STATUS ON INDUCED RESISTANCE AGAINST PLANT BACTERIAL DISEASES

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RESUMEN

El fenómeno de resistencia inducida describe el incremento de la resistencia de las plantas contra las enfermedades. A través de la utilización de agentes bióticos y químicos, llamados inductores de resistencia, *se activa el potencial de resistencia que existe de forma latente en las plantas y lo lleva a un nivel superior de resistencia. En contraste con un control directo contra enfermedades de plantas, la resistencia inducida define la capacidad de una planta para inhibir el desarrollo de factores dañinos. En general se han postulado tres factores para que un compuesto se considere inductor de resistencia:*

1. *La planta tratada es resistente al mismo espectro de la enfermedad que aquellos en los que la resistencia se induce biológicamente.*
2. *La carencia de actividad antimicrobiana y la no conversión del compuesto en la planta en metabolitos antimicrobianos.*
3. *La inducción de los mismos procesos biológicos que los observados en el tejido vegetal con posterioridad a la inducción biológica de resistencia.*

La resistencia inducida puede subdividirse en dos categorías amplias. La primera es resistencia sistémica adquirida (RSA). Este tipo se describió inicialmente como una respuesta a infección de patógeno. Subsecuentemente se encontró que el tratamiento de plantas con compuestos de bajo peso molecular puede inducir RSA, la cual puede desarrollarse local o sistémicamente en respuesta a un patógeno que cause una lesión necrótica o una respuesta hipersensitiva (RH). La reacción de resistencia está asociada con la producción de proteínas relacionadas (PR) a la patogénesis, y vía mediada al proceso que depende del ácido salicílico. El segundo tipo de resistencia inducida se desarrolla sistémicamente. Se conoce como resistencia sistémica inducida *(RSI), y está mediada por la vía sensitiva del jasmonato/etileno, y no implica la expresión de proteínas PR.*

Patógenos bacterianos incompatibles, agentes abióticos y estrés se han utilizado por mucho tiempo para inducir resistencia contra enfermedades bacterianas. Los primeros estudios de la infiltración de hojas de tabaco con células de Ralstonia solanacearum *muertas por procesos térmicos inducirían resistencia local contra el mismo patógeno. La resistencia inducida o adquirida a patógenos bacterianos se ha informado también como una disminución en los síntomas necróticos; sin embargo, muchos estudios revelaron que el efecto de la inducción de resistencia contra enfermedades bacterianas es la suspensión del crecimiento en las plantas inducidas de uno de los tres órdenes de magnitud en comparación con las plantas control. Esto sugiere que los inhibidores del crecimiento bacterial se producen como un resultado de la inducción de resistencia. Las plantas deben responder rápidamente a la inoculación por la producción de los inhibidores del crecimiento bacterial.*

Aquí se presenta una reseña sobre varios nuevos compuestos sintéticos, como por ejemplo Acibenzolar-S-metilo (ASM), DL-3-aminobutyric ácido (BABA) y otros, con sus efectos de biocontrol contra patógenos bacteriales, y los primeros estudios sobre sus modos de acción. Además se discuten algunos inductores naturales como extractos de plantas y aceites etéricos sobre su actividad inductora de resistencia contra enfermedades bacterianas.

Palabras clave: *resistencia, control biológico, enfermedad de planta*

ABSTRACT

The phenomenon of induced resistance describes the increase of resistance in the plant against diseases. Through the use of biotic or chemical agents, so called resistance inductors, the latent existing resistance potential of treated plants is activated and brought to a higher resistance level. In contrast to a direct control against plant diseases induced resistance describes the capability of a plant to inhibit the development of damaging factors. In general three criteria have been postulated for a resistance inducing compound:

1. *The treated plant is resistant to the same spectrum of disease as those in which resistance is induced biologically*
2. *A lack of antimicrobial activity and no conversion of the compound in plant in antimicrobial metabolites*
3. *Induction of the same biochemical processes as observed in plant tissue after biological induction of induced resistance.*

Induced resistance can be subdivided into two broad categories. The first is systemic acquired resistance (SAR), this type of resistance was first described as a response to pathogen infection. Subsequently, it has been found that treatment of plants with low molecular weight compounds can induce SAR, which can develop locally or systemically in response to a pathogen that causes a necrotic lesion or a hypersensitive response (HR). The resistance reaction is associated with the production of pathogenesis related (PR) proteins, and mediated via a salicylic acid depended process. The second type of induced resistance develops systemically, known as induced systemic resistance (ISR) and is mediated by a jasmonate/ethylene sensitive pathway and does not involve expression of PR-proteins.

Incompatible bacterial pathogens, abiotic agents and stress have been largely used to induce resistance against bacterial diseases. Early studies demonstrated that infiltration of tobacco leaves with heat-killed cells of Ralstonia solanacearum *would induce local resistance against the same pathogen. Systemic induced or acquired resistance to bacterial pathogens has also been reported as a decrease in necrotic symptoms. Most studies, however, revealed that the effect of resistance induction against bacterial diseases is suppression of bacterial growth in induced plants of one or three orders of magnitude as compared to control plants. This suggests that inhibitors of bacterial growth are produced as a result of resistance induction; plants may respond quickly to inoculation by production of bacterial growth inhibitors.*

In the following a review on several new synthetic compounds, as for instance Acibenzolar-S-methyl (ASM) , DL-3-aminobutyric acid (BABA) and others are presented with their biocontrol effects against bacterial pathogens and first studies on their mode of action. Moreover some natural inductors as plant extracts and etheric oils are discussed on their resistance inducing activity against bacterial diseases.

Key words: *resistance, biological control, plant disease*

INTRODUCTION

The phenomenon of induced resistance describes the increase of resistance in the plant against diseases. Through the use of biotic or chemical agents, so called resistance inductors, the latent existing resistance potential of treated plants is activated and brought to a higher resistance level. In contrast to a direct control against plant diseases induced resistance describes the capability of a plant to inhibit the development of damaging factors. As resistance inducers biotic and chemical (synthetic) agents have been reported, in most cases the reaction was achieved by preinoculation with apathogenic or pathogenic microorganisms in low concentrations or culture filtrates, as for instance in early studies of Mc Intire *et al.* (1973), who could protect apple plants against infection with virulent *Erwinia amylovora* strains with a pathogenic bacteria of the pathogen.

In general three criteria have been postulated for a resistance inducing compound:

1. The treated plant is resistant to the same spectrum of disease as those in which resistance is induced biologically.
2. A lack of antimicrobial activity and no conversion of the compound in plant in antimicrobial metabolites.
3. Induction of the same biochemical processes as observed in plant tissue after biological induction of induced resistance [Kessmann *et al.*, 1994].

Induced resistance to pathogens can be subdivided into two broad categories. The first of these is systemic acquired resistance (SAR). This type of resistance was first described as a response to pathogen infection. Subsequently, it has been found that treatment of plants with low molecular weight compounds can induce SAR [Ryals *et al.*, 1994]. SAR develops either locally or systemically in response to a pathogen that causes a necrotic lesion. The necrotic lesion can either be the result of a successful infection or a hypersensitive response (HR). The resistance expressed is generally effective against a broad range of pathogens, is associated with the production of pathogenesis related (PR) proteins, and is mediated via a salicyclic acid depended process [Hammerschmidt and Becker, 1997; Hammerschmidt, 1999]. As has been mentioned above, SAR can also be induced by exogenous application of some synthetic compounds [Zeller and Zeller, 1999; Baysal *et al.*, 2002; Siegrist *et al.*, 2000].

The second type of induced resistance develops systemically, known as induced systemic resistance (ISR) [Van Loon *et al.*, 1998]. It is mediated by a jasmonate/ethylene sensitive pathway and does not involve expression of PR-proteins.

Incompatible bacterial pathogens, abiotic agents and stress have been largely used to induce resistance against bacterial diseases [Goodman *et al.*, 1986]. Early studies by Lozano and Sequeira (1970) demonstrated that infiltration of tobacco leaves with heat-killed cells of *Ralstonia solanacearum* would induce local resistance against the same pathogen. Systemic induced or aquired resistance to beacterial pathogens has also been reported as a decrease in necrotic symptoms [Caruso and Kuc, 1979]. Most studies, however, revealed that the effect of resistance induction against bacterial diseases is suppression of bacterial growth in induced plants of one or three orders of magnitude, as compared to control plants [Caruso and Kuc 1979; Lawton *et al.*, 1996]. This suggests that inhibitors of bacterial growth are produced as a result of resistance induction; plants may respond quickly to inoculation by production of bacterial growth inhibitors. Moreover, induced *Arabidopsis* plants respond to *Pseudomonas syringae* pv. *syringae* inoculation with enhanced salicyclic acid accumulation and induction of PR-1 gene transcription [Cameron *et al.*, 1999]. SAR can activate in plants a series of substances inhibiting infections and spreading of diseases [Kessmann *et al.*, 1994; Ovadia, 2001].

Synthetic resistance inducers

Chemical inducers of disease resistance play the key role for the integration of the SAR concept in modern plant protection strategies [Lyon and Newton, 1997]. Acibenzolar-S-methyl (ASM) known under the commercial name Bion or Actigard, is one of the non-toxic synthetic resistance inducers used against plant pathogens. The compound is known to elicit SAR against fungal and bacterial diseases of several plants including tobacco, cucumber [Lawton *et al.*, 1996] and apple [Zeller and zeller, 1999; Brisset *et al.*, 2000; Baysal *et al.*, 2002].

The compound was also found to be effective in controlling bacterial black spot of mango, caused by *Xanthomonas campestris* pv. *mangiferaeindicae* [Boshoff *et al.*, 1998]. Pretreatment of rose shoots with 50 μM ASM led to resistance against *Agrobacterium tumefaciens* and *Diplocarpon rosae* by significantly reducing the disease severity of crown gall and blackspot [Suo and

Leung, 2001]. Resistance inducing effects of ASM have been demonstrated in apple against *Erwinia amylovora* in recent studies [Baysal *et al.*, 2002; Brisset *et al.*, 2000].

In physiological studies, a marked increase of peroxidase and, as a component of antioxidative protection system, gluthatione-S-transferase activities were found after ASM application in inoculated and uninoculated apple plants [Baysal *et al.*, 2002]. This was considered to be an indication of induction of resistance in fire blight in host plants protected with ASM. In further studies, Maxson-Stein *et al.* (2002) reported that expression of putative genes related to SAR induction was elevated in ASM-treated apple seedlings. The level of PR-1 and PR-8 mRNA were increased 10-fold and PR-2 mRNA was increased 100-fold in ASM-treated seedlings compared to levels in untreated seedlings. The role of plant defense activator ASM in inducing resistance in rice against leaf blight caused by *Xanthomonas oryzae* pv. *oryzae* was also studied [Babu *et al.*, 2003]. In rice plants pretreated with ASM, infection was significantly reduced. Induced systemic resistance was found to persist for up to three days in treated plants. Increased phenolic content and accumulation of pathogenesis-related proteins, e.g. chitinase, beta-1,3-glucanase and thaumatin-like protein (TLP; PR5) were also observed in rice plants pretreated with ASM after inoculation with *X oryzae* pv. *oryzae* [Babu *et al.*, 2003].

The effectiveness of resistance inducers prohexadione calcium (Regalis) and ASM against fire blight on apple and pear trees was evaluated in a greenhouse. Both compounds induced resistance to fire blight on terminal shoots, but they were not able to protect pears against infection by *E. amylovora* at high concentration of inoculum (10^8 cfu/mL). On the other hand, a decrease of disease severity was found when ASM or Regalis were applied with a lower bacterial concentration of bacterial inoculum (10^6 cfu/mL) [Sobiczewski *et al.*, 2001]. Thomson *et al.* (1999) reported that ASM alone provided significant protection against fire blight but was not as effective as streptomycin. The combination of ASM plus streptomycin was often the best or near best treatment. This would be logical since each compound has a different mode of action. In the case of streptomycin, the action is directed towards the pathogenic bacteria whereas ASM elicits the SAR response in the host plant. On the other hand, in experiments under greenhouse conditions ASM treatment showed a marked resistance induction effect against fire blight [Zeller *et al.*, 1999].

DL-3-aminobutrytic acid (BABA) is a non-protein amino acid which also induces resistance against a large number of plant pathogens [Zimmerli *et al.*, 2001]. BABA has a broad spectrum of activity against many disease causing organisms such as viruses, bacteria, fungi and nematodes [Jakob *et al.*, 2001; Cohen, 2002], and the compound reduced disease severity when applied following foliar, soil drench and leaf discs treatments [Ovadia *et al.*, 2000]. BABA operates through a variety of defense mechanisms, including physical barriers and biochemical changes leading to resistance [Cohen, 2002].

Some authors reported that prohexadione calcium (Regalis) is a growth retardant reducing shoot length in apple (Byers and Yoder, 1999) and pear [Theron *et al.*, 2002]. The compound also induced resistance to fire blight in apple and pear [Fernando and Jones, 1999; Jones *et al.*, 1999]. The severity of fire blight was reduced significantly on apple shoots inoculated 13 days after treatments with 250 mg/L prohexadione calcium compared with untreated shoots [Momol *et al.*, 1999].

Biotic resistance inducers

As natural compounds with resistance induction effect against fire blight several plant extracts, etheric oils and metabolic substances have been tested. Mende *et al.* (1993) observed induced resistance effect in the high susceptible host plant *Cotoneaster watereri* with several plant extracts from ivy (*Hedera helix*), mistletoe (*Viscum album*) and *Alchemilla vulgaris*, by causing a reduction of disease severity and lower multiplication of the pathogen in the host plant. The same results could be achieved with extracts from *Hedera helix* and *Viscum album* on detached leaves of quince (*Cydonia oblonga*) and in field experiments with the apple variety 'James Grieve' [Mosch *et al.*, 1996].

In another experiment the potential of the *Hedera helix* extract to protect M26 apple rootstocks against fire blight was determined under controlled conditions in the greenhouse. The plant extract applied prior to inoculation of the *E. amylovora* strain Ea 7/74 suppressed disease development and in correlation bacterial multiplication up to 58% vice versa 72%. Also in this host-parasite interaction, the *H. Helix*-extract caused induced resistance against fire blight on M26 apple rootstocks [Baysal and Zeller, 2005].

Besides plant extracts also an etheric oil has been tested against *E. amylovora* on its resistance induction effect. Although the essential oil of thyme has been described as an antibacterial natural agent against the fire blight pathogen besides others from origanum, savory, cinnamon, the etheric oil of the thyme variety *Thymbra spicata* showed in a low concentration of 0,05% also a reaction of systemic acquired resistance (SAR).

In the meantime this thyme oil has been registered in Turkey and Germany under the names Aksebio 2 and BioZell-2000B and was tested in several experiments under greenhouse and field conditions. Reduction of disease index was correlated with a significantly lower bacterial population in the plant tissue of M26 rootstocks compared to untreated inoculated plants.

In the studies with the extract of ivy (*Hedera helix*), which showed a suppressed disease development and bacterial multiplication of *E. amylovora* in various host plants local induced resistance was caused resulting in significant increase of polyphenol oxidation activity with higher activities of enzymes of phenol metabolism as peroxidase (PO), polyphenoloxidase (PPO) and phenylalanin-lyase (PAL). Recently Baysal and Zeller (2005) analyzed the mechanism of action of *H. helix*-extract, concerning alterations in the levels of key defense-relating enzymes, PO, chitinase and 1,3 β-glucanase. In this study a correlation was found between plant extract treatment and increase of PO and these both PR-proteins, which possess direct antimicrobial activity by degrading microbial cell walls. From these findings the authors concluded, that the extract of *H. helix* was responsible for a stimulation of resistance to fire blight in the host plant and can accelerate the defense response to stop bacterial migration in the plant tissue up to seven days.

Also with BioZell-2000B, the natural compound of the etheric oil of thyme (*Thymbra spicata*) a similar resistance inducing effect could be observed [Zeller *et al.*, 2004]. Besides a marked reduction in the severity of the disease in M26 rootstock shoots and apple blossom blight and decrease of the multiplication of *E. amylovora* in the host plant, the following physiological changes in inoculated and non-inoculated apple shoots could be found:

A higher phenol content in BioZell-2000B treated plant with increased activities of phenol metabolism (PO, PPO and PAL); moreover higher amounts of the PR-proteins of chitinase and β-1,3 glucanase, which led to the conclusion, that also this natural product is responsible for a stimulation of resistance to fire blight and acts as a SAR inducing compound in this host-parasite interaction.

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