



# PGPR-Mediated Defense Priming: A Sustainable Paradigm for Combating Biotic and Abiotic Stresses in Agriculture

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## Abstract

In the face of complex biotic and abiotic stresses, modern agriculture seeks innovative solutions to ensure sustainable crop production. Plant Growth-Promoting Rhizobacteria (PGPR) emerges as powerful allies, offering a sustainable approach to fortifying plant defense mechanisms. This review delves into harnessing PGPR-mediated defense priming to combat both biotic and abiotic stresses in agriculture. Defense priming, a sophisticated mechanism acquired through exposure to primary stimuli, empowers plants to mount quicker and more resilient defense responses against subsequent challenges. PGPR induce a pre-conditioned state of heightened alertness, enabling rapid and robust defense responses upon stress encounters. This paradigm not only enhances plant resilience to pathogens and environmental stressors but also promotes sustainable practices by reducing chemical inputs. The review critically evaluates the mechanisms underlying PGPR-mediated priming, emphasizing its potential to modulate plant physiology, metabolite production, increased antioxidants enzymes, defense related enzymes activities and enhance stress tolerance. It further explores how PGPR can improve plant responses to a spectrum of stressors. This review also highlights PGPR-mediated defense priming as a cost-effective, enduring, chemical-free, and sustainable method for managing abiotic and biotic stresses in agriculture. Implementing this strategy offers effective crop protection with minimal fitness and environmental costs, even in harsh conditions.

**Keywords:** PGPR; Defense Priming; Biotic and Abiotic Stresses; Plant Immunity; Sustainable Agriculture

**Abbreviations:** PGPR: Plant Growth-Promoting Rhizobacteria; BABA:  $\beta$ -aminobutyric Acid; DMRs: Differentially Methylated Regions; IGIP: Intergenerational Immune Priming; TGIP: Transgenerational Immune Priming; JA: Jasmonic Acid; SA: Salicylic Acid; ET: Ethylene; SAR: Systemic Acquired Resistance; ISR: Induced Systemic Resistance; ROS: Reactive Oxygen Species; CAT: Catalase; POX: Peroxidase; APX: Ascorbate Peroxidase.

## Introduction

Amidst the accelerating pace of global warming and the persistent impacts of climate variability, the integrity of agricultural productivity hangs in the balance. These concerns are further compounded by environmental degradation, pollution, and the prevalence of biotic stresses on food crops, all of which jeopardize global food security [1,2]. Environmental stressors can lead to substantial

reductions in crop yields, ranging from 30% to 70% [3]. Both biotic and abiotic stressors inflict severe constraints on plant growth, yield, and survival. As the global population hurtles towards an anticipated 9-10 billion by 2050, the pressure intensifies on the agro-economic sector to meet burgeoning demand [2,4]. This has increased a reliance on synthetic agrochemicals, deployed to temper stress severity, combat pathogens and pests, and amplify yields and overall crop productivity.

Current efforts are directed towards enhancing crop productivity without reliance on pesticides and fertilizers. Traditional breeding, which harnesses natural genetic diversity, has been pivotal in improving crops and strengthening their resilience against pathogens. However, conventional breeding's lack of precision can lead to unpredictable results and require significant time and resources. On the other hand, genome editing techniques like CRISPR-Cas9 provide precise modifications but encounter regulatory obstacles and public resistance, with concerns about unintended side effects [5]. Despite their limitations, both approaches struggle with addressing complex traits and adapting to rapidly changing environmental conditions.

Plant defense priming is an innovative approach to crop protection. Various biological, physical, and chemical stimuli, as highlighted by Yang, et al. [6], can induce the primed state of the plant immune system, while beneficial interactions with root-colonizing microorganisms, as noted by Yu, et al. [7], have been identified as potential triggers for establishing this primed state. This enables primed plants to remember prior interactions with beneficial microbes, allowing them to mount quicker and more targeted defences against invading pathogens [6,7]. This readiness, known as priming, enhances the plant's defense mechanisms, offering more effective protection against pathogens when they attack [8]. Unlike direct defense activation, priming conserves resources by only activating defences when needed, avoiding negative impacts on plant growth and development [9-14]. Additionally, priming provides broad-spectrum protection in challenging environments, boosting productivity with minimal fitness costs [15].

Upon receiving initial priming cues, plants undergo various physiological, transcriptional, metabolic, and epigenetic changes [9]. Some alterations in plants can lead to somatic immune memory, while others extend to reproductive tissues, forming intergenerational or transgenerational immune memory, benefiting future generations [6,16-18]. Epigenetic modifications, such as DNA methylation and histone modifications, are crucial for establishing memory in plants [19,20]. These changes enable plants to "remember" previous stress events and pass this information on to subsequent generations, thus supporting long-term

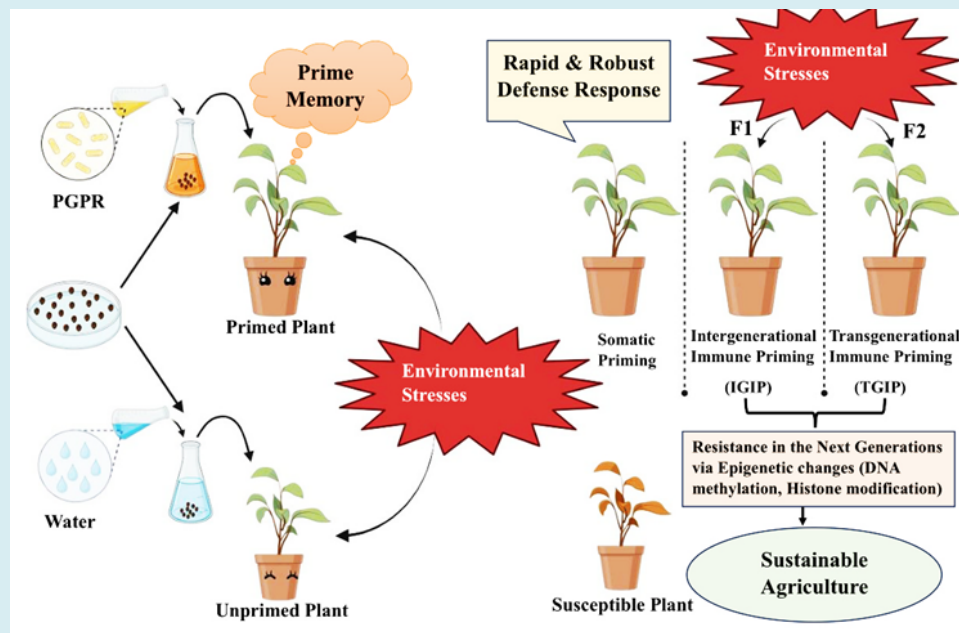
adaptation strategies [21]. Catoni, et al. [22] discovered that priming tomato plants with  $\beta$ -aminobutyric acid (BABA) significantly reduced global cytosine methylation, particularly in CHH sequence contexts. This hypomethylation predominantly occurred in differentially methylated regions (DMRs) and might influence priming indirectly by affecting regulatory genes that control stress responses, rather than directly modifying defense genes. The heritability of DNA methylation marks over several generations highlights the potential of using epigenetic mechanisms to develop crops with improved stress resilience [23].

Histone acetylation and methylation have been identified as key regulators of defense priming, occurring at specific histone residues and often alongside transcriptional reprogramming due to pathogen challenges or environmental stimuli. This process results in a sustainable reconfiguration of the nucleosome structure, as highlighted by Espinas, et al. [24]. Remarkably, in *Arabidopsis*, researchers examined stress memory in response to hyperosmotic stress priming. This priming resulted in histone modifications such as H3K27me3, which persisted in certain genes even after ten days of normal growth, indicating that the H3K27me3 marks were passed on through mitosis [21]. Geng, et al. [25] investigated the epigenetic diversity and memory in *Thlaspi arvense*, an oilseed crop, under salinity stress. They found that, compared to control plants, *T. arvense* plants showed increased epigenetic diversity in response to salinity stress. These changes persisted in the second and third generations, suggesting that the plants retained the stress memory and could pass it on to future generations. This process, where epigenetic marks are inherited across multiple generations without recurrent stress, is known as transgenerational epigenetic inheritance. Thus, the stress tolerance resulting from epigenetic priming could be harnessed to cultivate plants with enhanced tolerance.

This inheritance of epigenetic changes can lead to intergenerational immune priming (IGIP) or transgenerational immune priming (TGIP) as shown in Figure 1 [9,26]. Such phenomena have been observed in various crop plants, where primed plants produce resilient offspring [13,14,18,27,28]. For instance, recent studies have shown that *Trichoderma*-mediated priming in barley results in progeny that perform better under drought stress compared to non-primed barley. The expression of the epigenetic regulator gene *HvDME* was notably higher in primed barley and its subsequent generations, indicating the inheritance of priming through these epigenetic markers [20]. Another study demonstrated that primed common bean (*Phaseolus vulgaris* L.) with INA (2,6-dichloro-isonicotinic acid) provides resistance against *Pseudomonas syringae* pv. *phaseolicola*, with this resistance being transgenerationally transmitted via epigenetic modifications of INA-responsive

genes like *PvPRI* [28]. One more research further showed that DNA methylation changes in BABA-primed potatoes confer intergenerational resistance to *Phytophthora infestans*, with stress memory passed through R3a promoter

methylation. Similarly, Meller, et al. [29] found that in BABA-primed plants, the H3K4me2 label acts as a heritable mark for intergenerational regulation of resistance in potato.



**Figure 1:** PGPR-mediated defense priming enhances plant resilience to environmental stresses and induces somatic memory, termed as somatic priming. Furthermore, this priming can be inherited by progeny, resulting in intergenerational and transgenerational immune priming. Epigenetic modifications, including DNA methylation and histone modification, facilitate this inheritance mechanism. Compared to unprimed plants, primed plants display heightened resilience to stresses and transmit this enhanced defense capability to future generations through epigenetic mechanisms, offering sustainable solutions in agriculture.

Recent research has demonstrated that PGPR-mediated priming in wheat against *Bipolaris sorokiniana* extends beyond the parent generation, establishing intergenerational immune priming. This inheritance mechanism provides sustained protection against *B. sorokiniana*, highlighting the potential of PGPR-based strategies for long-term disease management in agriculture [14]. Utilising beneficial microorganisms not only boosts plant defense mechanisms but also reduces reliance on chemical pesticides, promoting eco-friendly agriculture. PGPR plays a pivotal role in promoting plant growth and development through the secretion of a diverse array of modulatory compounds [30,31].

In this context, this review aims to explore the concept of harnessing PGPR-mediated defense priming as a sustainable paradigm for combating both biotic and abiotic stresses in agriculture. We will delve into the mechanisms underlying PGPR-induced defense priming, examine its potential applications in enhancing crop resilience, and discuss its implications for sustainable agricultural practices.

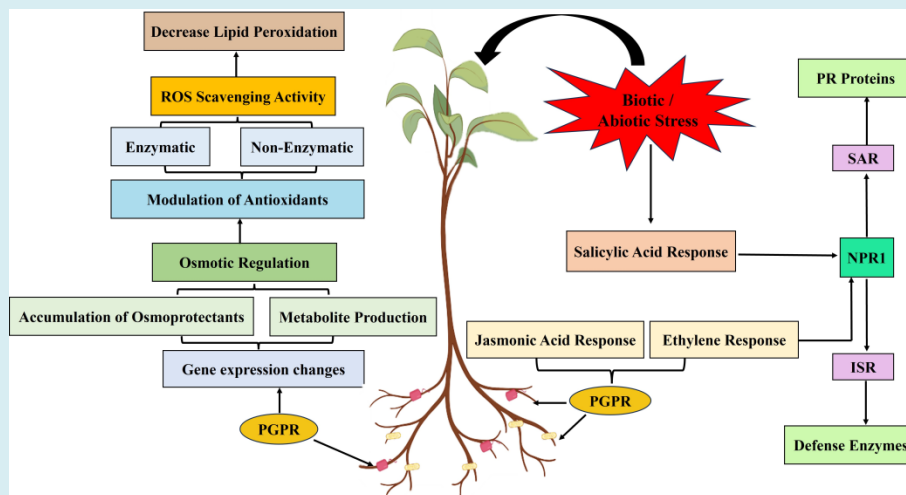
Additionally, further research is needed to explore the mechanism of intergenerational and transgenerational effects of PGPR defense priming, elucidating its long-term benefits for crop protection and food security.

### Efficacy of PGPR Priming for Enhancing Plant Resilience in Alleviating Environmental Stresses

A crucial aspect of plant defense mechanisms involves phytohormones like jasmonic acid (JA), salicylic acid (SA), and ethylene (ET), which play pivotal roles in PGPR-mediated priming to enhance plant immunity [32]. PGPR-induced defense priming and ISR rely on intricate crosstalk between signalling pathways, particularly involving JA, ethylene, and NPR proteins [33]. Understanding this network is vital for enhancing plant immunity. Perception of PGPR signals triggers cascades, activating modulating phytohormones like JA and ethylene, priming defense genes and enhancing PR protein production. This primes plants for rapid, robust responses to pathogens and provides enduring protection

against diverse stresses. Additionally, PGPR-mediated ISR primes PR protein expression, linked to NPR proteins and modulation of JA and ethylene pathways [34]. JA activates defense responses against necrotrophic pathogens and herbivorous insects by promoting the expression of defense genes. SA is crucial for systemic acquired resistance (SAR), providing long-lasting protection against a broad spectrum of pathogens [35]. Ethylene works synergistically with both JA and SA to modulate defense responses, fine-tuning the balance between different hormone pathways. Certain PGPR strains can trigger ISR through the synergistic activation of JA/ET and SA pathways [36]. For example, *Bacillus thuringiensis* primes tomato plants by inducing all three hormonal signaling pathways (SA, JA, and ET), thereby enhancing resistance to various pathogens [37]. *Bacillus subtilis* MBI600 also activates JA and SA pathways simultaneously in tomato plants to control soil-borne pathogens [38]. Similarly, *Bacillus cereus* AR156 can trigger immune responses against *Pseudomonas syringae* pv. Tomato DC3000 through ISR stimulated by both the JA/ET and SA signaling pathways

[39]. In addition, *B. cereus* AR156 mediates priming in *Arabidopsis thaliana* by simultaneously activating salicylate- and jasmonate/ethylene-dependent signaling pathways [36]. NPR (Non-expressor of Pathogenesis-Related) proteins, particularly NPR1, are key regulators in the SA signaling pathway, activating the expression of PR genes and enhancing resistance. NPR proteins serve as central integrators, merging signals from SA, JA, and ethylene pathways [40]. During pathogen attack, NPR1 modulates the cross-communication between SA and JA pathways to prioritize suitable defense mechanisms [40]. Together, these phytohormones and NPR proteins form a complex network that underpins PGPR-mediated priming, enabling plants to effectively respond to and withstand environmental stresses. Furthermore, PGPR-induced defense priming not only enhances secondary metabolite production and boosts antioxidant activity but also increases osmolyte accumulation, thereby enhancing the plant's resilience to environmental stresses (biotic and abiotic) as shown in Figure 2 [2].



**Figure 2:** This schematic illustrates the signaling network underlying PGPR-induced defense priming and ISR in plants. PGPR-derived signals initiate a cascade of events, including modulation of phytohormone signaling, particularly involving JA and ethylene. This primes defense-related genes, activates defense enzymes, and increases production of PR proteins, preparing the plant for rapid defense against environmental stresses. Additionally, PGPR-mediated ISR primes PR protein expression through NPR proteins and modulates JA and ethylene pathways, facilitating streamlined defense responses. PGPR-induced defense priming also enhances secondary metabolite production and antioxidant activity, reducing oxidative stress.

## Biotic Stress

Recent studies have consistently highlighted the effectiveness of plant growth-promoting rhizobacteria (PGPR) in fortifying plant defenses against diverse pathogens. For example, Sufyan, et al. [41] demonstrated that PGPR priming of chickpea seeds not only increased overall plant biomass but also decreased disease incidence

caused by *Fusarium oxysporum* f. sp. *ciceris*. Likewise, Dehkan, et al. [42] showed that priming tomato plants with *Bacillus thuringiensis* boosted the expression of defensive genes against *Fusarium oxysporum* (Fol), leading to diminished disease severity. In wheat plants challenged by *Puccinia striiformis* f. sp. *tritici* (Pst), Mashabela, et al. [43] observed notable metabolic changes induced by PGPR priming, including heightened levels of phenolic

compounds, indicating adaptive responses to stripe rust infection over time.

Moreover, Carlson, et al. [44] employed metabolomics to reveal that PGPR-primed sorghum seedlings exhibited enhanced upregulation of defense-related metabolites against *Fusarium pseudograminearum*, suggesting evidence of induced systemic resistance (ISR) and a primed state in the plants. Additionally, Devi, et al. [14] underscored the protective effects of PGPR priming in wheat against *Bipolaris sorokiniana*, attributing this to increased levels of enzymatic and non-enzymatic antioxidants, as well as heightened activities of defense-related enzymes in primed plants compared to non-primed ones.

In a recent contribution, Tahir Ali, et al. [45] demonstrated that priming *Crocus sativus* with the *Bacillus sp.* D5 strain enhanced biomass and fortified resistance against *Fusarium oxysporum* infection by inducing various defense enzymes. Collectively, these studies emphasize the potential of PGPR priming as a sustainable strategy for enhancing plant defense mechanisms and reducing pathogen-induced losses in agricultural contexts.

### Abiotic Stress

Due to their immobile nature, plants face a variety of abiotic stresses like drought, heat, heavy metal toxicity, and salinity, all of which hinder their growth and development [46-48]. These stresses adversely affect critical physiological processes such as photosynthesis, floral formation, seed germination, and even induce responses like stomatal closure. By 2050, it is anticipated that drought-affected crop lands will double, while water resources will diminish by thirty percent [49]. Abiotic stresses disrupt the delicate balance between reactive oxygen species (ROS) generation and scavenging, leading to the acceleration of ROS propagation and subsequent damage to crucial macromolecules and photosynthetic complexes, ultimately resulting in cell death [49]. PGPR priming enhances crop growth by activating antioxidant defense systems, regulating both enzymatic (CAT, SOD, APX, GR) and non-enzymatic antioxidants, thus shielding plants from oxidative damage [50].

The efficacy of priming techniques in enhancing drought tolerance across various crops is highlighted by recent research findings. For instance, priming maize with PGPR boosts phenolic acid flavonoids and enhances the activity of antioxidant enzymes such as SOD, CAT, and APX under drought conditions [51]. Furthermore, studies have demonstrated the effectiveness of priming in other crops. Priming *Oryza sativa* seeds with *Bacillus pumilus* SH-9 not only enhances germination metrics but also improves seedling characteristics compared to the control group, even under drought stress [52]. Similarly, priming wheat seeds

with the endophytic strains *B. subtilis* 104 and 26D enhances growth, elevates photosynthetic pigment content, increases leaf area, and mitigates oxidative and osmotic cell damage under combined herbicide and drought stress conditions [53]. Additionally, priming wheat seeds with *Bacillus subtilis* 10-4 increases drought tolerance by augmenting photosynthetic pigments, relative water content, and reducing lipid peroxidation and electrolyte leakage during drought stress [54]. Moreover, priming okra seeds with *Pseudomonas fluorescence* enhances drought stress tolerance by maintaining relative water content, elevating the activity of both enzymatic and non-enzymatic antioxidants (e.g., AsA, GSH, SOD, CAT, APX, and GPX), and promoting metabolite accumulation, thereby improving growth under drought stress conditions [55]. In another study by Arafa SA, et al. [56], priming pea seeds with *Bacillus thuringiensis* MH161336 and carrot extract enhances growth, biochemical, and physiological traits. This includes increased relative water content and chlorophyll levels (a and b), up-regulation of antioxidant enzymes, higher seed yield, and reduced lipid peroxidation and reactive oxygen species during drought stress. Collectively, these findings underscore the potential of priming techniques to mitigate oxidative stress and bolster crop resilience against drought.

Soil salinity poses a significant global concern, detrimentally impacting agricultural yields in numerous countries [57]. In the realm of salinity tolerance, PGPR priming demonstrates remarkable efficacy across various crops. In peas, it modulates biochemical parameters, reducing electrolyte leakage and H<sub>2</sub>O<sub>2</sub> levels during salinity stress [58]. Similarly, in wheat, this priming enhances water content and photosynthetic pigments while bolstering antioxidant activity under salinity stress conditions. Furthermore, PGPR priming triggers the upregulation of *SOS* genes (*SOS1* & *SOS4*) in wheat during salinity stress, indicating a pathway to enhance salinity resilience [59]. Additionally, seed priming with endophytic *B. subtilis* strains 10-4 and 26D was found to enhance growth attributes and mitigate oxidative and osmotic damage to *Phaseolus vulgaris* L. plants, while also increasing lignin accumulation in plant roots under salinity stress conditions [60]. Moreover, recent research discovered that priming tomato seeds with *Bacillus paralicheniformis* resulted in improved germination percentage, shoot length, root length, vigor index, and dry matter production compared to the control group under salinity stress conditions [61]. Furthermore, a study revealed that seed bio-priming of maize with *Bacillus spp.* mitigates salt stress damage on seedlings, resulting in elongated roots. This effect is achieved by increasing the activity of catalase (CAT), peroxidase (POX), and ascorbate peroxidase (APX), while also upregulating the expression of miR160d [62]. Ultimately, these findings underscore the potential of microbial priming techniques in bolstering crop

resilience to salinity stress. Another study demonstrated that priming wheat with PGPR resulted in several benefits. Primed wheat exhibited enhanced chlorophyll content and increased expression of various redox enzymes, along with the accumulation of osmolytes. This resulted in reduced membrane damage during heat stress compared to non-primed wheat plants [63]. Furthermore, another study by Jayanwita Sarkar et al. [64] demonstrated that priming wheat plants with *Bacillus safensis* enhanced resilience against high temperature stress. This was achieved through improvements in antioxidant enzymes, dynamic expressions of HSPs, osmolyte accumulation, and reduced chloroplast damage. Cold stress poses a significant challenge to crop development and global food security, prompting diverse molecular, physiological, and biochemical adaptations in plants across varying cold environments [65]. A study revealed that *Burkholderia phytofirmans* PsJN enhances Grapevine tolerance to low temperatures by upregulating stress-related genes. This priming significantly boosts the plant's resilience compared to non-primed ones [66].

Heavy metal toxicity poses a significant threat to crop production, affecting stomata structure and function, RuBisCO activity, and disrupting photosynthesis [67,68]. Recent research by Ahmet Direk, et al. [69] discovered that wheat seeds primed with *Bacillus cereus* showed enhanced growth, reduced oxidative stress markers ( $H_2O_2$  and TBARS), and increased activity of antioxidant enzymes (SOD, GST, and APX). This priming led to improved yields under cadmium and arsenic stress. Similarly, a study by Aditya Banerjee & Aryadeep Roychoudhury, et al. [70] explored the priming of *Oryza sativa* seeds with *Acinetobacter indicus*, resulting in enhanced growth physiology and antioxidant capacity by activating key enzymatic antioxidants under arsenic-fluoride co-toxicity.

### Conclusions and Future Perspectives

In conclusion, PGPR-mediated defense priming offers a holistic approach to mitigate both biotic and abiotic stresses in sustainable agriculture, enhancing crop resilience and reducing reliance on harmful chemicals. Future research should focus on identifying novel PGPR strains with superior priming capabilities, elucidating PGPR-plant interactions, and optimizing field application methods. Additionally, understanding the long-term impact of PGPR on plant health and soil sustainability, and integrating PGPR with other sustainable agricultural practices, will be critical for maximizing the benefits of this technology in diverse agricultural settings. By leveraging PGPR's defense-enhancing capabilities, researchers aim to bolster plant immunity, paving the way for more enduring and resilient agriculture. Exploring transgenerational effects, elucidating molecular mechanisms, and identifying synergies with other

management practices are key research avenues. Ultimately, PGPR-mediated priming presents a promising, eco-friendly tool for advancing agriculture sustainably amidst growing population demands and climate change challenges.

### Author Contributions

PS and BD conceived the idea. BD, NY and PS prepared the manuscript. BD, NY and PS edited and finalised the manuscript. All authors contributed to the article and approved the submitted version.

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### Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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