

Stimulating Natural Plant Defences for Disease Control

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There are problems associated with repeated pesticide use including the build up of toxic residues, the development of pathogen resistance, and adverse effects on nontarget beneficial organisms. The withdrawal of some very effective fungicides and a global trend towards lower pesticide inputs has generated greater interest in the development of disease control strategies that are safer and more environmentally acceptable. One possible alternative, induced resistance, involves the use of treatments which increase disease resistance in plants by stimulating their natural defence mechanisms. Induced resistance has been demonstrated to be effective in controlling disease development in several economically important crops. The integration of induced resistance with other biological control approaches such as the use of antagonistic microorganisms and antimicrobial natural products may offer practical methods for controlling plant diseases and reducing our dependency on synthetic pesticides.

INTRODUCTION

Plants defend themselves against pathogens using a combination of chemical and physical resistance mechanisms, some of which are preformed and others which are induced after infection (Dixon et al., 1994). Recent advances in our understanding of plant/pathogen interactions indicates that disease often occurs because of a delay in the defence response rather than because of the absence or inactivation of any particular defence mechanism. Indeed, many of the defence responses observed in resistant plants are also observed in susceptible plants, although usually later and to a lesser extent.

Plant defences can also be activated in the absence of infection by compounds called elicitors. Several elicitors have been identified, including extracts of microbial and plant origin, as well as several organic and inorganic compounds (Kuc, 1987; Lyon et al., 1995a). The use of elicitors to activate defence mechanisms in susceptible plants and thereby increase their resistance to pathogens has been suggested as an alternative approach for crop disease control (Kuc, 1987; Lyon et al., 1995a). This has sometimes been called "induced resistance" and it is proposed that elicitor treatment accelerates and intensifies the plants defence response to subsequent infection. Induced resistance against fungal, bacterial, and viral pathogens has been demonstrated in several important crops worldwide, including cereals, legumes, solanaceous plants, trees, and small fruits (Tuzun and Kuc, 1991). This paper presents an overview of different methods which have been shown to induce plant resistance and discusses the practical integration of induced resistance into disease management strategies.

MICROBIAL ELICITORS

Previous inoculation of plants with either avirulent strains of a pathogen or with non-pathogens have been shown to induce resistance to subsequent infections. This phenomenon was first documented nearly 100 years ago (Ray, 1901; Beauverie,

1901) when attenuated strains of *Botrytis cinerea* were shown to induce resistance in *Begonia*. Plants previously injected with the attenuated strain or grown in soil inoculated with the attenuated strain were shown to be resistant to subsequent inoculation with highly virulent strains of *Botrytis*. Interest in this approach to plant protection continued in the early part of this century and in 1933 Chester published a review in which he documented several examples where the "vaccination" of plants, whether with attenuated strains or with extracts of pathogens, resulted in increased resistance towards subsequent infection.

The first detailed laboratory analysis of induced resistance was published by Ross in 1961 who demonstrated systemic induction of resistance against tobacco mosaic virus (TMV) in tobacco plants following inoculation of lower leaves with TMV. More recently stem injection of tobacco with spores of the blue mould fungus (*Peronospora tabacina*) was shown to induce systemic resistance to blue mould under glasshouse and field conditions (Tuzun and Kuc, 1991). Resistance was elicited by a single injection and was reported to persist throughout the growing season. Induced resistance was shown to coincide with the accumulation of pathogenesis-related (PR) proteins including beta-1,3-glucanase and chitinase. A single elicitor application has been shown to protect plants against a broad range of pathogens. For example, resistance against fungi, bacteria, and viruses (Tuzun and Kuc, 1991) as well as some insects (McIntyre et al., 1981) was induced in cucumber following inoculation of the first true leaves with a necrosis-forming organism. Gregersen and Smedegaard-Petersen (1989) demonstrated that not only pathogens and nonhost pathogens but also saprophytes are capable of inducing resistance in barley. There are numerous other examples of induced resistance in response to pathogens and nonpathogens, however, it has been suggested that the use of such organisms in the field may be problematic if handled carelessly (Tuzun and Kloepper, 1995).

FUNGAL EXTRACTS

Carbohydrate components from fungal cell walls are amongst some of the most potent elicitors of plant defence. Yeast cell-wall extracts (YE) have been shown to induce resistance against important diseases such as barley powdery mildew, grey mould and stem rot on lettuce, and chocolate spot on beans (Reglinski et al., 1994a,b; 1995; Lyon et al., 1995b). Yeast cell-wall extracts induced a rapid stimulation of phenylalanine ammonia-lyase activity in barley and accelerated papilla formation leading to a 90% reduction in powdery mildew infection (Reglinski et al., 1994a,b).

Chitosan is a structural component of fungal cell walls and has received a lot of attention as a potential agent for controlling postharvest diseases (Wilson et al., 1994; El Ghaouth, 1997). Application of chitosan to stem scars in tomato, strawberry, and bell pepper fruit was shown to induce defence-related enzymes including peroxidase and beta-1,3-glucanase. Chitosan is also directly antimicrobial and was shown to inhibit the radial growth of a range of postharvest pathogens. The combination of antifungal and resistance-eliciting properties is potentially very useful for crop protection.

MICROBIAL METABOLITES

Metabolites produced by some saprophytic bacteria and fungi were shown to induce resistance in a number of hosts against fungal pathogens, without any direct antagonistic effect on the pathogen (Schonbeck et al., 1986). The metabolites gave

a high degree of disease control in the field against powdery mildew of cucumber and, in particular, wheat where mildew was reduced by over 90%, but were less effective against mildew on grape. The induction of resistance with microbial metabolites was associated with a reduction in the number and size of mildew colonies and a reduced sporulation rate (Steiner et al., 1988).

Some fungi that have been used for the biological control of plant pathogens have been shown to produce extracellular enzymes and metabolites that induce the plant hypersensitive response. This defence response is characterised by a rapid collapse and desiccation of host tissues adjacent to the site of attempted infection. A commercially available cellulase preparation from *Trichoderma viride* (Onozuka R-10) has been shown to stimulate production of antimicrobial compounds and the hypersensitive response in grape cell cultures (Calderon et al., 1993).

COMPOSTS

The benefits of using composts to maintain soil fertility and plant health have been known for centuries. In addition to providing essential nutrients compost-amended soils have been shown to reduce the severity of root rots, vascular wilts, and nematode diseases. Composts are believed to control disease through direct antifungal activity and also indirectly through the induction of host plant defences. In cucumber and arabidopsis plants grown on a compost mix, antifungal hydrolytic enzymes were only induced following pathogen infection so indicating that the compost-induced resistance involved priming of the host defences rather than direct activation (Zhang et al., 1998). Aqueous extracts of composts, from both animal sources and plant sources, have been used to control botrytis, downy mildew, and powdery mildew (Elad et al., 1996). The active component(s) in these sprays have not yet been identified.

Resistance induced by different composts against anthracnose in cucumber (Zhang et al., 1996) and *Xanthomonas* in radish, tomato, and lettuce was highly variable (Miller et al., 1997). This may be partly explained by the highly complex nature of composts which contain a variety of chemical and microbial components. Many of these individual components have been shown to induce systemic resistance in plants. Little is known about the interactions which occur between these components in a compost and how they influence the ability of compost to induce disease resistance. However, sterilization of composts resulted in a loss in their ability to induce plant resistance and so microbial populations appear to play a crucial role (Hoitink et al., 1997). The variability of composts as elicitors of resistance is likely to prove the biggest problem for their practical implementation at present.

PLANT GROWTH-PROMOTING RHIZOBACTERIA

Some soil and root colonising bacteria promote plant growth either directly, by producing plant growth regulators, or by stimulating nutrient uptake, or indirectly by suppressing pathogens. These bacteria are often referred to as plant growth-promoting rhizobacteria (PGPR). There is increasing evidence that selected PGPR (mainly *Pseudomonas* spp.) can also induce systemic protection against pathogens (Wei et al., 1991, 1996). Spatial separation of PGPR strains and pathogenic strains, using split root systems, demonstrated that disease control was not due to direct effects but rather due to the induction of plant resistance (van Peer et al., 1991). Plant growth-promoting rhizobacteria are effective as either a seed or as a soil treatment and have been shown to induce resistance in a number of plants against

fungi, bacteria, and viruses (Maurhofer et al., 1994; Hoffland et al., 1996). In recent field studies seed treatments with PGPR strains were shown to promote early season growth and to induce resistance against angular leaf spot (*Pseudomonas syringae*), and anthracnose (*Colletotrichum orbiculrae*) in cucumber (Wei et al., 1996).

Several studies have shown that PGPR-induced resistance is associated with the stimulation of host defence mechanisms. For example, induction of resistance by *P. fluorescens* was associated with an accumulation of phytoalexins in carnation (van Peer et al., 1991) and an increase in pathogenesis-related (PR) protein levels in tobacco (Maurhofer et al., 1994). However, the accumulation of PR proteins is not a prerequisite for the expression of resistance suggesting that different pathways of induction may be involved (Pieterse et al., 1996). Soluble chemicals produced by PGPR as well as structural components of the microorganism itself appear to play important roles in the induction of plant defences (Leeman et al., 1995; De Meyer and Hofte, 1997).

PLANT EXTRACTS

There are several reports indicating the potential of plant extracts as elicitors. Aqueous extracts from barley leaves stimulated papilla formation and induced resistance to powdery mildew in barley seedlings (Yokoyama et al., 1991). A number of products containing seaweed extracts are available which are reported to enhance plant health. Synermix (a seaweed extract plus AlCl_3 hexahydrate) was shown to elicit phytoalexins in grapes and reported to increase the efficacy of iprodione against *B. cinerea* (Jeandet et al., 1996).

Extracts of the perennial weed *Reynoutria sachalinensis* have been shown to control powdery mildew on apple, tomato, and begonia (Herger and Klingauf, 1990). Biochemical studies showed that the plants treated with the extract had increased levels of defence-related enzymes including peroxidase, glucanase, and chitinase (Herger and Klingauf, 1990) and rapidly accumulated antifungal phenolics (Daayf et al., 1995). In 1990, a wettable powder formulation of these extracts was commercialised (Milsana, Compo, Munste, Germany) and more recently an aqueous formulation (Milsana flussig, BASF) was developed. Applications of Milsana at a concentration of 2% have been shown to reduce the incidence of powdery mildew on cucumber (Daayf et al., 1995) and *Septoria tritici* in wheat (Metcalf and Wale, 1997).

CHEMICAL INDUCERS

There are numerous chemicals that have been shown to induce plant resistance mechanisms (see reviews by Kessmann et al., 1994; Lyon et al., 1995a). Salicylic acid (SA) plays an important role in the establishment of both local- and systemic-induced resistance in plants and has been one of the most intensively studied elicitors over the last 20 years. White (1979) was the first to report that exogenously applied SA or acetylsalicylic acid induced resistance to tobacco mosaic virus in tobacco. Treatment with SA, or structurally related derivatives has been shown to induce resistance to viral, fungal, and bacterial pathogens in both dicotyledonous and monocotyledonous plants, including tobacco, parsley, wheat, kiwifruit, and radiata pine (Kauss et al., 1993; Gorchach et al., 1996; Reglinski et al., 1997, 1998). However, it has been suggested that field application of SA may be impractical because only a narrow margin separates the rates at which it is efficacious and the rate at which it is phytotoxic (Kessmann et al., 1994; Reglinski et al., 1997).

The synthetic compound 2,6-dichloroisonicotinic acid (INA) has been shown to

induce systemic resistance and to provide protection under field conditions against fungal and bacterial pathogens on pear, pepper, rice, and tobacco (Kessmann et al., 1994) and in green beans (Dann and Deverall, 1996). This compound is not antimicrobial and has been shown to induce the same set of gene families that are induced by either SA or pathogen infection. However, although INA showed early promise as a plant protection compound it was insufficiently tolerated by some crops to warrant practical use (Gorlach et al., 1996).

Benzo(1,2,3)thiadiazole-7-carbothioc acid *S*-methyl ester (BTH) is an elicitor that has been developed by Novartis Crop Protection AG. It shares structural and functional similarities with SA and INA but has been reported to be a more potent elicitor of plant defences (Gorlach et al., 1996). This compound is currently commercially available as BionTM and is being marketed for use against wheat powdery mildew. Bion represents the first of a new generation of crop protectants developed specifically to operate through the induction of plant defence mechanisms. However, induced resistance is also thought to contribute to the efficacy of several pesticides that were not specifically developed as elicitors, including probenazole, metalaxyl, fosetyl-Al, and tricyclazole.

RESISTANT CULTIVARS

The most effective and practical method of disease control is to have naturally resistant plant species. Unfortunately many modern high-yielding crop varieties appear to lack much of the natural resistance of old cultivars or related wild species. It is possible that breeding for high yield and other desirable traits has failed to retain genes that are essential for effective resistance (Davis et al., 1990). However, recent advances in molecular biology has led to the identification of genes required for disease resistance. The technical feasibility of engineering broad-spectrum and stable disease resistance is growing fast and several transgenic plants exhibiting high levels of resistance to fungal and bacterial pathogens have been reported (Shah et al., 1995). Further, progress in the cloning of resistance genes and a greater understanding of plant/pathogen interactions has opened the door for the production of crops with agronomically useful levels of resistance. However, public acceptance of genetic engineering to produce transgenic plants is not widespread and very likely be the subject of debate for many years to come.

PRACTICAL INTEGRATION OF INDUCED RESISTANCE

Induced resistance has been demonstrated as an effective method of disease control in a variety of plants and against a broad range of pathogens. However, there must be a high probability that its implementation will be of economic benefit to growers before it will find widespread acceptance. In the short term the most practical way for implementing induced resistance for crop protection will be to integrate it with existing disease management programmes. Elicitors have already proven themselves to be compatible with commercially available fungicides. Mixtures containing yeast cell-wall extracts with reduced rate fungicide produced yields similar to those obtained with full rate fungicide (Reglinski et al., 1994a). Similarly, BionTM can be used as a stand alone elicitor or in conjunction with fungicides for controlling wheat powdery mildew.

Induced resistance is also compatible with other natural control measures that promote plant health and reduce plant disease including the use of resistant

cultivars, cultural practise, and biological control. Inducer/cultivar interactions have been reported in field studies (Reglinski et al., 1994a; Steiner et al., 1988) suggesting that the selection of genotypes better able to respond to elicitors could be included in future breeding programmes. However, the development of crops with broad spectrum and stable disease resistance through breeding is a longer term strategy and not of immediate benefit to growers. The integrated use of elicitors with antagonistic biological control agents has recently shown promise for controlling bunch rot in grapes caused by *B. cinerea* (Reglinski and Elmer, unpublished data). Benhamou et al., (1998) also recently reported the combined use of PGPR and chitosan to induce resistance to fusarium wilt in tomato.

Possibly the most economic approach would be the development of PGPR seed treatments or composts specifically selected for their ability to stimulate natural disease resistance. These would offer additional benefits over foliar applied elicitors by protecting against seed decay and pre- and post-emergence damping-off. Seed treatment is particularly attractive because of the possible savings of labour, time, fuel, and machinery associated with foliar chemical application.

Are There any Problems That Are Likely to be Faced in the Application of Induced Resistance for Crop Protection? Induced resistance relies upon a physiological and biochemical response by the plant and so efficacy of any elicitor may be affected by different climatic and agronomic factors which influence general plant health.

Will Induced Resistance be Durable? The durability of any form of resistance depends on how easily random mutations in the pathogen population can produce some means of negating it. Induced resistance operates through stimulation of the plants multicomponent "immune system" and, therefore, is likely to be more durable than the use of chemical pesticides that target a single metabolic site. In addition induced resistance in crop plants appears to be relatively nonspecific and so is likely to offer broad spectrum disease control.

Will the Energetic Costs Associated with Induced Resistance Cause a Loss in Yield? Smedegaard-Petersen (1990) attributed loss in yield, following induction of host resistance mechanisms in cereals, to a redirection of plant metabolites. However, this appears to be an exception rather than the rule and most studies on induced resistance have reported either no effect on yield or have actually observed yield benefits (Steiner et al., 1988; Reglinski et al., 1994a).

Is Induced Resistance Safe? Fears have been expressed about safety of using elicitors on foods and the induction of high levels of plant defence compounds which themselves may be toxic. Induced resistance is likely to be as safe for health as disease resistant plants since the mechanisms activated in both are the same.

Exploitation of induced resistance in the field is not yet widespread and is still at a relatively early stage in its development. There are prospects for improving the efficacy of elicitor treatments through formulation optimisation. Frequency and timing are also critical components as elicitors need to be applied before a pathogen becomes established. Disease prediction models may provide useful information to achieve maximum benefit from elicitor treatment. Research into the practical implementation of induced resistance is likely to become an area of intense activity

over the next few years. However, there is already ample evidence to suggest that the integration of induced resistance, and other natural-based control methods, with more conventional control methods can offer an economic and environmentally safe crop protection strategy.

LITERATURE CITED

- Beauverie, J.** 1901. Essais d'immunization des vegetaux contre de maladies cryptogamiques. C.R. Acad. Sci. series III 133:107-110.
- Benhamou, N., J.W. Kloepper, and S. Tuzun.** 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.
- Calderon, A.A., J.M. Zapata, R. Munoz, M.A. Pedreno, and A. Ros Barcelo.** 1993. Resveratrol production as a part of the hypersensitive-like response of grapevine cells to an 'elicitor' from *Trichoderma viride*. *New Phytol.* 124:455-463.
- Chester, K.S.** 1933. The problem of acquired physiological immunity in plants. *Quart. Rev. Biol.* 8, 275-324.
- Daayf, F., A. Schmitt, and R.R. Belanger.** 1995. The effects of plant extracts of *Reynoutria sachalinensis* on powdery mildew development and leaf physiology of long English cucumber. *Plant Dis.* 79 (6):577-580.
- Dann, E.K. and B.J. Deverall.** 1996. 2,6-dichloroisonicotinic acid (INA) induces resistance in green beans to the rust pathogen, *Uromyces appendiculatus*, under field conditions. *Austral. Plant Pathol.* 25:199-204.
- Davis, D.W., C.A. Engelkes and J.V. Groth** 1990. Erosion of resistance to common leaf rust in exotic-maize during selection for other traits. *Phytopathol.* 80:339-342.
- De Meyer, G. and M. Hofte.** 1997. Salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 induces resistance to leaf infection by *Botrytis cinerea* on bean. *Phytopathol.* 87:588-593.
- Dixon, R.A., M.J. Harrison, and C.J. Lamb.** 1994. Early events in the activation of plant defence responses. *Annu. Rev. Phytopathol.* 32:479-501.
- Elad, Y., N.E. Malathrakis, and A.J. Dik.** 1996. Biological control of *Botrytis*-incited diseases and powdery mildews in greenhouse crops. *Crop Prot.* 15:229-240.
- El Ghaouth, A.** 1997. Biologically based alternatives to synthetic fungicides for the control of postharvest diseases. *J. Ind. Microbiol. Biotechnol.* 19:160-162.
- Gorlach, J., S. Volrath, G. Knauf-Belter, G. Hengy., U. Beckhove, K-H. Kogel, M. Oostendorp, T. Staub, E. Ward, H. Kessmann, and J. Ryals.** 1996. Benzothiadiazole, a novel class of inducers of systemic acquired resistance, activates gene expression and disease resistance in wheat. *Plant Cell* 8:629-643.
- Gregersen, Per L. and V. Smedegaard.** 1989. Induction of resistance in barley against *Erysiphe graminis* f.sp. *hordei* after preinoculation with the saprophytic fungus, *Cladosporium macrocarpum*. *J. Phytopathol.* 124:128-136.
- Herger, G. and F. Klingauf.** 1990. Control of powdery mildew fungi with extracts of the giant knotweed *Reynoutria sachalinensis* (Polygonaceae). *Med. Fac. Landbouww. Rijksuniv. Gent* 55:1007-1014.
- Hoffland, E., J. Hakulinen, and J.A. van Pelt.** 1996. Comparison of systemic resistance induced by avirulent and nonpathogenic *Pseudomonas* species. *Phytopathol.* 86:757-762.
- Hoitink, H.A.J., W. Zhang, D.Y. Han, and W.A. Dick.** 1997. Making compost to suppress plant disease. *BioCycle* April pp. 40-42.
- Jeandet, P., M. Adrian, J.M. Joubert., F. Hubert, and R. Bessis.** 1996. Stimulating the natural defences of grape. A complement to phytosanitary control of *Botrytis*. *Phytoma* No. 488:21-22, 24-25.

- Kauss, H., R. Franke, K. Krause, U. Conrath, W. Jeblick, B. Grimming, and U. Matern.** 1993. Conditioning of parsley (*Petroselinum crispum* L.) suspension cells increases 'elicitor'-induced incorporation of cell wall phenolics. *Plant Physiol.* 102:459-466.
- Kessmann, H., T. Staub, C. Hofmann, T. Maetzke, and J. Herzog.** 1994. Induction of systemic acquired resistance in plants by chemicals. *Annu. Rev. Phytopathol.* 32:439-459.
- Kuc, J.,** 1987. Plant immunization and its applicability for disease control. pp. 255-274. In: I. Chet. (ed.). *Innovative approaches to plant disease control.* John Wiley and Sons, New York.
- Lyon, G.D., T. Reglinski, and A.C. Newton.** 1995a. Novel disease control compounds: The potential to "immunize" plants against infection. *Plant Pathol.* 44:407-427.
- Lyon, G.D., T. Reglinski, R.S. Forrest, and A.C. Newton** 1995b. The use of resistance elicitors to control plant diseases. *Aspects Appl. Biol.* 42:227-234.
- Leeman, M., J.A. van Pelt, F.M. den Ouden, M. Heinsbroek, P.A.H.M. Bakker, and B. Schippers.** 1995. Induction of systemic resistance against fusarium wilt of radish by lipopolysaccharides of *Pseudomonas fluorescens*. *Phytopathol.* 85:1021-1027.
- Maurhofer, M., C. Hase, P. Meuwly, J.P. Mettraux, and G. Defago.** 1994. Induction of systemic resistance of tobacco to tobacco necrosis virus by the root colonising *Pseudomonas fluorescens* strain CHA0: Influence of the *gacA* gene and of pyoverdine production. *Phytopathol.* 84:139-146.
- McIntyre, J.L., J.A. Dodds, and J.D. Hare.** 1981. Effects of localised infections of *Nicotiana tabacum* by tobacco mosaic virus on systemic resistance against diverse pathogens and an insect. *Phytopathol.* 71:297-301.
- Metcalf, R.J. and S.J. Wale.** 1997. Evaluation of milsana for the control of *Septoria tritici* in wheat. *Ann. Appl. Biol.* 130(suppl):52-53.
- Miller, S.A, F. Sahin, M. Krause, J. Al-Dahamani, A. Stone, and H.A.J. Hoitink.** 1997. Control of bacterial leaf spot of radish in compost-amended potting mixes. *Phytopathol.* 87:S66 (Abstract).
- Pieterse, C.M.J., S.C.M. van Wees, E. Hofflan, J.A. van Pelt, and L.C. van Loon.** 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.
- Ray, J.,** 1901. Les maladies cryptogamiques des vegetaux. *Rev. Gen. Bot.* 13:145-151.
- Reglinski, T., G.D. Lyon, and A.C. Newton.** 1994a. Assessment of the ability of yeast-derived resistance elicitors to control barley powdery mildew in the field. *J. Plant Dis. Prot.* 101(1):1-10.
- Reglinski, T., G.D. Lyon, and A.C. Newton.** 1994b. Induction of resistance mechanisms in barley by yeast-derived elicitors. *Ann. Appl. Biol.* 124:509-517.
- Reglinski, T., G.D. Lyon, and A.C. Newton.** 1995. The control of *Botrytis cinerea* and *Rhizoctonia solani* on lettuce using 'elicitors' extracted from yeast cell walls. *J. Plant Dis. Prot.* 102:257-266.
- Reglinski, T., P.R. Poole, G. Whitaker, and S.M. Hoyte.** 1997. Induced resistance against *Sclerotinia sclerotiorum* in kiwifruit leaves. *Plant Pathol.* 46:716-721.
- Reglinski, T., F.J.L. Stavely, and J.T. Taylor.** 1998. Induction of phenylalanine ammonia lyase activity and control of *Sphaeropsis sapinea* infection in *Pinus radiata* by 5-chlorosalicylic acid. *Eur. J. For. Pathol.* 28:153-158.
- Ross, A.F.** 1961. Systemic acquired resistance induced by localized virus infections in plants. *Virol.* 14:340-358.
- Schonbeck, F. and H-W. Dehne.** 1986. Use of microbial metabolites inducing resistance against plant pathogens. pp. 363-375. In: N.J. Fokkema and J. Van den Heuvel (eds.). *Microbiology of the Phyllosphere.* Cambridge University Press.

- Shah, D.M., C.M.T. Rommens, and R.N. Beachy.** 1995. Resistance to diseases and insects in transgenic plants: progress and applications to agriculture. *Trends Biotechnol.* 13:362-368.
- Smedegaard-Petersen, V.** 1990. Induction of defence reactions against powdery mildew in barley. *Proc. Crop Prot. Conf. Northern Britain.* pp. 233-242.
- Steiner, U., E.C. Oerke, and F. Schonbeck.** 1988. The efficiency of induced resistance under practical conditions. IV. Powdery mildew and grain yield of winter barley cultivars with induced resistance and fungicide treatment. *Z. Pflanz. Pflanz.* 95(5):506-517.
- Tuzun S. and J. Kuc.** 1991. Plant immunization: An alternative to pesticides for control of plant diseases in the greenhouse and field. pp. 30-39. In: *The biological control of plant diseases. Food and Fertilizer Technology Centre Book Series. No. 42.*
- Tuzun, S. and J. Kloepper.,** 1995. Practical application and implementation of induced resistance. pp 152-168. In: R. Hammerschmidt and J. Kuc (eds). *Induced resistance to disease in plants.* Kluwer Academic Publishers.
- van Peer, R., G.J. Niemann, and B. Schippers.** 1991. Induced resistance and phytoalexin accumulation in biological control of *Fusarium* wilt of carnation by *Pseudomonas* sp. strain WCS417r. *Phytopathol.* 81:728-734.
- Wei, G., J.W. Kloepper, and S. Tuzun.** 1991. Induction of systemic resistance of cucumber to *Colletotrichum orbiculare* by select strains of plant growth-promoting rhizobacteria. *Phytopathol.* 81:1508-1512.
- Wei, G., J.W. Kloepper, and S. Tuzun.** 1996. Induced systemic resistance to cucumber diseases and increased plant growth by plant growth-promoting rhizobacteria under field conditions. *Phytopathol.* 86(2):221-224.
- White, R.F.** 1979: Acetylsalicylic acid (aspirin) induces resistance to tobacco mosaic virus in tobacco. *Virology.* 99:410-412.
- Wilson, C.L., A. El Ghaouth, E. Chalutz, S. Droby, C. Stevens, J.Y. Lu., V. Khan, and J. Arul.** 1994. Potential of induced resistance to control postharvest diseases of fruits and vegetables. *Plant Dis.* 78:837-844.
- Yokoyama, K., J.R. Aist, and C.J. Bayles.** 1991. A papilla-regulating extract that induces resistance to barley powdery mildew. *Physiol. Mol. Plant Pathol.* 39:71-78.
- Zhang, W., W.A. Dick, and H. A. J. Hoitink** 1996. Compost-induced systemic acquired resistance in cucumber to *Pythium* root rot and anthracnose. *Phytopathol.* 86(10):1066-1070.
- Zhang, W., D.Y. Han, W.A. Dick, K.R. Davis, and H.A.J. Hoitink** 1998. Compost and compost-water-extract induced systemic acquired resistance in cucumber and arabidopsis. *Phytopathol.* 88:450-455.