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### Chemical priming for abiotic stress management in plants

<sup>1</sup>Kenny Zohmingliana, <sup>2</sup>K. Lalmalsawmi, <sup>3</sup>Dr.T. Vanlalngurzauva

<sup>1</sup>PhD Scholar, College of Post Graduate Studies in Agricultural Science, Umiam, Meghalaya, India

<sup>2</sup>Subject Matter Specialist, Krishi Vigyan Kendra, Serchhip District, Mizoram, India

<sup>3</sup>Senior Scientist & Head, Krishi Vigyan Kendra, Serchhip District, N. Vanlaiphai, Mizoram, India

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Corresponding Author: Kenny Zohmingliana

#### Abstract

Plants, as sessile organisms, are continuously confronted with a plethora of environmental stresses, including drought, salinity, extreme temperatures, and heavy metal toxicity, which collectively impede their growth, development, and overall productivity. To mitigate the detrimental effects of these abiotic stresses, plants have evolved intricate defense mechanisms, involving a complex interplay of physiological, biochemical, and molecular responses. Chemical priming, an innovative and cost-effective strategy, has emerged as a promising approach to fortify plants against abiotic stress by pre-exposing them to specific chemical compounds, thereby potentiating their defense responses and enhancing their tolerance to subsequent stress encounter. This review aims to provide a comprehensive overview of the role of chemical priming in plant abiotic stress management, elucidating the underlying mechanisms, exploring the diverse range of priming agents, and highlighting the potential applications of this technology in sustainable agriculture. Plants, being immobile organisms, are inevitably exposed to a multitude of environmental constraints that can significantly compromise their survival and productivity. These abiotic stresses, encompassing drought, salinity, heat, cold, and heavy metal toxicity, pose a major threat to global food security. To combat these adverse conditions, plants have developed sophisticated defense mechanisms that involve a complex network of physiological, biochemical, and molecular processes. Seed priming, which involves carefully hydrating seeds to initiate pre-germinative metabolic processes before re-drying, is a simple and effective method that can improve seedling establishment, yields, and stress tolerance in a variety of crops. Priming allows plants to activate their metabolism and repair any damage before the root emerges, leading to faster and more uniform germination and improved plant resistance. Plants exhibit morphological, physiological, and biochemical responses to environmental stresses, and understanding these responses is crucial for effective management.

**Keywords:** Abiotic stress, chemical priming, toxicity, tolerance, environmental stresses

#### 1. Introduction

Abiotic stresses, encompassing environmental challenges like drought, salinity, and extreme temperatures, exert a substantial toll on global crop production, exacerbating food security concerns in a changing climate (Duary, 2020) [33]. Plants, being sessile organisms, are particularly vulnerable during their early developmental stages, such as seed germination and seedling establishment, rendering them susceptible to the detrimental effects of these environmental constraints (Rhaman *et al.*, 2020) [101]. To mitigate the adverse impacts of abiotic stresses, innovative strategies are required to fortify plant resilience and enhance their ability to withstand and adapt to these challenges (Chakraborti *et al.*, 2021) [20]. Seed priming, a pre-sowing treatment involving controlled hydration, has emerged as a promising technique to enhance seed performance and seedling vigor, ultimately improving crop productivity under stressful conditions (Devika *et al.*, 2021; Duary, 2020; Srivastava *et al.*, 2021) [29, 33, 114]. Phytohormone priming stands out as a potent method within seed priming, modulating biochemical and molecular processes to bolster plant tolerance against abiotic stresses (Rhaman *et al.*, 2020) [101]. Seed priming techniques can be used to enhance the "pregerminative

metabolism" depending on the plant species, seed morphology, and physiology (Gianella *et al.*, 2020) [44]. The process of osmopriming entails exposing seeds to solutions characterized by low water potential before sowing (Chu *et al.*, 2021) [24].

#### 2. Chemical Priming Agents and Their Applications

Chemical priming involves the application of various chemical compounds to seeds before sowing, aiming to enhance germination, seedling establishment, and subsequent plant growth, particularly under adverse environmental conditions (MacDonald & Mohan, 2025) [71]. A range of chemicals have been identified and employed as priming agents, each exhibiting unique mechanisms of action and eliciting specific physiological responses in plants (Srivastava *et al.*, 2021) [114]. Hydropriming, a simple and cost-effective technique, involves soaking seeds in water for a specific duration to initiate the germination process without radicle emergence (Jaiswal *et al.*, 2017) [52] (Patra *et al.*, 2020) [92]. This hydration jumpstarts metabolic activities, such as enzyme activation and protein synthesis, leading to faster and more uniform germination (Forti *et al.*, 2020; Wiszniewska, 2021) [41, 130]. Halopriming, another

widely used method, utilizes salt solutions, such as potassium nitrate or sodium chloride, to regulate water uptake and improve germination under saline conditions (Sharma *et al.*, 2013) <sup>[107]</sup>. Hormopriming employs plant growth regulators, like gibberellic acid or abscisic acid, to modulate hormonal balance and enhance stress tolerance. These exogenous applications have been demonstrated to significantly improve seed germination and seedling growth in various crops (Debbarma & Das, 2017) <sup>[28]</sup>. Seed priming, as a cost-effective approach, is being used for different crops and countries to improve yield (Farooq *et al.*, 2019) <sup>[40]</sup>. The use of spermidine and gibberellic acid for priming seeds has been shown to improve growth disturbances caused by salinity, leading to increases in anthocyanins, chlorophyll, the Na<sup>+</sup>/K<sup>+</sup> ratio, proline, and phenol compounds (Budiastuti *et al.*, 2020) <sup>[17]</sup>. Furthermore, priming with GA3 and ammonium molybdate can activate enzyme synthesis and repair subcellular damage caused by accelerated aging (Al-Haidary *et al.*, 2018) <sup>[3]</sup>.

### 3. Physiological and Molecular Mechanisms Underlying Chemical Priming:

The beneficial effects of chemical priming are attributed to a complex interplay of physiological and molecular mechanisms that enhance a seed's ability to germinate rapidly and uniformly, resulting in vigorous seedling establishment even under stress (Duary, 2020) <sup>[33]</sup>. Priming treatments have been shown to trigger the accumulation of osmoprotectants, such as proline and glycine betaine, which help maintain cellular turgor and protect enzymes and cellular structures from dehydration stress. Furthermore, priming can enhance the antioxidant defense system by increasing the activity of enzymes like superoxide dismutase and catalase, scavenging reactive oxygen species generated during stress. At the molecular level, priming can induce changes in gene expression patterns, leading to the upregulation of stress-responsive genes involved in detoxification, osmotic adjustment, and signal transduction (Rhaman *et al.*, 2020) <sup>[101]</sup>. These molecular changes enable primed seeds to respond more quickly and effectively to subsequent stress exposure. Priming with small molecule-based biostimulants such as polyamines can also promote plant growth and improve stress tolerance (Hernández *et al.*, 2022) <sup>[49]</sup>. When exposed to salinity stress, seed germination is often delayed or prevented due to reduced water availability, altered mobilization of stored reserves, and structural changes in proteins (Ibrahim, 2016) <sup>[50]</sup>. Priming seeds with plant growth regulators and osmoprotectants has been shown to improve plant stand establishment and crop productivity in several crops of the tropical region (Al-Haidary *et al.*, 2018) <sup>[3]</sup>. In plants primed with chitosan, nitric oxide production is triggered via the activation of mitogen-activated protein kinases and the subsequent increase in antioxidant enzyme activity and proline content.

The influence of priming extends beyond immediate stress responses, and has the ability to induce a "stress memory" within the plant (Sen & Puthur, 2020) <sup>[105]</sup>. Priming treatments can induce epigenetic modifications, such as DNA methylation and histone acetylation, which alter gene expression patterns and contribute to long-lasting stress tolerance (Murgia *et al.*, 2015) <sup>[80]</sup>. These epigenetic marks can be stably maintained through cell divisions and even

transmitted to subsequent generations, leading to improved stress resilience in offspring. This transgenerational epigenetic inheritance of stress memory has significant implications for crop improvement, suggesting that priming can be used to develop stress-tolerant varieties with enhanced adaptation to changing environmental conditions (Koç *et al.*, 2020) <sup>[62]</sup>. Seed bio-priming facilitates the entry and adherence of bacteria to seeds, promoting microbial acclimatization to prevalent conditions (Kumar *et al.*, 2020) <sup>[104]</sup>. Priming approaches can lead to a primed state in plants, making them more tolerant to stress (Wiszniewska, 2021) <sup>[130]</sup>. This approach involves the activation of signaling molecules, the regulation of primary metabolism, and the activation of genes that produce secondary defense metabolites (Mhlongo *et al.*, 2018) <sup>[74]</sup>. Priming agents stimulate the antioxidant defense system and the synthesis of compatible solutes to protect plants from damages caused by abiotic stresses (Bryksová *et al.*, 2020) <sup>[16]</sup>. Seed priming enhances stress adaptation in seedlings growing in salinity stressed conditions (Dai *et al.*, 2017) <sup>[27]</sup>.

### 4. Abiotic Stress in Plants: An Overview

Abiotic stresses are non-biological environmental factors that negatively affect plant growth, development, and productivity. These stresses include drought, salinity, extreme temperatures, nutrient deficiency, and heavy metal toxicity, and are becoming increasingly prevalent due to climate change and unsustainable agricultural practices. Plants have evolved complex mechanisms to perceive and respond to these stresses, involving intricate signaling networks, changes in gene expression, and metabolic adjustments (Zhang *et al.*, 2023) <sup>[135]</sup>. Abiotic stress curtails crop production across the globe (Sankhla *et al.*, 2020) <sup>[104]</sup>. Abiotic stresses elicit a cascade of molecular events in plants, encompassing alterations in gene expression, protein synthesis, and metabolic pathways (Rehman & Tanti, 2020) <sup>[100]</sup>.

Abiotic stresses, including drought, salinity, waterlogging, heat/cold, and heavy metals, significantly reduce agricultural production worldwide (Wang *et al.*, 2022) <sup>[127]</sup>. The impact of abiotic stress is further amplified when stresses occur in combination, leading to even more devastating effects on plant growth and yield (Wang *et al.*, 2016) <sup>[121]</sup>. Abiotic stresses cause a range of effects, from inhibition of photosynthesis and disruption of water balance to oxidative damage and impaired nutrient uptake. The combined effects of drought and salinity, for example, affect almost 50% of the world's cultivated lands (Fadiji *et al.*, 2023) <sup>[38]</sup>. Plants often recover rapidly and fully when stress is relieved (Bostock *et al.*, 2014) <sup>[14]</sup>. The non-living components of an ecosystem exert selective pressure on living organisms, affecting their survival, reproduction, and distribution (Enebe & Babalola, 2018) <sup>[36]</sup>. These abiotic factors can limit plant growth and development, influence plant morphology and physiology, and determine the composition and structure of plant communities. (Bulgari *et al.*, 2019) <sup>[18]</sup>.

Salinity stress, a major abiotic stress, arises from high concentrations of soluble salts in the soil, disrupting the Na<sup>+</sup> /K<sup>+</sup> ratio in the cytoplasm of the plant cell, leading to osmotic stress, ion toxicity, and nutrient imbalances (Brini & Masmoudi, 2012) <sup>[15]</sup>. Salinity stress is an intense abiotic

stress that negatively affects plant physiological and biochemical processes, which leads to a serious reduction in growth and yield (Wu *et al.*, 2023) <sup>[131]</sup>. In leaves, salinity causes premature senescence and reduces photosynthetic activity, which is related to stomatal closure and non-stomatal limitations, like impairment of the photosynthetic machinery. Plants are frequently exposed to a variety of abiotic stressors such as drought, soil acidity and salinity, UV radiation, high light, temperature, nutritional deficits, and toxicity, all of which have a considerable detrimental influence on crop production globally (Fadiji *et al.*, 2023) <sup>[38]</sup>. It is also a major cause of land degradation, rendering soil infertile and unsuitable for agriculture. Due to climate change, abiotic and biotic stresses have a negative impact on global crop output and productivity (Begna, 2020) <sup>[9]</sup>. Insufficient rainfall is a major factor in crop production, particularly in regions where crop production is totally dependent on rainfall, there is always a chance of crop failure or yield loss owing to moisture stress (Begna, 2020) <sup>[9]</sup>. Environmental stresses have substantial influence on agricultural productivity, causing substantial reduction in crop yield (Kumar *et al.*, 2024; Michael, 2021) <sup>[98, 76]</sup>. Abiotic stresses are responsible for average yield losses of more than 50% in major crops (Wang *et al.*, 2022) <sup>[127]</sup>. Plants respond to abiotic stresses at the molecular level through altered gene expression, protein synthesis, and metabolic pathways. These alterations result in a variety of physiological and biochemical changes that enable plants to cope with the stress.

#### 4.1 Chemical Priming: A Strategy for Abiotic Stress Management:

Chemical priming involves the pre-treatment of plants with specific chemicals or compounds that enhance their ability to withstand subsequent stress exposure. This priming approach triggers a cascade of physiological and molecular responses that prime the plant's defense mechanisms, leading to enhanced stress tolerance (Wang & Frei, 2011) <sup>[125]</sup>. Chemical priming has emerged as a promising strategy to improve plant tolerance to abiotic stresses such as drought, salinity, and temperature extremes (Pirasteh-Anosheh & Hashemi, 2020) <sup>[94]</sup>. This method activates the plant's defense mechanisms, leading to improved stress tolerance (Vinocur & Altman, 2005) <sup>[119]</sup>. The effects of abiotic environmental stresses on crop quality are seen in protein, lipids, non-structural carbohydrates, minerals, antioxidants, feed value for ruminant herbivores, and physical/sensory traits (Wang & Frei, 2011) <sup>[125]</sup>. Seed priming has been shown to improve plant establishment and yield under a variety of environmental conditions.

Priming agents can be applied through various methods, including seed treatment, foliar spray, or root drenching, depending on the specific chemical and plant species. These compounds, often applied at low concentrations, trigger physiological and molecular changes that enhance the plant's ability to withstand subsequent stress exposure. Chemical priming has been shown to be effective in improving plant tolerance to a wide range of abiotic stresses, including drought, salinity, heat, and cold (Morcillo & Manzanera, 2021) <sup>[78]</sup>. Chemical priming offers several advantages over traditional breeding approaches for stress tolerance, including its rapid implementation, broad applicability across plant species, and potential for use in

combination with other stress management strategies. Several naturally synthesized and artificial priming agents have been identified that enhance abiotic stress tolerance in plants (Sako *et al.*, 2020) <sup>[103]</sup>.

#### 4.2 The Concept of Chemical Priming

Chemical priming can be described as pre-stress conditioning that prepares plants for future stress encounters. Priming enhances the speed and intensity of defensive responses when plants encounter subsequent stress. Priming agents are perceived by the plant and activate a variety of signaling pathways, leading to the upregulation of defense-related genes and the accumulation of protective metabolites. Priming enables plants to activate their defense responses more rapidly and effectively when exposed to subsequent stress (Hernández-Apaolaza, 2022) <sup>[96]</sup>. This enhanced responsiveness translates to improved stress tolerance and reduced yield losses.

The mechanisms underlying chemical priming are complex and involve a range of molecular and physiological processes. These include changes in gene expression, protein synthesis, hormonal signaling, and metabolic pathways. Pre-treatment of seeds with phytohormones is a physiological method that involves hydrating and drying seeds to boost metabolic activities before germination, increasing the percentage and rate of germination (Rhaman *et al.*, 2020) <sup>[101]</sup>.

#### 5. Objectives of the Review

- To explore the roles of chemical priming agents.
- To highlight the mechanisms underlying chemical priming-mediated stress tolerance.
- To provide a comprehensive overview of chemical priming agents.

One effective strategy to boost germination, seedling development, and crop productivity is seed priming (Lewandowska *et al.*, 2020) <sup>[67]</sup>. This study found that priming seeds with potassium nitrate and zinc oxide enhanced water stress tolerance and nutrient uptake in chili plants (Maphalaphathwa & Nciizah, 2025) <sup>[73]</sup>. Seed priming by hydration and drying was created to enhance seed quality and, as a result, their agricultural value (Wiszniewska, 2021) <sup>[130]</sup>. Priming has been shown to have an impact on seed longevity (Fabrissin *et al.*, 2021) <sup>[37]</sup>. Expanding our fundamental understanding of the molecular mechanisms underlying the seed response to priming is critical (Pagano *et al.*, 2023) <sup>[89]</sup>. The review gives specifics on the potential mechanisms by which nano-priming causes seed dormancy to be broken, seed germination to be accelerated, and their effects on the production of primary and secondary metabolites (Nile *et al.*, 2022) <sup>[82]</sup>.

Nanoparticles have been shown to have antimicrobial properties and can be used to protect plants from pathogens (Review of Literature, n.d.).

#### 6. Chemical Priming Agents: Types and Mechanisms

A variety of chemical compounds have been identified as effective priming agents for enhancing abiotic stress tolerance in plants (Zulfiqar, 2021) <sup>[137]</sup>. These agents can be broadly classified into several categories, including:

**6.1 Salicylic Acid (SA):** SA is a plant hormone involved in regulating plant defenses against pathogens. SA plays a crucial role in regulating plant defense responses against pathogens and abiotic stresses (Review of Literature, n.d.). It has been shown to enhance plant tolerance to drought, salinity, and temperature stress. SA-induced priming involves the activation of signaling pathways that lead to the expression of defense-related genes and the accumulation of protective metabolites (Alharbi *et al.*, 2022) <sup>[4]</sup>. SA pretreatment has been shown to mitigate the adverse effects of drought stress in various plant species.

### 6.2 Jasmonic Acid

JA is another plant hormone involved in regulating plant defenses. It plays a crucial role in regulating plant defense responses against insects and herbivores. JA-induced priming involves the activation of signaling pathways that lead to the expression of defense-related genes and the accumulation of protective metabolites.

### 6.3 Jasmonic Acid (JA) and Methyl Jasmonate (MeJA)

JA and MeJA are lipid-derived plant hormones that play important roles in plant defense and development. MeJA is a volatile derivative of JA that can act as an airborne signal to trigger defense responses in neighboring plants. JA and MeJA have been shown to enhance plant tolerance to a wide range of abiotic stresses, including drought, salinity, and temperature extremes. JA and MeJA signaling pathways, which involve the activation of transcription factors and the expression of defense-related genes are essential in plants.

### 6.4 Ethylene (ET)

Ethylene is a gaseous plant hormone that plays a crucial role in regulating plant development and stress responses. It is involved in various physiological processes, including fruit ripening, senescence, and abscission. Ethylene has been shown to enhance plant tolerance to flooding and hypoxia. The phytohormones abscisic acid, salicylic acid, jasmonic acid, and ethylene are the primary ones that are generated in response to biotic and abiotic stresses (Svoboda *et al.*, 2021) <sup>[115]</sup>. The production of ethylene is accelerated by environmental stresses.

### 6.5 Abscisic Acid (ABA)

Abscisic acid is a crucial phytohormone that orchestrates plant responses to various environmental stresses, including drought, salinity, and cold (Chen *et al.*, 2010) <sup>[22]</sup>. ABA regulates stomatal closure, which reduces water loss from leaves and helps plants conserve water under drought conditions. ABA-induced priming involves the activation of signaling pathways that lead to the expression of stress-related genes and the accumulation of compatible solutes.

### 6.6 Polyamines

Polyamines are aliphatic amines that are ubiquitous in plants and play essential roles in cell growth, development, and stress responses. Polyamines have been shown to enhance plant tolerance to drought, salinity, and heavy metal stress.

### 6.7 Brassinosteroids

Brassinosteroids are a class of plant steroid hormones that regulate a wide range of developmental processes, including

cell elongation, cell division, and differentiation. They have been shown to enhance plant tolerance to drought, salinity, and temperature stress.

Jasmonic acid is a crucial phytohormone involved in regulating plant responses to both biotic and abiotic stresses (Ali & Baek, 2020; Jang *et al.*, 2020; Wang *et al.*, 2021) <sup>[5, 53, 126]</sup>. It interacts with salicylic acid and abscisic acid signaling pathways (Ku *et al.*, 2018). Understanding the intricate crosstalk between these signaling pathways is crucial for developing effective strategies to enhance plant stress tolerance (Ku *et al.*, 2018; Wang *et al.*, 2020) <sup>[63, 136]</sup>. Phytohormones can interact antagonistically or synergistically, depending on the specific stress and plant species (Caarls *et al.*, 2015) <sup>[19]</sup>. These complex networks enable plants to grow and survive under different stress environments, with overlapping responses that confer tolerance to multiple stresses. The phytohormone crosstalk also influences the expression of stress-responsive genes, with abscisic acid acting as a central hub for integrating stress signals (Dhar *et al.*, 2020; Jogawat, 2019) <sup>[30, 19]</sup>.

Plants have evolved intricate mechanisms to perceive and respond to various abiotic stressors, with phytohormones playing a pivotal role in orchestrating these responses (Bittencourt *et al.*, 2023; MacDonald *et al.*, 2009; Pri-Tal *et al.*, 2023) <sup>[11, 70, 95]</sup>. Abscisic acid signaling is a central regulator that controls gene expression and generates physiological adaptation to various stressful conditions in plants (Wang *et al.*, 2018) <sup>[124]</sup>. ABA-mediated stomatal closure reduces transpirational water loss, while ABA-induced synthesis of compatible solutes helps maintain osmotic balance and protect cellular structures from dehydration. Jasmonic acid can induce the expression of genes involved in plant defense responses.

## 7. Molecular Mechanisms Underlying Chemical Priming

Priming enhances plant stress tolerance through various molecular mechanisms, including the activation of stress-responsive genes, the accumulation of compatible solutes, and the modulation of antioxidant defense systems. Upon exposure to stress, primed plants exhibit faster and stronger activation of defense responses, leading to enhanced tolerance (Osakabe *et al.*, 2014) <sup>[86]</sup>. Chemical priming can induce epigenetic modifications, such as DNA methylation and histone modification, that alter gene expression patterns and contribute to enhanced stress tolerance (Mao *et al.*, 2022; Wang *et al.*, 2020) <sup>[72, 136]</sup>. Jasmonates mediate plant responses to desiccation, ozone, UV, osmotic, cold, or light stress, as well as the formation of secondary metabolites and adaptation to seasonal and circadian rhythms (Wasternack, 2013) <sup>[129]</sup>.

### 7.1 Hydrogen Peroxide (H<sub>2</sub>O<sub>2</sub>)

Pre-treatment with hydrogen peroxide has been shown to improve seed germination under salt stress (Chen *et al.*, 2017). Hydrogen peroxide can activate defense mechanisms by affecting the expression of genes (Brini & Masmoudi, 2012) <sup>[23]</sup>.

### 7.2 Nitric Oxide (NO)

Nitric oxide is a signaling molecule involved in various physiological processes in plants, including stress responses. Induced systemic tolerance is influenced by antioxidants,

osmotic adjustment, phytohormone production and defense strategies (Fukami *et al.*, 2018) <sup>[42]</sup>. These signaling molecules can induce a wide array of physiological and biochemical changes that fortify the plant against future stress encounters (Osakabe *et al.*, 2013) <sup>[89]</sup> (Sharma *et al.*, 2020) <sup>[108]</sup>.

### 7.3 Cell Wall Remodeling

Environmental stress can trigger cell wall remodeling, a process mediated by plant hormones like jasmonic acid and brassinosteroids (Novaković *et al.*, 2018) <sup>[83]</sup>. This dynamic modification of the cell wall not only provides a physical barrier against stress but also contributes to cell signaling, thereby influencing the overall stress response of the plant (Song *et al.*, 2022) <sup>[113]</sup>.

The intricate relationship between plant growth-promoting rhizobacteria and plants has been observed to enhance drought resistance, in addition to salt tolerance (Hartmann *et al.*, 2021) <sup>[45]</sup>.

### 7.4 Silicon (Si)

Silicon is an abundant element in the earth's crust and has been shown to play a role in enhancing plant tolerance to abiotic stresses (Khan *et al.*, 2021) <sup>[60]</sup>. Silicon impacts the signaling of phytohormones during salinity, drought, and metal stresses, with detailed molecular and proteomic research still needed to fully understand the underlying mechanisms (Kim *et al.*, 2015) <sup>[61]</sup>.

Plants employ a wide array of adaptive mechanisms to cope with abiotic stresses, including osmotic tolerance, ionic tolerance, and tissue tolerance (Johnson & Puthur, 2021) <sup>[55]</sup>. Osmotic tolerance involves the accumulation of compatible solutes that help maintain cell turgor and protect cellular structures from dehydration (Hartmann *et al.*, 2021) <sup>[45]</sup>. Maintaining ion homeostasis by regulating ion uptake, transport, and compartmentalization prevents toxic build-up in sensitive tissues is achieved by ionic tolerance. Tissue tolerance involves the ability of plant cells and tissues to withstand stress-induced damage. Stress-responsive genes orchestrate salinity stress adaptation via synchronized action and crosstalk with other components of stress signal transduction pathways (Tuteja *et al.*, 2012) <sup>[117]</sup>. Understanding the molecular mechanisms underlying these tolerance mechanisms is crucial for developing strategies to enhance plant stress tolerance.

### 7.5 Other Potential Priming Agents

Further investigation into the role of other potential priming agents, such as polyamines, is necessary to broaden the scope of chemical priming strategies for plant abiotic stress management. Acquired tolerance to multiple stresses can be achieved through genetic engineering (Dhariwal *et al.*, 1998) <sup>[31]</sup>. Understanding the molecular mechanisms underlying priming is crucial for optimizing its application in agriculture and developing sustainable strategies for enhancing plant stress tolerance.

## 8. Abiotic Stresses and Chemical Priming

**8.1 Drought Stress:** Drought represents a major constraint to plant growth and productivity, particularly in arid and semi-arid regions. Seed priming enhances drought tolerance in crop plants through morphological, physiological,

biochemical, and molecular mechanisms (Vishvanathan *et al.*, 2020) <sup>[120]</sup>. Priming treatments can improve water uptake, enhance root growth, and promote stomatal closure, ultimately improving water use efficiency and drought tolerance. Plants respond to environmental stresses by activating a complex network of molecular and cellular mechanisms, including changes in gene expression, protein synthesis, and metabolic pathways (Slama *et al.*, 2015) <sup>[111]</sup>. Inadequate and inconsistent rainfall are among the abiotic stresses that have a negative impact on crop production worldwide (Duary, 2020) <sup>[33]</sup>. Drought stress causes a series of changes in plants, including morpho-anatomical, physiological, and biochemical changes, that are designed to limit water loss through transpiration and increase plant water use efficiency (Kapoor *et al.*, 2020) <sup>[57]</sup>.

### 8.2 Salinity Stress

Salinity is a major environmental stress that affects crop production in many regions of the world (Rhaman *et al.*, 2020) <sup>[101]</sup>. Salt stress can lead to ion toxicity, osmotic stress, and nutrient imbalance, ultimately inhibiting plant growth and development (Miceli *et al.*, 2021) <sup>[75]</sup>. Priming treatments can mitigate the adverse effects of salinity stress by enhancing ion homeostasis, improving osmotic adjustment, and activating antioxidant defense systems (Zaid *et al.*, 2018) <sup>[132]</sup>. Additionally, priming prepares plants to respond more effectively to protect against stress (Duary, 2020) <sup>[33]</sup>.

### 8.3 Temperature Stress (Heat and Cold)

#### 8.3.1 Heat Stress

Heat stress is a pervasive abiotic factor that adversely affects plant growth and productivity, especially in the face of global climate change. Priming treatments can enhance plant thermotolerance by upregulating heat shock proteins, stabilizing cell membranes, and modulating antioxidant defense systems.

#### 8.3.2 Cold Stress

Low-temperature stress poses a significant threat to plant productivity, particularly in temperate and cold regions. Priming treatments can improve plant tolerance to chilling and freezing temperatures by enhancing cold acclimation, modulating membrane fluidity, and accumulating cryoprotective compounds.

Abiotic stresses, encompassing drought, salinity, and extreme temperatures, exert a profound influence on plant physiology, instigating a cascade of molecular, biochemical, and physiological responses (Chakraborti *et al.*, 2021) <sup>[20]</sup>. Plants respond to these stresses through a variety of mechanisms, including morphological adaptations, physiological adjustments, and the activation of stress-responsive genes (Fahad *et al.*, 2017) <sup>[39]</sup>. Abiotic stress is the primary contributor to diminished quality and productivity in global crops (Neves *et al.*, 2020) <sup>[81]</sup>. These stresses induce a variety of changes at the physiologic, proteomic, metabolomic, and genomic levels, impacting plant growth and development (Swapna, 2016) <sup>[116]</sup>. Climate change has exacerbated the severity of environmental stressors and affects crop production worldwide (Ilangumaran & Smith, 2017) <sup>[51]</sup>. Plants have evolved sophisticated mechanisms to perceive stress signals and

activate appropriate defense responses. Plants employ a variety of biochemical and molecular responses to cope with stress, including selective formation or elimination of salt ions, control of root absorption of ions and transport to leaves, synthesis of compatible osmotic agents, stimulation of hormones, regulation of gene expression, etc. (Sewelam *et al.*, 2016)<sup>[106]</sup>.

Reactive oxygen species are produced as by-products of normal cellular metabolism and in response to environmental stresses (Rao *et al.*, 2025)<sup>[99]</sup>. The accumulation of ROS can lead to oxidative damage of lipids, proteins, and DNA, ultimately impairing cellular function and causing cell death. To mitigate the harmful effects of ROS, plants have evolved a complex antioxidant defense system that includes enzymatic and non-enzymatic components (Ma *et al.*, 2022)<sup>[68]</sup>. The physiological function of ROS involves a dual role as toxic by-products and as regulatory signaling molecules in plant cells (Dumanović *et al.*, 2021)<sup>[34]</sup>. Thus, ROS production and associated redox regulation is one of the most common plant responses to stress (Zhang *et al.*, 2017)<sup>[134]</sup>. ROS are produced in various cellular compartments, including chloroplasts, mitochondria, peroxisomes, and the plasma membrane (Hasan *et al.*, 2018)<sup>[47]</sup>.

#### 8.4 Oxidative Stress

Plants possess intricate defense mechanisms, including enzymatic and non-enzymatic antioxidants, to scavenge ROS and maintain redox homeostasis (Ma *et al.*, 2022; Mishra *et al.*, 2023)<sup>[68, 77]</sup>. The first line of plant defense against ROS damage involves the production of antioxidants (Gao *et al.*, 2023)<sup>[43]</sup>.

Enzymatic antioxidants, such as superoxide dismutase, catalase, and peroxidase, catalyze the dismutation or reduction of ROS, converting them into less harmful molecules. Non-enzymatic antioxidants, such as ascorbic acid, glutathione, and carotenoids, directly scavenge ROS and protect cellular components from oxidative damage (Rao *et al.*, 2025)<sup>[99]</sup>. Manipulation of genes that protect and maintain cellular functions or that maintain the structure of cellular components has been the major target of attempts to produce plants that have enhanced stress tolerance (Valliyodan & Nguyen, 2006)<sup>[118]</sup>. Environmental stresses trigger enhanced production of reactive oxygen species, causing an oxidative stress in the organism (Kumar, 2018)<sup>[66]</sup>. ROS are produced rapidly in plant cells after pathogen attack, are potentially involved in many defense processes including the hypersensitive response, phytoalexin synthesis and oxidative cross-linking of plant cell wall proteins (Singh & Upadhyay, 2014)<sup>[110]</sup>. Plants have developed a complex antioxidant defense system to overcome oxidative stress, consisting of enzymatic and non-enzymatic antioxidants (Zha *et al.*, 2019)<sup>[133]</sup>.

#### 8.5 Heavy Metal Stress

Heavy metal stress poses a significant threat to plant health and productivity, particularly in contaminated soils. Priming treatments can enhance plant tolerance to heavy metal stress by reducing metal uptake, enhancing metal detoxification, and activating antioxidant defense systems. Plants respond to heavy metal stress by producing phytochelatin, which are peptides that bind to heavy metals and facilitate their

sequestration in vacuoles. Plants under environmental stress produce reactive oxygen species that can cause oxidative stress and damage to lipids (Rao *et al.*, 2025)<sup>[99]</sup>. Plants experience oxidative stress upon exposure to heavy metals that leads to cellular damage and disturbance of cellular ionic homeostasis (Singh *et al.*, 2011)<sup>[109]</sup>. Malondialdehyde, a product of lipid peroxidation, serves as a marker for free radical activity and its levels, along with chlorophyll and carotenoids, increase under metal stress (Soleimani *et al.*, 2011)<sup>[112]</sup>. Plants respond to heavy metal stress by activating antioxidant defense systems to scavenge ROS and mitigate oxidative damage (Bojko *et al.*, 2013; Pan *et al.*, 2021; Sankhla *et al.*, 2020)<sup>[13, 91, 104]</sup>. Plants exposed to high concentrations of heavy metals must respond to avoid the deleterious effects of heavy metal toxicity at the structural, physiological and molecular levels (Ovečka & Takáč, 2013)<sup>[88]</sup>.

#### 8.6 Osmotic Stress

Osmotic stress, caused by drought or salinity, disrupts cellular water balance and induces a variety of physiological and biochemical changes in plants (Kaushal, 2020)<sup>[59]</sup>.

Osmotic stress leads to dehydration, ion toxicity, and disruption of nutrient uptake, ultimately inhibiting plant growth and development. Osmotic stress can lead to a decrease in photosynthetic activity, reduced protein synthesis, and impaired nutrient uptake. Osmotic stress is associated with dramatic changes in plant metabolism, including the accumulation of several organic osmolytes such as proline, glycinebetaine, and sugars. Proline and glycinebetaine contribute to osmotic adjustment, protect cellular structures, and scavenge ROS. Osmotic stress is created when plants are in an environment with low water potential.

#### 9. Physiological and Molecular Responses to Chemical Priming:

Priming agents can trigger a wide range of physiological and molecular responses in plants, leading to enhanced stress tolerance. Priming enhances the plant's defense potential, increasing its ability to survive and thrive under stress, ultimately leading to temporary stress tolerance (Wiszniewska, 2021)<sup>[130]</sup>.

Priming induces changes in gene expression, leading to the upregulation of stress-responsive genes and the accumulation of protective metabolites. Plants employ sophisticated mechanisms to perceive stress signals and activate appropriate defense responses. Plants have evolved complex mechanisms to perceive stress signals, transduce them into intracellular signals, and activate appropriate defense responses (Sen & Puthur, 2020)<sup>[105]</sup>. The outcome of priming depends on the type of inducer, its concentration, the plant species, and the developmental stage. Priming treatments can enhance photosynthetic efficiency, improve water use efficiency, and promote nutrient uptake under stress conditions (Osakabe *et al.*, 2014)<sup>[86]</sup>. Priming treatments can improve plant performance and productivity in stressful environments by triggering a cascade of physiological and molecular events (Srivastava *et al.*, 2021)<sup>[114]</sup>. Priming agents can activate signaling pathways, such as the mitogen-activated protein kinase cascade and the calcium signaling pathway, which regulate stress-responsive gene expression (Mhlongo *et al.*,

2018) [74]. Priming may lead to enhanced expression of genes involved in stress tolerance, resulting in an increased capacity to cope with stress.

### 9.1 Enhanced Antioxidant Defense Systems

Priming agents can enhance the activity of antioxidant enzymes, such as superoxide dismutase, catalase, and peroxidase, leading to improved ROS scavenging and reduced oxidative damage (Kaushal, 2020) [59]. Plants use various enzymatic and non-enzymatic systems to scavenge excessive ROS and to protect themselves from oxidative damage. Plants may develop enhanced tolerance to environmental stresses by manipulating the genes encoding proteins that protect and maintain cellular functions or that maintain the structure of cellular components. Plants possess an antioxidant defense system that includes enzymes such as superoxide dismutase, catalase, and glutathione reductase, which play a crucial role in ROS scavenging and detoxification. (Challenges and Potentials of Microbial Consortia for Plant Disease Management and Sustainable Productivity, 2024) [21]. Plants also have the capacity to change the metabolism of carbon and nitrogen to cope with stress (Bohnert & Шевелева, 1998) [12].

### 9.2 Accumulation of Compatible Solutes

Priming agents can promote the accumulation of compatible solutes, such as proline, glycine betaine, and trehalose, which protect cellular structures and maintain osmotic balance under stress conditions (Dutta *et al.*, 2019) [35]. Priming can trigger the accumulation of proline, glycine betaine, and other compatible solutes, which protect cellular structures, maintain osmotic balance, and scavenge ROS.

### 9.3 Improved Photosynthetic Efficiency

Priming agents can improve photosynthetic efficiency by enhancing chlorophyll content, increasing CO<sub>2</sub> assimilation, and protecting photosynthetic machinery from damage. Priming can also improve photosynthetic efficiency by protecting the photosynthetic apparatus from damage and enhancing CO<sub>2</sub> assimilation. Priming can protect chlorophyll from degradation, increase the efficiency of light capture, and enhance the activity of enzymes involved in carbon fixation.

### 9.4 Regulation of Stress-Related Genes

Priming induces the expression of stress-related genes, encoding proteins involved in stress perception, signal transduction, and downstream defense responses. Priming can activate the expression of stress-related genes, encoding proteins such as heat shock proteins, dehydrins, and late embryogenesis abundant proteins, which protect cellular structures and maintain cellular functions under stress. Priming can activate a suite of stress-responsive genes, leading to the production of proteins involved in detoxification, osmoprotection, and stress signaling (Rampino *et al.*, 2006) [97].

### 9.5 Modulation of Hormone Signaling Pathways

Priming agents can modulate hormone signaling pathways, such as those involving abscisic acid, salicylic acid, and jasmonic acid, to regulate plant defense responses. Hormonal seed priming is an effective way to control

abiotic stresses by manipulating biochemical and molecular processes, which has shown encouraging results (Rhaman *et al.*, 2020) [101]. Priming can also alter hormone signaling pathways, enhancing the plant's ability to perceive and respond to stress signals. Seed priming is a cost-effective strategy employed across various crops and countries to boost yields, functioning as a complementary approach to grain biofortification (Farooq *et al.*, 2019) [40]. Notably, seed priming enhances germination rates by managing critical parameters during the early stages of development (Gianella *et al.*, 2020) [44]. Priming with various agents has led to modified strategies like osmopriming, halopriming, hormonal priming, PGR priming, and nutrimpriming (MacDonald & Mohan, 2025) [71].

Seed priming, a pre-sowing treatment that partially hydrates seeds to initiate pre-germinative metabolic activity without actual germination, followed by drying back to near their original moisture content for easy handling, represents a simple yet effective strategy (Farooq *et al.*, 2019) [40]. The benefits of seed priming include improved stand establishment, increased economic yields, and enhanced tolerance to both biotic and abiotic stresses in a variety of crops by inducing a range of biochemical, physiological, molecular, and subcellular changes in plants (Jaiswal *et al.*, 2017; Patra *et al.*, 2020; Sharma *et al.*, 2013; Srivastava *et al.*, 2021) [52, 92, 107, 114].

Priming, a technique that involves pre-soaking seeds in water or specific solutions under controlled conditions, enhances germination speed and uniformity, contributing to higher yields and improved plant resistance (Kareem *et al.*, 2020; Waskow *et al.*, 2021) [58, 128]. Hydropriming, the most basic form of seed priming, entails soaking seeds in water for a specified period and then drying them back (Forti *et al.*, 2020) [41]. Different priming methods, including halopriming (using inorganic salts), osmopriming (using osmotic solutions), hormonal priming (using plant growth regulators), and solid matrix priming (using moistened solid carriers), can be tailored to specific plant species and stress conditions. These methods modulate various physiological processes, such as nutrient uptake, photosynthesis, and antioxidant defense mechanisms (Budiastuti *et al.*, 2020) [17].

### 9.6 Epigenetic Modifications

Priming can induce epigenetic modifications, such as DNA methylation and histone modification, which alter gene expression patterns and contribute to long-lasting stress tolerance (Lewandowska *et al.*, 2020) [67]. Priming can induce epigenetic modifications that alter gene expression patterns and lead to long-lasting stress tolerance.

### 9.7 Root System Development

Priming can promote root system development, increasing the plant's ability to access water and nutrients under stress conditions (Wisniewska, 2021) [130]. Priming can stimulate root growth, allowing plants to access water and nutrients more efficiently, which is especially important under drought conditions. Priming can also enhance root development, leading to improved water and nutrient uptake, further contributing to stress tolerance (Debbarma & Das, 2017) [28].

Seed osmopriming, a pre-sowing treatment where seeds are soaked in osmotic solutions, initiates the first stage of

germination without radicle protrusion, by exposing seeds to low-water-potential solutions (Chu *et al.*, 2021) <sup>[24]</sup>. This controlled hydration enhances germination speed, uniformity, and seedling vigor, particularly under stressful conditions (Pirasteh-Anosheh & Hashemi, 2020) <sup>[94]</sup>. Priming enhances seed performance by initiating various physiological and biochemical changes, including the activation of enzymes, the synthesis of proteins, and the accumulation of osmoprotectants (Al-Haidary *et al.*, 2018; Duary, 2020) <sup>[3, 33]</sup>. The improved activity of antioxidant enzymes helps mitigate the damaging effects of reactive oxygen species produced during stress conditions (Vishvanathan *et al.*, 2020) <sup>[120]</sup>. These improvements collectively contribute to enhanced germination rates and seedling establishment.

Hydropriming, a straightforward and economical method, substantially boosts yields by enhancing germination and seedling vigor (Rhaman *et al.*, 2020) <sup>[101]</sup>. Nutrient seed priming is a promising technique for enhancing nutrient uptake and improving crop growth, especially under water stress conditions (Maphalaphathwa & Nciizah, 2025) <sup>[73]</sup>. Seed priming enhances stress tolerance by activating a range of physiological and biochemical processes, including improved antioxidant defense mechanisms. Seed biopriming, which integrates beneficial microorganisms into the priming process, not only improves seed germination and seedling development but also enhances plant resistance to biotic and abiotic stresses (Kumar *et al.*, 2020) <sup>[104]</sup>. Halo-priming is another effective method to improve germination in halophytes (Ramírez *et al.*, 2022) <sup>[96]</sup>.

## 10. Application Methods and Considerations

Priming agents can be applied through various methods, including seed soaking, seed coating, and foliar spraying, depending on the specific agent and the target plant species. Careful consideration should be given to the concentration, duration, and timing of application to avoid phytotoxicity and ensure optimal results. Different priming methods, including hydropriming, osmopriming, halopriming, hormonal priming, and solid matrix priming, can be tailored to specific plant species and stress conditions. For hydropriming, it is difficult to avoid the radicle growth since hydropriming is a non-controlled water uptake (Corbineau *et al.*, 2023) <sup>[25]</sup>.

Seed priming enhances the plant's ability to cope with stress by fine-tuning its physiological and molecular responses (Wiszniewska, 2021) <sup>[130]</sup>. Seeds with high quality can successfully establish themselves, germinating uniformly and rapidly, producing robust seedlings, showing resilience to external factors, and germinating across diverse environmental conditions (Corbineau *et al.*, 2023) <sup>[25]</sup>.

### 10.1 Seed Priming

Seed priming, a pre-sowing treatment, readies seeds for faster germination and more uniform seedling emergence by partially hydrating them before planting (Ibrahim, 2016) <sup>[50]</sup>. Seed priming involves carefully controlling water uptake by the seed, allowing pre-germinative metabolic processes to begin without actual germination, and then drying the seeds back for storage (Adhikary *et al.*, 2021) <sup>[1]</sup>. This process enhances germination speed and uniformity, leading to better stand establishment and higher yields. During

priming, seeds go through the first two phases of germination, so when they are sown, they can finish the process more quickly once water is available (Pawar & Laware, 2018) <sup>[93]</sup>. The method involves hydrating seeds in a controlled manner, activating early germination processes without allowing radicle emergence, followed by drying the seeds to their original moisture level. This pre-sowing treatment enhances germination speed, uniformity, and seedling vigor, especially under stress conditions, ensuring better crop establishment and productivity.

### 10.2 Non-ionizing Radiation

Non-ionizing radiation methods offer an eco-friendly and cost-effective alternative to conventional priming techniques. Being eco-friendly and cost-effective approaches, priming with extra-terrestrial or physical agents offers many advantages along with ensuring enhanced production over conventional methods (Bera *et al.*, 2021) <sup>[20]</sup>.

### 10.3 Foliar Application

Foliar application of priming agents allows for direct delivery of protective compounds to the plant canopy, enhancing stress tolerance by modulating physiological and molecular responses. Foliar application of priming agents is a method of directly delivering protective compounds to the plant canopy.

### 10.4 Soil Application

Soil application of priming agents can improve plant tolerance to soil-borne stresses, such as salinity and nutrient deficiency, by modifying the rhizosphere environment and promoting root growth. Soil application of priming agents is a method of applying the protective agent to the soil. Effective priming requires careful selection of the appropriate agent, concentration, and application method, taking into account the specific plant species, stress condition, and environmental factors (Zulfiqar, 2021) <sup>[137]</sup>.

## 11. Molecular Mechanisms Underlying Priming-Mediated Stress Tolerance:

Priming induces a variety of molecular changes in plants, including changes in gene expression, protein synthesis, and metabolite accumulation, that contribute to enhanced stress tolerance (Ashraf & Foolad, 2005) <sup>[7]</sup>. At the molecular level, priming triggers a cascade of events that enhance the plant's ability to perceive and respond to stress signals. One of the key mechanisms underlying priming-mediated stress tolerance is the activation of antioxidant defense systems. This includes the upregulation of genes encoding antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase, which scavenge reactive oxygen species and protect cellular components from oxidative damage (Bryksová *et al.*, 2020) <sup>[16]</sup>. Priming also modulates the expression of stress-responsive genes involved in various protective mechanisms, including osmotic adjustment, detoxification, and protein stabilization (Koç *et al.*, 2020) <sup>[62]</sup>. Furthermore, priming can induce epigenetic modifications, such as DNA methylation and histone modification, which alter gene expression patterns and contribute to long-lasting stress tolerance. Nano-priming affects primary and secondary metabolite production (Nile *et al.*, 2022) <sup>[82]</sup>.

The improved stress tolerance observed in primed plants is often associated with changes in hormonal signaling pathways, particularly those involving abscisic acid, salicylic acid, and jasmonic acid. These hormones play critical roles in regulating plant responses to stress, and priming can enhance their biosynthesis, signaling, and downstream effects. Priming-induced changes in ion homeostasis, such as increased potassium uptake and reduced sodium accumulation, also contribute to stress tolerance by maintaining cellular functions and preventing ion toxicity (Dimkpa *et al.*, 2009)<sup>[32]</sup>.

### 11.1 Optimal Concentrations and Timing

Optimal concentrations and timing are critical for achieving effective priming without causing phytotoxicity or adverse effects on plant growth.

The use of small molecule-based biostimulants, like polyamines, has shown promise in promoting plant growth and improving stress tolerance, although further research is needed to fully understand their mechanisms of action (Hernández *et al.*, 2022)<sup>[49]</sup>.

Beneficial rhizosphere microbes are being increasingly exploited for biofertilization, disease and pest control, and alleviation of environmental constraints (Palma *et al.*, 2018)<sup>[90]</sup>. The effectiveness of microbial phytohormones in enhancing abiotic stress tolerance and defense responses in crops has been demonstrated (Ma *et al.*, 2019)<sup>[69]</sup>. However, more research is needed to determine the optimal application methods, timing, and combinations of priming agents for different plant species and stress conditions. To increase crop productivity, scientists are exploring plant- and microbial-based solutions, such as biostimulants and bioprotectants, which enhance plant growth and reduce the impact of abiotic and biotic stresses (Mrid *et al.*, 2021)<sup>[79]</sup>. Biostimulants, which include substances and/or microorganisms, improve nutrient uptake, stimulate growth, and enhance stress tolerance in plants (Oosten *et al.*, 2017)<sup>[85]</sup>.

### 11.2 Potential Risks and Side Effects

Potential risks and side effects associated with chemical priming, such as phytotoxicity, environmental contamination, and unintended effects on non-target organisms, need to be carefully evaluated and mitigated. The use of chemical pesticides in agriculture has been reported to have residual effects, necessitating the use of biological control agents for plant disease management (Olowe *et al.*, 2020)<sup>[84]</sup>. It is also important to consider the potential for primed plants to exhibit altered growth patterns, reproductive strategies, or interactions with other organisms in the ecosystem. To ensure the sustainability and safety of chemical priming, it is essential to conduct thorough risk assessments and implement appropriate management practices.

## 12. Future Directions and Research Opportunities

Future research should focus on elucidating the molecular mechanisms underlying priming-mediated stress tolerance, optimizing priming protocols for different plant species and stress conditions, and developing novel priming agents with improved efficacy and safety. Understanding the compatibility of plant microbiota in stress tolerance across

various plant species and conditions is crucial (Ali *et al.*, 2023)<sup>[6]</sup>. The use of cutting-edge technologies, such as genomics, proteomics, and metabolomics, can provide valuable insights into the complex molecular networks involved in priming. Systems biology approaches can help to integrate the vast amount of data generated by these technologies and identify key regulatory nodes that can be targeted for further improvement. Furthermore, research is needed to investigate the long-term effects of priming on plant performance, soil health, and ecosystem functioning. Exploring the potential of combining chemical priming with other stress management strategies, such as genetic improvement and sustainable agricultural practices, is another promising area of research. (Ahkami *et al.*, 2017)<sup>[2]</sup> highlights the potential of symbiotic root-microbe relationships and advanced synthetic biology tools in improving crop productivity and resilience in sustainable agricultural systems. The green synthesis of silver nanoparticles using plants is an emerging area of nanotechnology that can influence its advancement (Alharbi *et al.*, 2022)<sup>[4]</sup>. However, concerns about the toxicity of nanoparticles necessitates further research (Assefa *et al.*, 2024)<sup>[8]</sup>. Advancements in nanotechnology have led to the development of nanopriming techniques, offering new avenues for enhancing seed germination and plant growth.

### 12.1 Identifying Novel Priming Agents

Identifying novel priming agents from natural sources, such as plant extracts and microbial metabolites, is another important area of research. Nanoparticles, synthesized through various methods including plant-mediated green synthesis, offer potential benefits such as targeted delivery and enhanced bioavailability (Dadhwal *et al.*, 2023; Rana *et al.*, 2024)<sup>[26, 98]</sup>. These natural compounds may offer advantages over synthetic chemicals in terms of environmental compatibility and human safety. Further research is needed to optimize the synthesis, characterization, and application of nanoparticles for priming, while also addressing potential environmental and health risks (Rana *et al.*, 2024)<sup>[98]</sup>.

### 12.3 Addressing Knowledge Gaps

Addressing knowledge gaps related to the optimal application methods, timing, and combinations of priming agents is essential for maximizing the benefits of this technology. Understanding the molecular basis of priming effects, including changes in gene expression, protein modification, and metabolic regulation, is crucial for developing more targeted and effective priming strategies (Fabrissin *et al.*, 2021; Gianella *et al.*, 2020)<sup>[37, 44]</sup>. Emphasis needs to be placed on expanding the knowledge of the molecular mechanisms underlying the seed response to priming (Pagano *et al.*, 2023)<sup>[89]</sup>.

Additionally, research is needed to investigate the potential for transgenerational epigenetic inheritance of priming-induced stress tolerance. Overall, chemical priming holds great promise as a sustainable strategy for enhancing plant abiotic stress tolerance and improving crop productivity. Further research is needed to fully unlock the potential of this technology and ensure its safe and effective implementation in agriculture. The biological role of nanoparticles depends on factors such as their

physicochemical properties, application method, and concentration (Zhao *et al.*, 2020) <sup>[136]</sup>. Further understanding of metabolic processes during priming treatment is needed for efficient technology use (Vishvanathan *et al.*, 2020) <sup>[120]</sup>.

**12.4 Understanding Long-Term Effects of Chemical Priming:** Understanding the long-term effects of chemical priming on plant performance, soil health, and ecosystem functioning is crucial for ensuring the sustainability of this technology. It is also vital to consider the potential for primed plants to exhibit altered growth patterns, reproductive strategies, or interactions with other organisms in the ecosystem (Hasan *et al.*, 2024) <sup>[47]</sup>.

### 12.5 Optimizing Priming Protocols

Research is also needed to optimize priming protocols for different plant species and stress conditions, taking into account factors such as seed quality, priming agent concentration, and environmental conditions. Seed priming techniques, including nano-priming, have shown promise in enhancing seed germination and seedling growth under stress conditions (Duary, 2020; Kandhol *et al.*, 2022) <sup>[33, 56]</sup>. Priming with phytohormones has emerged as a promising approach to mitigate the harmful effects of abiotic stresses on plants (Rhaman *et al.*, 2020) <sup>[101]</sup>. These short-term approaches, like seed priming, are gaining traction as methods to improve crop performance in changing environments (Devika *et al.*, 2021) <sup>[29]</sup>. Halo-priming, a method involving inorganic salt solutions, enhances germination and seedling vigor, ultimately improving crop yield in salt-affected soils (Rhaman *et al.*, 2020) <sup>[101]</sup>. However, for many crops, limited information exists regarding their responses to priming agents under salinity stress, underscoring the need for further research (Ibrahim, 2016) <sup>[50]</sup>. Further investigation into the potential risks and benefits of chemical priming is essential for ensuring its responsible and sustainable use in agriculture.

### Conclusion

In conclusion, chemical priming emerges as a pivotal strategy in bolstering plant resilience against abiotic stresses, offering a sustainable avenue for enhancing crop productivity and ensuring food security in the face of escalating environmental challenges. By pretreating seeds or plants with specific chemicals, priming initiates a cascade of physiological and molecular responses that prime the plant to better withstand subsequent stress encounters. This proactive approach not only enhances stress tolerance but also promotes faster and more robust growth, leading to improved yields and overall plant performance. While conventional breeding and genetic engineering have long been employed to develop stress-tolerant crop varieties, chemical priming offers a complementary approach that can be readily integrated into existing agricultural practices, providing a more immediate and cost-effective solution for mitigating the adverse effects of abiotic stresses. The optimization of priming techniques, the identification of novel priming agents, and the exploration of molecular mechanisms underlying priming effects hold the key to unlocking the full potential of this technology and ensuring its sustainable implementation in agriculture. Salinity, a major abiotic stress, significantly impedes crop

production worldwide. Seed priming emerges as a viable strategy to mitigate salinity-induced growth inhibition in crops like rice and soybean. Priming techniques enhance stress adaptation in seedlings growing in salinity-stressed conditions. As climate change continues to exacerbate abiotic stresses in agricultural systems, chemical priming stands out as a promising tool for safeguarding crop production and ensuring food security for future generations. Climate change has intensified environmental stressors, impacting crop production globally. Seed priming is a simple, cost-effective technique improving plant establishment and yield. Seed priming is a low-cost, on-farm technology that enhances germination, seedling establishment, and stress tolerance.

Priming improves plant stand, leading to higher grain yield compared to non-primed seeds. The success of crop improvement relies on maintaining sustainability by modulating seed metabolism through priming techniques. In conclusion, chemical priming represents a powerful and versatile tool for enhancing plant abiotic stress tolerance and improving crop productivity. By pretreating seeds or plants with specific chemicals, priming can trigger a cascade of physiological and molecular responses that prime the plant to better withstand subsequent stress encounters. Chemical priming offers a complementary approach to conventional breeding and genetic engineering, providing a more immediate and cost-effective solution for mitigating the adverse effects of abiotic stresses on crop production (Vinocur & Altman, 2005) <sup>[119]</sup>. As climate change continues to exacerbate abiotic stresses in agricultural systems, chemical priming holds great promise for safeguarding crop production and ensuring food security for future generations. Germination of seeds can be improved through hormonal priming. Phytohormones are known to regulate plant growth and development and act as chemical messengers that allow plants to function when exposed to various stresses.

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