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Review Article

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Efficacy of Biotic and Chemical Inducers of SAR in Management of Plant Viruses

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Abstract

The objective of this study was to review the published research works on management of viral diseases of crop plants in recent years using microbial antagonists and chemical inducers of SAR. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistance; in both SAR and ISR, plant defenses are preconditioned by prior infection or treatment that results in resistance (or tolerance) against subsequent challenge by a pathogen or parasite. Much of this knowledge is due to the identification of a number of chemical and biological elicitors, some of which are commercially available for use in conventional agriculture. The biocontrol potential of *Bacillus* spp. and *Pseudomonas* spp in relation with their antagonizing attributes against plant viruses revealed their efficacy against *Tobacco Mosaic Virus* (TMV), *Cotton leaf curl virus* (CLCuV), *Cucumber mosaic virus* (CMV) and some other plant viruses are discussed in this review. Recent researches on mechanisms of biological control by PGPR revealed that several plant growth promoting rhizobacteria (PGPR) strains protect plants against viral infection through induction of systemic resistance. Studies were done to evaluate specific strains of PGPR for induced resistance in indicator plants like *Chenopodium* and *Arabidopsis thaliana*. The classic form of SAR can be triggered by exposing plant to virulent, avirulent, and nonpathogenic microbes viz. microbial antagonist, or artificially with chemicals such as salicylic acid 2,6-dichloro-isonicotinic acid (INA) or benzo (1, 2, 3) thiadiazole-7-carbothioic acid *S*-methyl ester (BTH) etc. which are considered as chemical inducers of SAR. Progress with efficient use of different biological agents against plant viruses is a worthwhile approach in context of sustainable crop health management.

Keywords: Elicitors, induced resistance, plant defense

1. Introduction

Plant infection by viruses causes physiological disorders responsible for plant diseases of economic and agronomic significance in many crops. Plant viruses cause epidemics on all major cultures of agronomic importance, representing a serious threat to global food security. As strict intracellular pathogens, they cannot be controlled chemically and prophylactic measures consist mainly in the destruction of infected plants and excessive pesticide applications to limit the population of vector organisms. The years of dependence and extensive use of the agrochemicals have led to undesirable effects on the environment, on non-target organisms and development of carcinogenicity in humans (Heydari, 2007). Taking into account the requirement of alternative approaches, biological control seems effective and beneficial. In simple terms, biological control involves the control of one organism using another organism or products derived from another organism (Cook, 1993). The induction of plant resistance using microbial antagonist or other abiotic elicitors is also a form of biological control (Schouten et al., 2004).

It is widely known that plants can defend themselves against pathogen infection through a variety of mechanisms that can be either local, constitutive, or inducible (Franceschi et al., 1998; 2000). Inducible resistance mechanisms such as systemic acquired resistance (SAR) are broad spectrum plant defense responses that can be induced biologically by challenging a plant with a weaker strain of a specific pathogen or exposing a plant to natural and/or synthetic chemical compounds (Elliston et al., 1977). SAR has been studied by plant biologists for the past 100 years as a means to increase resistance to fungal, bacterial, and viral pathogens in crop plants such as potato, wheat, and rice (Agrios, 1997). In this review, different aspects of biological control of viral plant diseases including induction of resistance using different microbial antagonists and chemical SAR activators, the mechanisms involved and their methods of application in different crops have been covered.

2. Biotic and Chemical Inducers of Systemic Acquired Resistance against Plant Viruses

Plants develop a generalized resistance in response to infection by a pathogen or to treatment with certain natural or synthetic chemical compounds. At first, it is localized around the point of infection and subsequently spreads to distal uninoculated plant parts. This is known as systemic acquired resistance or SAR (Agrios, 2005). The advantages of SAR in plant protection can be enlisted as described by Conrath (2006). It leads to the development of the enhanced resistance in the distal, uninoculated plant organs. It confers a long-lasting protection that can last for weeks to month, and sometimes throughout an entire season. (Conrath, 2006).

Systemic acquired resistance is characterized by the accumulation of salicylic acid (SA), along with enhanced expression of pathogenesis-related proteins and activation of phenylpropanoid pathway. This leads to the synthesis of higher phenolic compounds that are associated extensively with the defense of plants against microbes (Metraux and Raskin, 1993). Various mechanisms such as phytoalexin production, proteinase inhibitors, cell wall strengthening , lignifications and synthesis of hydrogen peroxide has been suggested to be an important regulator of disease resistance that are associated with hypersensitive response (HR) and systemic acquired resistance (Levine et al., 1994).

The classic form of SAR can be triggered by exposing plant to virulent, avirulent, and nonpathogenic microbes viz., microbial antagonist (Table 1), or artificially with chemicals such as salicylic acid 2,6-dichloro-isonicotinic acid (INA) or benzo (1,2,3) thiadiazole-7-carbothioic acid *S*-methyl ester (BTH) etc. (Table 2) which are considered as chemical inducers of SAR.

In the year 1996, two microbial antagonist namely *Pseudomonas fluorescens* and *Serratia marcescens* were studied for their capacity to induce resistance in cucumber and tomato plants against CMV. It is to be noted that these antagonist had already shown resistance in cucumber against some fungal and bacterial diseases. It was observed that the plants that developed from seed treated with the antagonist showed low number of mean symptomatic plant even after mechanical inoculation with CMV. The viral antigen has detected at negligible amounts in the microbial antagonist treated plants (Raupach et al., 1996).

In an experiment done in the year 2000, three species of *Bacillus* were studied for their capacity to induce resistance against ToMoV. In field trials conducted over 3 seasons, commercial spore preparation of the antagonist were applied as seed treatments, as powder amendments to the planting medium, or as a combined seed and powder treatment. The results demonstrated that under natural conditions along with high levels of vector–virus inoculums present, the PGPR treatments showed reduced ToMoV incidence and disease severity also, a corresponding increase in fruit yield in some cases (Murphy et al., 2000).

In several experiments carried out separately, many microbial antagonist have been shown to be effective against CMV. *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Bacillus megaterium*, *Agrobacterium chorococcum*, *Frateuria aurantia* have shown effective result in inducing resistance in different crops like cucumber, pepper and tomato. The result was observed as a significant reduction in disease severity and disease incidence. The analysis of the treated plants also showed high free salicylic acid and peroxide activity contents (Shami et al., 2017; Lee and Ryu, 2016; El-Borollosy et al., 2012).

Similar works have also been demonstrated in tobacco and

Table 1: Effective biotic inducers of SAR used in protection of crop plants against viruses

Sl. No.	Plant Virus	Biotic Inducers	Source
1.	CMV (Cucumber mosaic virus)	*Bacillus subtilis*	El-Borollosy et al., 2012
2.	CMV (Cucumber mosaic virus)	*Pseudomonas fluorescens*	El-Borollosy et al., 2012
3.	CMV (Cucumber mosaic virus)	*Azotobacter chroococcum*	El-Borollosy et al., 2012
4.	CMV (Cucumber mosaic virus)	*Bacillus amyloliquefaciens*	Lee and Ryu, 2016
5.	CMV (Cucumber mosaic virus)	*Azotobacter chroococcum*	Shami et al., 2017
6.	CMV (Cucumber mosaic virus)	*Bacillus megaterium*	Shami et al., 2017
7.	CMV (Cucumber mosaic virus)	*Frateuria aurantia*	Shami et al., 2017
8.	ToMV (Tobacco mottle virus)	*Bacillus amyloliquefaciens*	Murphy et al., 2000
9.	ToMV (Tobacco mottle virus)	*Bacillus subtilis*	Murphy et al., 2000
10.	ToMV (Tobacco mottle virus)	*Bacillus pumilus*	Murphy et al., 2000
11.	TMV(Tobacco mosaic virus)	*Bacillus subtilis*	Wang et al., 2009
12.	TMV(Tobacco mosaic virus)	*Bacillus amyloliquefaciens*	Wang et al., 2009
13.	CLCuV (Chilli leaf curl virus)	*Pseudomonas aeruginosa*	Ramzan et al., 2015
14.	CLCuV (Chilli leaf curl virus)	*Bacillus spp*	Ramzan et al., 2015
15.	Broad bean wilt virus and Pepper mottle virus	*Bacillus amyloliquefaciens strain 5B6*	Lee and Ryu, 2016

indicator plants like *Chenopodium* and *Arabidopsis thaliana.* Tobacco treated with two different strains each of *Bacillus subtilis* and *B. amyloliquefaciens* showed a fair level of resistance induced against TMV. The results demonstrated that the treatments enhanced the plant height and fresh weight, and also lowered the disease severity rating of the tobacco mosaic virus (TMV). RT-PCR analysis indicated an increase in the activity of regulatory genes and defense genes (Wang et al., 2009). In separate studies, *Trichoderma asperellum* induced resistance in *Arabidopsis thaliana* and *Streptomyces* spp. induced resistance in *Chenopodium* against CMV (Elsharkawy et al., 2013). Results have also been obtained in fibre crops like cotton. Treatment of cotton plants with *Pseudomonas aeruginosa* and *Bacillus* spp isolated from rhizosphere and phyllosphere of the cotton plants showed reduction of CLCuV virus (Ramzan et al., 2015).

According to Kessmann et al. (1994), three criteria need to be fulfilled before a chemical agent can be classified as an “activator” of the SAR response: 1) the treated plants are resistant to the same number and type of diseases as those plants in which SAR has been biologically induced, 2) the chemical used has no direct antimicrobial activity or can be converted by the tree into antimicrobial metabolites, and 3) the same pre-infectional biochemical processes are induced as recorded in plant tissues after biological induction of SAR.

SA is an endogenous signal for the activation of SAR; therefore there has been an increase in characterization of synthetic chemicals that can mimic SA in terms of SAR induction (Table 2). The first such chemical to be characterized was 2,6-dichloroisonicotinic acid and its methyl ester. Thereafter benzo (1,2,3) thiadiazole (BTH) has been widely used for inducing a similar signaling mechanism like SA (Kessmann et al., 1994; Gorlach et al., 1996). A study on tobacco showed that application of 2,6-Dichloroisonicotinic acid (INA) has similar effect as an exogenous application of SA, both bind and inhibit tobacco catalase correlates their biological activity to induce PR-1 gene expression and enhance resistance to tobacco mosaic virus (Conrath et al., 1995). In another study, resistance was induced in pepper plants against PepGMV infection. Pepper plants treated with BTH were characterized for resistance depending on symptom appearance, virus accumulation and viral movement (Trejo-Saavedra et al., 2013).

Table 2: Chemical inducers of SAR used in protection of crop plants against viruses

Sl. No.	Plant virus	Chemical inducers	Source
1.	PepGMV (Pepper green mottle virus)	Benzothiadiazole (BTH)	Trejo-Saavedra et al., 2013
2.	Cucumber mosaic virus (CMV)	Benzothiadiazole (BTH)	Lee and Ryu, 2016
3.	TMV(Tobacco mosaic virus)	Salicylic acid	Van Loon and Antoniw, 1982
4.	TMV(Tobacco mosaic virus)	Acetylsalicylic acid (aspirin	White, 1979
5.	TMV(Tobacco mosaic virus)	2,6-Dichloroisonicotinic acid (INA) and salicylic acid (SA)	Conrath et al., 1995

3. Mechanisms of Biological Control of Viruses

Among the different plant diseases, viral diseases cause serious problems once they occur in the field because virus control methods tend to mostly targeted its vectors and not to the pathogen directly. Most common control measures include monitoring and chemical control of the vector causing the viral disease (Perring et al., 1999; Mandadi and Scholthof, 2013). The methods of viral resistance breeding and transformation based genetic engineering are also used for control of viral diseases, but, the use of these techniques are limited due their time constrains involved (Agrios, 2005).

The microbial antagonist control various disease causing pathogens by different mechanism like hyperparasitism, hypoparasitism, antibiosis, metabolite production, competition etc (Heydari and Pessarakli, 2010). However, the biological control of viruses mainly involves the mechanism of induction of resistance. In response to different stimuli, resistance may be induced in plants via the increase in certain biochemical activities. Induced host defenses may be local or systematic depending on the simulation agents (Kloepper et al., 1980; Leeman et al., 1995; Moyne et al., 2001).

Induced resistance responses in plants can be subdivided into two categories, systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR is mediated via salicylic acid pathway and involves local and systemic increase of salicylic acid levels, along with expression of pathogenesis-related genes (Malamy et al., 1990; Ryals et al., 1996). ISR, on the other hand, is independent of salicylic acid or pathogenesis related proteins and depends on pathways regulated by jasmonic acid and/or ethylene (Knoester et al., 1999; Pieterse et al., 1996; Yan et al., 2002). These inducible defense mechanisms have been shown to be effective in many plant species against different viruses (Murphy, 2006). In 1960-61, the inducible plant resistance against viruses by a localized virus or weak virulent strain of virus introduced prior to infestation by the virulent virus was observed (Ross, 1961; Yarwood, 1960). Later in 1990s, a group of root associated plant growth promoting rhizobacteria was found to elicit plant defense mechanism (Maurhofer et al., 1994). Thereafter, the works done by various researchers across the globe has shown the efficacy of various microbial antagonist especially PGPR in inducing systemic resistance against viruses in different crop plants. Similar effective results are obtained on exogenous application of salicylic acid, jasmonic acid, benzothiadiazole (BTH) and their derivatives (Singh et al., 2004; Heil and Baldwin, 2002).

4. Methods of Application of biotic and chemical SAR Activators

Application time, site and method hold importance in order to receive successful biological control. The same holds true for control of viruses using microbial agents (Baker, 1987). Intensive knowledge in aspects as to when and where biological control of plant pathogens can be profitable is the basis of forming an efficient integrated pest management system. For formulating one such disease management program in an cropping system involves cultural practices that can promote crop health (Cook, 1993) viz., crop rotations, proper use of tillage, proper preparation of seed beds, management of soil fertility etc.

The next line of defense is the use of quality crop germplasm i.e. those showing traits of resistance or tolerance (Cook, 1993). After considering the above factors, growers can further focus on biological and/or chemical inputs to regulate the diseases. The following points highlights the different methods of application of microbial antagonists and SAR activators based on the articles under this review:

4.1. Seed treatment

This method involves treating seeds of the crop in a solution of the microbial antagonist that is being used prior to sowing of the seeds. It is to be noted that the antagonist in use may be a commercial formulation or culture filtrate obtained from cultures grown in suitable media. For commercial formulations, the standard dosage is to be followed (Raupach et al., 1996; Murphy et al., 2000; Wang et al., 2009; Shami et al., 2017).

4.2. Soil application

Microbial antagonist can also be applied as soil amendment prior to planting of the crops plants. The soil should be properly sterilized prior to application of the antagonist so that there is no competition from the secondary soil microbes present. The soil application can be redone every 10-15 days after transplantation of the crop to ensure that adequate population of the antagonist is maintained (Raupach et al., 1996; Wang et al., 2009).

4.3. Spray application

This is the most common method of application. Spray solutions of adequate strengths are prepared and sprayed on above ground portion of the crop. Similar to soil application, the crops should be sprayed at an interval of 10-15 days. This method has shown efficient results in many studies (El-Borollosy et al., 2012; Lee and Ryu, 2016; Ramzan et al., 2015).

4.4. Application with irrigation water

Microbial antagonist can also be applied via incorporation with irrigation water. This method has been found to be effective in greenhouse condition especially in potted crops. The irrigation is to be repeated every 3-4 days for about a period of 15 days (El-Borollosy et al., 2012; Shami et al., 2017). Many studies also indicate effective results on combined use of two or more of the above methods.

4.5. Application of chemical SAR activators

Most studies showing efficient activity of chemical SAR activators follow spray application of the chemicals. The spraying of solution ranging in concentrations of 0.5 mM to 1 mM has shown positive results (Kessmann et al., 1994; Gorlach et al., 1996; Conrath et al., 1995; Trejo-Saavedra et al., 2013).

5. Future Outlook

Ultimately, the main objective of research on plant virus management consists of implementation of efficient antiviral resistances and antiviral immune mechanisms in crop plants. Ever since there has been manifold development in the subject and it is now supported by researches being carried out and published in many different scientific journals. At present, there is an intensive knowledge bank regarding various organisms with potential to act as biocontrol agents, mechanism of biocontrol in different crops and against different pests. Some of the research criteria that will advance our understanding of biological control of plant viruses and the conditions under which it can be applied, can be the study of the ecology of antagonistic microbes, study of new strains of microbes that originates in the rhizosphere and phyllosphere of the particular crops, targeting the different genes that are activated in different plant species as a response to various SAR activators, exploring the potential of possible new SAR chemicals etc.

6. Summary

The growing awareness of the adverse effects of chemical pesticides on environment and human health has made it unavoidable to search for alternative methods of control of viral diseases. Biological control, therefore, stands as a promising alternative. Although,tremendous research is being carried out in the aspect, the number of methodologies developed is more in controlling fungal and bacterial diseases. However, at grassroot level, biological control of viral diseases is still mostly focused on control of vectors using entomopathogenic agents. With development of SAR mechanisms, research is being directed to the exploitation of this mechanism to control viral disease and many fruitful results have been achieved. The future success of the biological control industry depends on innovative business management, product marketing, extension education and research (Joshi and Gardener, 2006). Along with directing research towards the study of newer antagonist that can control viruses, the studied antagonists should be tried in field conditions and should directed towards commercialization of these organisms.

7. Conclusion

Although tremendous research is being carried out in biological management aspect, the number of methodologies developed is more in controlling fungal and bacterial diseases. However, at grass root level, biological control of viral diseases is still mostly focused on control of vectors using entomopathogenic agents. With development of SAR mechanisms, research is being directed to the exploitation of this mechanism to control viral disease and many fruitful results have been achieved.

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