbibitional oxidative bursts, thus preserving membrane integrity and hydrolytic enzyme activity for timely radicle protrusion. The physiological response to the photosynthetic capacity of seedlings links chlorophyll a/b accretion and carotenoid accretion with measurements of net CO_2, assimilation measurements to confirm that the preconditioning of photoprotective antioxidants translates into functional light harvesting and carbon fixation in nascent leaves. On the cellular scale, biochemical markers of physiological response encompass the accumulation of osmolyte (proline, soluble sugars) and phenolic antioxidant pools alongside ROS, H_2O_2, and malondialdehyde (MDA) quantification, which together reveal the robustness of the redox buffer network and its role in osmotic homeostasis. With oxidative stress held in check, growth & biomass physiological response quantifies downstream structural gains, fresh and dry mass, leaf area expansion, and total biomass that arise from uninterrupted cell division and expansion. Finally, the seedling performance dimension group physiological response integrates these early-stage readouts, vigour, water relations, morphology, and photochemical efficiency into a predictive cascade that culminates in yield-related traits, thereby closing the mechanistic loop from antioxidant activation through seedling establishment to agronomic performance.

3.1.1. Germination and seedling vigour

Nitrate-salt priming with 7.5 mM $Mg(NO_3)_2$ accelerated the accumulation of osmolytes (soluble sugars, proline) and increased chlorophyll retention in polyethylene glycol (PEG) stressed seeds, doubling the percentage of germination and seedling vigour in an unspecified genotype evaluated by Singh *et al.* (2020b). A 20-40% *Plantago ovata* extract elicited an equivalent antioxidant surge while conferring additional phenolic protection, which translated into an enhanced photosynthetic rate and stomatal conductance in the elite cv. Cimmyt-Pak under water-deficit conditions (Nawaz M. *et al.*, 2021). Hormonal priming with 0-200 ppm gibberellic acid (GA_3) further demonstrated that coupling redox activation to hydrolase-driven reserve mobilisation shortened the mean germination time by 35 h and raised relative water content under NaCl-imposed osmotic stress (Gnawali and Subedi, 2021).

Chemical hardening, soaking in distilled water with thermal pulses and the fungicide Amistar Xtra, increased seed survival by 30% across combined drought, waterlogging, and heat episodes, confirming that membrane repair and ROS scavenging act synergistically (Khaeim *et al.*, 2022). Polymer-based hydro-, osmo-, and thermo-priming with 1-2% chitosan reinforced CAT, POD, and APX activity, elevated proline and pigment levels, and fully restored germination and vigour indices in the drought-challenged landrace 'Pearl, Sargodha 2002 White' (Kakar *et al.*, 2023). Melatonin soaking (250-1 000 μM) delivered the largest absolute gains, 101% higher germination, 133% longer shoots, and a 424% increase in stomatal aperture by synchronising redox buffering with chloroplast and stomatal protection under severe drought (Muhammad *et al.*, 2023). Finally, a thiol-micronutrient cocktail (3 mM glutathione + 0.5% $ZnSO_4$) outperformed either component alone, amplifying SOD/POD/CAT/APX, raising pigment pools, and improving emergence on water-deficit media (Saeed *et al.*, 2023).

On the other hand, salicylic acid (SA) or EDTA (1 M) raised CAT and SOD while lowering MDA in Nigerian cvs SWAN-LSR-Y, BR9928-OMR-SR-Y, and OMR-LSR-Y, but phenotypic translation was genotype-dependent. SWAN-LSR-Y lost germination at 50 mM NaCl, whereas BR9928-OMR-SR-Y maintained radicle and plumule elongation (Olayinka *et al.*, 2022). Follow-up comparisons of hydropriming, KNO_3 osmopriming, and ascorbic- or salicylic-acid chemical priming on the same germplasm showed that ascorbate delivered the broadest antioxidant profile (SOD, CAT, APX, and glutathione) and the highest vigour index, reinforcing the principle that breadth of redox mobilisation, not merely strength, governs salt resilience (Olayinka *et al.*, 2023).

Microbial consortium priming with combinations of *Pseudomonas spp.*, *Azospirillum lipoferum, Bacillus spp.*, and cyanobacteria coordinated energy metabolism and DNA-repair pathways alongside classical redox defences, increasing ATP, nucleic acids, and sterols in parallel with antioxidants. These treatments substantially enhanced seedling biomass (69-91% increases) and vigour indices (75–117% increases) under combined stress conditions including salinity, nitrogen limitation, and heavy metal exposure (Cardarelli *et al.*, 2022).

Allelochemical hydropriming with *Moringa oleifera* leaf extract (0.5-3%) intensified CAT and POD while reducing H_2O_2 levels; at 3% extract, the salt-tolerant hybrid Pioneer 30Y87 accrued 22-56% higher antioxidant activity, CO_2 assimilation, and stomatal conductance, whereas the sensitive Pioneer 30T60 derived only modest benefit (Khaliq *et al.*, 2024). Thiol-micronutrient co-priming (3 mM GSH + 0.5% $ZnSO_4$) simultaneously boosted antioxidant enzymes, elevated K^+/Na^+ and Ca^{2+}/Na^+ ratios, and suppressed Na^+ uptake at 120 mM NaCl, illustrating how redox cycling dovetails with membrane transport regulation to deliver compound salt tolerance (Kasana *et al.*, 2025).

Hydropriming of the chilling-sensitive hybrid PEHM-5 (CM-150 × CM-151) increased SOD, CAT, and POX activities, improved membrane repair, and halved imbibitional leakage, shortening the mean germination time from 4.9 days to 2.8 days and tripling the vigour index (Mir *et al.*, 2021). By contrast, cytokinin priming with benzylaminopurine and kinetin in the inbred Knezha 310 mitigated both accelerated-ageing heat stress and cold-storage injury, suppressing H_2O_2 and MDA while sustaining leaf biomass and chlorophyll, which translated into 16-18% grain-mass gains (Chipilski *et al.*, 2023). A dual hydro-/bio-priming protocol with *Trichoderma harzianum* in cold-resistant AR68 and cold-sensitive KSC703 hybrids elevated auxin/cytokinin ratios, proline levels, and nutrient uptake in parallel with catalase activity, driving a 99.7% field-establishment rate and an 11.8 g increase in root dry weight (Afrouz *et al.*, 2023).

Physical priming with multi-walled carbon nanotubes (0-200 mg L^{-1}) in cadmium-sensitive waxy hybrids Yuebaitiannuo 7 and Yuecainuo 2 provoked a transient oxidative burst that was rapidly neutralised by POD, CAT, and SOD, concomitantly reducing MDA and raising germination by 11% (M100) and 25% (M200), as well as increasing shoot and root biomass under 50 M Cd stress. Raffinose priming (50 mM, 12 h soak) of waxy inbreds SYKN167 and SD88 activated -galactosidase, stimulated RFO biosynthesis, and simultaneously boosted SOD, POD, and CAT, thereby suppressing ROS generated by cold storage, artificial ageing, and oxidative challenge; germination rose by 7.8% (SYKN167) and 20.5% (SD88), confirming that carbohydrate-mediated osmoprotection and enzymatic redox buffering act synergistically when membrane stability is compromised (Zhu *et al.*, 2024).

A summary of the priming type, agent/material (if available), activated mechanism, quantitative outcome (if available), physiological response, stress type, and genotype/variety (if available) for each research is presented in Table 1.

These studies delineate a hierarchical mechanistic template for maize seed priming across stress categories: (i) rapid induction of the antioxidant triad (SOD-CAT-POD/APX) is indispensable; (ii) the chemical identity of the priming agent dictates the secondary pathway, ion/osmolyte homeostasis for nitrate salts and biostimulants, reserve mobilisation for GA_3, membrane repair for chemical hardening, stress memory for chitosan, chloroplast-stomatal stabilisation for melatonin, metabolic cycling for GSH + Zn, broad redox breadth for ascorbate, energy-DNA repair coupling for microbial consortia, phenolic-driven photosynthetic enhancement for *Moringa* extract, or source–sink fortification for cytokinins; and (iii) genotype background modulates quantitative, but not qualitative, gains, as evidenced by the superior responses of 'Pearl', Sargodha 2002 White, Vega F1, SYKN167, and other tolerant lines versus their sensitive counterparts. This integrative evidence underscores that effective maize-priming strategies must harmonise robust early redox fortification with stress-matched auxiliary mechanisms tailored to varietal physiology. This integrative mechanistic evidence is visually synthesised in Fig. 1a.

3.1.2. Seedling photosynthetic capacity

Every elicitor, whether hormonal, nutrient, biostimulant, microbial, or physical, mobilises the antioxidant redox network (SOD, CAT, POD and, where assayed, APX), thereby curbing reactive-oxygen build-up and safeguarding

Table 1. Antioxidant/redox defence mechanism in germination and seedling vigour physiological response

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Singh *et al*., 2020b)	Nitrate salt-based	Magnesium nitrate ($Mg(NO_3)_2$), 7.5 mM	↑SOD, POX, CAT activity, induces osmoregulatory compounds; ↓ROS	↑Chlorophyll in T5-T6 treatments; ↓Phytotoxicity in shoot and root *vs*. controls	↑ Germination, ↑ Seedling vigour, ↑ Chlorophyll, ↑ Sugar	Proline accumulation	Moisture stress (PEG-6000, 1.5-4.5%)
(Nawaz M. *et al*., 2021)	Natural extract	*Plantago ovata* (20%, 40%) extract	↑Antioxidant activity (SOD, POD, CAT, APX); ↓ROS; ↑enzymatic	↓non-enzymatic defence	↑ Germination and growth under drought; 20% extract was most effective ↓	↑ Germination rate, ↑ photosynthesis, ↑ stomatal traits, ↓ oxidative stress indicators ↓	Water deficit stress (PEG-induced) ↓
(Gnawali and Subedi, 2021)	Hormonal	Gibberellic acid GA_3 at 0-200 ppm	↑Embryo growth, ↑reserve mobilisation, ↑antioxidant enzymes, ↓lipid peroxidation	↑Germination %, ↑shoot length from 2.9 to 6.4 cm under 1.05 MPa	↑ Germination rate, ↑ shoot length, ↑ RWC under low water potential	Drought stress (NaCl-induced osmotic stress)	Not reported
(Mir *et al*., 2021)	Hydropriming	Not reported	↑SOD, POX, CAT activity, ↑membrane repair, ↓imbibitional leakage, ↑seed vigour index	↑Vigour index (3907.2 vs 1438.1), ↑germination %, ↓ MGT (4.9 to 2.8 days)	↑ Germination, ↑ seed vigour, ↑ membrane stability	Chilling stress	PEHM-5 (CM-150 × CM-151)
(Chen *et al*., 2021)	Physical (nanomaterial treatment)	Multiwall carbon nanotubes (MWCNTs) at 0, 100, 200 mg L	↑ POD, CAT, SOD, ↓ MDA	↑Germination; ↑shoot/root weight; ↓MDA	↑ Germination rate, ↑ seedling growth, ↑ antioxidant activity under Cd stress	Abiotic stress: cadmium (Cd) toxicity	Yuebaitiannuo7 and Yuecainuo2
(Olayinka *et al*., 2022)	Chemical	Salicylic acid (SA, 1.0 M), EDTA (1.0 M)	↑CAT/SOD, ↓ROS, ↑water uptake, ↓MDA	↓Germination %; ↑seedling length; ↑CAT/SOD	BR9928-OMR-SR-Y	↑Germination, ↑seedling growth, ↑radicle/plumule length	Salinity
(Khaeim *et al*., 2022)	Antifungal	distilled water, temperature treatment, amistar xtra, and hypo	↑SOD, ↓ROS	↑Survival by 30%	↑Germination, ↑Seedling growth	Drought, waterlogging, temperature	Not reported
(Cardarelli *et al*., 2022)	Hydro-, Osmo-, Physicochemical-, Hormonal-, Matric, Micro-priming,	*Trichoderma harzianum*, *Bacillus spp*., *Paenibacillus yonginensis*, *Rhizoglomus intraradices*, *Trichoderma atroviride*	↑ATP, ↑nucleic acids/proteins, ↑sterols, ↑DNA repair, ↑antioxidants	↑Germination +4%; ↑shoot length +14%; ↑root length +26%; ↑root number +46%; ↑fresh weight +9%	↑Germination, ↑seedling vigour, ↑biomass	Heat, osmotic, salt, suboptimal temperature	Not reported
(Kakar *et al*., 2023)	Hydropriming, Osmopriming, Thermopriming	Chitosan (1, 2%), distilled water, and 4°C thermo-priming	↑Antioxidant enzymes (CAT, POD, APX), ↑proline, ↑ROS scavenging	↑Germination %, ↑seed vigour index, ↑pigments	proline (with priming); ↓under stress w/o priming	↑Seed germination, ↑seedling growth, ↑photosynthetic pigments, ↑proline, ↑antioxidant activity	Osmotic (PEG-4000), Drought

Table 1. Antioxidant/redox defence mechanism in germination and seedling vigour physiological response

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Chipilski *et al*., 2023)	Hormonal	BAP, KIN (synthetic CKs)	↑Antioxidants, ↓MDA, ↓H_2O_2	↑Grain mass: +18% (KIN), +16% (BAP); ↓Oxidative markers	↑Germination, ↑Leaf wt, ↑Chlorophyll, ↓Oxidative stress	Heat (AIS), Cold storage	Knezha 310
(Afrouz *et al*., 2023)	Hydropriming, Biopriming	*Trichoderma harzianum*, water	↑Auxin/CK, ↑Antioxidants, ↑Proline, ↑Nutrient uptake	↑Establishment rate: 99.7%; ↑Fm: 994; ↑Root dry wt: 11.8	↑Catalase activity, ↑Emergence, ↑Root dry wt	Cold	AR68 (cold-resistant), KSC703 (cold-sensitive)
(Muhammad *et al*., 2023)	Melatonin	Melatonin: 250, 500, 1000 µM	↑ SOD, ↑ POD, ↑ CAT, ↑ GSH, ↑ AsA, stabilizes chloroplast, improves stomata	↑Germination, ↑root length, ↑shoot length, ↑fresh weight, ↑proline, ↑protein, ↑sugar, ↑chlorophyll, ↑stomatal aperture 424, ↑SOD, ↑POD, ↑CAT, ↑GSH, ↑AsA	↑Germination, ↑root/shoot length, ↑fresh weight, ↑proline, ↑protein, ↑sugar, ↑chlorophyll, ↑stomatal aperture	Drought	Not reported
(Olayinka *et al*., 2023)	Hydropriming, Osmopriming	H_2O_2, KNO_3, Ascorbic acid, Salicylic acid	↑SOD, ↑CAT, ↑APX, ↑glutathione (antioxidant activity)	↑Germination %, ↑Speed of germination, ↑Seedling vigour index (ascorbic acid highest)	↑Germination, ↑Seedling vigour, ↑Radicle length, ↑Anti-oxidative potential	Salt	SWAN-LSR-Y, BR9928-OMR-SR-Y, OMR-LSR-SY (maize cultivars, Nigeria)
(Saeed *et al*., 2023)	Organic (GSH), Nutrient	Glutathione (GSH), Zn (0.5%)	↑SOD/POD/CAT/APX (antioxidants), ↑Metabolic activity	3 mM GSH + Zn: ↑Germination, ↑Growth, ↑Pigments vs. water stress	↑Germination, ↑Seedling growth, ↑Photosynthetic pigments	Water deficit	Not reported
(Zhu *et al*., 2024)	Oligosaccharide, Exogenous substance	Raffinose solution	↑ α-GAL, ↑RAFS, ↑SOD/POD/CAT, ↓ROS	↑Germination: +7.8% (SYKN167), +20.5% (SD88); ↑antioxidant activity, ↓ROS	↑Seed vigor, ↑germination, ↑antioxidant enzymes, ↓ROS	Low temperature, oxidative, artificial aging	SYKN167, SD88 (waxy corn inbreds)
(Khaliq *et al*., 2024)	Hydropriming	*Moringa oleifera* leaf extract (MLE), 0.5–3\%	↑CAT, ↑POD (antioxidant); ↓H_2O_2; ↑Growth, ↑Photosynthesis	MLE (3%) ↑Antioxidant (CAT, POD) by 22–56%; ↑Germination under salinity (best at 2.5%, 3%)	↑Germination, ↑Photosynthesis, ↑Antioxidants (CAT, POD), ↑Growth, ↑Internal C, ↑Stomatal conductance	Salt	Pioneer 30Y87 (salt-tolerant), Pioneer 30T60 (salt-sensitive)
(Kasana *et al*., 2025)	Seed, Combo	GSH (1.5–4.5 mM), $ZnSO_4$ (0.5%)	↑Antioxidants, ↑K^+Na^+, ↑$Ca^{2+}Na^+$, ↓Na^+	Combo (3 mM GSH + Zn): ↑Germ, ↑Emergence, ↑K^+Na^+, ↓Na^+ uptake	↑Germ, ↑Emergence, ↑Salt tolerance	Salt	Not reported

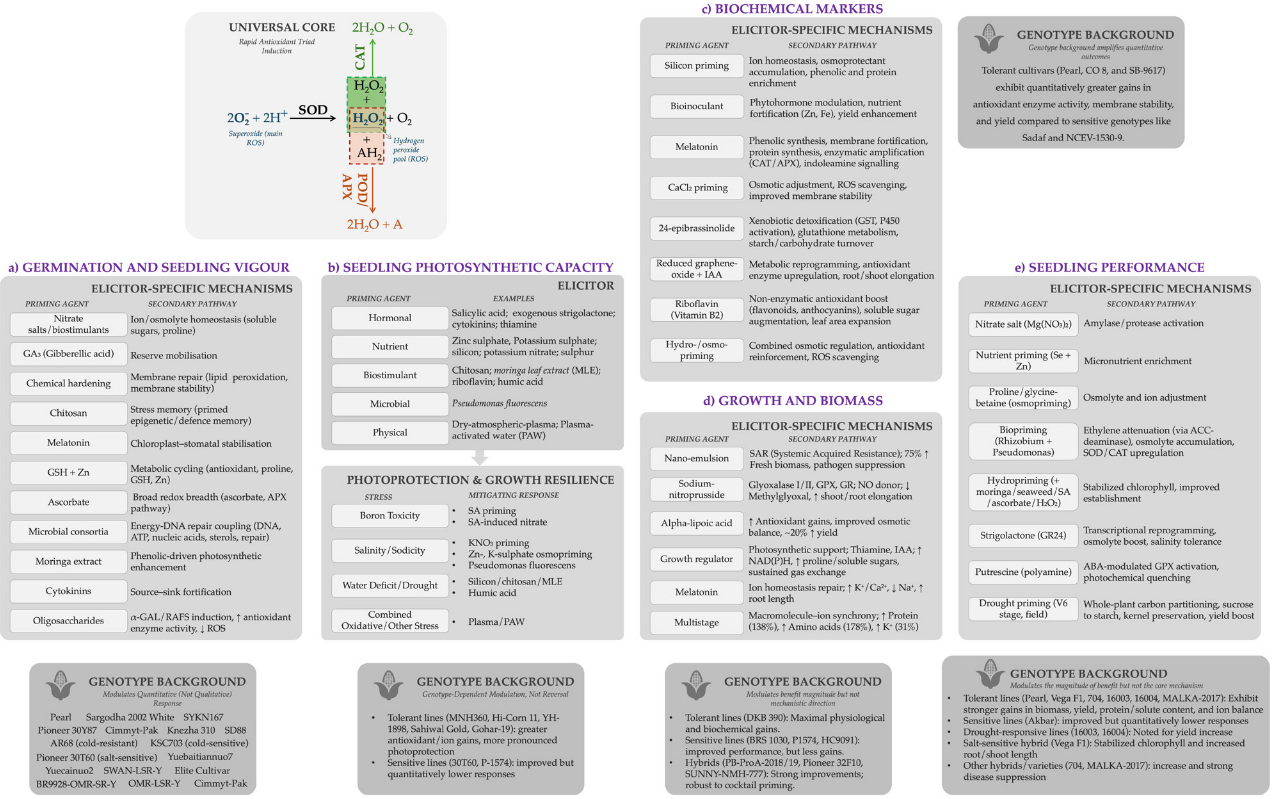


Fig. 1. Antioxidant/Redox defence activated mechanism in the physiological response to: a) germination and seedling vigour, b) photosynthetic capacity of seedlings, c) biochemical markers, d) growth and biomass, e) multidimensional assessment of seedling performance.

the photosynthetic machinery under boron toxicity, salinity/sodicity, water deficit, or combined oxidative stress. This redox pre-conditioning is consistently accompanied by improved carbon assimilation, chlorophyll retention, and osmotic adjustment, underscoring ROS surveillance as the pivotal gateway to photoprotection in maize.

A summary of priming types, agents, activated mechanisms, quantitative outcomes, physiological responses, stress types, and genotypes for each study is presented in Table 2.

Researchers have found that salicylic-acid soaking 100 µM) in the cultivar Gohar-19 boosted proline and glycine-betaine while attenuating ROS, culminating in greater shoot-root recovery under 30 mg B kg^{-1} soil (Nawaz M. *et al.*, 2020). Zinc- and potassium-sulphate osmopriming elevated CAT, POD, and SOD and lifted shoot dry mass by 69% under combined salinity-sodicity, despite the genotype not being reported (Basit *et al.*, 2020). Silicon and chitosan treatments increased the photosynthetic rate by up to 24.7% and grain yield by up to 56.9% during water stress (Younas *et al.*, 2022). Under salt stress, 1.5% KNO_3 priming raised K^+ uptake, enhanced CAT, APX, and POD, and suppressed ROS, with the tolerant hybrid MNH360 outperforming the sensitive 30T60 (Rehman *et al.*, 2024). Thus, these studies show that ion-homeostatic agents are most effective when their nutrient functions dovetail with redox reinforcement.

Exogenous strigolactone (GR24, 0.1 mg L^{-1}) induced a controlled H_2O_2/NO burst that closed stomata, raised osmolytes, and ultimately improved CO_2 assimilation and seed set in hybrids HY-1898 and FH-1046 at 60% field capacity (Luqman *et al.*, 2023). Cytokinin-mediated gains reported elsewhere were paralleled here by SA-induced nitrate remobilisation, indicating that hormone priming can couple antioxidant induction with nitrogen economy.

Pseudomonas fluorescens (NAFP-19) inoculation enhanced CAT/APX activity, osmolyte pools, and chlorophyll fluorescence, lengthening shoots by up to 65% under salinity (Naz *et al.*, 2024). Humic-acid soaking (100 mg L^{-1}) increased chlorophyll and water status while offsetting drought-induced biomass losses by up to 59% (Abu-Ria *et al.*, 2024). A combined *moringa* leaf-extract/thiamine/riboflavin regime amplified SOD, CAT, and POD; however, only *moringa* (5%) sustained biomass at 60% field capacity in YH-1898 and Sahiwal Gold, highlighting that natural phenolic matrices can outperform single vitamins when drought limits carbon gain (Ahmad *et al.*, 2025). These findings suggest that multi-pathway stimulation, including redox, osmotic, and hormonal pathways, is the hallmark of effective biostimulant priming.

Physical plasma priming offered a non-chemical alternative: dry-atmospheric-plasma (DAP) raised germination to 90% (*vs.* 65% control) and halved the median germina-

Table 2. Antioxidant/redox defence mechanism in seedling photosynthetic physiological response

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
Nawaz *et al*., 2020b)	Hormonal priming (Salicylic Acid)	Salicylic acid (SA), 0-150 µM (100 µM most effective)	↑ Proline and GB, ↓ ROS, ↑ Antioxidant enzymes; promotes defense and nutrient uptake	↓ Nitrate content by 20%, ↑ root/shoot recovery at 100 µM SA	↑ Root/shoot length, ↑ Biomass, ↑ Chlorophyll a/b and carotenoids under B stress	Boron toxicity, salt	Gohar-19 (Maize and Millets Research Institute, Pakistan)
(Basit *et al*., 2020)	Hydro-priming (water) and osmopriming (ZnSO$_4$, K$_2$SO$_4$)	Water, 4 mM ZnSO$_4$, 23 mM K$_2$SO$_4$ ↓	↑ Antioxidant enzyme activity (CAT, POD, SOD); ↑ Ascorbic acid, ↓ reduced glutathione	↑Shoot dry biomass; ↑ Shoot K by 74% (water/K$_2$ SO$_4$), 62% (ZnSO$_4$); ↑ Root K by 43% (water), 33% (ZnSO$_4$) ↓	↑ Chlorophyll content, ↑ photosynthesis rate, ↑ biomass yield under saline conditions ↓	Salt	Not reported
(Younas *et al*., 2022)	Chemical priming	Silicon, Chitosan, Si+Chitosan	↑Antioxidant enzymes (CAT, POD, SOD), ↓MDA, ↑chlorophyll	↑Photosynthetic rate: 19.7-24.7%; ↑chlorophyll-a: 31.6-79.3%; ↑grain yield: 9.86-56.9% (Si, Chitosan, Si+Chitosan, at 100/50% FC)	↑Photosynthetic rate, ↑stomatal conductance, ↑transpiration, ↑RWC, ↑chlorophyll-a, ↑MSI, ↑yield	Water	Not reported
(Farman *et al*., 2022)	Si priming	Silicon (3 mM Na$_2$SiO$_3$), S foliar spray (0.5-1%)	↑CAT, ↑POX, ↑SOD (antioxidants), ↓oxidative damage, ↑ROS-scavenging enzymes	↑Catalase 45%, ↑POX 38%, ↑SOD 55%, ↑NPK 40-63%, ↑yield traits under drought; Si+S treatments most effective	↑RWC (25%), ↑chlorophyll a (56%), ↑carotenoids (26%), ↑photosynthetic rate (64%), ↑stomatal conductance (56%), ↑CO$_2$ (48%)	Drought	Hi-Corn 11 (tolerant), P-1574 (susceptible)
(Luqman *et al*., 2023)	Hormonal (Strigolactone priming)	GR24 (strigolactone analogue, 0 0.1 mg L, 16 h soak)	↑H$_2$O$_2$ and NO (stomatal closure), ↑osmoprotectants (glycinebetaine, proline), ↑antioxidants, ↑photosynthetic efficiency	↑Chlorophyll b, ↑total chlorophyll, ↑carotenoids, ↑CO$_2$ assimilation rate, ↑seeds/cob, ↑seeds/plant; no effect on chlorophyll a	↑CO$_2$ assimilation rate, ↑stomatal conductance, ↑chlorophyll b, ↑total chlorophyll, ↑carotenoids	Drought	HY-1898, FH-1046
(Rehman *et al*., 2024)	Chemical (KNO$_3$), Physical	KNO$_3$ (0-1.5%)	↑K$^+$ uptake, ↑CAT, ↑POD, ↑APX, ↓ROS, ↑MDA	↑Growth in MNH360 (*vs* 30T60); ↑CAT, ↑APX, ↑POD, ↑MDA, ↑TSP; ↓ROS	↑Growth, ↑Chlorophyll, ↑Carotenoids, ↓ROS	Salt	MNH360, 30T60
(Naz *et al*., 2024)	Bio-priming	*Pseudomonas fluorescens* (NAFP-19)	↑CAT/APX activity, ↑Glycine betaine/proline, ↑Osmotic adjustment, ↑Chlorophyll fluorescence, ↑Photosynthetic genes	↑Shoot length (64.7, 45.6% in corn); ↑Root length (23.3, 30.5% in corn) under salt stress; ↑water, chlorophyll, conductance	↑Shoot/root length, ↑Relative water content, ↑Osmotic potential, ↑Chlorophyll, ↑Stomatal conductance	Salt	Not reported
(Abu-Ria *et al*., 2024)	Biostimulant priming	Humic acid (HA, 100 mg L)	↑APX, ↑CAT, ↑POD, ↑soluble carbs, ↑proline, ↑proteins, ↑osmotic homeostasis	↑Photosynthetic rate by 29.2% (maize), ↑RWC, ↑chlorophyll, maize biomass ↓37-58.7% under drought	↑Growth, ↑dry matter, ↑water status, ↑photosynthetic efficiency, ↑chlorophyll, ↑RWC, ↑sugars, ↑carbohydrates, ↑proline, ↑proteins	Drought	Not reported
(Ahmad *et al*., 2025)	Natural (MLE), Synthetic (B1, B2)	*Moringa* leaf extract (MLE, 5%), thiamin (B1, 100 mM), riboflavin (B2, 100 µM), combined application	↑SOD, ↑CAT, ↑POD, ↑osmolytes	↓Biomass at 60% F.C.; MLE (5%) best for ↑growth	↑Growth, ↑Chl, ↑phenolics	Drought	YH-1898, Sahiwal Gold
(Kamseu-Mogo *et al*., 2024)	DAP (pre), PAW (post)	Dry Atmospheric Plasma (DAP), Plasma-Activated Water (PAW)	↑ROS, ↑Signal transduction, ↑Growth genes, ↓Photosynth.	DAP: ↑Germ (90% *vs.* 65%), ↓Median time (−37.5%); DAP+PAW: most robust growth	↑Germ (90%), ↓Median time (−37.5%), ↑Growth, ↓Chlorophyll	Drought, oxidative	ATP-SR-Y

tion time, while subsequent plasma-activated water (PAW) maintained robust growth but reduced chlorophyll, suggesting a trade-off between rapid establishment and long-term photo-assimilatory capacity (Kamseu-Mogo *et al.*, 2024). Transient ROS spikes appear to act as a signalling cue that reprograms antioxidant and growth genes before photosynthetic acclimation sets in.

Genotype responsiveness modulated, but did not reverse, the direction of priming benefits. Drought-tolerant Hi-Corn 11 and sensitive P-1574 both profited from silicon plus sulphur, yet antioxidant gains (SOD +55%) were larger in the tolerant line (Farman *et al.*, 2022). Similarly, salt-tolerant MNH360 exhibited stronger K^+ retention and ROS suppression than 30T60 after KNO_3 priming, validating the premise that a robust basal ion-transport capacity amplifies redox-centred priming effects.

The collective evidence indicates that successful photoprotective priming hinges on synchronising ROS detoxification with stress-specific auxiliary processes, ion exclusion under salinity, osmolyte accumulation under drought, nitrate remobilisation under boron toxicity, or early signalling under plasma exposure. This integrative mechanistic framework is summarised in Fig. 1b.

Future work should quantify the temporal coupling between antioxidant gene expression and chloroplast redox poise across diverse genetic backgrounds to refine predictive markers of priming efficacy in maize.

3.1.3. Biochemical markers

Every treatment, whether silicon salt, bacterial inoculant, melatonin, calcium chloride, 24-epibrassinolide, reduced graphene oxide, IAA, riboflavin, or multi-mode hydro/osmo-priming, rapidly elevated superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD/APX), thereby curbing reactive oxygen species accumulation and stabilising membranes at imbibition. Silicon priming with sodium-metasilicate (1-2 mM) in the alkaline-tolerant *cv.* CO 8 intensified SOD and CAT activity (48.1 and 17.2 U mg^{-1} protein, respectively) while enriching phenolics and soluble proteins, paralleling superior stress tolerance under Na_2CO_3 alkalinity (Natarajan *et al.*, 2022). By contrast, Zn-solubilising *Bacillus* consortia (strains ZM20, ZM31, S10, ZM63) acted primarily through APX-, POD-, and SOD-driven ROS scavenging coupled to phytohormone modulation, translating into 1.5-fold gains in grain-Zn and substantial yield increases under soil Zn deficiency (Mumtaz *et al.*, 2022).

Salinity studies reinforce this pattern. A three-way comparison of hydro-priming (water), osmo-priming (2% $CaCl_2$), and melatonin priming (1 000 μM) in hybrids SB-9617, YH-1898, and NCEV-1530-9 demonstrated parallel rises in SOD (+32%), POD (+18%), and CAT (+17%), with melatonin additionally boosting phenolics (+61%) and membrane stability index, consequently suppressing electrolyte leakage by 17% (Hussain *et al.*, 2023). Under paraquat-induced oxidative stress in sweet-corn var. saccharata, 150 μM melatonin cut herbicide injury 4.6-fold while multiplying CAT activity 4.6-fold and APX 2.4-fold, affirming indoleamine signalling as an efficient amplifier of enzymatic defences (Fathi *et al.*, 2023).

Hormonal and biochemical primers extend the mechanistic palette beyond ROS detoxification. Ultra-low 24-epibrassinolide (0.01 μM) simultaneously activated glutathione reductase, GST, cytochrome-P450 monooxygenase, and carbohydrate turnover, yielding higher net CO_2 assimilation (P_n) and lower MDA under the broad-spectrum pesticide diazinon (Mehrian *et al.*, 2023). Independent melatonin seed-soaking work likewise promoted SOD/CAT/POD gains and improved seedling biomass under salinity (Anggarda Gathot Subrata *et al.*, 2023), indicating that disparate signalling molecules converge on the same redox nodes while delivering ancillary benefits, starch remobilisation in the case of brassinosteroid and protein synthesis in the case of melatonin. Engineered and vitamin-based elicitors confirm the centrality of redox buffering while adding novel functional layers. Reduced graphene-oxide and IAA priming enhanced APX, CAT, and POD. They drove significant shoot-root elongation under undefined abiotic pressure (Bhattacharya *et al.*, 2023), suggesting that nano-carbon surfaces can act as ROS-signal modulators. Riboflavin (50–75 ppm) priming of the salt-sensitive *cv.* 'Sadaf' and the tolerant CV. 'Pearl' increased both enzymatic (SOD, POD, CAT, APX, GPX) and non-enzymatic (flavonoids, anthocyanins) antioxidants, augmented soluble sugars and leaf area, and ultimately improved photosynthetic performance under 70 mM NaCl (Iftikhar and Perveen, 2024).

An overview of the types of priming, agents, mechanisms activated, quantitative outcomes, physiological responses, stress types, and genotypic variations for each study is provided in Table 3.

Collectively, these findings reveal a consistent mechanistic hierarchy: (i) rapid induction of SOD-CAT-POD/APX is indispensable for priming success across all stress categories; (ii) secondary layers, ion homeostasis in silicon or $CaCl_2$ priming, phytohormone crosstalk in bacterial or melatonin treatments, xenobiotic detoxification in epibrassinolide priming, and metabolic reprogramming under vitamin or nano-carbon stimuli, determine the magnitude and durability of physiological gains; and (iii) genotype background modulates but does not invert treatment efficacy, as evidenced by stronger responses of tolerant Pearl versus Sadaf or of SB-9617 versus NCEV-1530-9.

This integrative mechanistic evidence is summarised in Fig. 1c. Future biomarker work should couple time-resolved transcriptomics of antioxidant and osmoprotective pathways with metabolite flux analysis across contrasting

Table 3. Antioxidant/redox defence mechanism in biochemical markers physiological response

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Natarajan *et al*., 2022)	Silicon priming	Sodium meta silicate (1-2 mM)	↑SOD, ↑catalase, ↑proline, ↑soluble proteins; ↑osmo-protectants; ↓ROS	↑Phenols (60.4 µg g^{-1}), ↑soluble proteins (30.2 mg g^{-1} DW), ↑SOD (48.1 U mg^{1} protein), ↑CAT (17.2 U mg^{1}) at 75 mM alkali stress, 2 mM Si	↑Phenols, ↑soluble proteins, ↑antioxidants, ↓proline (stress tolerance)	Alkaline (pH, NaCO)	*Zea mays L.* cv CO 8
(Mumtaz et al.*, 2022)*	Bioinoculant	Zn-solubilizing *Bacillus* (ZM20, ZM31, S10, ZM63)	↑APX, ↑POD, ↑SOD; modulated phytohormones	↑Grain Fe (×1.69-1.77), ↑Grain Zn (×1.41-1.50), ↑yield traits (grain wt, stover, HI)	↑Antioxidant enzyme activity, ↑growth, ↑yield, ↑nutrient accumulation	Abiotic (Zn deficiency)	Not reported
(Hussain *et al*., 2023)	Chemical priming	HP (water), $CaCl_2$ 2% (CaP), melatonin 1000 µM (MP)	↑ SOD, ↑ POD, ↑ CAT, ↑ proline, ↑ phenolics, ↑ sugars, ↑ ROS scavenging, ↑ membrane stability, ↑ RWC, ↓ MDA, ↓ HO, ↓ EL	↑ Total soluble sugar 34.6%, ↑ phenolics 61.1%, ↑ proline 45.1%, ↑ protein 34.8%; ↑ SOD 32.5%, ↑ POD 18.2%, ↑ CAT 17.1%; ↓ MDA 35.1%, ↓ H_2O_2 31.3%, ↓ EL 16.9%	↑ Membrane stability index, ↑ RWC, ↓ electrolyte leakage, ↑ antioxidant defense, ↑ physiological parameters	Salt	SB-9617, YH-1898, NCEV-1530- 9
(Fathi *et al*., 2023)	Si priming	↑ Antioxidant enzymes (SOD, CAT, APX, POD), ↑ Photosynthetic pigments, ↑ Fv/Fm index	↑ Antioxidant defense, ↓ Membrane permeability, ↑ Membrane integrity, ↑ Photosynthesis, ↓ H_2O_2, ↓ MDA	Melatonin 150 M: ↓ Herbicide injury (4.6× less), ↑ SOD (2.9×), ↑ CAT (4.6×), ↑ APX (2.4×), ↑ POD (2.0×) under PQ	↑Growth, ↑Photosynthetic pigments, ↑Antioxidant activity, ↓H_2O_2, ↓MDA, ↑Stress tolerance	Oxidative (paraquat)	Sweet corn (*Zea mays L.* var saccharata)
(Mehrian *et al*., 2023)	Hormonal (Strigolactone priming)	24-epibrassinolide (EBL, 10, 0.1, 0.01 µM) and diazinon (DZ)	↑SOD, ↑CAT, ↑POD, ↑APX, ↑ GR, ↑GST, ↑P450 monooxygenas,↑Peroxidase, ↑Carboxylesterase, ↑Starch degradation	0.01 µM EBL: ↑Enzyme activity, ↑ DPPH, ↑ FRAP, ↑Pn, ↑Gs, ↑Proline/protein, ↓MDA (in DZ stress)	↑ Photosynthesis (Pn), ↑ Stomatal conductance (Gs), ↑ Proline, ↑ Protein, ↓ Lipid peroxidation (MDA)	Abiotic (DZ pesticide, salt, drought, heat, metals); Biotic (implied)	Not reported
(Anggarda Gathot Subrata *et al*., 2023)	Biochemical (seed priming)	Melatonin	↑SOD, ↑CAT, ↑POD (antioxidants); ↓lipid peroxidation	↑Shoot/root dry biomass (SDB/RDB), ↑Pn, ↑SOD, ↑CAT, ↑POD, ↑soluble protein	↑Shoot/root biomass, ↑photosynthetic rate (Pn), ↑SOD activity	Salt	Not reported
(Bhattacharya *et al.,* 2023)	Biostimulant	rGO (reduced graphene oxide) + IAA	↑APX/CAT/POD (antioxidants), ↑Plant defence	↑Root length, ↑Shoot length, ↑Biomass (significant)	↑Root/shoot length, ↑Biomass, ↑Antioxidant levels	Abiotic	F2 pollinated maize seeds
(Iftikhar and Perveen, 024)	Chemical priming	Riboflavin (vitamin B2) 0, 50, 75 ppm	↑Antioxidant enzymes (SOD, POD, CAT, APX, GPX), ↑non-enzymatic antioxidants (flavonoids, anthocyanins)	Riboflavin priming ↑leaf area, ↑proteins, ↑soluble sugars, ↑photosynthesis *vs*. non-primed under salt stress	↑Growth rate, ↑total leaf area, ↑total free proteins, ↑total soluble sugars, improved antioxidant defense	Salt	Sadaf, Pearl (maize var.)

genotypes to identify predictive early markers of priming efficacy and clarify how ancillary mechanisms interface with the canonical redox shield in maize.

3.1.4. Growth and biomass

These studies converge on a common biochemical backbone: each priming agent, ranging from a *Peganum harmala/Ailanthus altissima* nano-emulsion to multistage $H_2O \rightarrow KNO_3 \rightarrow H_2O_2$ conditioning, rapidly elevates the canonical antioxidant triad (SOD, CAT, POD/APX), thus restricting early oxidative damage and unlocking stress-specific auxiliary pathways. The 20% nano-emulsion priming of maize variety 704 triggered a transient ROS burst that subsequently upregulated CAT and POD, activated systemic acquired resistance, disrupted pathogen membranes, and boosted fresh biomass by 75% while suppressing soil-borne fungal disease (Almasian *et al.*, 2024). Under abiotic chemical stress, sodium-nitroprusside priming enhanced glyoxalase I/II alongside SOD, GPX, and GR, lowering methylglyoxal toxicity and promoting shoot–root elongation, despite the genotype not being specified (Yiğit and Atici, 2022). Alpha-lipoic-acid seeds exposed to drought showed parallel antioxidant gains together with improved osmotic regulation, translating into approximately 20% grain-yield increases in water-stressed lines 16003 and 16004 (Manavalagan *et al.*, 2024).

Growth-regulator priming with thiamine or IAA under arsenic toxicity raised the NAD(P)H pool, enriched proline and soluble sugars, and sustained photosynthetic gas exchange in the sensitive cultivar ‘Akbar’ and the tolerant ‘Pearl’, confirming that metabolic-reductant buffering can augment classical ROS detoxification (Atif *et al.*, 2022). Melatonin priming of the salt-sensitive hybrid Vega F1 reinforced K^+ and Ca^{2+} retention while lowering Na^+, stabilising chlorophyll and increasing root length, evidence that indoleamine signalling couples antioxidant activation with ion-homeostatic repair (Sezer *et al.*, 2021). Finally, sequential hydro-, osmo-, and redox-priming in hybrid MALKA-2017 elevated total soluble protein by 138%, free amino acids by 178%, and K^+ by 31%, illustrating how staged conditioning can synchronise protein synthesis, compatible-solute accrual, and ion balance to counter soil alkalinity (Imran *et al.*, 2022).

Table 4 presents a comprehensive overview of the priming types, agents, activated mechanisms, quantitative outcomes, physiological responses, stress, and genotypic variations associated with each study.

Taken together, these data reveal a hierarchical mechanistic model depicted in Fig. 1d: (i) rapid antioxidant upregulation is indispensable across all genotypes and stressors; (ii) the chemical identity of the primer dictates the secondary pathway, SAR for nano-emulsion, glyoxalase detoxification for NO donors, osmotic and metabolic-reductant buffering for ALA, thiamine or IAA, ion-homeostatic recalibration for melatonin, and macromolecule–ion synchrony for multistage conditioning; and (iii) the genotype background modulates quantitative but not qualitative gains, as shown by the differential responses of ‘Pearl’ versus ‘Akbar’ and of lines 16003/16004 under drought. This evidence underscores that future maize-priming strategies should tailor auxiliary mechanisms to the anticipated stress while ensuring robust early redox fortification.

3.1.5. Multidimensional assessment of seedling performance

Antioxidant-centred redox fortification serves as the fundamental mechanism that unites all types of focused priming investigations. However, each elicitor engages an auxiliary pathway, such as ethylene regulation, reserve mobilisation, ion or osmolyte homeostasis, or hormone-mediated transcription, to adapt to specific stress conditions and genetic context.

Table 5 provides an exhaustive analysis of the priming types, agents, activated mechanisms, quantitative results, physiological responses, stress factors, and genotype varieties relevant to each study.

Under laboratory moisture stress, magnesium-nitrate salt priming of the single-cross SUNNY-NMH-777 accelerated endosperm catabolism through amylase- and protease-mediated starch mobilisation, doubling germination and vigour indices, evidence that nitrate signalling can synchronise energy release with early ROS surveillance (Singh *et al.*, 2020a). Likewise, nutrient priming with 0.075 mM Se and 10 mM Zn enhanced GPX and APX, while enriching kernel Se and Zn in the droughted *cv.* P1574, translating antioxidant gains directly into a 54% spike in emergence indices (Nawaz F. *et al.*, 2021). Proline and glycine-betaine osmopriming lowered Na^+, raised K^+ and CAT/POX, and improved biomass in an unreported genotype, reinforcing that compatible solutes integrate ionic balance with enzymatic detoxification (Rhaman *et al.*, 2024).

In the drought-sensitive hybrid HC9091, biopriming with *Rhizobium phaseoli* RS-1 plus *Pseudomonas spp.* combined with hydropriming suppressed ethylene *via* ACC-deaminase, intensified SOD, CAT, and osmolyte accumulation, and consequently enhanced photosynthesis, water-use efficiency, and grain yield under 50% field-capacity drought (Nawaz H. *et al.*, 2020). The spring hybrid Pioneer 32F10 benefited when hydropriming was stacked with *moringa* or seaweed extracts plus salicylic acid, ascorbate, or hydrogen peroxide: the cocktail elevated CAT, POD, and SOD, stabilised chlorophyll, and improved stand establishment and yield during alternating heat-and-chill episodes (Afzal *et al.*, 2020). The strigolactone analogue GR24 (0.001-0.1 mg L^{-1}) simultaneously boosted SOD, POD, CAT, and osmolytes in salt-challenged hybrids PB-ProA-2018 and PB-ProA-2019, coupling redox protection with transcriptional reprogramming for salinity tolerance (Iftikhar *et al.*, 2024). Under water deficit, low-dose putrescine priming invoked ABA-modulated GPX

Table 4. Antioxidant/redox defence mechanism in growth and biomass physiological response

Author	Priming Type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Yiğit and Atici, 2022)	Chemical	Sodium nitroprusside (0, 0.5, 0.75 mM)	↑Glyoxalase I and II, ↑SOD, GPX, GR activity, ↓MG accumulation	↑Germination, ↑shoot/root growth, ↓MG, ↑enzyme activity	↑Root/shoot growth, ↓oxidative stress under MG toxicity	methylglyoxal toxicity	Not reported
(Sezer *et al*., 2021)	Melatonin	Melatonin (0, 50, 100, 200 µM)	↑ Photosynthesis, ↓ ROS, ↑ ion homeostasis (↑ K^+, Ca^{2+}; ↓ Na^+); improved chlorophyll content	↑Root length (23.2 cm), ↑Root FW (18.9 g), ↑Root DW (2.9 g); ↓stem length up to 41.67%	↑Stomatal conductance, ↑ion ratios (K^+/Na^+, Ca^{2+}/Na^+), ↑growth parameters	Salt	Vega F1
(Manavalagan *et al*., 2024)	Alpha-lipoic acid	Alpha-lipoic acid (ALA)	↑CAT, ↑SOD, ↑POD activity; ↓lipid peroxidation; better osmotic regulation; improved water relations; ↑non-enzymatic antioxidants	↑Shoot fresh weight (29, 28%), ↑shoot dry weight (27, 24%), ↑100-grain weight (24, 23%), ↑total grain yield (20, 21%) (water-stressed lines 16003, 16004)	Improved growth, ↑shoot fresh/dry weight, ↑grain yield, ↑photosynthetic performance	Water	Not reported
(Imran *et al*., 2022)	Hydropriming, Osmopriming, Redox-priming	H_2O, KNO_3, and H_2O_2	↑Antioxidant enzymes, ↑Protein synthesis, ↑Ion homeostasis, ↓Na^+	RWC ↑16.4%, TSP ↑138%, FAA ↑178%, K^+ ↑31%	↑RWC, ↑TSP, ↑FAA, ↑growth	Alkalinity	Maize hybrid 'MALKA- 2017'
(Atif *et al*., 2022)	Growth regulator	Thiamine (250 mg/L), IAA (30 µM), alone/combined	↑ Antioxidants (↓ H_2O_2, ↓ MDA), ↑ NAD(P)H, ↑ nutrient uptake	↑Proline (34.69, 34.83%), ↑TSS (65.78, 25.84%)	↑Photosynthesis, ↑transpiration, ↑stomatal conductance, ↑ biomass	Arsenic	Akbar (sensitive), Pearl (tolerant)
(Almasian *et al*., 2024)	Nanoemulsion	*P. harmala* 20% and *A. altissima*	↑ROS, ↑Catalase, ↑Peroxidase, Systemic Acquired Resistance (SAR), antifungal membrane/protein disruption	↑Fresh weight (75.2 g), ↑Dry weight (25.2 g), ↑Catalase (6.2 U mg^{-1} min^{-1}), ↑Peroxidase (2.4 U mg^{-1} min^{-1}), ↓Disease symptoms	↑Fresh/dry weight, ↑Enzyme activity, ↓Disease symptoms	Biotic (soil-borne fungi)	*Zea mays* variety 704

Table 5. Antioxidant/redox defence mechanism in seedling performance dimensions physiological response

Author	Priming Type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Nawaz *et al.*, 2020a)	Biopriming, Hydropriming	Rhizobium phaseoli-RS-1 + *Pseudomonas spp.* (bio- priming); distilled water (hydropriming)	↑ ACC-deaminase activity → ↓ ethylene, ↑ ROS defence, ↑ osmolyte regulation, ↑ nutrient uptake	↑ Plant height, ↑ Cob weight, ↑ Grain yield vs control; ↑ under drought	Water-Relation Response: ↑ Photosynthesis, ↑ Transpiration, ↑ WUE, ↑ Stomatal conductance, ↑ Relative water content	Terminal drought (50% field capacity during reproductive stage)	Hybrid cultivar HC9091 (DuPont Pioneer, Pakistan)
(Singh *et al.*, 2020a)	Salt	Magnesium nitrate salt	↑ Amylase & protease activity, ↑ Endosperm catabolism → energy for cell division under stress (biochemical activation)	↑ Germination (↑100% in T5), ↑ SVI, ↑ TI (vs. non-primed)	Vigour Indices Response: ↑ Germination, ↑ Vigour Index (SVI), ↑ Tolerance Index (TI)	Moisture	SUNNY- NMH-777
(Afzal *et al.*, 2020)	Hydropriming, biopriming	MLE + HO, SWE + ASA, SA, 2O2 (various combinations) ↑	↑ ROS-scavenging enzymes (CAT, POD, SOD), ↑ stomatal regulation, ↑ chlorophyll biosynthesis, ↑ thermotolerance ↑	↑ Transpiration rate (MLE+HO, SWE+ASA), ↑ stand establishment, ↑ grain yield ↑	Water-Relation Response: ↑ Photosynthesis, ↑ transpiration, ↑ stomatal conductance, ↑ internal CO2 ↑	Heat, low temperature	Pioneer 32F10 (single-cross hybrid spring maize)
(Nawaz *et al.*, 2021a)	Nutrient priming	Se (0.075 mM), Zn (10 mM), Se+Zn (12 24 h)	↑ Antioxidant enzyme activity (CAT, GPX, SOD, APX), ↑ seed vigour	↑ Se (154%) and Zn (114%) content; ↑ germination indices with Se+Zn	Vigour Indices Response: ↑ GP (52%), ↑ PI (54%), ↑ EI (42%), ↑ VI (35%) with Se+Zn	Drought	*Zea mays* cv. P1574
(Liu *et a*l., 2024)	Drought priming	Not reported	↑Sugar-starch conversion, ↑Seed setting, ↑Starch synthesis, Attenuation of tapetal cell wall invertase (↓sucrose breakdown)	↑Yield: 6.4–33.4% (T5–T8 vs T1); ↑KNS loss mitigated; ↑Fertilized florets by 2.7%	Yield Attributes: ↑Kernel number (KNS), ↑Kernel weight (KW), ↑Seed setting, ↑Yield	Drought, Heat, Combined	Not reported
(Rhaman *et al.*, 2024)	Osmopriming	Proline (Pro), Glycine betaine (GB), Pro+GB	↑CAT, ↑POX, ↓H_2O_2, ↓MDA, ↑K^+, ↓Na^+ (ionic homeostasis)	↑FGP, ↑GI, ↑Biomass, ↑SVI, ↓MGT, ↓MDA, ↓H2O2 with Pro, GB, and Pro+GB under salt stress	Vigor Indices: ↑FGP, ↑GI, ↑Shoot/Root biomass, ↑SVI, ↓MGT, ↑Chlorophyll, ↑RWC, ↑K^+, ↑Stomatal size	Salt	Not reported
(Toledo *et al.*, 2024)	Putrescine priming	Putrescine (10, 100 µM)	↑Free radical elimination, ↑ABA regulation, ↓lipid peroxidation, ↑protein folding, ↑secondary metabolites, ↑GPX (DKB)	↑Root growth (BRS with 10 µM Put), ↑reducing sugars (DKB, 100 µM Put), ↑GPX activity (DKB, stress)	Photochemical Efficiency: ↑Root growth (BRS DKB), ↑photochemical & non-photochemical quenching, ↑stress response	Drought	DKB 390 (tolerant), BRS 1030 (sensitive)
(Iftikhar *et al.*, 2024)	Seed priming (hormonal, synthetic)	GR24 (synthetic strigolactone analogue, 0.001, 0.01, 0.1 mg L)	↑SOD, ↑POD, ↑CAT, ↑ascorbic acid, ↑glycine betaine, ↑free proline, ↑stress gene expression	↑Root length by 31.3%, ↑leaf area by 62%, ↑SOD by 29.6%, ↑POD by 68.3%, ↑CAT by 25%, ↑ascorbic acid by 23.1%, ↑free proline by 42.3%, ↑phenolics by 13%	↑Root length (+31.3%), ↑total leaf area (+62%), ↑enzyme activities, ↑osmolytes	Salt	PB-ProA- 2018 (H1), PB-ProA-2019 (H2)

activity; the tolerant DKB 390 showed stronger root growth and photochemical quenching than the sensitive BRS 1030, demonstrating genotype-dependent translation of redox signals into root architecture (Toledo *et al.*, 2024).

At field scale, an unspecified hybrid exposed to V6 drought priming re-channelled sucrose towards starch, preserved kernel number, and raised yield by up to 33%, underscoring that whole-plant carbon partitioning is orchestrated downstream of redox cues (Liu *et al.*, 2024).

Collectively, these findings define a hierarchical template: rapid activation of SOD – CAT – POD/APX is obligatory; the priming agent then dictates the secondary pathway, ethylene attenuation for rhizobial consortia, hydrolase activation for nitrate salts, micronutrient enrichment for Se + Zn, osmolyte/ion adjustment for Pro/GB, or ABA and strigolactone signalling for polyamines and GR24. Genotype background modulates the quantitative benefit but never reverses the direction, affirming that effective varietal priming in maize must synchronise the canonical redox shield with stress-matched auxiliary mechanisms. This integrative mechanistic evidence is visually summarised in Fig. 1d.

3.2. Hormone crosstalk mechanism

The Hormone Regulation category encompasses priming-induced mechanisms in which endogenous phytohormones and ROS-detoxifying enzymes act in concert to fine-tune stress responses. Hormone crosstalk refers to the dynamic interplay among auxin, gibberellin, abscisic acid, ethylene, salicylic acid, and other signalling molecules, whereby the up-regulation of one pathway modulates the synthesis, sensitivity, or downstream signalling of the others. In seed priming, this coactivation of the antioxidant triad with phytohormone networks ensures that redox homeostasis is synchronised with reserve mobilisation, osmotic adjustment and transcriptional reprogramming, thereby securing germination, seedling vigour, and eventual yield under diverse abiotic stresses.

In four Serbian inbreds (NS 6030, NS 4030, NS 4023, NS 3022), distilled-water hydropriming followed by 4 mM $ZnSO_4$ nutrient soaking amplified DNA-repair activity, metabolic turnover, and multiple phytohormones; the Zn load rose to 298-361 mg kg^{-1} and germination climbed to 93-96%, culminating in an 18% biomass gain in NS 3022 under combined low-temperature and water stress (Gatan *et al.*, 2019). This study illustrates how mineral-driven hormonal cues integrate with antioxidant activation to stabilise chilling-compromised membranes and sustain protein synthesis.

Salicylic-acid priming (1 mM) in the salt-tolerant hybrid PAC 571 and the sensitive SG 17 elevated aldose-reductase, ascorbate-peroxidase, and abscisic acid, while boosting proline accumulation; root dry mass and cob yield rose by 43 and 45%, respectively, at 6 dS m^{-1} NaCl (Islam *et al.*, 2022). The data confirm that SA-induced hormonal and redox adjustments synchronise osmolyte buffering with photosynthetic and stomatal maintenance, yet the magnitude of the benefit scales with the cultivar's intrinsic Na^+-K^+ management capacity.

Polyamine priming with 50-75 ppm spermine or spermidine in the drought-exposed hybrid COH(M) 8 up-regulated GA and IAA, stimulated hydrolytic enzymes and chlorophyll synthesis, and improved osmotic balance. Field emergence reached 91% (*vs*. 86% control) and seed yield increased by 26.7%, underscoring that polyamines act as hormonal amplifiers coupling reserve mobilisation with cell division and elongation during water deficit (Tolay, 2024).

Bio-priming with talc-based *Deinococcus radiodurans* formulations (10 g pot^{-1}, 10^8 CFU g^{-1}) in the maize cultivar PSM3 enhanced shoot length (47.7 cm) and seedling vigour index (5,791.6), with potential mechanisms including phospho-solubilisation via pyrroloquinoline quinone and hormone production (Chitara *et al.*, 2024).

A dual $ZnSO_4$ (0.5%) + *Pseudomonas fluorescens/P. aeruginosa* protocol further exemplified multi-layered signalling: bacterial auxin–gibberellin production, siderophore-mediated micronutrient delivery, and ethylene regulation interacted with Zn-driven redox fortification to raise grain yield by 48% and rows per cob by 15% under drought (Khaledi *et al.*, 2025).

Table 6 summarises the hormone crosstalk priming type, agent material, activated mechanism description, quantitative outcome, physiological response, stress type, and genotype/variety.

Collectively, these studies define a hierarchical template for hormone-centred priming in maize: (i) rapid antioxidant-phytohormone co-activation is obligatory; (ii) the priming agent sets the auxiliary track, Zn-mediated DNA repair, SA-linked osmoprotection, polyamine-driven reserve mobilisation, microbe-facilitated nutrient and hormone delivery, or combined Zn-bacteria ethylene modulation; and (iii) genotype background modulates quantitative but not qualitative gains.

This integrative hormone crosstalk model is illustrated in Fig. 2, which maps the dynamic interaction among the main phytohormones, redox enzymes, and elicitor-specific secondary pathways in maize priming.

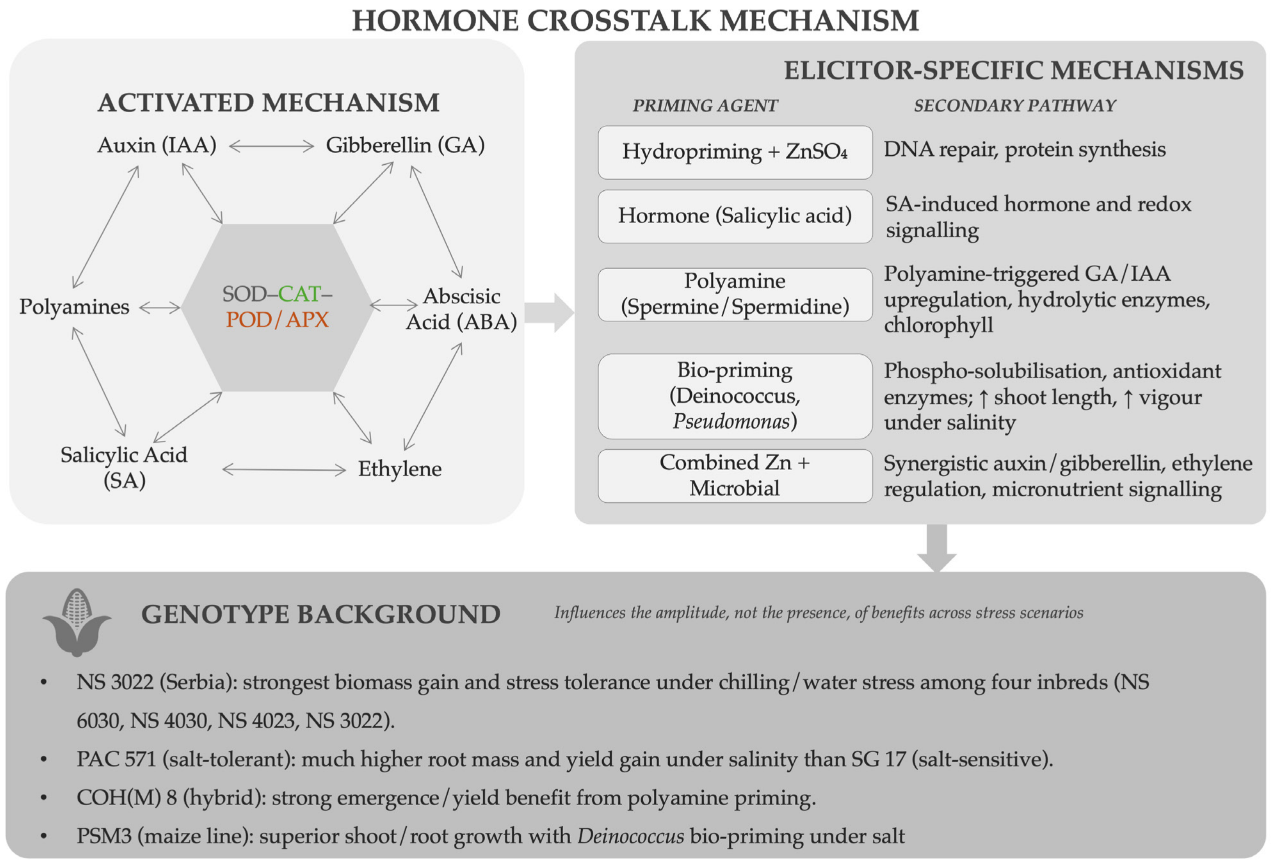
Future work should quantify temporal hormone-ROS kinetics and integrate transcriptomics across contrasting cultivars to refine predictive markers of priming efficacy.

3.3. Osmoregulation and water relations

This mechanism describes the suite of processes by which primed maize seeds and seedlings maintain cellular hydration, turgor, and metabolic continuity under drought or salinity stress. Central to this mechanism is the rapid synthesis or mobilisation of compatible solutes (osmolytes such as proline and glycine betaine), the selective uptake and compartmentation of ions (*e.g.*, Na^+, Cl^-), and enhanced

Table 6. Hormone crosstalk mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Gatan *et al.*, 2019)	Hydropriming and Nutrient priming	Distilled water (hydro), and 4 mM $ZnSO_4$ (nutrient)	↑ DNA repair, ↑ metabolic activity, ↑ phytohormones, ↑ enzyme activation	Zn ↑ to 298-361 mg kg^{-1}; germination 93-96.3%; NS 3022 ↑ 18% weight vs. hydro	↑ Biomass, ↑ seedling dry weight, ↑ protein synthesis & stress tolerance	Low temperature and water stress	Sahiwal-2002 (salt-tolerant), Sadaf (salt- sensitive)
(Islam *et al.*, 2022)	Hormonal	Salicylic acid (SA) 1 mM	↑Aldose reductase, ↑ascorbate peroxidase, ↑ABA, ↑proline	↑Root dry matter by 43%, ↑cob yield by 45%, ↑leaf RWC by 5%, ↑proline by 7% at 6 dS/m	↑Root dry matter, ↑cob yield, ↑leaf RWC, ↑proline, ↑photosynthesis, ↑stomatal conductance	Salt	Not reported
(Tolay, 2024)	Hydropriming	Spermine (50/75 ppm) and Spermidine (50/75 ppm)	↑Phytohormones (↑GA, ↑IAA), ↑hydrolytic enzymes, ↑photosynthesis, ↑chlorophyll, ↑osmolyte balance, improved cell division & elongation	↑Field emergence 91% (vs. 86% control), ↑seed yield 26.7% (5.73 kg/plot *vs.* 4.52 kg/plot control), max height 205.7 cm at 45 DAS	↑Stress tolerance, ↑plant height, ↑biomass, ↑yield, ↑field emergence, ↑photosynthesis, ↑chlorophyll	Drought	Nakhon Sawan 3
(Chitara *et al.*, 2024)	Biopriming	*Deinococcus radiodurans* 38 and R1 (talcum-based, 1×10^8 CFU/g, 10 g/pot)	↑Auxin/gibberellin synthesis, ↑enzyme activity, PQQ production (↑P solubilization), possible novel stress tolerance pathways	↑Shoot length (47.72 cm), ↑root length (10.19 cm), ↑fresh shoot/root weight (3.44/0.39 g), ↑vigour (5791.6)	↑Seed germination, ↑shoot/root length, ↑fresh/dry weight, ↑seedling vigour	Salt	Not reported
(Khaledi *et al.*, 2025)	Zn seed priming + bio-priming	ZnSO4 (0.5%) + *Pseudomonas fluorescens* & *P. aeruginosa*	↑N assimilation, ↑Protein/Nitrate/ Nitrite, ↑Photosynthesis, ↓H_2O_2/MDA, ↑OEC efficiency	ZnSO4 + *P. aeruginosa*: ↑grain yield by 48%, ↑biological yield by 8.9%; ZnSO + both strains: ↑cobs/m2 by 12.5%, ↑rows/cob by 15%	↑Relative water content, ↑cobs/m^2, ↑rows/cob, improved drought resilience	Drought	Not reported



PRIMING AGENT	SECONDARY PATHWAY
Hydropriming + $ZnSO_4$	DNA repair, protein synthesis
Hormone (Salicylic acid)	SA-induced hormone and redox signalling
Polyamine (Spermine/Spermidine)	Polyamine-triggered GA/IAA upregulation, hydrolytic enzymes, chlorophyll
Bio-priming (Deinococcus, *Pseudomonas*)	Phospho-solubilisation, antioxidant enzymes; ↑ shoot length, ↑ vigour under salinity
Combined Zn + Microbial	Synergistic auxin/gibberellin, ethylene regulation, micronutrient signalling

Influences the amplitude, not the presence, of benefits across stress scenarios

- NS 3022 (Serbia): strongest biomass gain and stress tolerance under chilling/water stress among four inbreds (NS 6030, NS 4030, NS 4023, NS 3022).
- PAC 571 (salt-tolerant): much higher root mass and yield gain under salinity than SG 17 (salt-sensitive).
- COH(M) 8 (hybrid): strong emergence/yield benefit from polyamine priming.
- PSM3 (maize line): superior shoot/root growth with *Deinococcus* bio-priming under salt

Fig. 2. Hormone crosstalk activated mechanism in maize (*Zea mays* L.).

water-uptake capacity during imbibition. Together, these adjustments preserve membrane integrity, sustain enzyme activity, and support photosynthetic function by maintaining favourable water potentials and stomatal behaviour. When activated alongside antioxidant defences, osmoregulatory priming ensures that dehydration- or ion-induced water deficits are mitigated before they can compromise seedling establishment.

Phenylalanine soaking, even when described simply as an "implied hormonal/biochemical" treatment, accelerated hydrolase-mediated endosperm weakening and water uptake, thereby elevating total chlorophyll and putative salt tolerance in the contrasting genotypes Sahiwal-2002 and Sadaf (Zahra *et al.*, 2020). In a field context, El-Sanatawy *et al.* (2021a) demonstrated that halopriming with 4 000-8 000 ppm NaCl imparted a molecular "stress memory" characterised by proline accumulation and enhanced osmotic adjustment; this translated into an 8.5% rise in water-use efficiency and a grain-yield advantage of up to 256 kg ha^{-1} under 60-80% evapotranspiration replacement. Complementarily, silicon priming (1 mM) in Nakhon Sawan 3 intensified Rubisco activity, boosted soluble sugars, and raised photochemical efficiency and electron-transport rate by 30%, culminating in a 38% yield increase under 50% field-capacity drought (Sirisuntornlak *et al.*, 2021b).

Multi-factor priming by Ansari *et al.* (2022), combining hydro, halo, and hormonal treatments, showed that salicylic acid each enhanced PSII efficiency, osmotic adjustment, and relative water content (up to 96%), confirming that ion- or hormone-mediated signalling can converge on thylakoid proton-gradient reinforcement to sustain photosynthesis during salinity stress. Finally, a simpler 5 g L^{-1} NaCl soak in the short-duration Nepalese cultivar Arun-2 improved imbibition, dormancy break and enzymatic activation, giving higher germination, shoot length, and water-use efficiency under saline conditions (Mahara *et al.*, 2022).

Table 7 summarises the osmoregulatory priming studies, activated mechanisms, quantitative outcomes, type of stress, and genotype/variety in maize.

Collectively, the evidence delineates a hierarchical mechanism: (i) rapid activation of osmolyte synthesis or osmotic ions (proline, soluble sugars, Na^+/Cl^-) is obligatory; (ii) the priming agent dictates auxiliary pathways, endonuclease/hydrolase acceleration for phenylalanine, proline-centred stress memory for NaCl halopriming, carbon-fixation enhancement for silicon, thylakoid proton-coupling for multi-factor treatments, and seed-enzyme activation for short-term NaCl soaks; and (iii) genotype background modulates the quantitative payoff but not the qualitative direction of the physiological gains.

Table 7. Osmoregulation and water relations mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Zahra *et al*., 2020)	Not specified in terms of type; implied hormonal/biochemical priming	Phenylalanine ↑ salinity tolerance; NaCl used to induce stress	↑ Hydrolase activity → endosperm weakening, ↑ water uptake; activation of stress- response pathways	Not reported	↑ Chlorophyll a, b, and total chlorophyll (suggested); im- plied ↑ salt tolerance	Salt	Sahiwal- 2002 (salt- tolerant), Sadaf (salt- sensitive)
(Attia *et al*., 2022)	Biochemical / Organic biostimulant (algal extract priming)	Seaweed extracts: Halimeda opuntia, Padina pavonica	↑ Stress memory, ↑ proline accumulation, ↑ osmoregulation; improved biochemical stability	↑ Grain yield: 7055 kg/ha (4000 ppm) vs 6799 kg/ha (control); ↑ WUE by 8.5%; ↑ cob traits	↑ Germination %, ↑ vigour index, ↑ biomass, ↑ drought tolerance	Drought	Not reported
(Sirisuntornlak *et al*., 2021b)	Silicon	Silicon	↑ Rubisco activity; ↑ photosynthetic rate; ↑ TSS; ↓ proline	↑ Growth and yield (↑ 38%) with 1 mM Si under drought	↑ Photochemical efficiency (33%), ↑ ETR (31%), ↓ proline, ↑ sugar	Drought	Nakhon Sawan 3
(Ansari *et al*., 2022)	Hydropriming, Halopriming, Hormonal	Distilled water, NaCl (75, 150 mM), Salicylic acid (1, 2 mM), $CaCl_2$ (34 mM), $Ca(NO_3)_2$ (20 mM)	↑ PSII efficiency, ↑ active RCs, ↑ osmotic adjustment, ↑ proton gradient in thylakoid	↑ FV/FM, ↑ FV/FO, ↑ qP, ↑ water uptake	↑ CCI (up to 2.99), ↑ RWC (up to 96.3%), ↑ osmotic adjustment	Salt	Not reported
(Mahara *et al*., 2022)	Chemical	*Azotobacter vinelandii* (40%, 80%)	↑N assimilation, ↑Protein/Nitrate/Nitrite, ↑Photosynthesis, ↓H_2O_2/MDA, ↑OEC efficiency	↑Germination %, ↑shoot length, ↑leaf number	↑WUE, ↑germination %, ↑seedling vigour	Salt	DK-8148 (moderately salt-sensitive)

Table 8. Photosynthetic protection mechanism

Author	Priming Type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Seifikalhor *et al*., 2020)	Biostimulant priming: *Spirulina platensis*, Salep gum, *Spirulina platensis* + Salep gum	*Spirulina platensis* (cultured in liquid), Salep gum (3%)	SP enhances PSII efficiency and NPQ, minimizes oxidative stress, improves water absorption and reduces Cd uptake	↑ Growth under Cd stress; ↓ Cd root-to-shoot translocation after 12 days	↑ Fv/Fm, ↑ NPQ, ↓ Cd accumulation in shoots	Cadmium toxicity	*Zea mays L.* var. ”260” (Karaj Agricultural Research Institute, Iran)
(Attia *et al*., 2022)	Biochemical / Organic biostimulant (algal extract priming)	Seaweed extracts: Halimeda opuntia, Padina pavonica	↑Secondary metabolite biosynthesis, ↑photosynthetic pigment synthesis, ↑defence enzyme activity	SWE treatment ↑root/shoot fresh/dry weight, ↑pigment & K^+ content *vs.* untreated stressed plants	↑Root/shoot weight, ↑K^+, ↑chlorophyll a/b, ↑carotenoids, ↓Na^+, ↓proline, ↑protein, ↑phenols/alkaloids	Salt	*Zea mays* (TWC 310)
(Nida *et al*., 2024)	Microbial	*Azotobacter vinelandii* (40%, 80%)	↑N assimilation, ↑Protein/Nitrate/Nitrite, ↑Photosynthesis, ↓H_2O_2/MDA, ↑OEC efficiency	↑Growth and photosynthetic efficiency, ↑Osmotic adjustment, especially at 40% priming	↑N assimilation, ↑Chlorophyll, ↑Photosynthetic efficiency, ↓Stress markers	Salt	DK-8148 (moderately salt-sensitive)

The integrated osmoregulation and water-relations model is illustrated in Fig. 3, mapping the pathway from osmolyte synthesis and ion regulation to downstream seedling vigour, yield, and physiological adaptation.

Therefore, designing osmoprotective priming protocols for maize should integrate a robust water-relation trigger with stress-specific auxiliary processes while accounting for varietal osmotic capacity.

3.4. Photosynthetic protection

Across maize varieties, photosynthetic-protection priming consistently stabilises the photo-system II (PSII) apparatus and downstream carbon assimilation, irrespective of the stressor applied. Biostimulant seed conditioning with *Spirulina platensis* and Salep gum in '260' maize enhanced PSII quantum efficiency (↑ Fv/Fm) and non-photochemical quenching, curtailed Cd root-to-shoot transfer, and ultimately sustained biomass production under 200 mg Cd kg^{-1} soil, indicating that improved water uptake and reduced Cd permeability are pivotal to the observed tolerance (Seifikalhor *et al.*, 2020).

Under ionic (NaCl) stress, organic biochemical priming with *Halimeda opuntia* and *Padina pavonica* seaweed extracts in *cv*. TWC 310 intensified secondary-metabolite biosynthesis and pigment accumulation, leading to higher root-shoot dry matter, elevated K^+/Na^+ ratios, and suppressed proline build-up, responses that collectively denote efficient osmotic adjustment and ion homeostasis (Attia *et al.*, 2022). Complementarily, microbial priming with *Azotobacter vinelandii* (40% suspension) in the moderately salt-sensitive hybrid DK-8148 increased nitrate reduction, chlorophyll content, and oxygen-evolving complex efficiency, while lowering H_2O_2 and MDA, thereby coupling enhanced nitrogen metabolism with reinforced antioxidant defence to secure photosynthetic capacity under salinity (Nida *et al.*, 2024).

Table 8 summarises the photosynthetic protection priming studies, activated mechanisms, quantitative outcomes, type of stress, and genotype/variety in maize.

Collectively, these studies reveal that, whether the elicitor is algal-derived metabolites, cyanobacterial biomass, or diazotrophic bacteria, the mechanistic convergence lies in safeguarding PSII integrity, optimising ionic balance, and minimising oxidative load, which together translate into improved growth metrics across cadmium- and salt-challenged maize genotypes.

3.5. Reserve mobilisation

Reserve Mobilisation refers to the priming-induced activation of seed-resident hydrolases, principally amylases and proteases, which break down starch and storage proteins into soluble sugars and amino acids. These readily usable substrates fuel early metabolic processes, support ATP synthesis for radicle protrusion, and generate osmolyte

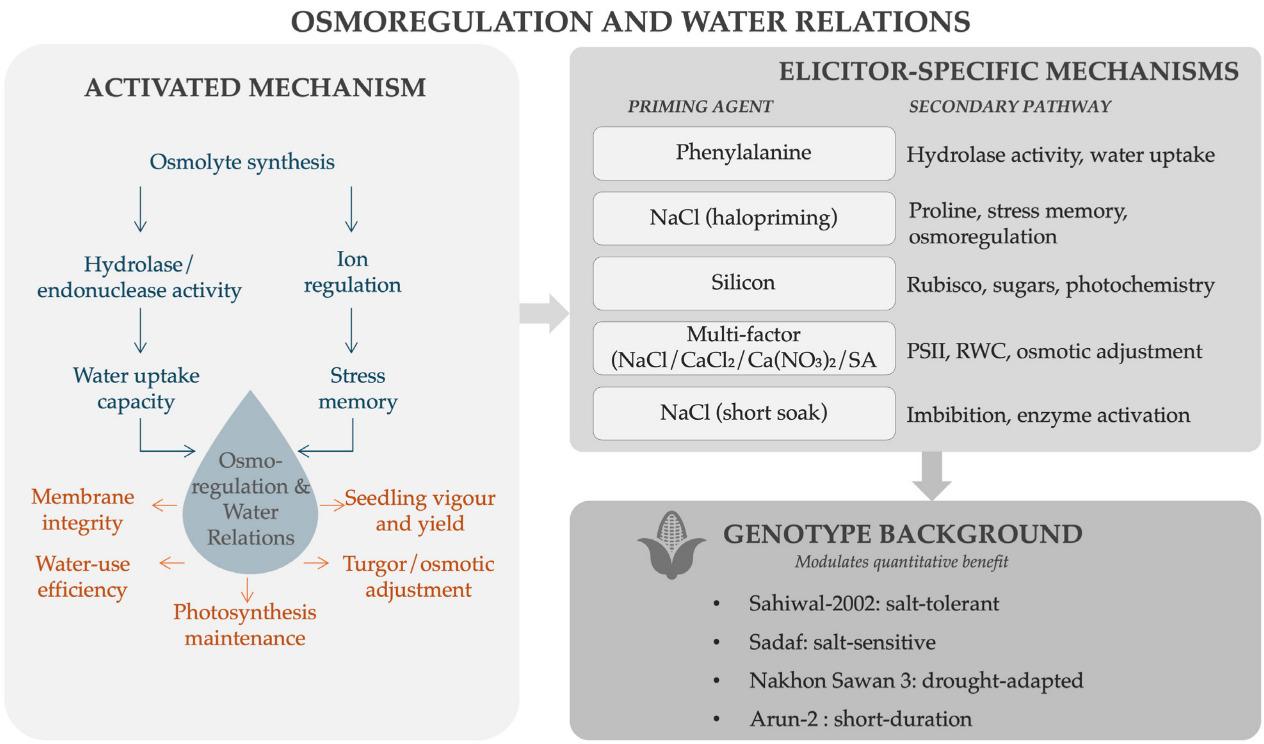


Fig. 3. Osmoregulation and water relations activated mechanism in maize (*Zea mays* L.).

precursors for cell expansion. By synchronising reserve degradation with stress-buffering pathways (*e.g.* antioxidant defence, osmotic adjustment), this mechanism ensures that emerging maize seedlings possess both the energetic and structural resources required to establish vigour and withstand subsequent abiotic challenges.

Table 9 summarises the reserve mobilisation priming studies, activated mechanisms, quantitative outcomes, type of stress, and genotype/variety in maize.

Hydropriming combined with seed hardening using distilled water promoted marked increases in α- and β-amylase activities and ATP generation; these biochemical shifts translated into superior emergence, greater seedling vigour, longer root–shoot axes and, ultimately, a 4-6% rise in grain yield and crop water productivity under both moderate and severe water-deficit regimes (El-Sanatawy *et al.*, 2021b). When the priming agent was switched to botanically derived biostimulants, such as garlic and *Moringa oleifera* extracts, a similar mobilisation of carbohydrate reserves (α-amylase) was accompanied by heightened chitinase and peroxidase activities, indicating simultaneous reinforcement of defence pathways.

These molecular adjustments improved germination parameters and seedling biomass of the single-cross hybrid 168 exposed to 100 mM NaCl and other biotic–abiotic challenges, underscoring the versatility of enzyme-centred reserve mobilisation across distinct stressors (Ahmed, 2023). Extending the concept to materials science, biopolymer-based priming with crab-shell and green polymers, and especially a synthesised BP1 formulation (1.6%), intensified amylase- and protease-mediated degradation of starch and storage proteins. The resultant surge in soluble substrates was reflected in higher seed vigour indices, faster germination, and enhanced seedling growth even in dual salt stress imposed by NaCl and Na_2CO_3 (Ponnarmadha, 2022).

Collectively, these studies demonstrate that, irrespective of the priming matrix, aqueous, phytochemical, or polymeric, the mechanistic hallmark is a coordinated up-regulation of reserve-degrading enzymes that augments metabolic energy pools. This enzymatic acceleration supplies both the respiratory ATP required for radicle protrusion and the osmolyte precursors essential for cell expansion under osmotic or drought pressure. The consistent positive translation of these biochemical events into agronomic performance (yield, water productivity) and early-stage physiological metrics (vigour, biomass) confirms reserve mobilisation as a central lever for priming-induced resilience across maize genotypes and stress spectra.

3.6. Gene/signal modulation

Gene/Signal Modulation refers to priming-induced alterations in gene expression and signal-transduction cascades that act as the upstream triggers for all downstream physiological defences. By modulating transcription factors, kinases, and second-messenger pathways (*e.g.* Ca^{2+}, ROS, phytohormone cross-talk), this mechanism reprogrammes the seed's stress-response "blueprint" during imbibition, ensuring that antioxidant-defence enzymes, osmotic-adjustment systems, and reserve-mobilisation pathways are deployed in a coordinated fashion.

Table 10 summarises the gene/signal modulation priming type, agent material, activated mechanism description, quantitative outcome, physiological response, stress and genotype/variety.

Hydropriming, achieved through on-farm water soaking, re-establishes osmotic balance in dry-land Ethiopian soils by allowing a controlled, stepwise rehydration of the embryo, thereby preventing imbibitional injury, restoring redox poise, and accelerating respiratory restart. Sime and Aune (2020) showed that the drought-adapted cultivar Melkassa-2 primed in this way emerged earlier and more uniformly, shortened its vegetative phase, and ultimately yielded 6-11% more grain under rain-fed conditions and up to 75% more when hydropriming was combined with micro-dosed nutrients. These physiological gains are best explained by the rapid activation of antioxidant enzymes and ATP-generating pathways that sustain seedling growth during intermittent moisture deficits.

By contrast, silicon priming at 1-2 mM in the Thai hybrid Nakhon Sawan 3 operated through structural fortification and osmoprotective chemistry. Sirisuntornlak *et al.* (2021a) demonstrated that Si deposition in cell walls and the concurrent up-regulation of antioxidant defences increased relative water content, leaf area, and photosynthetic integrity under controlled drought stress; this translated into an 11% increase in cob length, 47% more kernels, and an overall 11% yield boost. The data indicate that Si strengthens mechanical barriers and scavenges ROS, thereby preserving tissue hydration and sink strength during dehydration events.

Collectively, these studies confirm that priming-induced gene and signal modulation provides a versatile entry point for drought resilience in maize. While both hydro- and silicon-based treatments activate core antioxidant and metabolic pathways, the dominant physiological levers differ: hydropriming optimises early water-uptake kinetics and metabolic reactivation, whereas silicon priming fortifies structural and antioxidant safeguards that prolong tissue hydration. Aligning the chemistry of the priming agent with a genotype's inherent stress-adaptation strategy is therefore critical for maximising agronomic returns.

3.7. Growth and primary metabolism

This mechanism describes the priming-induced reactivation and optimisation of central metabolic pathways that supply energy, reducing power and carbon skeletons for cell division and expansion during early imbibition. This mechanism encompasses the upregulation of plasma-membrane H^+-ATPase to restore the proton-motive force, enhanced

Table 9. Reserve mobilisation mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(El-Sanatawy *et al*., 2021b)	Hydropriming and hardening	Distilled water and hardening solution	↑ - and -amylase, ↑ ATP production	↑ Yield (7468-7612 *vs*. 7186 kg/ha), ↑ CWP	↑ Germination, ↑ seedling vigour, ↑ root/shoot length	Water deficit (moderate/ severe)	Not reported
(Ahmed, 2023)	Natural extract priming	Garlic extract (0.25-1.0 g), *Moringa oleifera* extract (0.25 g)	↑Enzyme activities (chitinase, peroxidase), ↑- amylase, ↑metabolic activity	Not reported	↑Germination, ↑seedling vigour, ↑shoot/root length, ↑seedling weight	Salt	Maize single cross hybrid 168
(Ponnarmadha, 2022)	Biopolymer	Crab shell extract (CE), green polymer (GP), synthesised biopolymer (BP 1; 1.6%)	↑Amylase, ↑Protease activity, ↑starch/protein mobilisation	BP1 (0.4–1.6%) ↑seed vigour, ↑germination, ↑enzyme activity vs. control, CE, GP	↑Seedling growth, ↑seed vigour index, ↑germination, ↑enzyme activity (amylase, protease)	Salt	Not reported

Table 10. Gene/signal modulation mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
Sime and Aune (2020)	Hydropriming	Water (on-farm soaking, surface-drying)	Not molecularly detailed; general ↑ biochemical activity, ↑ seedling vigour, ↑ stand uniformity	↑ Grain yield: 11% (Melkassa), 8% (Ziway), 6% (Hawassa); ↑ with micro-dosing: 75, 69, 33%	↑ Emergence, ↑ Vigour, ↑ Uniformity, ↑ Flowering earliness (2–3 days), ↑ Maturity earliness (10–13 days)	Soil moisture stress (semi-arid, variable rainfall, dry spells)	*Zea mays L. var*. Melkassa-2 (120-130 days to maturity)
Sirisuntornlak *et al*. (2021a)	Seed priming with silicon	Si (0, 1, 2 mM)	↑ Biochemical defense, ↑ water status (general)	↑ Cob length (11%), ↑ kernels/cob (47%), ↑ grain yield (11%)	↑ RWC, ↑ leaf area, ↑ plant height, ↑ kernel number	Water-deficit stress	Nakhon Sawan 3

respiratory flux through NAD(P)H turnover, and increased carbon partitioning via the pentose phosphate and shikimate pathways, collectively ensuring that both ATP and precursor molecules are available to sustain growth under stress.

Table 11 summarises the growth and primary metabolism priming type, agent material, activated mechanism description, quantitative outcome, physiological response, stress, and genotype/variety.

Acid priming of the Baghdad-3 cultivar with humic, ascorbic, and citric acids promoted a sharp rise in plasma-membrane H^+-ATPase activity, thereby strengthening the proton-motive force that drives nutrient uptake and energises downstream respiration (Kadhim and Hamza, 2021). The resulting acceleration of enzymatic reactions translated into higher emergence percentages, shorter emergence time, and enhanced seedling vigour under the combined constraints of low temperature and drought, outcomes that underscore the centrality of membrane energisation for sustaining metabolism when water availability and thermal energy are both limiting. By contrast, nitrate-based physiological conditioning with calcium and potassium nitrates intensified cytosolic redox turnover, as evidenced by elevated NAD(P)H oxidation and greater flux through the pentose-phosphate and shikimate pathways (Burin *et al.*, 2021). These reactions increased the supply of reducing equivalents and aromatic precursors, thereby reinforcing both antioxidant capacity and the provision of carbon skeletons for growth. Under low-temperature incubations and in broader abiotic stress scenarios that included hypoxia, salinity, and drought, this biochemical reprogramming boosted first-count germination, total germination, and speed indices, indicating a robust enhancement of early metabolic readiness even though the specific genotype was not reported.

Collectively, both studies confirm that priming-induced modulation of primary metabolism is a versatile route to stress resilience in maize, but the operative mechanisms differ. Acid priming amplifies proton pumping to secure nutrient inflow and respiratory restart, a mechanism well-suited to cultivars like Baghdad-3 that confront concurrent drought and chilling. Nitrate priming, in turn, augments cytosolic redox cycling and carbon diversion into anabolic pathways, providing a broader buffer against multiple abiotic stresses. These complementary modes of action highlight the need to align priming chemistry with anticipated stress factors and cultivar physiology to maximise agronomic gains.

3.8. Defence and immunity

This mechanism refers to those priming-induced processes that bolster a maize seedling's capacity to resist biotic threats by activating both innate and induced immune responses. This mechanism encompasses the stimulation of antimicrobial metabolite synthesis (*e.g.*, phytoalexins, siderophores), the elevation of hydrolytic enzymes (chitinases, glucanases), the modulation of phytohormones (auxin, salicylic acid, jasmonates), and the reinforcement of membrane integrity through antioxidant protection. By pre-arming the rhizosphere and cellular defence networks, priming ensures that seedlings can rapidly detect and neutralise pathogen incursions while maintaining growth under concurrent abiotic stresses.

Table 12 summarises the defence and immunity priming type, agent material, activated mechanism description, quantitative outcome, physiological response, stress, and genotype/variety.

Biopriming with *Pseudomonas spp*. K3HPSB2 and biochemical-hydropriming with melatonin both reinforce maize defence pathways, yet they do so through distinct proximal signals tailored to different stressors. Indhuja *et al.* (2021) demonstrated that coating seed with a *Pseudomonas migulae* analogue elevates indole-3-acetic acid, siderophore release, hydrolytic enzymes, and antifungal metabolites, thereby strengthening rhizosphere-mediated immunity against root-wilt disease. The resulting enhancement of germination percentage and seedling-vigour index indicates a rapid transition from innate to induced systemic resistance, even though cultivar identity was not disclosed, an information gap that limits genotype-specific extrapolation.

Conversely, Hussain *et al.* (2024) applied 500-1 500 µM melatonin during hydropriming, targeting salt-induced oxidative imbalance across six inbred and composite genotypes (MMRI-Yellow, NCEV-1530-9, YH-1898, Composite, SB-9617, FH-949). Melatonin suppressed lipoxygenase activity while boosting nutrient assimilation and protein biosynthesis, thereby reducing membrane injury. These biochemical adjustments translated into promptness-index gains of up to 6.25 and a threefold improvement in the seedling-vigour index, with SB-9617 showing the greatest responsiveness.

Collectively, the data underscore that defence-oriented priming leverages either microbe-driven phytohormone and metabolite secretion (biopriming) or exogenous antioxidant provisioning (melatonin priming) to converge on enhanced early growth. While both strategies elevate vigour metrics, biopriming primarily mobilises rhizosphere signalling against biotic challenges, whereas melatonin recalibrates cellular redox status to counter ionic and osmotic toxicity.

Integrating cultivar-specific responses, absent in but explicit in, will be essential for refining priming prescriptions that align mechanistic triggers with both stress profile and genetic background.

3.9. Stress memory/root development

The Stress Memory/Root Development mechanism describes how early mild drought episodes act as a biological "primer" that induces lasting adaptations in root architecture and water-foraging capacity. Through transient elevations of abscisic acid and reactive-oxygen species, these *in situ* cues trigger chromatin remodelling

Table 11. Growth and primary metabolism mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Kadhim and Hamza, 2021)	Acid priming (Hu-mic, Ascorbic, Citric)	Humic acid, Ascorbic acid, Citric acid	↑ H-ATPase activity, ↑ nutrient transport	↑ Emergence %, ↓ emergence time	↑ Respiration, ↑ enzymatic reactions, ↑ seedling vigor	Low temp +drought	Baghdad 3 cultivar
(Burin *et al*., 2021)	Chemical priming (physiological conditioning)	Calcium nitrate, potassium nitrate, other nitrates (unspecified)	↑ NAD(P)H oxidation, ↑pentose phosphate pathway, ↑ shikimic acid pathway, ↑ low-temp tolerance	↑ First germination count, ↑ total germination, ↑ speed index with nitrate treatments	↑ Germination %, ↑ speed,↑ early vigor under low- temperature	Abiotic stress: low-temp, hypoxia, salt, drought	Not reported

Table 12. Defence and immunity mechanism

Author	Priming type	Agent / Material	Activated mechanism	Quantitative outcome	Physiological response	Stress type	Genotype / Variety
(Indhuja *et al*., 2021)	Biopriming	Green fluorescent *seudomonas spp.* K3HPSB2 (99% match with *P. migulae*)	↑ IAA, antifungal metabolites, siderophores, hydrolytic enzymes	↑ Germination %, ↑ seedling igour vs control	↑ Germination %, ↑ seedling vigour index	Biotic stress: root wilt disease (RWD); also mentions nutrient/ water uptake (abiotic)	Not reported
(Hussain *et al*., 2024)	Hydropriming, Biochemical	Melatonin (500, 1000, 1500 µM), H_2O (control)	↓Lipoxygenase activity, ↑Nutrient use, ↑Protein formation, ↓Membrane damage	PI: SB-9617=6.25; max PI with 1500µM=5.56; SVI: SB-9617=763.4, Composite = 247.8; melatonin reduced adverse effects on germination/seedling	↑Promptness index (PI), ↑Seedling vigour index (SVI), ↑Shoot length, ↑Fresh shoot weight	Salt	MMRI-Yellow, NCEV-1530-9, YH-1898, omposite, SB-9617, FH-949

Table 13. Stress memory/Root development mechanism

Author	Priming type	Activated mechanism	Physiological response	Stress type	Genotype / Variety
(Aguilar *et al*., 2021)	Stress-induced priming (early drought)	↑ Root system development; earlier mild drought → improved stress memory and root response	↑ Root depth and density; ↑ drought tolerance; ↑ detection rates	Abiotic stress: drought at different growth stages	H003, H014 (among four hybrids tested)

and hormonal reprogramming at key root-growth loci, effectively "remembering" the stress and hard-wiring enhanced meristematic activity. The result is deeper and denser root systems that maintain hydraulic function and growth during subsequent water deficits, without the need for exogenous chemical priming.

Table 13 summarises the stress memory/root development priming type, agent material, activated mechanism description, quantitative outcome, physiological response, stress, and genotype/variety.

Early-season mild drought events can function as an *in situ* priming cue that establishes "stress memory," thereby re-programming root developmental pathways for improved water foraging in later growth stages. In maize hybrids H003 and H014, Aguilar *et al.* (2021) showed that an imposed early drought episode, without any exogenous chemical agent, enhanced both root depth and lateral density, effects that persisted through subsequent drought cycles. The authors linked this phenotype to a mechanistic axis centred on stress-induced chromatin and hormonal remodelling: transient water deficit is proposed to elevate ABA and ROS signalling, which in turn reshapes histone-modification patterns at root-growth loci, locking in a higher baseline of meristematic activity. Although quantitative yield gains were not reported, the documented increases in root system architecture, drought tolerance scores, and soil-water detection rates provide physiological evidence that the primed plants not only survive but also maintain growth under repeated water limitation.

Collectively, these results underscore that endogenous drought priming, even in the absence of added biochemical agents, can hard-wire plastic root architectures through epigenetic and hormonal circuits, offering a genotype-specific route (effective in H003 and H014 but less so in the other two hybrids tested) to sustain productivity in water-scarce environments.

4. DISCUSSION

This review answers the central research question: *How do distinct seed priming strategies in maize map onto core mechanistic pathways and physiological responses under varying stress conditions?* The findings demonstrate that distinct seed priming strategies in maize, despite their diversity in agent and application, converge upon a core mechanistic pathway centred on rapid antioxidant/redox defence (notably SOD-CAT-POD/APX induction), which is universally necessary for early stress protection across all stress types.

The chemical identity of the priming agent determines the secondary pathway, whether osmoregulation, hormone crosstalk, reserve mobilisation, or gene/signal modulation, thus tailoring the physiological response to the specific stress condition (*e.g.*, drought, salinity, heat).

Physiological outcomes such as germination, seedling vigour, growth, and yield are therefore orchestrated by a hierarchical, context-dependent mechanism in which robust redox fortification is layered with stress-matched auxiliary processes.

Genotype background modulates the quantitative magnitude of these responses but does not alter their direction, with tolerant varieties consistently translating priming-induced mechanisms into greater physiological gains. This multi-level mapping is visually summarised in the Sankey diagram and substantiates the centrality of harmonised antioxidant induction and auxiliary mechanisms as the cornerstone of effective maize seed priming under variable stress environments.

The diagram depicted in Fig. 4 shows that, regardless of the priming type or stress context, the antioxidant/redox defence mechanism stands as the principal convergence point. This mirrors extensive experimental findings, *e.g.*, SOD, CAT, and POD/APX induction consistently marks the first defence line, as repeatedly documented in nitrate, silicon, and biostimulant priming. All classes, hydropriming, chemical, hormonal, biostimulant, and even biopriming, ultimately channel their effects through this pathway.

This supports the Results section's observation that early-stage ROS detoxification is both necessary and broadly sufficient to preserve membrane stability, promote germination, and secure seedling vigour.

Multiple priming types intersect with similar stress types and mechanisms, confirming the redundancy and robustness of the system. For instance, hydropriming, osmopriming, and biostimulant priming all connect with drought/water deficit and salinity stresses, each mobilising both redox and osmoprotective processes. Conversely, unique pathways are visible, *e.g.*, hormonal priming and polyamine treatments diverge into hormone crosstalk or gene/signal modulation, underscoring the results on agent-specific auxiliary mechanisms (Tolay, 2024; Chitara *et al.*, 2024).

The intermediate stress type column demonstrates how priming effects are filtered by the prevailing abiotic or biotic constraint. For example, drought and salinity consistently map onto osmotic/ion homeostasis and antioxidant activation, whereas heat, heavy metals, and oxidative stresses see greater engagement of reserve mobilisation, gene regulation, or photosynthetic protection (Sezer *et al.*, 2021; Chen *et al.*, 2021; Basit *et al.*, 2020; Fathi *et al.*, 2023).

Downstream physiological responses (germination, vigour, photosynthetic capacity, biochemical markers, growth, yield, and more) are reached by both direct (*e.g.*, antioxidant to vigour) and indirect/multistep (*e.g.*, priming → gene modulation → hormone crosstalk → yield) pathways.

The presence of parallel connections to multiple responses underscores that no single mechanism is sufficient for broad-spectrum stress resilience; rather, the strongest outcomes are achieved when early antioxidant fortification is layered with context, specific auxiliaries

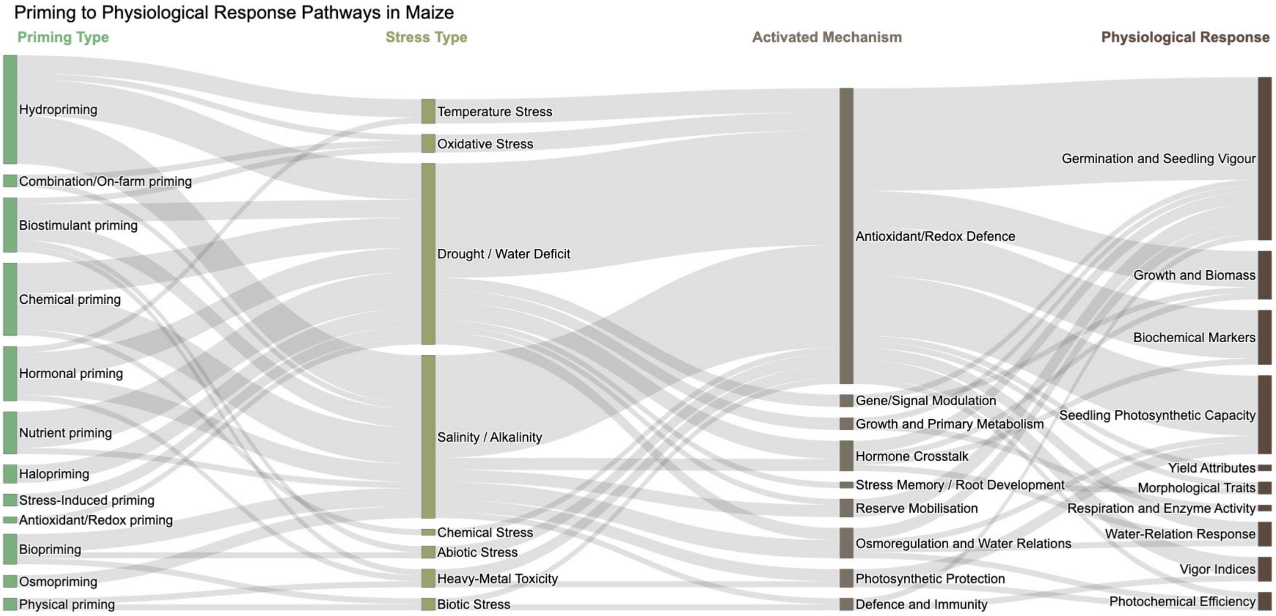


Fig. 4. Multi-stage Sankey diagram mapping priming type, stress context, activated mechanism, and physiological response in maize seed priming studies.

like osmotic regulation, hormone synchrony, or reserve mobilisation (Singh *et al.*, 2020b; Mehrian *et al.*, 2023; Imran *et al.*, 2022).

While genotype is not explicitly a node in the diagram, the Results clearly indicate that varietal background modulates the quantitative outcome along these paths. For instance, the more robust physiological gains seen in tolerant lines like 'Pearl', 'SB-9617', 'Vega F1', or 'Pioneer 30Y87' compared to their sensitive counterparts are always routed through the same mechanistic core, but with amplified magnitude (Kakar *et al.*, 2023; Khaliq *et al.*, 2024; Sezer *et al.*, 2021).

Collectively, this mechanistic mapping highlights the essential role of robust early redox fortification, supplemented with auxiliary mechanisms specific to context and genotype, in providing sustained stress resilience to maize.

4.1. Mechanistic breadth and depth

Recent literature on maize seed priming reflects a pronounced advance in mechanistic understanding, particularly regarding the rapid activation of superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD/APX), across nearly all priming contexts and stress types (Hussain *et al.*, 2023; Kakar *et al.*, 2023; Nawaz M. *et al.*, 2021; Fathi *et al.*, 2023; Manavalagan *et al.*, 2024). These findings substantiate the centrality of redox homeostasis as a universal gateway to stress resilience in maize. However, comparative analysis reveals that studies diverge in the breadth of secondary mechanisms explored: while some works focus exclusively on ROS detoxification and membrane stability (Mir *et al.*, 2021; Muhammad *et al.*, 2023), others provide nuanced delineations of ion/osmolyte homeostasis (Kasana *et al.*, 2025), reserve mobilisation (Gnawali and Subedi, 2021), metabolic cycling (Bhattacharya *et al.*, 2023), or hormone crosstalk (Tolay, 2024; Chitara *et al.*, 2024). The present synthesis demonstrates that the most effective priming agents not only induce rapid redox fortification but also engage multiple context-dependent auxiliary pathways, producing robust and durable physiological gains under complex stress regimes (Rehman *et al.*, 2024; Afrouz *et al.*, 2023).

4.2. Integration of genotype-dependent responses

A critical finding of this synthesis is that genotype background modulates the quantitative but not qualitative outcomes of seed priming. Across all 72 studies analysed, tolerant genotypes (*e.g.*, 'Pearl', Sargodha 2002 White, MNH360, AR68) consistently translated priming-induced mechanisms into larger absolute improvements in germination, antioxidant activity, and physiological markers compared to their sensitive counterparts (*e.g.*, 'Sadaf', 30T60, KSC703, Yuecainuo2). However, the *direction* of priming benefit remained positive in all cases, regardless of genotype. For example, *Moringa oleifera* leaf extract priming increased antioxidant activity by 22-56% in the salt-tolerant Pioneer 30Y87 but yielded only modest gains in the sensitive Pioneer 30T60 (Khaliq *et al.*, 2024). Similarly, melatonin priming stabilised chlorophyll and improved ion homeostasis in Vega F1, with the magnitude of K^+/Ca^{2+} retention scaling with the cultivar's intrinsic stress tolerance (Sezer *et al.*, 2021). This pattern suggests that the universal antioxidant core (SOD-CAT-POD/APX) operates across all genetic backgrounds, while genotype-specific ion transport capacity, membrane stability, and osmotic adjustment systems amplify or attenuate the downstream physiological gains. Formal statistical analysis of genotype × mechanism × stress interactions was not possible in this review due to the heterogeneity of experimental designs, measurement protocols, and stress intensities across the review. Future work should employ standardised factorial designs testing multiple genotypes under multiple stress intensities with common measurement protocols to enable robust partitioning of genotype, environment, and management effects, thereby refining predictive models for cultivar-specific priming recommendations.

4.3. Mechanism-physiology mapping across stress types

A systematic comparison highlights that successful priming strategies exhibit precise mechanisms-physiology mapping tailored to the predominant stressor. Under drought and salinity, osmoregulatory and ion-homeostatic adjustments, often mediated by proline, glycine-betaine, or potassium-nitrate priming, consistently enhance water-use efficiency, chlorophyll retention, and yield components (Rhaman *et al.*, 2024; Rehman *et al.*, 2024; Nawaz M. *et al.*, 2021). In contrast, heat, cold, and oxidative stress contexts benefit from priming regimes that augment membrane repair, stress memory, and metabolic cycling (Afrouz *et al.*, 2023; Kamseu-Mogo *et al.*, 2024; Natarajan *et al.*, 2022). These trends confirm that the secondary mechanism mobilised by a given primer, be it reserve mobilisation, DNA repair, or hormonal amplification, determines the magnitude and durability of the physiological response (Chipilski *et al.*, 2023; Farman *et al.*, 2022). Thus, the integration of multi-level mechanistic readouts is essential for matching priming interventions to specific environmental constraints.

4.4. Agronomic and functional translation

While most studies report significant improvements in early-stage germination, seedling vigour, and biochemical markers, relatively few extend these mechanistic insights to field-scale agronomic performance. Notable exceptions include the demonstration of enhanced yield, kernel number, and drought resilience following hydropriming, biostimulant, or multi-modal priming treatments in field trials (Liu *et al.*, 2024; Manavalagan *et al.*, 2024; Afzal *et al.*, 2020; Mumtaz *et al.*, 2022). This review highlights a critical gap in the literature: the need for integrative studies that bridge physiological measurements with harvestable yield and economic outcomes. Future research should employ multi-season, multi-location trials to validate the functional translation of laboratory and greenhouse findings to agronomic reality.

4.5. Hierarchical and multidimensional framework

A key outcome of this review is the proposal of a hierarchical, multidimensional framework that integrates the type of priming, the activated mechanism, the stress context, the physiological response, and the genotype. This approach reveals that single-factor interventions do not govern successful maize priming but rather by harmonising rapid antioxidant induction with stress-matched auxiliary pathways, each modulated by varietal background (Imran *et al.*, 2022; Tolay, 2024). The Sankey diagram provided in this work visually encapsulates these inter-connections, serving as a model for future synthesis and predictive modelling in seed priming research.

4.6. Limitations

Despite the significant advances made, several critical gaps remain. Foremost among these is the insufficient elucidation of the temporal dynamics and crosstalk interactions among primary and secondary mechanisms, especially between redox and hormone signalling (Chitara *et al.*, 2024; Khaledi *et al.*, 2025). Secondly, omics approaches, while increasingly prevalent, are often not coupled with functional validation or direct physiological readouts, limiting their mechanistic impact. Thirdly, genotype-by-environment-by-treatment interactions are rarely resolved with sufficient statistical power to inform breeding and precision agronomy.

The studies employed diverse experimental protocols that limit direct cross-study comparison. Key sources of heterogeneity include: (i) priming duration (ranging from 6 h to 72 h), (ii) stress imposition timing (pre-germination *vs*. post-emergence), (iii) stress intensity (often not standardised or reported inconsistently), (iv) measurement techniques for antioxidant enzymes (spectrophotometric methods varied across laboratories), and (v) statistical approaches (some studies lacked factorial designs or adequate replication). For example, SOD activity was quantified using at least three different assay protocols across the reviewed studies, complicating absolute comparisons of enzyme induction magnitude. This methodological diversity, while reflecting the real-world complexity of maize production environments, limits our ability to establish universal dosage-response relationships or absolute thresholds for priming efficacy.

Furthermore, we cannot partition the variance attributable to genotype, environment, or their interaction, nor can we identify whether certain priming agents are universally superior or context-dependent. For example, melatonin priming was highly effective under drought in hybrid

YH-1898 (Muhammad *et al.*, 2023) and under salinity in Vega F1 (Sezer *et al.*, 2021), but we lack parallel studies testing both stresses in the same genetic background to determine whether melatonin confers broad-spectrum or stress-specific resilience.

Most studies measured antioxidant enzyme activity, osmolyte content, and gene expression at single time points (typically 7-14 days post-priming), providing static snapshots rather than dynamic trajectories. The temporal coupling between priming-induced transcriptional reprogramming, enzyme synthesis, and physiological adaptation remains largely uncharacterised. For instance, we do not know whether the observed SOD/CAT/POD induction peaks within hours, days, or weeks post-imbibition, nor whether these enzymes remain elevated throughout seedling development or decay after stress alleviation. Time-course studies integrating transcriptomics, enzyme kinetics, and physiological phenotyping are needed to resolve these dynamics and identify critical windows for intervention.

These limitations underscore the need for standardised experimental protocols, transparent reporting of negative results, multi-location field validation, and systems-level integration of temporal, genotypic, and environmental factors in future maize seed priming research.

4.7. Future directions

Future studies should prioritise: (i) integrated transcriptomic, proteomic, and metabolomic profiling with validation through biochemical and agronomic assays; (ii) time-resolved analyses of mechanistic cascades; and (iii) factorial field trials across diverse genotypes and environments to enable robust, predictive frameworks for maize seed priming.

- Experimental work should continue to move beyond the antioxidant triad: While the Results demonstrate that rapid SOD-CAT-POD/APX induction is universal, true resilience requires deploying a synergistic, multilayered defence, especially in diverse or marginal environments (Afrouz *et al.*, 2023; Manavalagan *et al.*, 2024; Luqman *et al.*, 2023).
- Explicit genotype-pathway mapping is a priority: Integrating genotype as a factor within such mechanistic diagrams (or in predictive models built from them) will be crucial for delivering precision priming in maize.
- Expand mechanistic endpoints and validate agronomic translation: The Sankey shows where evidence is strong (antioxidants, osmolytes, photosynthesis) and where it is thin (*e.g.*, signal transduction, stress memory, root architecture).
- Many priming protocols require controlled conditions (specific temperatures, durations, drying rates) that may be impractical for smallholder farmers. For instance, osmopriming with PEG-6000 or chitosan requires precise concentration control, specialised equipment, and safe disposal protocols, limiting on-farm adoption. Even simple hydropriming demands access to clean water, shade drying facilities, and knowledge of optimal soaking duration, resources not universally available in semi-arid maize-growing regions. Extension services must develop simplified, low-tech priming protocols validated under diverse infrastructural constraints, accompanied by training materials in local languages and demonstration trials in farmer fields.

Critical knowledge gaps include the temporal sequence of molecular and physiological events during imbibition and the persistence of priming effects through the crop cycle. Field studies tracking primed vs. non-primed cohorts through the entire crop cycle, with periodic tissue sampling for biochemical and transcriptomic analysis, are needed to determine whether priming-induced changes persist to flowering, grain-filling, and maturity, or dissipate after stress alleviation. Additionally, research must test whether priming confers constitutive stress tolerance (effective regardless of stress timing), developmental-stage-specific protection, or adaptive priming (where the mechanism activated matches the anticipated stress type and timing). Future studies should fill these gaps, validating how molecular/biochemical shifts translate into yield, water productivity, and stress adaptation at scale (Liu *et al.*, 2024; Aguilar *et al.*, 2021).

5. CONCLUSIONS

This review establishes that seed priming in maize is governed by a core, hierarchical mechanistic logic. Across all priming strategies and stress contexts, the early and robust induction of the antioxidant enzyme triad (SOD, CAT, POD/APX) emerges as the universal foundation for stress resilience. This primary defence is consistently layered with auxiliary mechanisms, such as ion homeostasis, hormone crosstalk, osmoregulation, and reserve mobilisation, whose activation is dictated by the chemical nature of the priming agent and the specific stress encountered. The outcomes of priming are further modulated quantitatively, but not qualitatively, by the genetic background of the variety; tolerant genotypes invariably realise greater physiological benefit, yet all lines share the same direction of response.

The integration of redox fortification with context-specific pathways supports not only improved seedling establishment and growth, but also more efficient water use, enhanced photosynthetic performance, and ultimately, superior yield attributes under adverse conditions. Collectively, these findings indicate that effective priming strategies must be both mechanistically sound and tailored to the physiological and genetic profile of the target maize population. Importantly, this synthesis moves beyond descriptive “omics” correlations to clarify functional causality between priming treatment, activated mechanism, and physiological benefit.

Despite recent progress, several avenues remain open for further research. First, there is a need for temporally resolved studies that couple transcriptomic and metabolomic profiling with physiological assays, enabling the identification of predictive early biomarkers for priming efficacy across diverse genotypes and environmental scenarios. Future research should also strive to dissect the crosstalk between antioxidant and hormonal pathways at finer spatial and temporal scales, using targeted gene editing and functional validation rather than correlative data alone.

A second priority is the development of genotype-specific priming protocols, particularly for sensitive and hybrid varieties, through systems-level modelling and controlled field trials. Such approaches would allow for the rational design of multi-component priming agents capable of synchronising redox, hormonal, and osmotic responses in a context-dependent manner. Additionally, integration with precision agriculture technologies could enable the real-time monitoring and adaptive management of priming interventions at scale.

Finally, translating mechanistic insights into practice will require collaboration across disciplines, linking plant physiology, biochemistry, genetics, agronomy, and data science, to ensure that priming strategies not only enhance crop resilience under current climatic pressures but are also robust to future environmental uncertainties. By anchoring future work in mechanistic and functional frameworks, researchers can accelerate the adoption of seed priming as a cornerstone of sustainable maize production.

Conflicts of Interest: The authors declare no conflicts of interest.

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