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Induced systematic resistance by beneficial microbes

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Abstract

Beneficial microbes in the microbiome of plant roots improve plant health. Induced systemic resistance (ISR) emerged as an important mechanism by which selected plant growth-promoting bacteria and fungi in the rhizosphere prime the whole plant body for enhanced defense against a broad range of pathogens and insect herbivores. A wide variety of root-associated mutualists, including Pseudomonas, Bacillus, Trichoderma, and mycorrhiza species sensitize the plant immune system for enhanced defense without directly activating costly defenses. This review focuses on molecular processes at the interface between plant roots and ISR-eliciting mutualists, and on the progress in our understanding of ISR signaling and systemic defense priming. The central role of the root-specific transcription factor MYB72 in the onset of ISR and the role of phytohormones and defense regulatory proteins in the expression of ISR in aboveground plant parts are highlighted. Finally, the ecological function of ISR-inducing microbes in the root microbiome is discussed.

Keywords: defense priming; plant growth–promoting microbes; plant immunity

Introduction

With the rapid growth of the world's population, people's demand for agricultural products is increasing. Plants are sessile organisms, frequently exposed to a myriad of microorganisms, including pathogenic and beneficial ones. The pursuit of productivity has led to the abuse of fertilizers and pesticides, causing serious environmental pollution and ecological damage. During development, the main concerns in the agricultural industry have changed from yield to food quality and environmental impact. The use of environmentally friendly agricultural inputs has arisen since then. Biological control uses beneficial organisms to suppress harmful organisms and promote plant growth. Currently, many beneficial microorganisms, such as *Bacillus*, *Pseudomonas*, and *Trichoderma*, are used as biological control agents to control field plant diseases.

Main body

Plants possess an innate ability to sense and recognize potential invading microorganisms and to activate defense responses . On the contrary, to perceive the beneficial microorganisms and form a symbiotic relationship with them, plants adopt similar, yet distinct, cell surface receptors . Plants can recognize microbial- or pathogen-associated molecular patterns (MAMPs or PAMPs), such as bacterial flagellin and fungal chitin, through transmembrane pattern recognition receptors (PRRs), and this process triggers the first layer of immune defense, named pattern-triggered immunity (PTI). The complex and precise immune system built from host–pathogen competition allows beneficial microorganisms to induce plant immunity through targeting the key elements in the process of PTI and ETI by modulating host small RNAs.

Plant systemic resistance can be divided into induced systemic resistance (ISR) and systemic acquired resistance (SAR), induced by non-pathogenic microbes and pathogenic microbes, respectively. Colonization by beneficial microbes induces a physiological state of plant host called "priming", plants display stronger and faster defense responses against the following invasion of pathogens, demonstrated as a common feature of systemic resistance induced by beneficial microorganisms. SAR was first discovered in 1961 and identified as a salicylic acid (SA)-dependent plant defense, featured by accumulation of SA and activation expression of pathogenic-related (PR) genes. Nevertheless, thre are multiple reports demonstrating activation of both SA and JA/ET signaling pathways in ISR triggered by beneficial microbes revealed the complexity and diversity of signal pathways involved in ISR

Various beneficial microorganisms have shown the potential to induce systemic resistance. Beneficial bacteria, such as *Bacillus* spp. and *Pseudomonas* spp., can stimulate defense responses and help plants to obtain broad-spectrum disease resistance. Beneficial fungi, such as *Trichoderma* spp. and Arbuscular mycorrhizal fungi (AMFs), have been considered to be widespread potential biocontrol agents. Roottreatment with *Trichoderma harzianum* T39 induced ISR in bean against *Botrytis cinerea* . AMFs, which form symbiotic associations with many plant root systems, have been proved to induce local and systemic resistance to *Phytophthora parasitica* in tomato roots .

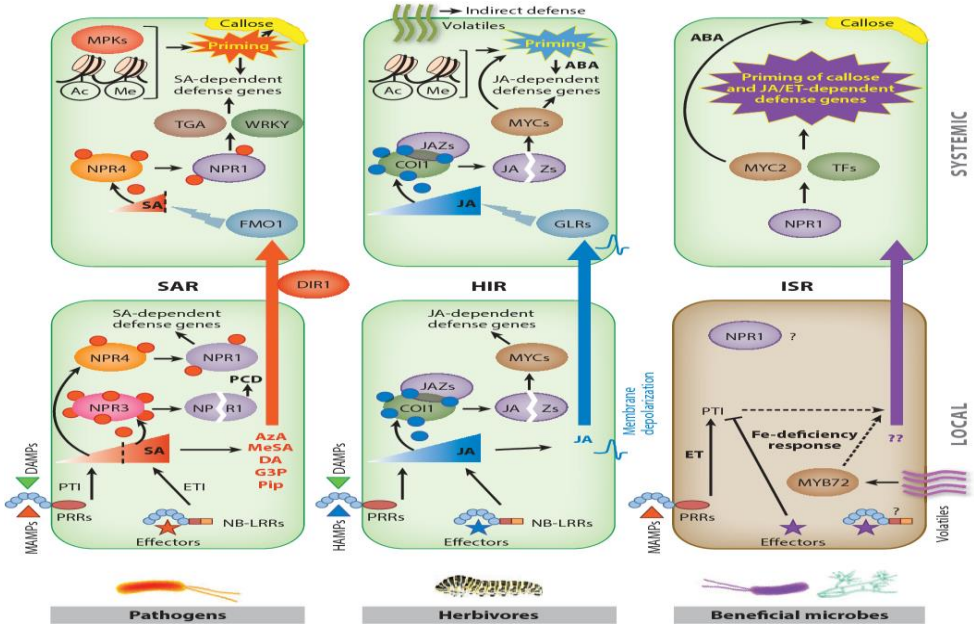

Figure 1: Schematic representation of biologically induced resistance triggered by pathogen (red arrow), insect herbivory (blue arrow), & colonisation of roots by beneficial microbes purple arrow).

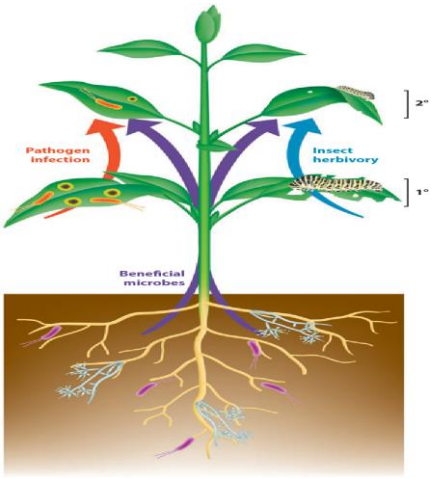

Fig 2: Schematic representation of molecular components & mechanisms involved in pathogen-induced Systemic Acquired Resistance (SAR), Herbivore-Induced Resistance (HIR) & Induced Systemic Resistance (ISR) triggered by beneficial soil borne microbes.

Beneficial microorganisms are able to stimulate defense responses of host plants through different pathways, thereby endowing plants with resistance to multiple pathogens.

RESISTANT MECHANISM OF BENEFICIAL MICROBES			
Strain	**Pathogen**	**Disease**	**Resistance Mechanism**
Bacillus amyloliquefaciens Ba13	Tomato yellow leaf curl virus	Tomato yellow	*PR1*, *PR2*, and *PR3* gene (antimicrobial effects, beta-1,3

		leaf curl virus disease	glucanase, and chitinase activities); enhanced activities of phenylalanine ammonia lyase (regulation of plant growth and stress tolerance), beta-1,3 glucanase (inhibition of the mycelial growth and spore germination), and chitinase (inhibition of mycelial growth).
Bacillus amyloliquefaciens FZB42	*Meloidogyne incognita*	Root-knot nematode	Volatiles-dimethyl disulfide, methyl isovalerate, and 2-undecanone (regulation of antioxidant enzymes, protection from oxidative stress, and against *M. incognita*).
Bacillus cereus AR156	*Pseudomonas syringae* pv. tomato (Pst) DC3000		Suppression of miR825 and miR825* (activating the targeted defense-related genes).
Bacillus cereus C1L	*Botrytis cinerea*, *Cochliobolus heterostrophus*	Foliar and soil diseases	Volatile metabolites-dimethyl disulfide (induction of ISR).
Bacillus megaterium DE BABY TRS-4	*Fomes lamaoensis*	Brown root rot	Enzymes activity-peroxidase, chitinase, beta-1,3-glucanase (inhibition of the mycelial growth and spore germination), and phenyl alanine ammonia lyase (regulation of plant growth and stress tolerance); enhanced phosphate solubilization and production of IAA (promotion of plant growth); regulation of siderophore and antifungal metabolite (inhibition of pathogen growth)
Bacillus subtilis FB17	*Pseudomonas syringae* pv. tomato (Pst) DC3000		Malate efflux (enabling stable colonization).
Bacillus subtilis M4	*Colletotrichum lagenarium*, *Pythium aphanidermatum*		Metabolic and transcriptomic changes (enhanced defense response).
Bacillus subtilis OTPB1	*Alternaria solani*, *Phytophthora infestans*	Early and late blight	Defense-related enzymes—peroxidase, polyphenol oxidase, and superoxide dismutase (inhibition of the mycelial growth and spore germination, and protection from oxidative stress).
Bacillussubtilis UMAF6639	*Podosphaera fusca*	Cucurbit powdery mildew	Reactive oxygen species (inhibition of the mycelial growth and spore germination); cell wall reinforcement (reduction in pathogen invasion); metabolites—surfactin lipopeptide (stimulation of the immune response).
Paenibacillus alvei K165	*Verticillium dahliae*		*PR-1*, *PR2*, and *PR-5* genes (antimicrobial effects, beta-1,3 glucanase, and chitinase

			activities, markers for SA-mediated activation of SAR).
Pseudomonas aeruginosa 7NSK2	*Magnaporthe grisea*; *Rhizoctonia solani, Botrytis cinerea*	Rice blast and sheath blight	Metabolites-phenazine pyocyanin and pyochelin (induction of ISR); ROS (inhibition of the mycelial growth and spore germination); SA (expression of acquired resistance).
Pseudomonas fluorescens SS101	*Pseudomonas syringae* pv tomato (Pst)		Metabolic and transcriptomic changes (induction of resistance responses).
Pseudomonas fluorescens PTA-CT2	*Plasmopara viticola, Botrytis cinerea*	Downy mildew and gray mold diseases	Activation of SA, JA, and ABA defensive pathways, HR (reduction in pathogen invasion).
Pseudomonas fluorescens WCS417		Broad spectrum	Transcription factor MYB72 (regulation of iron-uptake responses).
Streptomyces lydicus M01	*Alternaria alternataon* cucumbers	Foliar disease	ROS (inhibition of the mycelial growth and spore germination).
Streptomyces pactum	Tomato yellow leaf curl virus	Tomato yellow leaf curl virus disease	ROS (inhibition of the mycelial growth and spore germination); enzyme activity-peroxidase, chitinase, beta-1,3-glucanase (inhibition of the mycelial growth and spore germination), and phenyl alanine ammonia lyase (regulation of plant growth and stress tolerance); defense-related genes *PR-1*, *PR2*, and *PR-5* genes (antimicrobial effects, beta-1,3 glucanase, and chitinase activities, markers for SA-mediated activation of SAR); JA/ET (induction of immune response and reduction in pathogen invasion).
Acrophialophora jodhpurensis	*Rhizoctonia solani* AG4-HG II	Tomato root and crown rot	Direct antagonistic activity; ROS (inhibition of the mycelial growth and spore germination); enzyme activity—peroxidase, chitinase, beta-1,3-glucanase (inhibition of the mycelial growth and spore germination), and phenyl alanine ammonia lyase (regulation of plant growth and stress tolerance); iron restriction (inhibition of pathogen growth and promotion of plant growth).
Mortierella hyaline	*Alternaria brassicae*		JA (response to external and biological stresses); Ca2+ (regulating the permeability of plant cell membrane, enhance resistance).

Serendipita vermifera	*Bipolaris sorokiniana*		ROS (inhibition of the mycelial growth and spore germination); enzyme activity—hydrolytic enzymes (activation of defence).
Trichoderma atroviride	*Trichoderma atroviride*		Glutamate: glyoxylate aminotransferase GGAT1 (stimulation of plant growth and induction of the plant systemic resistance); WRKY transcription factors (active defense response to biotics and abiotic stresses).
Trichoderma harzianum	*Bipolaris sorokiniana*, *Rhizoctonia solani*	Spot blotch, wilt	Phenylpropanoid activities (reduction in cell wall disruption and tissue disintegration and increased suberization and lignification of the plant cell); secondary metabolite Harzianic acid (inducing the expression of several genes involved in defense response).
Trichoderma longibrachiatum MK1	*Botrytis cinerea*, *Alternaria alternata, Pythium ultimum*, and *Rhizoctonia solani*		Type II hydrophobin (direct antifungal as well as a microbe-associated molecular pattern and a plant growth promotion (PGP) activity).
Trichoderma harzianum OTPB3	*Alternaria solani*, *Phytophthora infestans*	Early and late blight	Defense-related enzymes—peroxidase, polyphenol oxidase, and superoxide dismutase (inhibite the mycelial growth and spore germination, and protection from oxidative stress).

Conclusion

In this article, we summarize the recognition of beneficial microorganisms and early events that occur during induced systemic resistance, highlighting reactive oxygen species burst, callose deposition that can inhibit the infection and expansion of pathogens, calcium signaling, and transcriptional factors, that play a significant role in regulating the expression of downstream defense-related genes and diseases control. The crosstalk of signaling transduction pathways and the function of secondary metabolites and stomatal regulation in ISR will be discussed. Finally, we will highlight recent advances about the role of small RNAs in rhizobacteria-induced ISR.

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