

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

Waheed Akram* and Tehmina Anjum

Institute of Agriculture Sciences, University of the Punjab, Pakistan

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-

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 Saksirat 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>	Verticilium 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.

REFERENCES

- Abd-El-Kareem F, EL-Mougy NS, EL-Gamal NG, Fatouh YO (2006). Use of chitin and chitisan against tomato root rot disease under greenhouse conditions. *Research J. Agric.Biological sciences*. 2(4): 147-152.
- Amel A, Soad H, Ahmed M, Ismail AA (2010). Activation of Tomato Plant Defense Response Against *Fusarium* Wilt Disease Using *Trichoderma Harzianum* and Salicylic Acid under Greenhouse Conditions. *Research Journal of Agriculture and Biological Sciences*, 6(3): 328-338.
- Anith KN, Momol MT, Kloepper JW, Marois JJ, Olson SM, Jones JB (2004). Efficacy of plant growth-promoting rhizobacteria, acibenzolar-S-methyl, and soil amendment for integrated management of bacterial wilt on tomato. *Plant Dis*. 88:669-673.
- Attitalla IH, Johnson P, Brishammar S, Quintanilla P (2001). Systemic resistance to *Fusarium* wilt in tomato induced by *Phytophthora cryptogea*. *J. Phytopathol.* 149:373– 380.
- Audenaert K, Pattery T, Cornelis P, Hofte M (2002). Induction of systemic resistance to *Botrytis cinerea* in tomato by *Pseudomonas aeruginosa* 7NSK2: role of salicylic acid, pyochelin and pyocyanin. *Mol. Plant Microb. Interact.* 15:1147–1156.
- Audenaert K, Pattery T, Cornelis P, Hofte M (2002). Induction of systemic resistance to *Botrytis cinerea* in tomato by *Pseudomonas aeruginosa* 7NSK2: role of salicylic acid, pyochelin, and pyocyanin. *Mol. Plant-Microbe Interact.* 15:1147-1156.
- Austin MB, Noel AJP (2003). The chalcone synthase superfamily of type III polyketide synthases. *Nat. Prod. Rep.* 20:79–110.
- Bangera MG, Thomashow LS (1999). Identification, and characterization and of gene cluster for synthesis of the polyketide antibiotic 2,4- diacetylphloroglucinol from *Pseudomonas fluorescens* Q2-87. *J. Bacteriol.* 181:3155–3163.
- Beauvène J (1901). Essais d'immunization des vegetaux contre de maladies cryptogamiques. *Cr. Acad. Sci. Paris* 133:107–110.
- Beauvène J (1899). Le *Botrytis cinerea* et la maladie de la toile. *Cr. Acad. Sci. Paris* 128:846–849.
- Benhamous N, and B'elanger RR (1998). Benzothiadiazole-mediated induced resistance to *Fusarium oxysporum* f. sp. *radicis-lycopersici* in tomato. *Plant Physiol.* 118:1203– 1212.
- Benhamous N, Kloepper JW, Tuzun S (1998). Induction of resistance against *Fusarium* wilt of tomato by combination of chitosan with an endophytic bacterial strain: ultrastructure and cytochemistry of the host response. *Planta* 204:153–168.
- Benhamous N, Kloepper JW, Quadt-Hallmann A, Tuzun S, (1996). Induction of defense related ultrastructural modifications in pea root tissues inoculated with endophytic bacteria. *Plant Physiol.* 112:919–929.
- Benhamous N (1992). Ultrastructural and cytochemical aspects of chitosan on *Fusarium oxysporum* f. sp. *Radicis-lycopersici*, agent of tomato crown and root rot. *Phytopathology* 82: 1185-1193.
- Benhamous N, Kloepper JW, Tuzun S (1998). Induction of resistance against *Fusarium* wilt of tomato by combination of chitosan with an endophytic bacterial strain: Ultrastructural and cytochemistry of the host response. *Planta* 204: 153-168
- Bloch CB, De-Wit PJGM, Kuc J (1984). Elicitation of phytoalexins by arachidonic acid and eicosapentaenoic acids: a host survey. *Physiol. Plant Pathol.* 25: 199-208.
- Broadbent P, Baker KF, Water-Worth Y (1977) Bacteria and actinomycetes antagonistic to fungal root pathogens in Australian soils. *Aust J Biol Sci.* 24: 925 - 944.
- Chen G, Hackett R, Walker D, Taylor A, Lin-Z., Grierson D (2002). Identification of a specific isoform of tomato lipoxygenase (TomloxC) involved in the generation of fatty acid-derived flavor compounds. *Plant Physiol.* 136:1-11.
- Broadbent P, Baker KB, Franks N, Holland J (1977) Effect of *Bacillus* spp. On increased growth of seedlings in steamed and in nontreated soil. *Phytopathology* 67 : 1027-1034.
- Cohen Y, Kuc JJ (1981). Evaluation of systemic resistance to blue mold induced in tobacco leaves by prior stem inoculation with *Peronospora tabacina*. *Phytopathology* 71:783–787.
- Cordier C, Pozo MJ, Barea JM, Gianinazzi S, Gianinazzi-Pearson V (1998). Cell defense responses associated with localized and systemic resistance to *Phytophthora parasitica* induced in tomato by an arbuscular mycorrhizal fungus. *Mol. Plant Microbe Interact.* 11:1017–1028.
- Cotxarrera L, Trillas-Gay MI, Steinberg C, Alabouvette C (2002). Use of sewage sludge compost and *Trichoderma asperellum* isolates to suppress *Fusarium* wilt of tomato. *Soil Biology and Biochemistry.* 34: 467–476.
- Crop Protection Compendium. (2002). CABI Publishing. Available at <http://www.cabicompendium.org/cpc/economic.asp>.
- De Meyer G, Bigirimana J, Elad Y, Hofte M (1998). Induced systemic resistance in *Trichoderma harizanum* T39 biocontrol of *Botrytis cinerea*. *Eur. J. Plant Pathol.* 104:279–286.
- Dixon RA, Harrison MJ, Lamb CJ (1995). Early events in the activation of plant defense response. *Annu. Rev. Phytopathol.* 32, pp 479-501.
- Duijff BJ, Gianinazzi-Pearson V, Lemanceau P (1997). Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol *Pseudomonas fluorescens* strain WCS417r. *New Phytol.* 135:325–334.
- Duijff BJ, Pouhair D, Olivain C, Alabouvette C, Lemanceau P (1998). Implication of systemic induced resistance in the suppression of fusarium wilt of tomato by *Pseudomonas fluorescens* WCS417r and by nonpathogenic *Fusarium oxysporum* Fo47. *Eur. J. Plant Pathol.* 104:903-910.
- Dunleavy J (1955). Control of damping-off of sugar beet by *Bacillus subtilis*. *Phytopathology* 45: 252–257.
- Durrant WE, Dong X (2004). Systemic acquired resistance. *Annu Rev Phytopathol.* 42:185-209.
- Elliston J, Kuc J, Williams E, Raje J (1977). Relation of phytoalexin accumulation to local and systemic protection of bean against anthracnose. *Phytopathol Z.* 88:114–130.
- Enebak SA, Carey WA (2004) Plant growth-promoting rhizobacteria

- may reduce fusiform rust infection in nursery-grown loblolly pine seedlings. *Southern J. Appl. Forestry*. 28: 185-188.
- Forster H, Adaskaveg JE, Kim DH, Stanghellini ME (1998). Effect of phosphate on tomato and pepper plants and on susceptibility of pepper to *Phytophthora* root and crown rot in hydroponic culture. *Plant Dis.* 82:1165–1170.
- Franceschi VR, Karokene P, Krekling T, Christiansen E (2000). Phloem parenchyma cells are involved in local and distant defense responses to fungal inoculation or bark-beetle attack in Norway spruce (Pinaceae). *Am. J. Bot.* 87(3):314-326.
- Franceschi VR, Krekling T, Berryman AA, Christiansen E (1998). Specialized phloem parenchyma cells in Norway spruce (Pinaceae) are a primary site of defense reactions. *Am. J. Bot.* 85:601–615.
- Hibar K, Daami-Remadi M, El-Mahjoub M (2007). Induction of resistance in tomato plants against *Fusarium oxysporum* f.sp. *radicis-lycopersici* by *Trichoderma* spp. *Tunisian J. plant protection*. 2(1): 47-58.
- Hibar K, Daami-Remadi M, Khiareddine H, El Mahjoub M (2005) Effet inhibiteur in vitro et in vivo du *Trichoderma harzianum* sur *Fusarium oxysporum* f. sp. *radicis-lycopersici*. - *Biotechnol. Agron. Soc. Environ.* 9: 163-171.
- Howell CR, Stipanovic RD (1979). Control of *Rhizoctonia solani* on cotton seedlings with *Pseudomonas fluorescens* and with an antibiotic produced by the bacterium. *Phytopathology* 69:480-482.
- Hunt MD, Ryals JA (1996). Systemic acquired resistance signal transduction. *Crit. Rev. Plant Sci.* 15:583–606.
- Jeun YC, Park KS, Kim CH, Fowler WD, Kloepper JW (2004). Cytological observations of cucumber plants during induced resistance elicited by rhizobacteria. *Biol. Control* 29:34–42.
- Kloepper JW (1993). Plant growth-promoting rhizobacteria as biological control agents. In: Metting FB, Jr (ed) *Soil Microbial Ecology – Applications in Agricultural and Environmental Management* (pp 255–274) Marcel Dekker, New York.
- Kring JB, Schuster DJ, Price JF (1991). Sweetpotato whiteflyvectored geminivirus on tomato in Florida. *Plant Disease Note*. 75: 1186-1193.
- Kuc J (1982). Induced immunity to plant disease. *Bioscience* 32:854-860.
- Lambais MR, Mehdy MC (1995). Differential expression of defense-related genes in arbuscular mycorrhiza. *Can. J. Bot.* 73:S533–S540.
- Larena I, Sabuquillo P, Melgarejo P, De-Cal A (2003). Biocontrol of *Fusarium* and verticillium wilt of tomato by *Penicillium oxalicum* under greenhouse conditions. *Journal of Pathology* 78: 488-492.
- M'Piga P, Belanger RR, Paulitz TC, Benhamou N (1997). Increased resistance to *Fusarium oxysporum* f. sp. *radicis-lycopersici* in tomato plants treated with the endophytic bacterium *Pseudomonas fluorescens* strain 63-28. *Physiol. Mol. Plant Pathol.* 50:301–320.
- M'Piga P, Belanger RR, Paulitz TC, Benhamou N (1997). Increased resistance to *Fusarium oxysporum* f. sp. *radicis-lycopersici* in tomato plants treated with the endophytic bacterium *Pseudomonas fluorescens* strain 63-28. *Physiol. Mol. Plant Pathol.* 50:301–320.
- M'piga P, Bélanger RR, Paulitz TC, Benhamou N (1997). Increased resistance to *Fusarium oxysporum* f.sp. *radicis-lycopersici* in tomato plants treated with the endophytic bacterium *Pseudomonas fluorescens* strain 63-28. *Physiol. Mol. Plant Pathol.* 50:301-320.
- Madi L, Katan J (1998). *Penicillium janczewskii* and its metabolites, applied to leaves, elicit systemic acquired resistance to stem rot caused by *Rhizoctonia solani*. *Physiol. Mol. Plant Pathol.* 53:163–175.
- Mandal S, Mallick N, Mitra A (2009). Salicylic acid- induced resistance to *Fusarium oxysporum* f.sp.*lycopersici* in tomato. *Plant Physiology and Biochemistry*. 47: 642-649.
- Mariutto M, Duby F, Adam A, Bureau C, Fauconnier ML, Ongena M, Thonart P, Dommès J (2011). The elicitation of a systemic resistance by *Pseudomonas putida* BTP1 in tomato involves the stimulation of two lipoxygenase isoforms. *Mariutto et al., BMC Plant Biology*, 11:29.
- Mathesius U, Mulders S, Gao MS, Teplitski M, Caetano-Anolles G, Rolfe BG, Bauer WD (2003). Extensive and specific responses of a eukaryote to bacterial quorum-sensing signals. *Proc. Natl. Acad. Sci. USA* 100:1444–1449.
- Maurhofer M, Keel C, Haas D, Defago G (1995). Influence of plant species on disease suppression by *Pseudomonas fluorescens* strain CHA0 with enhanced antibiotic production. *Plant Pathology*. 44:40-50.
- McGovern RJ, Polston JE, Stansly PA (1995). Tomato mottle virus. University of Florida Cooperative Extension Service Circular. pp:143.
- Métraux JP (2001). Systemic acquired resistance and salicylic acid : current state of knowledge. *Eur. J. Plant Pathol.* 107: 13-18.
- Meziane H, Van-der-Sluis I, Van-Loon LC, Höfte M, Bakker PAHM (2005). Determinants of *Pseudomonas putida* WCS358 involved in inducing systemic resistance in plants. *Mol. Plant Pathol.* 6:177-185.
- Murphy JF, Reddy MS, Ryu C-M, Kloepper JW, Li R (2003). Rhizobacteria mediated growth promotion of tomato leads to protection against *cucumber mosaic virus*. *Phytopathology*. 93:1301-1307.
- Murphy JF, Zehnder GW, Schuster DJ, Sikora EJ, Polston JE, Kloepper JW (2000). Plant growth-promoting rhizobacteria mediated protection in tomato against tomato mottle virus. *Plant Disease*. 84: 779–784.
- Necip T, Lale A N, Karabay U Effects of Salicylic Acid, Harpin and Phosphorus acid in Control of Late Blight (*Phytophthora infestans* Mont. De Barry) Disease and Some Physiological Parameters of Tomato. *Plant diseases*. 18:1042-1047.
- Nowak J, Shulaev V (2003). Priming for transplant stress resistance in in vitro propagation. *In Vitro Cell. Dev. Biol., Plant.* 39:107–124.
- Owney BH, Duffy BK, Weller DM (2003). Identification and manipulation of soil properties to improve the biological control performance of phenazine-producing *Pseudomonas fluorescens*. *Appl. Environ. Microbiol.* 69:3333–3343.
- Park KS, Kloepper JW (2000). Activation of PR-1a promoter by rhizobacteria which induce systemic resistance in tobacco against *Pseudomonas syringae* pv. *tabaci*. *Biological Control* 18: 2-9.
- Pieterse CMJ, Van-Wees SC, Hoffland E, Pelt JA, Van Loon LC (1998). Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. *Plant Cell*. 8:1225–1237.
- Pieterse CMJ, Risseuw EP, Davidse LC (1991). An *in planta* induced gene of *Phytophthora infestans* codes for ubiquitin. *Plant Mol. Biol.* 17:799-811.
- Pieterse CMJ, Van Wees SCM, Hoffland E, Van Pelt JA, Van Loon LC (1996). Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. *Plant Cell*. 8:1225-1237.
- Pieterse CMJ, Van Wees SCM, Van Pelt JA, Knoester M, Laan R, Gerrits H, Ping L, Boland W (2004). Signals from the underground: bacterial volatiles promote growth in *Arabidopsis*. *Trends Plant Sci.* 9:263–269.
- Ping L, Boland W (2004) Signals from the underground: bacterial volatiles promote growth in *Arabidopsis*. *Trends in Plant Science* 9: 263–266.
- Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Smayyappan R (2001). Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. *Crop Prot.* 20:1–11.
- Ramamoorthy V, Raguchander T, Samiyappan R (2002). Induction of defense-related proteins in tomato roots treated with *Pseudomonas fluorescens* Pf1 and *Fusarium oxysporum* f.sp. *lycopersici*. *Plant Soil.* 239:55-68.
- Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Smayyappan R (2001). Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. *Crop Prot.* 20:1–11.
- Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Smayyappan R (2001). Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. *Crop Prot.* 20:1–11.
- Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Smayyappan R (2001). Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. *Crop Prot.* 20:1–11.
- Raupach GS, Liu L, Murphy JF, Tuzun S, Kloepper JW (1996). Induced systemic resistance in cucumber and tomato against cucumber mosaic cucumovirus using plant growth promoting rhizobacteria (PGPR). *Plant Dis.* 80:891-894.

- Ray J (1901). Les maladies cryptogamiques des vegetaux. Rev. Gen. Bot. 13:163–175.
- Ross AF (1961). Localized acquired resistance to plant virus infection in hypersensitive hosts. Virology. 14:329–339.
- Ryan PR, Delhaize E, Jones DL (2001). Function and mechanism of organic anion exudation from plant roots. Annu. Rev. Plant Physiol. Plant Mol. Biol. 52:527–560.
- Ryu CM, Farag MA, Hu CH, Reddy MS, Kloepper JW, Pare PW (2004). Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiol. 134:1017–1026.
- Sabuquillo P, De Cal A, Melgarejo P (2006) Biocontrol of tomato wilt by *Penicillium oxalicum* formulations in different crop conditions. Biological Control 37: 256-265.
- Saksirirat W, Chuebandit M, Sirithorn P, Sanoamung N (2005). Species diversity of antagonistic fungus, *Trichoderma* spp. from seed production fields and its potential for control Fusarium wilt of tomato and cucurbits. The IV Int. Conf. on Biopesticides. 13-15 Feb 2006, Imperial Maeping, Chiang Mai, Thailand.
- Sankari Meena K, Jonathan EI, Kavitha PG (2010). Induction of systemic resistance by chitinase in tomato against *Meloidogyne incognita* by *Pseudomonas fluorescens*. Resistant Pest Management Newsletter. Vol. 20, No. 1.
- Schippers G, Baker AW, Bakker PAHM (1987). Interactions of deleterious and beneficial rhizosphere microorganisms and the effect on cropping practices. Annual Review of Phytobiology. 25: 339–358.
- Schneider M, Schweizer P, Meuwly P, Metraux JP (1997). Systemic acquired resistance in plants. Int. Rev. Cytol. 168:303–340.
- Shah J (2003). The salicylic acid loop in plant defense. Curr. Opin. Plant Biol., 6: 365-37 1.
- Sharma A, Johri BN, Sharma AK, Glick BR (2003). Plant growth-promoting bacterium *Pseudomonas* sp. strain GRP3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilzek). Soil Biol. Biochem. 38: 887–894.
- Silva HSA, Da Silva Romeiro R, Macagnan D, Halfeld-Vieira B, Peirera MCB, Mounter A (2004a). Rhizobacterial induction of systemic resistance in tomato plants: non-specific protection and increase in enzyme activities. Biol Control. 29:288-295.
- Silva HSA, Romeiro RS, Carrer Filho R, Pereira JLA, Mizubuti ESG, Mounter A (2004b). Induction of systemic resistance by *Bacillus cereus* against tomato foliar diseases under field conditions. J. Phytopathol. 152:371-375.
- Simone GW, Brown JK, Hiebert E, Cullen RE (1990). New geminivirus epidemic in Florida tomatoes and peppers. Phytopathology. 80:1063.
- Thordal-Christensen H (2003). Fresh insights into processes of nonhost resistance. Curr. Opin. Plant Biol. 6:351-357.
- Van Loon LC (2000). Systemic induced resistance. In: Mechanisms of Resistance to Plant Diseases. Kluwer Acad. Publ., Dordrecht, pp. 521-574.
- Van Loon LC, Bakker PAHM, Pieterse CMJ (1998). Systemic resistance induced by rhizosphere bacteria. Annu Rev Phytobiology 1998, 36:453-483.
- Van Loon LC, Bakker PAHM, Pieterse CMJ (1998). Systemic resistance induced by rhizosphere bacteria. Annu. Rev. Phytobiology. 36: 453–483.
- Van Peer R, GNiemann J, Schippers B (1991). Induced resistance and phytoalexin accumulation in biological control of *Fusarium* wilt of carnation by *Pseudomonas* sp. Strain WCS417r. Phytopathology 81:728–734.
- Van Peer R, Nieman GJ, Schippers B (1991). Induced resistance and phytoalexin accumulation in biological control of *Fusarium* wilt of carnation by *Pseudomonas* sp. strain WCS417r. Phytopathology 1991, 81:728-734.
- Vimala R, Suriachandraselvan M (2009). Induced resistance in bhendi against powdery mildew by foliar application of salicylic acid. J. Biopesticides, 2(1): 111-114.
- Viswanathan R, Samiyappan R (1999). Induction of systemic resistance by plant growth promoting rhizobacteria against red rot disease caused by *Colletotrichum falcatum* in sugarcane, p. 24–39. In Proceedings of the Sugar Technology Association of India, vol. 61. Sugar Technology Association, New Delhi, India.
- Weisbeek PJ, Van Loon LC (1998). A novel signaling pathway controlling induced systemic resistance in *Arabidopsis*. The Plant Cell 1998, 10:1571-1580.
- Yalpani N, Silverman P, Wilson TMA, Kleir DA, Raskin E (1991). Salicylic acid is a systemic signal and inducer of pathogenesis-related proteins in virus-infected tobacco, Plant cell 3; 809-818.
- Yan Z, Reddy MS, Ryu C-M, McInroy JA, Wilson M, Kloepper JW (2002). Induced systemic protection against tomato late blight elicited by plant growth-promoting rhizobacteria. Phytopathology 92:1329-1333.
- Yan Z, Reddy MS, Ryu C.-M, McInroy JA, Wilson M, Kloepper JW (2002). Induced systemic protection against tomato late blight elicited by plant growth-promoting rhizobacteria. Phytopathology 92:1329-1333.
- Yoshikawa M, Yamaoka N, Takeuchi Y (1993). Elicitors: Their significance and primary modes of actions in the induction of plant defense reactions. Plant Cell Physiol. 34: 1163-1173.
- Zehnder GW, Yao C, Murphy JF, Sikora ER, Kloepper JW (2000). Induction of resistance in tomato against cucumber mosaic cucumovirus by plant growth-promoting rhizobacteria. BioControl 45:127-137.
- Zehnder GW, Yao C, Murphy JF, Sikora ER, Kloepper JW (2000). Induction of resistance in tomato against cucumber mosaic cucumovirus by plant growth-promoting rhizobacteria. BioControl. 45:127-137.