

Review

Use of bioagents and synthetic chemicals for induction of systemic resistance in tomato against diseases

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Plants and pathogens have developed an intricate relationship based on mutual information. Pathogens develop various strategies to attack successfully plants and in return, plants develop strategies to protect themselves from pathogens. Over the last two decades, a number of approaches have been applied by pathologists to enhance disease resistance in plants. Among these, induction of systemic resistance as an integrated control strategy offers exciting opportunities. Induced resistance (IR) could be developed by two main mechanisms: Systemic acquired resistance (SAR) and induced systemic resistance (ISR). Systemic acquired resistance (SAR) is a phenomenon by which a plant activates its own defense under the influence of a bio-agent or a chemical. This resistance develops with changes in the biochemistry and physiology of the cell that is further accompanied by structural modifications in the plants that act as physical barriers to restrict pathogen penetration. It is effective under field conditions and is a natural mechanism for bio-control of plant diseases. Scientists have used several agents to induce systemic resistance in tomato including bacteria, fungi and chemicals. Major areas discussed in this paper are historical background, mechanism of IR and its induction in tomato by various bio-agents and chemicals.

Keywords: Induced systemic resistance ISR, systemic acquired resistance SAR, bacteria, fungi, tomato.

INTRODUCTION

Concept of induced resistance (IR) was recognized nearly 100 years ago by researchers and since then, it has been studied for its effectiveness to protect plants from fungi, bacterial and viral pathogens. In the past decade, discovery of biocontrol agents and knowledge regarding plant defense mechanism led to the understanding of the fact that inducing resistance in plant against diseases is the best prospect for management of plant diseases. Transcription of defense related genes can be stimulated by external signals. Plants can defend themselves from pathogens by variety of mechanism that can be either constituted or inducible (Franceschi et al., 1998: 2000). Inducible resistance can be developed by two mechanisms such as systemic acquired resistance (SAR) and induced systemic resistance (ISR); both have broad spectrum of action on pathogen. SAR is a phenomenon by which a plant activates its own defense

under the influence of a bio-agent, physical injury or a chemical. This resistance develops with changes in biochemistry and the physiology of cell that is further accompanied by structural modifications in the plants that act as physical barriers to restrict pathogen penetration. ISR is known to have originated from colonization of roots by certain non-pathogenic bacteria. SAR can be induced by bio-agent such as challenging plant with a weak strain of a specific pathogen or by using a chemical agent (Eliston et al., 1977). Bio-agents can induce resistance against diseases caused by fungi (Howell and Stipanovic, 1979), bacteria (Park and Kloepper, 2000) and viruses (Maurhofer et al., 1994). Chemicals used for ISR may be synthetically or naturally produced either by microorganisms or host plants (Dixon et al., 1995).

Tomato is an economically important crop cultivated in all parts of the world. This is used as a fruit, a vegetable and in medicinal industry. In the fields, tomatoes are vulnerable to numerous diseases caused by fungi, bacteria and viruses, leading to dramatic losses in the production. Farmers tend to use huge amounts of che-

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micals to get rid of plants diseases. Tolerances to pesticides increase the use of several hazardous agrochemicals that can destroy both human and animal life. Therefore, great efforts to develop new effective and environmentally safe approaches for management of plant diseases are needed. The objectives of this review are to discuss ISR history, its general mechanisms and the involvement of bio-agents and chemicals for the induction of systemic resistance in tomato.

Historical background

ISR was first studied by Ray (1901) and Beauvenc (1901). They worked on gray mold caused by *Botrytis cinerea*. At that time Beauvenc (1899) had already discovered that ISR could be induced in *Begonia* sp. which was under the influence of pathogen *B. cinerea*. The virulence was altered by cold shock. There are many ways of challenging the plants with the inoculum of bio-agent being used to induce systemic resistance. Soil inoculation, root priming, foliar spray and injection methods have been used by various authors in their experiments of ISR. In 1961, Ross carried out the first investigation under laboratory conditions on the induced systemic resistance in a single leaf of tobacco with tobacco mosaic virus. He observed a reduction in the disease severity in the rest of the plant leaves. After that, another experiment on ISR was carried out on tobacco under field conditions, where a suspension of *Peronospora tabacina* spores was injected in the stem of tobacco plants to control mold caused by the same virus (Cohen and Kuc, 1981). Since then, Scientists from different parts of the world have also carried out their studies on various types of plants to investigate phenomenon of ISR (Hunt and Ryals, 1996; Schneider et al., 1997). Rhizospheric bacteria were initially applied to improve growth of the plants but later they were used as bio-control agents for suppression of plant diseases (Dunleavy, 1955; Broadbent et al., 1971; Schippers et al., 1987; Kloepper, 1993). First, bio-control product was introduced by Gustafsons Inc. (Plano, Texas); bio-control agent used was *Bacillus subtilis* A-10 (Broadbent et al., 1977).

A wide range of chemical compounds such as oligosaccharides (Yokoshiwa et al., 1993), glycoprotein and peptides (Benhamou, 1992) and salicylic acid (Yalpani et al., 1991) has been used to demonstrate their effects for induction of systemic resistance in different plants. The first chemical agent used to induce the production of phenolics compounds in tomato plants was arachidonic acid (Bloch et al., 1984).

Mechanisms

Plant pathogenic agents, such as fungi and bacteria

cause the host plants to initiate defense response to restrict growth and invasion of pathogen. But this response is very slow and weak enough to prevent this pathogen colonization inside the host plant (Thordal-Christene 2003). These resistance reactions can be triggered before pathogens' attack to restrict their colonization of certain cells or by blocking their penetrating site (Kuc, 1982). If infection ceases along with the restriction of pathogen damage, this phenomenon is called induced systemic resistance ISR. ISR initiates a wide range of resistance phenomenon elicited by nonpathogenic organisms (Van Loon, 2000). This induced resistance is generally systemic, as it protects not only infection focus but also other parts of the plant (Ross, 1961). These distant sites are protected because of the pathogen related gene expressions and stimulation of other defense related mechanisms (Durrant and Dong, 2004). Non-pathogenic fungi induce systemic resistance in plants by stimulating production of pathogenesis related proteins. This mechanism closely resembles systemic resistance induced by pathogenic fungi (Lambais and Mehdy, 1995; Cordier et al., 1998). Fungi seem to activate defense response by producing auxins or auxins precursors. Auxin regulated IR pathway may be responsible for ISR in plants (Madi and Katan 1998).

In case of chemicals agents, salicylic acid has been used by several researchers to induce systemic resistance. It is believed that salicylic acid is involved in signaling transduction pathway that leads to the production of defense related proteins (Vimal et al., 2009; Shah, 2003; Metraux, 2001).

The way in which bacteria induce systemic resistance is not associated with salicylic acid production (Pieterse et al., 1991). Jasmonate and ethylene are involved in bacterial mediated ISR (Van Loon et al., 1998). Both ISR and SAR transductions are dependent on regulatory proteins NPR1 (Pieterse et al., 1996). Pathogen related genes are not expressed in ISR (Van Loon et al., 1998).

Increase of resistance to diseases in plants is usually associated with phenylpropanoid and oxylipin pathway. Volatile organic compounds may play a significant role in enhancing protection in plants against diseases (Ping and Boland, 2004; Ryu et al., 2004). This was confirmed by studying ISR mediated by volatile compounds secreted by *B. subtilis* GBO3 and *B. amyloquefaciens* IN937a (Ryan et al., 2001).

ISR protects plants from pathogens by inducing cell wall thickening and other changes in host physiology, such as enhancing the production of defense related compounds like phenolics and proteins (Nowak and Shulaev. 2003; Ramamoorthy et al., 2001; Duijff et al., 1997).

In most cases, where bacteria are used to induce systemic resistance in plants, there will be cell wall thickening due to the deposition of callos and increase in total phenolics contents at the site where pathogen

attacks (Benhamous et al., 1996; Benhamous et al., 1998; MPiga et al., 1997). It can also be due to accumulation of pathogenesis related (PR) proteins such as PR-1 and PR-2, chitinases, some peroxidases (Jenu et al., 2004; Maurhofer et al., 1994; MPiga et al., 1997; Park et al., 2000; Ramamoorthy et al., 20001; Viswanathan et al., 1999), increase in the quantities of peroxidase, phenylalanine ammonia lyase, phytoalexins, polyphenol oxidase, and/or chalcone synthase in plant cells (Chen et al., 2004; Ownley et al., 2003; Ramamoorthy et al., 2001; Van Peer et al., 1991) and the productions of antibiotics like pHID (Austin and Noel, 2003; Bangera and Thomashow, 1999). Recently, it is discovered that N-Acyl homoserine lactones are also involved in ISR mediated by bacteria which stimulate chalcone synthase in plants (Mathesi et al., 2003).

Use of bio-agents for the induction of systemic resistance

Bacteria

To check the efficacy of bacterial bioagents for induction of ISR in tomato, scientists had already carried out various experiments in laboratory, green houses and under field conditions. For example, they have carried out an experiment on tomato caused by *Meloidogyne incognita*. The highest accumulation of *chitinase* was observed in tomato cells which reduced nematode penetration in root tissues. Sharam et al., (2003) carried out an in vitro study using *Pseudomonas* sp. strain GRP3 against pre and post emergence damping off caused by *Pythium aphanidermatum* and *Phytophthora nicotianae* in tomato and chilli. In other studies, it was also stated that tomato mottle virus was a limiting factor in tomato production areas in Florida since 1990s Kring et al., 1991; McGovern et al., 1995; Simone et al., 1990). In order to manage mottle virus, Murphy and coworkers (2000) used two strains of PGPR (SE34 and IN937) as seed dressings under field conditions. A significant reduction in the disease severity and incidence was recorded. Another study was done by Sankari et al. (2010), who used *Pseudomonas fluorescens* strain Pf 128 to control root knot nematodes. *P. fluorescens* strain 89B-27 and *S. marcescens* strain 90-166 were used as seed dressing to protect tomato plants from Cucumber mosaic virus (CMV) (Raupach et al., 1996). *Bacillus subtilis* strain GB03 induced systemic resistance in CMV under greenhouse conditions (Murphy et al., 2003). Zehnder et al. (2000) used seed dressing technique to induce systemic resistance in tomato plants against CMV under field conditions.

Two bacterial strains *P. putida* 89B-61 and *B. subtilis* GB03 were incorporated in soilless media against late blight of tomato caused by *Phytophthora infestans* (Yan et al., 2002). In another study, *Bacillus cereus* caused

significant reduction in early blight of tomato when it was inoculated onto tomato seeds (Silva et al., 2004); a reduction of up to 18% was observed. Different bacterial agents used for induction of systemic resistance in tomato are summarized in Table 1.

Fungi

Numerous fungi have also been checked for their efficacy in induction of systemic resistance in tomato. A research work was carried by Saksirirat et al. (2005) to investigate effects of species of *Trichoderma* in induction of systemic resistance in tomato against *Fusarium* wilt disease. A significant reduction in symptoms was observed under field conditions. In another study, *Penicillium oxalicum* was used to suppress fungal wilting diseases in tomato under greenhouse conditions (Larena et al. (2003). Increase in pathogen related proteins was observed in treated plants as compared to untreated control. Fungal agents used for induction of systemic resistance in tomato are summarized in Table 2.

Use of synthetic chemicals to induce systemic resistance

Synthetic chemicals have also been used as elicitors of ISR in tomato plants. Benhamos et al. (1998) carried out an experiment to investigate the potential of chitosan in induction of systemic resistance in tomato plants. Plants were treated with chitosan as foliar spray or root coating. Growth of *Fusarium* sp. was restricted to epidermis and outermost cortical cell layer; fungal hyphae were unable to penetrate the inner most cortical layer. This localized colonization was associated with the induction of defense barriers in host plants when treated with chitosan. This was due to deposition of the callose that enhanced the level of phenolic compounds when under the influence of chitosan treatment. In addition, salicylic acid (SA) represents an interesting new opportunity in controlling fungal and bacterial diseases of tomato plants. Salicylic acid has been studied by various authors (Table 3) to induce defense in tomato plants. Table 3 shows different synthetic chemicals used for induction of systemic resistance in tomato.

CONCLUSION

Plant protection provided by induction of systemic resistance is an effective and simple approach of disease management. This approach also reduces the use of harmful agrochemicals. Nevertheless, this type of treatment has several limitations including stability, duration of induced systemic resistance, efficacy of such formulations under commercial conditions and their sta-

Table 1. Different bacterial strain used for induction of systemic resistance in tomato

Bacterial strain	Disease	Reference
<i>Bacillus cereus</i> B 101 R	Early blight	Silva et al. (2004)
<i>B. cereu</i> B 212 K		
<i>B. subtilis</i> GB03	CMV	Murphy et al. (2003)
<i>B. pumilus</i> strains SE34		
<i>B. amyloliquefaciens</i> IN937a		
<i>B. subtilis</i> IN937b		
<i>B. subtilis</i> GB03	Late blight	Yan et al. (2002)
<i>B. cereus</i>	Foliar diseases	Silva et al. (2004)
<i>B. pumilus</i> SE34	Bacterial wilt	Enebak and Carey (2000)
<i>Pseudomonas aeruginosa</i> 7NSK2	Grey mold	Audenaert et al. (2002)
<i>P. fluorescens</i> 89B-27	CMV	Raupach et al. (1996)
<i>P. fluorescens</i> 89B61	Bacterial wilt	Ryu et al. (2004)
<i>P. putida</i> WCS358	Grey mold	Meziane et al. (2005)
<i>P. aeruginosa</i> 7NSK2	Grey mold	Audenaert et al. (2002)
<i>P. fluorescens</i> 63-28	Fusarium wilt	MPiga et al. (1997)
<i>P. fluorescens</i> Pf1	Fungal and bacterial wilt	Ramamoorthy et al. (2002)
<i>P. fluorescens</i> WCS417r	Fusarium wilt	Duijff et al. (1998)
<i>P. putida</i> BTP1	Grey mold	Mariutto et al. (2011)
PGPR	Cucumber mosaic virus	Murphy et al. (2003)
		Zehnder et al. (2000)
PGPR	Late blight	Yan et al. (2002)
PGPR strain SE34	Tomato mottle virus	Murphy et al. (2000)
PGPR strain IN937		
<i>Pseudomonas</i> sp. GRP3	Pre and post emergence damping off	Sharma et al. (2003)
<i>Serratia marcescens</i> 90-166	CMV	Raupach et al. (1996)
<i>S. marcescens</i> 90-166	Bacterial wilt	Ryu et al. (2004)

Table 2. Different fungal strain used for induction of systemic resistance in tomato

Fungus	Disease	Reference
Actinomycete A 068 R	Early blight	Silva et al. (2004)
	Bacterial spots	
<i>Fusarium oxysporum</i> f.sp. <i>lycopersici</i>	Fungal and bacterial wilts	Ramamoorthy et al. (2002)
<i>Penicillium oxalicum</i>	Fungal Wilt diseases	Larena et al. (2003)
<i>Phytophthora cryptogea</i>	Fusarium wilt	Attitalla et al. (2001)
<i>T. harzianum</i>	Verticillium wilt	Khiareddine et al. (2009)
<i>T. viride</i>		
<i>T. virens</i>		
<i>T. asperellum</i>	Fusarium wilt	Cotxarrera et al. (2002)
<i>T. harizianum</i> T39	Grey mold	De Meyer et al. (1998)
<i>T. harzianum</i>	Fusarium wilt	Amel et al. (2010)
<i>Trichoderma</i> spp.	Fusarium wilt	Hibar et al. (2007)

bility under field conditions. In spite of these limitations, the advance in knowledge of the ISR phenomenon proves the great potential of its use in the near future. Actually, experiments have proven that pathogen growth

and development is restricted by structural and biochemical barriers in plant tissues under the influence of systemic resistance inducers. This approach can play a key role in the management of large number of plant

Table 3. Different synthetic chemicals used for the induction of a systemic resistance in tomato.

Chemical	Disease	Reference
Acibenzolar-S-methyl	Bacterial wilt	Anith et al. (2004)
Benzothiadiazole	Fusarium wilt	Benhamous and B'elanger (1998)
Chitosan	Crown and root rot	Benhamous (1992)
Chitosan	Fusarium wilt	Benhamous et al. (1998)
Harpin, Phosphorus acid	Late blight	Necip et al. (2003)
Phosphate	Late blight	F'orster et al. (1998)
Validamycin	Fusarium wilt	Teraoka et al. (2005)
Validoxylamine	Fusarium wilt	Teraoka et al. (2005)

diseases. This strategy also meets with the demand for sustainable and eco-friendly agriculture.

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