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Review

Induced resistance in the nematodes control

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Nematodes are serious problem, parasitizing plants and impairing the yields of various plant species, especially in tropical countries. Control of these organisms is complex and usually demands integrated management practices. One strategy that has attracted the interest of researchers is the use of resistance inducers. Resistance inducers or elicitors can take the form of a chemical compound or a live organism, whose function is to activate the plant's defense mechanisms. The last few years have seen numerous researches in search of efficient phytonematode resistance inducers. The aim of this review is to present some of the results of this work, indicating its potential and limitations.

Key words: Elicitors, management, phytonematode, resistance.

INTRODUCTION

Agricultural productivity is determined by factors such as cultivars, water availability, fertilizers, climate, pests and diseases (Gershenson, 2002). Plant diseases have posed a problem since the advent of cropping and controlling those demands enormous efforts (Sobrinho et al., 2005). Root diseases are among the main causes of impaired food crop yield, occurring with greater intensity in tropical regions. However, they have received little attention by comparison with leaf diseases (Michereff et al., 2005), and this is applied, in particular, to diseases caused by nematodes.

Nematodes that parasitize plants (phytonematodes) are responsible for a substantial part of the losses caused by destruction of root systems. Estimates put the losses to world production of maize at 10.2%, soybean 10.6%, citrus crops 12.0% and sugar cane 15.2%. In Brazil, losses vary from 5 to 35% for various annual, semi-perennial and perennial crops (Chaves and Araújo, 2007).

Controlling nematodes is complex and requires integrated management. The methods most widely used include both chemical and genetic approaches. However, the use of nematicides, apart from the expenses incurred, can result in chemical residues harmful to humans and the environment, as well as selecting for resistant nematodes (Ghini and Kimati, 2000). Genetic control is limited mainly by the scarcity of high-resistance material, but other factors are also important, such as restriction to region, climate and nematode species (Franzener et al., 2007).

In general, alternative cropping methods produce good results, especially if incorporated into integrated management system with crop rotation, organic soil amendment, biological control and induced resistance

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(Campos, 2001; Bettiol and Ghini, 2003; Dias-Arieira et al., 2012).

Induction of plant resistance to pathogens has been known since the beginning of the 20th century with the work of Bernard (1911) and Romeiro (2001), who observed that orchid bulbs grown in a culture medium with soil fungi did not show signs of infection (Romeiro, 2001). Induction has proved to be a high-potential alternative for reducing the severity of diseases in various crops, effectively controlling many pathogens using biotic or abiotic inducers (Benhamou and Belanger, 1998; Baysal et al., 2003; Silva et al., 2004; Bonaldo et al., 2005; Dias-Arieira et al., 2012), providing that the inducers sensitize the plant and activating defense mechanisms in response to the presence of the pathogen (Conrath et al., 2002). These mechanisms involve enzymes such as peroxidase, β-1, 3-glucanase, chitinase, phenylalanine ammonia-lyase and polyphenol oxidase (Cavalcanti et al., 2005).

There are two acknowledged ways of inducing plant resistance to disease: Systemic acquired resistance (SAR) and induced systemic resistance (ISR). Different metabolic pathways are used to produce SAR and ISR. SAR is characterized by an accumulation of salicylic acid and proteins related to pathogenesis, whereas ISR involves the accumulation of growth regulators, such as jasmonic acid and ethylene (Pieterse et al., 2002). There is some consensus among authors that ISR and SAR are distinct phenomena in regard to the form that the resistance begins, but the end results are fairly similar (Fabry et al., 2007).

A lot of researches are currently being conducted on resistance induction as people become more aware of the health implications of the food they eat and the environmental impact of pesticides. Resistance induction also provides a further alternative for integrated management (Soares et al., 2004; Bonaldo et al., 2005; Dias-Arieira et al., 2012). The study of resistance induction for controlling nematodes has been increasingly reported over the past few years, with research projects on a number of elicitors for resistance to a range of phytonematodes in a variety of crops (Fabry et al., 2007; Franzener et al., 2007; Molinari and Baser, 2010).

Phytonematode resistance induction can be applied to both annual and perennial crops, but some factors must be taken into consideration, such as the nature of the specific pathosystem's interaction, host plant genetics and the need to reactivate defense mechanisms, bearing in mind the temporary effect of the inducer. Furthermore, the absence of any direct toxic effect on the pathogen is one of the basic criteria for confirming the occurrence of induced resistance (Salgado et al., 2007).

Steiner and Schönbeck (1995) proposed two criteria for differentiating induced resistance from other biological control mechanisms that reduce the severity and incidence of plant diseases. First, the criterion of temporal separation must be satisfied, which means that the inducer must be applied prior to inoculation with the nematode so that there is time for the plant to activate and express the genes responsible for resistance. Second, it must be possible to eliminate toxic or competitive effects using the split-root method, in which part of the root is inoculated with the induction agent and another part with the disease-causing agent (Osman et al., 2012).

Van Loon et al. (1998) described a third criterion for differentiating induced resistance from other control mechanisms that involves observing the responses of different hosts in the knowledge that this depends on the plant genotype. In soybean, it has been observed that there is greater production and accumulation of phytoalexin glyceollin in the Centennial cultivar (resistant to *Meloidogyne incognita* (Kofoid and White) Chitwood), and less accumulation in the Pickett 71 cultivar (susceptible). However, when Centennial was inoculated with *Meloidogyne javanica* (Treub) Chitwood, to which it is susceptible; there was no significant accumulation of glyceollin (Kaplan et al., 1980).

In addition to these criteria, *in vitro* and *in vivo* activities can be compared, and pathogenesis-related proteins and the production of phytoalexins and secondary compounds can be quantified (Bettiol and Morandi, 2005). This is because plant defense response to nematodes include the activation of the metabolic pathways involved in phytoalexin biosynthesis, an increase in the activity of enzymes such as phenylalanine ammonia-lyase, deposition of callose and/or lignin and the accumulation of phenolic compounds, peroxidase, polyphenol oxidase, superoxide dismutase, chitinases and proteinase inhibitors (Mazzafera et al., 1989; Salgado and Silva, 2005).

Two major resistance responses have been studied, based on microscopic observation of various incompatible interactions between nematode and plant. The first blocks the development of nutrient cells (giant cells) in the infection sites and the second is characterized by a rapid hypersensitivity reaction, resulting in necrosis at the feeding site, occurring a few days after infection. The hypersensitivity reaction is a defense mechanism against a wide range of pathogens, and is characterized by an oxidative reaction resulting in the production of active kinds of oxygen, such as hydrogen peroxide (H_2O_2), the superoxide radical (O_2^-) and accumulation of phenylpropanoids (Bakker et al., 2006).

One of the most widely researched chemical inducers for controlling phytonematodes is acibenzolar-S-methyl (ASM). Sprayed onto vine leaves seven days prior to inoculation with *M. javanica* and *Meloidogyne arenaria* (Neal) Chitwood, ASM reduced the galls number and eggs by 40 to 80%, compared to untreated plants (Owen et al., 1998). Similar results have been obtained by prior application to the *M. incognita*-tomato pathosystem (Silva et al., 2002, 2004). ASM is thought to interfere in the

formation of giant cells via a protein essential to this process and to affect nematode reproduction (Silva et al., 2002). A significant increase in the activity of β-1, 3-glucanase in the roots has also been observed five days after application of ASM (Owen et al., 1998).

However, Rocha et al. (2000) observed insignificant effects for ASM on a population of *Heterodera glycines* Ichinohe in soybean, showing only a tendency towards reduction when ASM was applied during irrigation at a higher concentration. ASM was, also, ineffective in controlling *Meloidogyne exigua* Goeldi in coffee cv. Catuaí 144, and no significant differences were observed between treatments in terms of final population, galls number and reproduction factor, 90 days after inoculation (Salgado et al., 2007). When ASM was sprayed onto vine leaves (50 µg i.a. ml^{-1}), there was no change in the number of *Meloidogyne* spp. in the roots, three days after inoculation, but there was a drop in the population, three weeks after inoculation, a period compatible with the plant-nematode interaction involving the induction of giant cells in the host, enabling parasites to feed and increase (Owen et al., 2002).

Research has shown that ASM does not impair the formation of galls, probably because it does not inhibit penetration and induction of feeding sites, but rather the reproduction of the nematodes (Chinnasri et al., 2003; Molinari and Baser, 2010). This result is due to the time required to induce the plant's resistance mechanisms, since studies have indicated that ASM does not affect nematode hatching, survival or penetration into the host roots (Chinnasri et al., 2003; Salgado et al., 2007; Molinari and Baser, 2010), but does impede nematode development and reproduction (Chinnasri et al., 2003; Molinari and Baser, 2010), a result, also, was observed for other inducers, such as DL-β-amino-n-butyric acid (Oka and Cohen, 2001).

In general, the effectiveness of ASM has been directly proportional to the concentration applied (Chinnasri et al., 2003; Molinari and Baser, 2010). In caupi bean, the reduction in the population of *Rotylenchulus reniformis* Linford and Oliveira in the root system was proportional to an increase in concentration from 50 to 100 mgL^{-1} water (Chinnasri et al., 2003). In addition to the concentration, Molinari and Baser (2010) evaluated different ASM application methods for controlling *M. incognita* in tomato and observed that concentrations of 180 and 360 ppm reduced the nematode population when applied to the soil. However, when applied to the aerial part, only the higher concentration significantly reduced the eggs number in the root system and the nematode reproduction.

In addition to ASM, other chemical resistance inducers have been researched, such as salicylic acid, potassium phosphite and jasmonic acid. Molinari and Baser (2010) evaluated salicylic, methyl-salicylic acid and ASM in the control of *M. incognita* in tomato roots and observed that salicylic acid reduced 50% the egg masses number, and the reproduction by 57%. Methyl-salicylic acid was ineffective in reducing the variables assessed; this result was attributed to the low concentration used in the study since it was phytotoxic when applied at high concentrations. Kempster (1998) confirmed induction of resistance to *Heterodera trifolii* Goffart in bioassays on clover (*Trifolium repens* L.), applying salicylic acid and benzothiadiazole. Resistance was evidenced by a reduction in nematode fecundity, non-viability of cysts and fewer eggs in the cysts.

The use of methyl jasmonate and potassium silicate reduced the number of *M. incognita* per root gram and increased peroxidase enzyme activity in sugar cane. Furthermore, the parasitism by *M. incognita* increased peroxidase activity at 14 and 21 days after inoculation (Guimarães et al., 2010). Jasmonic acid plays a fundamental role in signaling the expression of plant defenses. Some defense genes are controlled by the jasmonate pathway, including those coding for proteinase inhibition. Proteinases are crucial for impeding nematode feeding and development (Gheysen and Fenoll, 2002). However, in the *Meloidogyne*-tomato pathosystem, jasmonic acid and methyl jasmonate did not induce resistance when sprayed onto the leaves or applied to the soil (Oka et al., 1999).

The capability of phosphites to trigger plant defense mechanisms, including the production of phytoalexins, was reported by Dercks and Creasy (1989). In a study conducted by Dias-Arieira et al. (2012), potassium phosphite was effective in decreasing the population of *Pratylenchus brachyurus* (Godfrey) and Filipjev and Schuurmans Steckhoven in maize. Similar results have been obtained for other nematode species (Oka et al., 2007). Although phosphites affect microorganisms directly (Guest and Grant, 1991), in a study conducted by Dias-Arieira et al. (2012), phosphite was applied to the aerial part, that is, spatially separated from the nematode, proving its capability of triggering plant defense mechanisms, which include the phytoalexins production (Dercks and Creasy, 1989). This hypothesis is backed up by the result that in a study carried out by Salgado et al. (2007), potassium phosphite increased hatching of *M. exigua*, but did not kill juveniles, that is, did not directly affect the parasite. Furthermore, Oka et al. (2007) observed that potassium phosphite applied to the aerial part was effective in controlling *Heterodera avenae* Wollenweber and *Meloidogyne marylandi* Jepson and Golden in wheat and oats. This result can be ascribed to potassium phosphite's capability of translocating through the xylem and phloem (Quimette and Coffey, 1990).

Silicon has also been used to induce resistance in various pathosystems, and although the mechanism by which silicon activated resistance in plants has not yet been elucidated; its deposition on the cell walls has resulted in the hypothesis of a possible physical barrier (Terry and Joyce, 2004). The silicon absorbed by plants is rapidly translocated to the aerial part and, during

transpiration, the dissolved silicon becomes supersaturated and polymerizes, forming solids that are incorporated into the cell walls enhancing rigidity (Epstein and Bloom, 2004). Although most of the silicon is polymerized or solidified, its role in resistance to disease is mainly due to the silicon fraction in solution within the plant, which would suggest that it helps produce defensive compounds by activating the synthesis of substances such as phenols, lignin, suberin and callose in the cell wall (Rodrigues and Datnoff, 2005).

Dutra et al. (2004) observed that applying calcium silicate caused a decrease in the number of galls and eggs of various species of *Meloidogyne* in common bean, tomato and coffee. The authors attributed the induced and enhanced resistance to the silicon was thought to stimulate the production of enzymes and substances related to defense mechanisms. Researching the biochemical resistance response of coffee to *M. exigua* mediated by silicon, (Silva et al., 2010) submitted evidence that the reproductive capability of nematodes in coffee roots supplied with silicon was impaired. The response was associated with the production of lignin and increased activity of peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase, especially in the susceptible cultivar studied. According to Guimarães et al. (2008), potassium silicate was effective in inducing resistance to *M. incognita* in sugar cane, since it reduced the number of nematode eggs in the RB867515 and RB92579 varieties. However, it did not affect aerial part biomass in the RB867515 and RB863129 varieties, nor the population density of *Pratylenchus zeae* Graham in the soil and roots, 100 days after transplanting.

Over the last decade, research has been conducted on the use of essential oils and plant extracts as resistance inducers. Bosenbecker et al. (2004) observed a significant difference in the final population and reproduction factor of *M. javanica* in *Solanum tuberosum* L. sprayed with extract of fennel (*Foeniculum vulgare* Mill.). Application of aqueous extracts of *Mucuna pruriens* var. *utilis* (L.) D.C. and *Ocimum basilicum* L., also, significantly impaired the reproduction of *M. incognita in* tomato (Lopes et al., 2005). Franzener et al. (2007) observed that an aqueous extract obtained from various parts of *Tagetes patula* L. was effective in reducing the galls and eggs number of *M. incognita* in tomato when applied weekly. Nonetheless, other studies have produced negative results, such as those obtained by Gardiano et al. (2011), showing that an aqueous extract of rosemary did not control *Rotylenchulus reniformis* Linford and Oliveira in cotton. Aqueous extracts of various medicinal plants applied to the aerial part of tomato, also, proved ineffective role in inducing resistance to *M. javanica*, although some treatments did reduce the number of galls (Gardiano et al., 2008).

In regard to biotic agents, plant-growth promoting rhizobacteria have attracted quite a much attention from resistance induction researches, since these organisms are capable of boosting plant growth with direct antagonistic action, and because they could easily be used as commercial inoculants by farmers (Ramamoorthy et al., 2001; Mafia et al., 2009). Oostendorp and Sikora (1989) observed that *Pseudomonas fluorescens* Migula rhizobacteria induced systemic resistance and reduced the penetration of *Heterodera schachtii* Schmidt in sugar beet. Similar results were obtained for the control of *Hirschmanniella oryzae* (van Breda de Hann) Luc and Goodey in rice (Swarnakumari et al., 1999).

Using the split-root method, Siddiqui and Shaukat (2002) observed that *Pseudomonas aeruginosa* Shroeter strain IE-6S$^+$ and *P. fluorescens* strain CHA0 rhizobacteria were effective in reducing the population of *M. javanica* in tomato, by 42 and 29%, respectively. The authors attributed the greater efficacy of the IE-6S$^+$ strain to its capability of colonizing plant tissues. In fact, research has shown that endophytic bacteria can both promote plant growth and attenuate the symptoms brought on by various phytopathogens (Pleban et al., 1995). Oliveira et al. (2009) confirmed that isolates of endophytic bacteria impaired the formation of galls and the reproduction of *M. javanica* in tomato roots, mainly through root bacterization.

Working with the *Rhizobium etli* (G12 isolate), Fabry et al. (2007) confirmed systemic induced resistance to *M. javanica* in tomato grown using the split-root method. The galls and egg numbers per root system was reduced by 35.3 and 38.8%. They also observed that *R. etli* was effective in reducing the galls and eggs number of *M. javanica* and *M. incognita* at both low and high concentrations of nematode inoculum (2000 and 4000 eggs). Furthermore, the capability of controlling nematodes using rhizobacteria to induce resistance was observed by applying humus, which increased nematode reproduction in the soil.

Mahdy et al. (2001) observed that *R. etli* and *Bacillus sphaericus* B43 were effective in inducing resistance to *Globodera pallida* Stone and *M. incognita* in potato. Reitz et al. (2000) had previously observed that applying lipopolysaccharide (LPS), extracted from *R. etli* G12, attenuated the infection caused by *G. pallida* in potato, even at low concentrations, confirming the systemic resistance induced by LPS. Surface carbohydrates of *Rhizobium* consist mainly of exopolysaccharides (EPS) as additional viscous or capsular layers around the bacterial cell and the LPS, forming an integral part of the external cell membrane. These carbohydrates play an important role during the recognition process in the symbiotic interaction between *Rhizobia* and legumes (Denny, 1995). Moreover, some authors have proposed that the degradation of rhizobial polysaccharides is involved in regulating the plant response (Mellor and Collinge, 1995). Hackenberg and Sikora (1994) observed that potato tubers treated with *R. etli* exhibited reduced penetration of *G. pallida* juveniles in greenhouse studies,

in addition to reducing the hatching of juveniles *in vitro*.

Using the split-root method, Hasky-Günther et al. (1998) showed the capability of *R. etli* G12 and *Bacillus sphaericus* B43 to trigger induced resistance to *G. pallida*, significantly attenuated the penetration of *G. pallida* juveniles into potato roots. Induced systemic resistance in the root system was caused by live bacterial killed by heat, and the effects of induced systemic resistance could be related to alterations in exudates or in the respective amounts of hatching factor in the roots, since *G. pallida* will hatch only in the presence of hatching factor produced by the host plant (Perry and Clarke, 1981). Specific exudates on the surface of the root are used by the cyst nematode to recognize the host (Zuckermann and Jansson, 1984). Root exudate components could be altered by the resistance-inducing rhizobacteria (Hasky-Günther et al., 1998).

A study conducted by Araújo and Marchesi (2009) proved that isolate of *Bacillus subtilis* (PRBS-1), in addition to impairing the reproduction of nematodes forming galls in tomato roots, also increased aerial part biomass. Araújo et al. (2002) observed that treating soybean roots with *B. subtilis* inhibited the attraction of *H. glycines* juveniles to the plant by comparison with roots not treated with the bacterium. Vonderwell et al. (2001) observed an increase in the concentration of indoleacetic acid (IAA) in plantlets of *Pinus taeda* L. inoculated with *B. subtilis* isolate INR7.

In contrast to the other studies, *B. subtilis* A-13 rhizobacterium was evaluated for controlling *M. incognita* in cotton and sugar beet, and *R. reniformis* in cotton. It was observed that, despite the reduction in the populations of *M. incognita* in sugar beet and *R. reniformis* in cotton, the population of *M. incognita* in cotton remained unaffected (Sikora, 1988). In a study by Russi (2012), it was also observed that *B. firmus* GN-126 induced resistance to *R. reniformes* in cotton at concentrations of 1×10^{6} cfu ml^{-1} and 1×10^{9} cfu ml^{-1}. The study did not reveal any significant differences in the fresh weights of both parts of the root, nor in the number of *R. reniformis* females and eggs. Some authors draw attention to factors that can cause variations in the results of induced resistance to nematodes, including application doses, methods and timing, and the genetic resistance of the host (Owen et al., 1998, 2002; Molinari and Baser, 2010). Application of the inducer, generally, requires inoculation at intervals ranging from three to fifteen days (Owen et al., 2002). According to Silva et al. (2004), applying ASM outside the period starting from three days before and seven days after transplanting does not effectively activate resistance mechanisms in tomato.

However, in practice, applying the inducer in advance restricts nematode control, since the nematodes are already present in the soil when the seeds germinate. On the other hand, if the inducer impairs the multiplication of the nematode in subsequent cycles, the damage that they cause can be minimized. But to be ascertaining of this hypothesis, researchers should work over a complete crop cycle, or at least with a longer observation period. Studies are still necessary on resistance inducers in seed treatments to find out whether host protection can be achieved in early stage of germination. Investigations are also required on the treatment of plants germinated on trays or nursery and subsequently transplanted in the field.

CONCLUSIONS

Resistance induction in plants has proved to be a method of control with potential to attenuate the severity of nematodes, but it is important to increase our knowledge of the mechanisms by which resistance inducers operate.

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