# *Role of Plant Growth in Promoting Rhizobacteria in Inducing Systemic Resistance in Plants: Molecular Mechanisms and Recent Advances*

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**ABSTRACT**

Plant growth-promoting rhizobacteria (PGPR) play a crucial role in enhancing plant defense by activating systemic resistance against a broad range of pathogens. This review explores the molecular basis of PGPR-mediated induced systemic resistance (ISR), with particular emphasis on defense signaling pathways regulated by jasmonic acid, ethylene, and salicylic acid. The induction of ISR involves multiple mechanisms, including the regulation of plant hormone signaling, synthesis of antimicrobial metabolites, and priming of plant defense systems. As a result, plants exhibit increased expression of defense-related genes and a strengthened immune response. A clear understanding of these molecular interactions is essential for promoting sustainable agricultural strategies and minimizing dependence on chemical pesticides. Recent progress in omics-based approaches and bioinformatic tools has significantly improved our understanding of PGPR-plant interactions, facilitating the discovery of new bacterial strains and key signaling components. Future studies should emphasize the integration of multi-omics data with field-based research to enhance the effective application of PGPR for improved crop protection and productivity.

## INTRODUCTION

Plant growth-promoting rhizobacteria (PGPR) represent a diverse group of beneficial soil bacteria that colonize the rhizosphere and support plant growth and health through a range of direct and indirect mechanisms (Gowtham *et al*., 2021). These bacteria contribute significantly to sustainable agriculture by enhancing nutrient availability, synthesizing plant growth regulators, and suppressing plant pathogens. Induced systemic resistance (ISR) is an important plant defense response initiated by specific PGPR strains. Through ISR, plants develop a heightened state of readiness that allows them to respond more rapidly and effectively to a wide range of pathogens and environmental stresses (Pieterse *et al*., 2014). This systemic defense response strengthens plant resilience while reducing dependence on chemical pesticides, thereby supporting environmentally sustainable crop management practices. Although several reviews have addressed PGPR-mediated ISR and its applications, many lack an integrated discussion of recent advances in molecular signaling pathways and the complex interactions among PGPR, ISR, and the plant-associated microbiome. Moreover, important knowledge gaps remain regarding the variability of ISR responses across different plant species and under diverse environmental conditions.

## OVERVIEW OF PGPR

Plant growth-promoting rhizobacteria (PGPR) are beneficial bacteria that colonize plant roots and support plant growth and health. Common PGPR genera include *Bacillus*, *Pseudomonas*, *Azospirillum*, *Rhizobium*, and *Enterobacter* (Shetty, Meghana & Shetty, 2025). These bacteria primarily inhabit the rhizosphere, the soil zone influenced by root secretions. PGPR benefit plants through several mechanisms: by Promoting plant growth by synthesizing phytohormones such as auxins, cytokinins, and gibberellins, Enhancing nutrient availability through processes like nitrogen fixation, phosphate solubilization, and siderophore-mediated iron chelation, Improving tolerance to abiotic stresses, including drought, salinity, and heavy metal stress, Protecting plants from pathogens by producing antimicrobial compounds, lytic enzymes, or by activating induced systemic resistance (Gowtham *et al*., 2021). PGPR differ from other soil microorganisms due to their direct and beneficial interactions with plants. Unlike general soil microbes, which may be neutral or harmful, PGPR actively enhance plant growth and health through specific biological mechanisms. Their efficient colonization of the rhizosphere and ability to influence plant physiological responses distinguish them from non-beneficial and free-living microbes.

## MOLECULAR SIGNALING IN PGPR-ISR

Induced systemic resistance (ISR) triggered by plant growth-promoting rhizobacteria (PGPR) is a complex defense process in which beneficial root-associated microbes prepare the entire plant for improved resistance against pathogens. In contrast to systemic acquired resistance (SAR), which is mainly mediated by salicylic acid (SA) following pathogen attack, ISR is typically regulated through jasmonic acid (JA) and ethylene (ET) signaling pathways(Zhang *et al*., 2025). The defining feature of PGPR-mediated induced systemic resistance (ISR) is the priming of plant defense, in which defense mechanisms remain inactive until pathogen attack, thereby conserving plant metabolic resources. **Triggering mechanisms:** Certain PGPR strains, such as *Pseudomonas fluorescens* and *Bacillus velezensis*, release elicitor molecules including lipopolysaccharides (LPS), flagellin, and volatile organic compounds (VOCs) such as 2,3-butanediol. These signals are perceived

by plant pattern recognition receptors (PRRs), leading to signal transduction that enhances sensitivity of the jasmonic acid and ethylene (JA/ET) pathways. **Key genes involved:** *MYC2* acts as a central transcription factor in the jasmonic acid signaling pathway and regulates the expression of jasmonate-responsive defense genes. **ERF1 (Ethylene Response Factor 1):** Functions as a key regulatory node where jasmonic acid and ethylene signaling pathways intersect (Lorenzo *et al*., 2003; Pieterse *et al*., 2014). **NPR1 (Non-expressor of PR genes 1):** Although NPR1 is best known as a central regulator of salicylic acid-dependent systemic acquired resistance, it also plays an essential role in JA/ET-mediated ISR in many plant species, primarily functioning in the cytoplasm rather than the nucleus.

**Recent crop examples (2018–2025):**

- In tomato (*Solanum lycopersicum*), *Pseudomonas canadensis* enhances resistance to *Botrytis cinerea* by stimulating jasmonic acid-associated defense genes such as *LOX*, consistent with ISR-mediated activation (Mazuecos-Aguilera *et al*., 2025).
- **Arabidopsis:** Volatile compounds produced by *Bacillus* spp. and other beneficial microbes activate jasmonate- and ethylene-related defense pathways, including the regulation of JA-responsive transcription factors such as *MYC2*, leading to enhanced resistance against herbivores and necrotrophic pathogens (Yu *et al*., 2022; Montejano-Ramírez & López, 2024).
- **Rice (*Oryza sativa*):** In rice, strains of *Bacillus amyloliquefaciens* have been reported to induce systemic resistance and enhance defense signaling pathways, contributing to disease suppression and improved host resilience (Yang *et al*., 2024).

## CROSS-TALK WITH SALICYLIC ACID

Traditionally, SA and JA/ET signaling pathways have long been described as mutually antagonistic, with SA-mediated defenses targeting biotrophic pathogens and JA/ET pathways primarily conferring resistance against necrotrophic pathogens and herbivorous insects (Glazebrook, 2005; Pieterse *et al*., 2012). Recent studies, however, reveal a more complex interaction between these pathways, often described as signaling crosstalk. Role of SA in plant defense: SA commonly induces the expression of pathogenesis-related (PR) genes such as *PR1* and forms the core signaling pathway underlying systemic acquired resistance (SAR). Points of intersection: Synergistic interaction: Certain PGPR, including specific *Bacillus* strains, can activate both SA and JA-dependent signaling pathways simultaneously, resulting in broad-spectrum resistance. For instance, studies published in 2025 on *Peribacillus frigoritolerans* demonstrated concurrent activation of both pathways in tomato plants. Antagonistic interaction: Under some conditions, elevated SA levels may suppress JA-responsive genes, and the reverse can also occur. PGPR assist plants in managing this regulatory balance by modulating transcription factors such as *WRKY70* (Li *et al*., 2004; Pieterse *et al*., 2012).

## DOWNSTREAM DEFENSE GENE ACTIVATION

Following activation of defense signaling pathways, plants enter a primed state that allows rapid mobilization of defense responses upon pathogen attack. Defense priming leads to the induction of genes encoding chitinases (PR3), β-1,3-glucanases (PR2), and thaumatin-like proteins (PR5), which directly degrade fungal and bacterial cell walls (Van Loon *et al*., 2020; Li *et al*., 2022). Studies published in 2024 reported that *Bacillus halotolerans*

increased the expression of *PR1* and *PR5* in cucumber plants, enhancing resistance to powdery mildew. Antioxidant enzymes: To regulate the oxidative burst associated with pathogen defense, PGPR stimulate the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) (Pieterse *et al*., 2014; Gill & Tuteja, 2010). This regulation limits oxidative damage to plant tissues while allowing reactive oxygen species (ROS) to function in pathogen suppression. Secondary metabolites: Phenylpropanoids: Enhanced phenylalanine ammonia-lyase (PAL) activity results in increased synthesis of lignin and tannins, which act as structural barriers to infection. Phytoalexins: PGPR induce the production of antimicrobial compounds such as camalexin in *Arabidopsis* and gossypol in cotton. Field and greenhouse studies on chickpea reported a significant increase (up to ~40%) in total phenolic content following inoculation with *Pseudomonas* spp., indicating enhanced defense metabolism (Sharma *et al*., 2025).

| PGPR Genus | Primary Elicitors | Target Signaling Pathways | Specific Gene Expression | Host Plant Example |
|---|---|---|---|---|
| *Bacillus* | VOCs (2,3-butanediol), Surfactin, Fengycin | JA/ET (Primarily), some SA | $MYC2$, $PDF1.2$, $PR1$ | Tomato, Arabidopsis, Cucumber |
| *Pseudomonas* | Flagellin (flg22), Pyoverdine, LPS | JA/ET, SA Crosstalk | $PAL$, $LOX$, $ERF1$, $NPR1$ | Rice, Tobacco, Wheat |
| *Serratia* | Prodigiosin, Siderophores | JA/ET | $PR2$, $PR3$ (Chitinases) | Maize, Bean |
| *Azospirillum* | Indole-3-acetic acid (IAA), VOCs | JA/ET, Auxin signaling | $AOS$ (Allene oxide synthase) | Wheat, Barley |

**Table1.** Comparative Overview of PGPR-Induced ISR: Elicitors, Signaling Networks, and Host Gene Expression

**Advances in integrated omics approaches**

Including genomics, transcriptomics, proteomics, and metabolomics have transformed the understanding of induced systemic resistance (ISR) from isolated gene-level observations to a comprehensive, systems-level perspective of how plant growth-promoting rhizobacteria (PGPR) modulate host defense networks (Sahoo *et al*., 2025). Transcriptome profiling through RNA-Seq has demonstrated that beneficial microbes extensively reprogram plant gene expression, establishing a primed defensive state characterized by the upregulation of key transcription factor families such as WRKY, MYC2, and ERF, as observed in recent studies on tomato and rice inoculated with *Peribacillus* spp. and *Bacillus amyloliquefaciens*. Notably, many defense-associated genes remain in a partially activated state, enabling a rapid and amplified transcriptional response upon subsequent pathogen attack. Complementary proteomic analyses further bridge gene expression with functional outcomes by revealing enhanced accumulation of pathogenesis-related proteins (PR1, PR2, PR5) and chitinases that directly contribute to pathogen cell wall degradation. Recent proteomic studies show increased abundance of ATP synthase subunits and ROS-scavenging enzymes such as SOD, CAT, and APX during PGPR-induced ISR, reflecting metabolic reprogramming to sustain defense while limiting oxidative stress (Zhang *et al*., 2024). Metabolomic profiling substantiates these molecular shifts by detecting elevated levels of defense-related secondary metabolites, including phenylpropanoids, flavonoids, and phytoalexins, as reported in recent studies on wheat and mustard, alongside increased concentrations of proline and sucrose that function as biomarkers of enhanced stress tolerance and defense signaling. Collectively, multi-omics evidence provides robust mechanistic support for ISR, demonstrating that PGPR-mediated resistance is orchestrated through coordinated transcriptional reprogramming, proteomic modulation, and metabolic reconfiguration, thereby equipping plants with a rapid, efficient, and sustainable defensive capacity against diverse pathogens.

| Omics Level | Key Findings (2018–2025) | Primary Outcome |
|---|---|---|
| Transcriptomics | Upregulation of $WRKY$, $MYC2$, and $RLKs$ | Transcriptional "Priming" |
| Proteomics | Accumulation of $PR$-proteins and SOD/CAT enzymes | Enhanced Protein Synthesis/Scavenging |
| Metabolomics | Higher Phenolics, Flavonoids, and Proline | Chemical Defense & Homeostasis |

**Table 2.** Multi-Omics Insights into PGPR-Induced Systemic Resistance (2018–2025) Source: Author's compilation based on recent ISR omics studies (2018–2025).

**Comparative case studies across diverse host**

species demonstrate that although the fundamental concept of induced systemic resistance (ISR) is evolutionarily conserved, its molecular execution varies considerably depending on host-specific signaling architectures and adaptive history. In *Arabidopsis thaliana*, ISR is mainly governed by jasmonic acid (JA) and ethylene (ET) signaling, with NPR1 acting in the cytoplasm to regulate defense priming without activating *PR1*, distinguishing ISR from SA-dependent SAR (Pieterse *et al*., 2014; Martínez-Medina *et al*., 2016). A defining characteristic in this system is the strong reliance on transcription factors such as MYC2 and downstream defense markers like PDF1.2, making Arabidopsis the principal reference framework for mechanistic ISR studies. In contrast, Solanum lycopersicum exhibits a more flexible signaling architecture, where significant crosstalk between JA and SA pathways contributes to ISR establishment. Notably, tomato plants display enhanced activation of the phenylpropanoid pathway, leading to lignin deposition and reinforcement of cell walls, and recent studies (2025) indicate that volatile organic compounds (VOCs) from *Pseudomonas canadensis* can systemically induce protease inhibitor genes, further strengthening defense capacity. In monocots such as Oryza sativa, ISR commonly involves synergistic interactions between SA and JA pathways; owing to inherently elevated basal SA levels, resistance is reinforced through WRKY45 and OsNPR1-mediated transcriptional regulation (Shimono *et al*., 2007; Nakayama *et al*., 2013). A distinctive feature in rice is the pronounced induction of antioxidant enzymes, including peroxidase (POD) and polyphenol oxidase (PPO), which enhance resistance against hemibiotrophic pathogens such as *Xanthomonas*. In legumes, which are naturally adapted to symbiotic interactions, ISR signaling partially overlaps with nodulation pathways, as PGPR-derived signals intersect with the common symbiosis signaling pathway (CSSP) (Oldroyd, 2013; Zipfel & Oldroyd, 2017; Venkateshwaran *et al*., 2015).This integration results in strong stimulation of flavonoid and phytoalexin biosynthesis, with compounds such as medicarpin in alfalfa playing dual roles in microbial communication and pathogen defense. Collectively, these comparative analyses underscore that while ISR is unified by the principle of microbial priming, its regulatory networks are finely tuned to host-specific physiological and evolutionary contexts, reflecting adaptive diversification of plant immune strategies.

| Host Plant | Primary Signaling | Key Biomarkers | Primary Defense Strategy |
|---|---|---|---|
| Arabidopsis | JA / ET | $VSP2$, $PDF1.2$ | Priming of JA-responsive genes |
| Tomato | JA / ET + SA | $COI1$, $PR$ proteins | Cell wall lignification & Phenolics |
| Rice | SA + JA / ET | $WRKY45$, $OsNPR1$ | ROS scavenging & Phytoalexins |
| Legumes | JA + Nod-Factors | Flavonoids, $PAL$ | Secondary metabolite accumulation |

**Table 3.** ISR Variations by Host

**CURRENT GAPS AND FUTURE DIRECTIONS**

Despite substantial progress in elucidating the molecular framework of PGPR-induced ISR, several critical knowledge gaps continue to hinder its consistent translation from controlled laboratory systems to variable field

environments. One major unresolved aspect concerns the longevity and stability of the primed state. Although experimental evidence suggests that ISR can persist for several weeks, the molecular mechanisms governing the maintenance, attenuation, or termination of this heightened defense readiness remain largely unknown. In particular, the signaling components responsible for resetting the plant immune system to its basal state have not been clearly identified. Additionally, ISR research has largely relied on bulk tissue analyses, which obscure spatial and cell-type-specific variations in signaling. Consequently, there is limited understanding of how ISR signals are transported through vascular routes such as the phloem and xylem, or how distinct tissues and cell populations perceive and interpret PGPR-derived cues, restricting precise mapping of systemic signal transmission.

Current omics-based approaches, while powerful, also present methodological constraints. Conventional transcriptomic and proteomic analyses depend on pooled tissue samples, generating averaged molecular profiles that mask cell-to-cell heterogeneity and prevent identification of the primary ISR perception sites. The absence of single-cell omics data represents a significant limitation in pinpointing the earliest cellular events in ISR initiation. Moreover, although vast datasets now exist across genomic, proteomic, and metabolomic layers, their integrative interpretation remains at an early stage. The application of artificial intelligence and machine-learning frameworks to synthesize multi-omics datasets into predictive, systems-level models of plant immune performance is only beginning to emerge, highlighting the need for computational advancements alongside biological experimentation.

Another pressing challenge is the persistent “lab-to-land” disconnect. Much of the current mechanistic understanding of ISR is derived from elite, well-characterized PGPR strains evaluated under controlled conditions; however, in natural soils these strains frequently face intense competition from indigenous microbial communities, resulting in inconsistent establishment and variable field performance. Furthermore, ISR efficacy is highly sensitive to environmental parameters such as soil pH, temperature, and water availability. In the context of increasing climatic variability, future research must prioritize the development of climate-resilient PGPR consortia capable of sustaining ISR induction under fluctuating agro-ecological conditions.

An emerging and relatively unexplored dimension of ISR research involves epigenetic regulation. A central question is whether PGPR-triggered priming induces stable epigenetic modifications such as alterations in DNA methylation patterns or histone modifications that maintain plants in a heightened defensive state. Preliminary evidence suggests the intriguing possibility that ISR-primed parent plants may transmit enhanced immune preparedness to their progeny, indicating a heritable component of defense priming. Deciphering these epigenetic signatures could open avenues for producing seeds with intrinsic disease resistance, thereby reducing reliance on repeated microbial applications and contributing to more sustainable crop protection strategies.

## CONCLUSION

Plant growth-promoting rhizobacteria (PGPR) activate induced systemic resistance (ISR) through a stable yet adaptable signaling network. Jasmonic acid (JA) and ethylene (ET) act as the central regulators, while salicylic acid (SA) participates depending on the plant species and environmental context. With agriculture under pressure from climate stress and the need to limit chemical inputs, PGPR-mediated ISR emerges as a sustainable biological strategy. It delivers broad and

durable protection against diverse threats, including fungal, bacterial, viral pathogens, and insect herbivores. Unlike synthetic pesticides, ISR activates the plant's inherent defense capacity, reducing environmental contamination and slowing the evolution of resistant pathogens.

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