Indian J. Microbiol. (December 2007) 47:289–297

REVIEW

Induced systemic resistance (ISR) in plants: mechanism of action

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Received: 10 July 2007 / Final revision: 26 October 2007 / Accepted: 30 October 2007

Abstract Plants possess a range of active defense apparatuses that can be actively expressed in response to biotic stresses (pathogens and parasites) of various scales (ranging from microscopic viruses to phytophagous insect). The timing of this defense response is critical and reflects on the difference between coping and succumbing to such biotic challenge of necrotizing pathogens/parasites. If defense mechanisms are triggered by a stimulus prior to infection by a plant pathogen, disease can be reduced. Induced resistance is a state of enhanced defensive capacity developed by a plant when appropriately stimulated. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistance wherein plant defenses are preconditioned by prior infection or treatment that results in resistance against subsequent challenge by a pathogen or parasite. Selected strains of plant growth-promoting rhizobacteria (PGPR) suppress diseases by antagonism between the bacteria and soil-borne pathogens as well as by inducing a systemic resistance in plant against both root and foliar pathogens. Rhizobacteria mediated ISR resembles that of pathogen induced SAR in that both types of induced resistance render uninfected plant parts more resistant towards a broad spectrum of plant pathogens. Several rhizobacteria trigger the salicylic acid (SA)-dependent SAR pathway by producing SA at the root surface whereas other rhizobacteria trigger different signaling pathway independent of SA. The existence of SA-independent ISR pathway has been studied in *Arabidopsis thaliana*, which is dependent on jasmonic acid (JA) and ethylene signaling. Specific *Pseudomonas* strains induce systemic resistance in viz., carnation, cucumber, radish, tobacco, and *Arabidopsis*, as evidenced by an enhanced defensive capacity upon challenge inoculation. Combination of ISR and SAR can increase protection against pathogens that are resisted through both pathways besides extended protection to a broader spectrum of pathogens than ISR/SAR alone. Beside *Pseudomonas* strains, ISR is conducted by *Bacillus* spp. wherein published results show that several specific strains of species *B. amyloliquifaciens*, *B. subtilis, B. pasteurii, B. cereus, B. pumilus, B. mycoides,* and *B.sphaericus* elicit significant reduction in the incidence or severity of various diseases on a diversity of hosts.

Keywords Induced systemic resistance · SAR · Signalling and expression · Jasmonate and ethylene signalling · Pathogenesis-related proteins

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Introduction

Imagine a place on Earth where an organism does not suffer from infectious disease and is unlikely to become infected even in presence of pathogens. Such rare places exist and one such habitat is natural suppressive soils[1]. In such soils the roots of crop plants are protected from diseases caused by soil-borne pathogenic microorganisms which include fungi, bacteria and plant-deleterious nematodes. Patho-

genic microorganisms affecting plant health are major and chronic threats to food production and ecosystem stability worldwide. Crop rotation, breeding for resistant plant varieties and the application of pesticides are insufficient to control root diseases of important crop plants. An initiative, simple explanation of how the biological control of soil-borne pathogens could work? There is a large body of literature describing potential use of plant associated bacteria, the so called plant growth-promoting bacteria (PGPB) as agents stimulating plant growth and managing soil and plant health. The most widely studied group of PGPB is plant growth-promoting rhizobacteria (PGPR) that colonize the root surface and the closely adhering soil interface, the rhizosphere. The widely recognized mechanism of biocontrol mediated by PGPB is competition for an ecological niche/substrate, production of inhibitory allelochemicals, and induction of systemic resistance (ISR) in host plants to a broad spectrum of pathogens[2]. Induced resistance is a physiological "state of enhanced defensive capacity" elicited by specific environmental stimuli, whereby the plant's innate defenses are potentiated against subsequent biotic challenges. This enhanced state of resistance is effective against a broad range of pathogens and parasites[15]. The two most clearly defined forms of induced resistance are systemic acquired resistance (SAR), and induced systemic resistance (ISR), which can be differentiated on the basis of the nature of the elicitor and the regulatory pathways involved (Fig. 1).

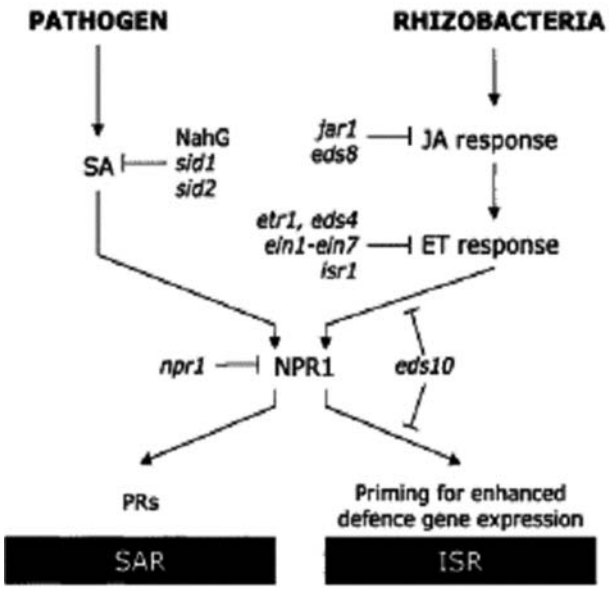

Fig. 1 The pathogen-induced SAR and the rhizobacteria-mediated ISR signal transduction pathways in *Arabidopsis* (From Pieterse et al (2002) "Signaling in Rhizobacteria-Induced Systemic Resistance in *Arabidopsis thaliana*". Reproduction with permission.

SAR can be triggered by exposing the plant to virulent, avirulent, and nonpathogenic microbes. Depending on the plant and elicitors, a set period of time is required for the establishment of SAR wherein accumulation of pathogenesis-related proteins (chitinase and glucanase), and salicylic acid takes place. ISR is potentiated by plant growth-promoting rhizobacteria (PGPR), of which best characterized are strains that belong to genus *Pseudomonas* that cause no visible damage to the plant's root system[3]. Unlike SAR, ISR does not involve the accumulation of pathogenesis-related proteins or salicylic acid, but instead, relies on pathways regulated by jasmonate and ethylene[5,52].

Plant roots release substantial amounts of C- and N-containing compounds into the surrounding soil. Microorganisms are attracted to this nutritous environment and use the root exudates and lysates for growth and multiplication on the surface of root and in the adjacent rhizosphere soil. Because of the rapid consumption of the nutrients, bacterial growth in the rhizosphere remains nutrient-limited where roots are seldom colonized for more than about 15% of their surface area. The rhizosphere micrflora plays an important role in plant development and acclimation to environmental stresses[3]. Since the rhizosphere microflora is extremely diverse, a dynamic interplay between the members of the microbial community occurs which is mediated by synergistic and antagonistic interactions within the limits of the nutrients available. In addition, signals are exchanged between fungi and bacteria and plant roots which reflect a highly dynamic belowground communication network. Plant growth-promoting rhizobacteria can suppress diseases through antagonism between bacteria and soil-borne pathogens, as well as by inducing a systemic resistance in the plant against both root and foliar pahogens. The induced resistance constitutes an increase in the level of basal resistance to several pathogens simultaneously, which is of benefit under natural conditions where multiple pathogens exist. Several specific *Pseudomonas* strains have been reported to induce systemic resistance in e.g., carnation, cucumber, radish, tobacco, and *Arabidopsis.* In addition, several other bacterial strains are reported to inducing resistance in different plant species, whereas others show specificity, indicating specific recognition between bacteria and plants at the root surface. In carnation, radish and *Arabidopsis*, the O-antigenic side chain of the bacterial outer membrane lipopolysaccharide acts as an inducing determinant along with other bacterial traits. Pseudobactin siderophores have been implicated in the induction of resistance in tobacco and *Arabidopsis* together with other siderophore, psedomonine. These siderophores may explain induction of resistance associated with salicylic

acid (SA) in radish. Although SA induces phenotypically similar systemic acquired resistance (SAR), it is not a necessary component of the systemic resistance induced by most rhizobacterial strains. Instead, rhizobacteria-mediated induced systemic resistance (ISR) is dependent on jasmonic acid (JA) and ethylene (ET) signaling in the plant. Upon challenge inoculation of induced plants with a pathogen, leaves expressing SAR exhibit a primed expression of SA-responsive defense-related genes, whereas leaves expressing ISR are primed to express JA/ET-responsive genes. A combination of ISR and SAR can increase protection against pathogens that are resisted through both pathways, as well as extend protection to a broader spectrum of pathogens than ISR or SAR alone[3,4]. Here we focus on ISR with emphasis on extensively studied group of biocontrol PGPR consisting of certain fluorescent pseudomonads and other organisms that protect a range of crop plants from important, mostly fungal root pathogens.

Induced-resistance systems in plants

An induced-resistance system in plants is very complex which has been partially elucidated in several model plant systems viz., *Arabidopsis*. There are three generally recognized pathways of induced resistance in *Arabidopsis* wherein two of these are involved in the direct production of pathogenesis-related (PR) proteins; in one pathway, the production of PR proteins is generally the result of attack by pathogenic microorganisms whereas in the other, PR proteins are generally produced as a result of wounding, or necrosis-inducing plant pathogens; both pathways however have alternate mechanisms for induction. Typically, the pathogen-induced pathway relies on salicylic acid (SA) that is produced by the plant as a signaling molecule, whereas the wounding pathway relies on jasmonic acid (JA) as the signaling molecule. These compounds and their analogues induce similar responses when they are applied exogenously and no doubt, there is considerable cross talk between the pathways[5]. The JA induced pathway has been designated as induced systemic resistance (ISR) and this term is also used to refer to quite different processes that are initiated by rhizobacteria.

The salicylate- and jasmonate-induced pathways are characterized by the production of a cascade of PR proteins which include antifungals (chitinases, glucanases and thaumatins), and oxidative enzymes (viz., peroxidases, polyphenol oxidases and lipoxygenases) respectively. Low-molecular weight compounds with antimicrobial properties (phytoalexins) can also accumulate. The third type of induced resistance is one which is provoked by non-pathogenic root-associated bacteria and is referred to as rhizobacteria induced systemic resistance (RISR) which led to development of systemic resistance to plant diseases. However, it is functionally very different, as the PR proteins and phytoalexins are not induced by root colonization by the rhizobacteria in the absence of attack by plant-pathogenic microorganisms. Once pathogen attack occurs, the magnitude of the plant response to attack is increased and disease is reduced. Thus, RISR results in potentiation of plant defence responses in the absence of cascade of proteins that is typical of the SA-induced system.

Arabidopsis as a model to study Rhizobacteria-Mediated ISR

To study rhizobacteria-mediated ISR, an *Arabidopsis*-based model system was developed because this plant species has been excellently studied for molecular genetic research on plant-microbe interaction wherein non-pathogenic rhizobacterial strain *Pseudomonas fluorescens* WCS 417r has been used as an inducing agent. Colonization of *Arabidopsis* roots by ISR-inducing WCS 417r bacterium protects the plants against different type of pathogens, including the bacterial leaf pathogen *Ps. syringae* pv. *tomato* and *Xanthomonas campestris* pv. *armoraciae*, the fungal root pathogen *Fusarium oxysporum,* the fungal leaf pathogen *Alternaria brassicicola* and the oomycete leaf pathogen *Peronospora parasitica*[6].

Role of ISR

It is envisaged that in suppressive soils plant roots are associated with microbial communities that have an overall beneficial effect on plant health. Indeed several biocontrol PGPR elicit ISR in the host plant which allows plants to withstand pathogen attack to the leaves/roots without offering total protection[7]. Many effective biocontrol PGPR elicit ISR, irrespective of antibiotic production[8]. The effects of three different strains of *Pseudomonas* spp. mediating ISR in *Arabidopsis thaliana* have been investigated through transcriptome (expressed level of proteins) analysis of plants with roots that were colonized by one of these strains (*P. fluorescens* WCS 417r, *P. thivervalensis* and *P. fluorescens* CHA0). In each instance, the transcript levels in the leaves were not markedly changed i.e., they varied by less than a factor of three, compared with the uninoculated control, and systemic responses that are typically seen after attack by necrotizing pathogens. Challenge inoculation of plants with a leaf pathogen e.g., *P. syringae* pv. *tomato*, showed that ISR-positive plants were 'primed' i.e., they reacted faster and more strongly to pathogen attack by induc-

ing defense mechanism[9]. Studies conducted with *A. thaliana* mutants indicated that JA/ethylene inducible defensive pathway was important for ISR, whereas the SA-inducible pathway was meant for mediating systemic acquired resistance (SAR). In bean, ISR elicited by *P. putida* strain, was associated with elevated level of hexenal (volatile antifungal compound) and with enhanced expression of enzymes that are involved in hexenal synthesis[8].

The foremost question that comes to mind is which bacterial signals elicit ISR? Phl^- (2,4-diacetylphloroglucinol) mutants of *P. fluorescens* CHA0 were less effective than the wild type in protecting *Arabidopsis* from the leaf pathogen *Peronospora parasitica* and application of phl to the roots triggered ISR to this pathogen[10]. Sharma et al[34] (2007) have been described molecular characterization of rhamnolipid which is considered to be determinant of biocontrol activity wherein a detailed screening of bacterial isolates from the Central Himalayan region for plant growth promoting and antimycelial activity against *Pythium* and *Phytophthora* strains have been employed. They afforded seven isolates of which three were particularly effective against the incidence of damping-off in field trials on chile and tomato. In this investigation an initial spectroscopic survey of the methanolic extracts of the seven bacterial isolates showed complex mixtures apart from those from *Pseudomonas* sp. GRP3, one of the most promising isolates based on field studies. Strain GRP3 was selected for structural characterization of its secondary metabolites, particularly glycolipids. The extracellular secondary metabolites were enriched by Amberlite XAD-16 adsorber resin followed by separation and structural analysis using TLC, LC-MS, MS-MS and NMR spectroscopy. Acquired data show the presence of a number of mono- and di-rhamnolipids, that include Rhamnose (Rha)-C8-C10, Rha-C10-C8, Rha-C10-C10, Rha- C10-C12:1, Rha-C10-C12, Rha-Rha-C8-C10, Rha-Rha-C10-C10, Rha-Rha-C10-C10:1, Rha-Rha-C10-C12, Rha-Rha-C10-C12:1, Rha-Rha-C12-C12:1, and Rha-Rha-C12-C12 in strain GRP3. Since rhamnolipids are involved in the lysis of the plasma membrane of zoospores of fungi, application of such rhamnolipid-producing rhizobacteria could facilitate control of damping-off plant pathogens.

SA-overproducing recombinant of *P. fluorescens* strain P3 showed enhanced protection of tobacco against TMV compared with the wild type P3 which indicate that –SA might also stimulate defence. In another *Pseudomonas* biocontrol strain, a combination of siderophores pyocyanin and pyochelin seem to be most effective for inducing resistance in tomato. The PGPR, *P. fluorescens* GRP3 showed ISR in rice against sheath blight. The plant-growth stimulating volatile 2,3-butanediol that is found in *Bacillus* spp. can also initiate ISR. It is difficult to recover specific ISR elicitors in several ISR-competent strains of fluorescent pseudomonads, therefore, it has been proposed that a combination of siderophore, O-antigen and flagella might account for the ISR effect[11,12,13,14].

Researchers have been described role of siderophores which is one of the determinants of ISR in effecting plant nutrition wherein they overcome problem of iron non-availability particularly in calcareous soils by incorporation of siderophore producing strains of fluorescent pseudomonads (FLPs). Sidrophore producing bacterium *Pseudomonas* strain GRP_3 was employed in a pot experiment to assess the role of microbial siderophores in the iron nutrition of mung bean employing Fe-citrate, Fe-EDTA, and $Fe(OH)_3$ in different concentration. The plant showed a reduction of chlorotic symptoms and enhanced chlorophyll level in bacterized plant. Bacterization with GRP_3 increased peroxidase activity and lowered catalase activity in roots. There was also a significant increase in total and physiologically available iron. Such siderophore producing system has the potential of improving iron availability to plants and reduce fertilizer usage[33]. Sharma et al[35] (2007) reported efficacy of bacterial isolate to protect chile and tomato plants under natural vegetable nursery and artificially created pathogen infested (*Pythium* and *Phytophthora* spp.) nursery conditions. Chile and tomato plants were harvested after 21 d of sowing and analysed for peroxidase and phenylalanine ammonia lyase (PAL) activities (ISR responsive proteins and not SAR-responsive). They found that *Pseudomonas* sp. strains FQP PB-3, FQP-PB-3 and GRP_3 were most effective in increasing shoot length together with increased activity of peroxidase and PAL., which are well known as indicators of an active lignification process.

The mechanism of rhizobacteria-induced systemic resistance (RISR)

The generally non-specific character of IR constitutes an increase in the level of basal resistance to several pathogens concomitantly, which is of benefit under natural conditions where multiple pathogens may be prevented[15]. To understand the phenomenon of rhizobacteria-mediated ISR it is important to gain insight into the bacterial plant mechanisms involved and to unravel the requirements for ISR induction, signaling, and expression.

Induction of ISR

Beneficial rhizobacteria do not obviously damage their host/cause localized necrosis, therefore, the eliciting factors produced by ISR-triggering rhizobacteria must be different

Table 1 Differential induction of systemic resistance (SR) by Pseudomonas spp. in different plant species

Plant Species	*P. putida* WCS 358	*P. fluorescens* WCS 374	*P. fluorescens* WCS 417	References
Arabidopsis	+	-	+	36
Bean and Tomato	+	ND	+	18
Carnation	-	ND	+	37
Radish	-	+	+	38

from elicitors of pathogens. There is comparatively little information on the bacterial determinants that trigger ISR. Mechanism of elicitation shows several similarities to the generation of certain non-specific defense reactions in plant cells that occur in response to general pathogen-associated molecular patterns (PAMPs); common components are present in microorganisms which appear to be recognized by eukaryotic cells[16]. Cell surface components viz., LPS and flagella can act as trigger of defence-associated reaction in suspension-cultured plant cells and leaves[17]. Both these factors of the rhizobacterial strain WCS 358 have the ability to elicit ISR when applied as purified components to root system of *Arabidopsis* plants upon challenge inoculation of treated plants with the causal agent of bacterial speck disease. The pathogenic bacterium *P. syringae* pv. *tomato* (Pst) which results in chlorotic and necrotic symptoms on the plants was reduced to an extent comparable to that on plants grown in soil containing wild type strain WCS 358[18].

A non-specific induction of ISR by rhizobacteria is also incompatible with an observed differential induction of systemic resistance in different plant species and in ecotypes. Several rhizobacterial strains appear to be equally effective in ISR in different plant species whereas others show narrow specificity which is indicative of a plant species-specific recognition between bacteria and receptors on the root surface. Three WCS strains of *P. fluorescens* mentioned earlier elicit ISR in different plant species (Table 1). For a limited number of ISR-eliciting rhizobacterial strains the inducing determinants (s) have been identified through mutant analysis and application of isolated components (Table 2).

Signalling in pathogen-induced SAR

Identification of critical steps in the signal transduction pathway for SAR has been studied by employing mutant and transgenic plants. A phenolic compound structurally resembling SA was required for the establishment of SAR was borne out when SA was determined to be an endogenous compound in plants which increased in amount upon elicitation. Recently, it has been hypothesized that local SA levels are increased upon induction which is associated with the generation of a mobile signal that is transported throughout the plant whereby initiating further local SA production in distant leaves. This level of SA is necessary and sufficient to confer the systemically induced state[19].

There is neither an understanding about the trigger which is responsible for increased SA production in the plant, nor has it been established how SA exerts its resistance-inducing action. The protein NPR1, an ankyrin-repeat family protein which structurally resembles the inhibitor of IF-kB, necessary for SA action in plant, plays a role in animal innate immunity. A redox change causes oligomers of NPR1 in the cytoplasm to be reduced to monomers under the influence of SA. These monomers are transported into the nucleus where they interact with specific TGA transcription factors to allow the expressions of genes encoding pathogenesis-related proteins (PRs)[20]. These conclusions led to the hypothesis that the status of SAR relies on the presence of PRs.

Signalling in rhizobacteria-induced systemic resistance (RISR)

Signalling in ISR appears more complex than that in SAR. Several ISR-eliciting rhizobacterial strains have been described which are also capable of producing SA whereas others do not. Two criteria can be used to explain this: (i) the ISR should be associated with the induction of PRs and, (ii) both ISR and the induction of PRs should be abolished in Nah G plants (SA deficient). ISR against tobacco mosaic virus (TMV) and *Botrytis cinerea* is abolished in tobacco and tomato plants upon challenge inoculation with 7NSK2, and in *Arabidopsis* against *P. syringae* pv. *maculicola* after elicitation by *B. pumilus* SE34[21,22] whereas it is maintained in all other combinations tested (Table 3). Strain WCS 358, which does not produce SA, elicit ISR in *Arabidopsis* whereas other rhizobacterial strain that can produce SA *in vitro* does not elicit ISR e.g., WCS 374 on *Arabidopsis* which otherwise elicits ISR in a SA-independent way viz., *Serratia marcescens* on tobacco or *P. fluorescens* CHA0 on *Arabidopsis*[10]; this data indicates that rhizobacterial production of SA is not generally required for induction of SAR.

Table 2 Bacterial determinants of induced systemic resistance in different plant species.

Bacterial strain	Plant species	Determinant	References
B. amyloliquefaciens IN 937a	*Arabidopsis*	2,3-butanediol	13
B. subtilis GB03	*Arabidopsis*	2,3-butanediol	13
P. aeruginosa 7 NSK2	Bean	SA	40
	Tobacco	SA	39
	Tomato	Pyochelin &Pyocyanin	11
P. fluorescens CHA0	*Arabidopsis*	2,4 DAPG	10
	Tobacco	Siderophore	41
	Tomato	2,4 DAPG	42
P. fluorescens Q2-87	*Arabidopsis*	2,4 DAPG	43
P. fluorescens WCS 374	Radish	LPS	44
		Siderophore and Fe-regulated compounds	45
P. fluorescens WCS 417	*Arabidopsis*	LPS	36
	Carnation	LPS	46
	Radish	LPS	44
		Fe-regulated compounds	45
P. putida WCS 358	*Arabidopsis*	LPS, Siderophore, Flagella	18
	Bean	LPS, Siderophore	18
	Tomato	LPS, Siderophore	18
P. fluorescens GRP3	Rice	Siderophore	12
Rhizobium etli G12	Potato	LPS	47
S.marcescens 90-166	Tobacco	Fe-regulated compounds	48

Several ISR-eliciting strains have also been shown to activate the PR-1α promoter in a transgenic GUS reporter line of tobacco, including *S. marcescens* 90-166, that was subsequently shown to induce resistance in tobacco in a SA-independent manner[23,24]. Downstream of SA in the SAR signaling pathway, the protein NPR1 plays an important role and this protein is necessary for ISR in *Arabidopsis*. Despite this SA is not necessary for ISR in this system. Mutant npr1 plants do not express ISR after treatment with WCS 417 and reflect that NPR1 seems to play a central role in reaching the induced state whether triggered by avirulant pathogens or by non-pathogenic rhizobacteria. Recently, evidence was provided which demonstrated that NPR1 is translocated to the nucleus upon induction of SAR, where it activates PR gene expression by physically interacting with a subclass of basic leucine zipper protein transcription factor that binds to promoter sequences required for SA-inducible PR gene expression both *in vitro* and *in vivo*[25,26,27]. However, downstream of NPR1, the signaling pathways must diverge again because SAR is associated with the accumulation of PRs whereas in ISR-induced plants such accumulation does not commonly occur (Fig. 1).

Expression of ISR

Expression of ISR is similar to SAR upon challenge inoculation with pathogen wherein disease severity is reduced; the number of diseased plants also diminishes. This reduction is associated with decreased growth of the pathogen and reduced colonization of induced tissues which reflects upon the ability of plant to resist the pathogen. The spectrum of diseases against which ISR and SAR are effective overlaps only partly, because of the differences in defense signaling. It has been demonstrated in *Arabidopsis*, that pathogens are resisted by either SA-dependent, or by JA- and/or ethylene dependent defenses or both. SA is an important signaling molecule in both locally and systemically induced resistance responses; however, research on rhizobacteria mediated ISR signaling has demonstrated that JA and ethylene play the key roles[28]. Thus, expression of ISR is phenotypically quite similar to SAR, and relies not only on a different type of biological induction but occurs also through different defense-related activities. Plant defense molecules i.e., phytoalexins can also contribute to plant resistance but available information shows that in mutants of *Arabidopsis* that are impaired in the

Table 3 Results of assays for induction of ISR on NahG plants.

Bacterial strain	Plant species	Pathogen	ISR	References
B. amyloliquefaciens IN 937a	*Arabidopsis*	*Erwinia carotovora*	+	13
B. pumilus SE34	*Arabidopsis*	*P. syringae* pv. Maculicola	+	22
	Tobacco	*Peronospora tabacina*	+	24
B. pumilus T4	*Arabidopsis*	*P. syringae* pv. Maculicola	+	22
B. subtilis GB03	*Arabidopsis*	*Erwinia carotovora*	+	13
P. aeruginosa 7NSK2	Tobacco	TMV	-	39
	Tobacco	*Botrytis cinerea*	-	11
	Tomato	*Meloidogyne javanica*	+	49
P. chlororaphis 06	Tobacco	*P. syrigae* pv. tabaci	+	50
P. fluorescens CHA0	*Arabidopsis*	*Peronospora parasitica*	+	10
	Tomato	*Meloidogyne javanica*	+	49
P .fluorescens WCS417	*Arabidopsis*	*P. syringae* pv. tomato	+	51
P .fluorescens 89B61	*Arabidopsis*	*P. syringae* pv. Maculicola	+	22
	Arabidopsis	*P. syringae* pv. tomato	-	22
	Tomato	*Phytophthora infestans*	+	52
S.marcescens 90-166	Arabidopsis	*P. syringae* pv. Maculicola	+	22
	Arabidopsis	*P. syringae* pv. tomato	-	22
	Tobacco	*P. syrigae* pv. tabaci	+	48

synthesis of the phytoalexin camalexin (pad1-pad4), there is normal expression of ISR against Pst which implies that ISR does not operate through stimulation of phytoalexin production.

In *Arabidopsis*, SAR is most effective against biotrophic pathogens- downy and powdery mildews as well as viruses that are sensitive to SA-dependent defenses whereas ISR is more active against nectrotrophic pathogens. It was earlier observed that SAR was not effective against typical necrotrophic fungi viz., *Botrytis cinerea* and *Alternaria brassicicola* [29]. In tobacco, the effectiveness of SAR and ISR against different type of pathogens is largely similar to their differential activities in *Arabidopsis*. Yet, in tomato the powdery mildew fungus *Oidium neolycopersici* was reported not to be resisted by SA-dependent defenses, while SA was involved in defense against *Botrytis*[30]. Thus, the conclusion, that SA- and JA- or ethylene-dependent defense mechanism can be effective against different pathogens in different plant species.

It was observed that upon challenge inoculation of *Arabidopsis* plants with Pst, SAR-induced plants showed an augmented expression of SA-dependent PR-1 mRNA, whereas plants with ISR accumulated mRNA of the JA-inducible gene vsp to higher levels than non-induced plant. This "priming" effect indicated that induced plants activate defense-related gene expression earlier and to a greater extent than non-induced plants[31]. As revealed by employing subtractive hybridization[32], ISR triggered by *P. chlororaphis* O6 upon root colonization of cucumber against target leaf spot-caused by *Corynespora cassiicola*-was associated with faster and stronger accumulation of transcripts of six distinct genes upon challenge inoculation.

Systemically induced resistance (SIR) and plant growth

SIR, whether SA-dependent SAR or JA- and ethylene –dependent ISR, both have to be expressed through an enhanced activation of defense responses upon challenge inoculation. Most of the ISR-triggering rhizobacteria have been selected primarily because of their plant-growth promotory properties, whereas SAR is associated with the accumulation of PRs and negatively affects plant growth[32]. Besides inducing ISR, PGPR can exert a protective action against soil-borne pathogens that are particularly prone to attack towards emerging seedlings. Stimulation of plant growth no doubt leads to increased plant vigour. ISR-eliciting rhizobacteria can be applied on seeds whereby they readily colonize emerging plant roots and thus such seedlings are better protected at an early stage.

Conclusively it is emphasized that ISR-inducing PGPR is a useful tool to reduce diseases caused by pathogens that are sensitive to JA- and ethylene-dependent defenses.

Integrating ISR-triggering PGPR into disease management programme in conjunction with other strategies will be a worthwhile approach to explore.

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