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Biocidal Mechanisms in Biological Control of Fusarium Wilt in Chickpea (*Cicer arietinum* L.) by Antagonistic Rhizobacteria: A Current Perspective in Soil Borne Fungal Pest Management

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A B S T R A C T

Fusarium wilt caused by *Fusarium oxysporum* f. sp. *ciceris*, one of the most important fungal pathogen of chickpea (*Cicer arietinum* L.), is a constant threat to this crop worldwide. It causes yield losses up to 100 % depending upon the varietal susceptibility, growth stage and climatic conditions. Strategies have been employed for controlling this pathogen such as use of cultural practices, resistant cultivars, fungicides etc., but have proven less effective and even the use of chemicals have hazardous effects, and also lead to the development of fungicide resistance in pathogens. As an environmentally sound alternative, biological control is an attractive method against such soil borne diseases. Several rhizospheric bacteria have the ability to control diseases and promote the plant growth under laboratory and field conditions. Among these, species of *Pseudomonas* and *Bacillus* are the most extensively studied for the biocontrol of a variety of root associated phytopathogens. The mechanisms mainly include synthesis and release of some metabolites such as antibiotics, lytic enzymes, siderophores, hydrogen cyanide (HCN) and other diffusible and volatile antifungal compounds. All these metabolites exert inhibitory effect on a range of phytopathogens present in close vicinity of the plant roots. Moreover they provide competitive nature to these rhizobacteria for survival and function under prevalence of such soil borne fungal pathogens. Additionally, the use of antagonistic plant growth promoting rhizobacteria increase the symbiotic efficacy of indigenous *Mesorhizobium ciceris* present in the soil and also help in inducing the plant's own defense mechanism against several phytopathogens. Thus use of biocontrol measures using bacterial antagonists, due to their perceived level of safety; reduced environmental impact and easy delivery improve the growth and hence yield.

Introduction

Chickpea is one of the most important grain legume crops in the world, and contributes about 48% of the total pulse production in India (Anonymous, 2015). Due to its high nutritive value (25-29% protein, 4-10% fat, 52-71% carbohydrate, and 10-23% fiber,

minerals and vitamins) chickpea occupy an important position in the largely vegetarian population of the country (Jukanti *et al.,* 2012; Ali and Kumar, 2006).

Amongst pulse crops, chickpea has maintained a significant status ranking second in the area and 3rd in the production (14.6%) (Hussain *et al.,* 2015). This pulse crop significantly imparts the management of soil fertility primarily due to its ability to fix atmospheric nitrogen in association with the bacterial symbiont *Mesorhizobium ciceri* (Maiti, 2001; Kantar *et al.,* 2007). Rhizobia offer the great advantage of symbiotic nitrogen fixation by symbiotic association with such leguminous crops (Arafoui *et al.,* 2006).

Fusarium wilt and its casual organism

Chickpea is usually attacked by wilt caused by *Fusarium oxysporum* f. sp. *ciceris*, worldwide and is one of the consistent threats to this crop (Moradi *et al.,* 2012). Fusarium wilt is prevalent in almost all chickpea-growing areas of the world, and resulted loss varies from 14% to 32% in the different states of India (Dubey *et al.,* 201; Kumari and Khanna, 2014). Even this plant disease causes yield losses up to 100% under favorable conditions in chickpea (Anjaiah *et al.,* 2003, Pande *et al.,* 2010, Landa *et al.,* 2004). In Pakistan it is reported that this disease incidence causes 10 to 50 % loss every year (Khan *et al.,* 2002).

Symptoms of fusarium wilt mainly include yellowing and stunting of the leaves followed by plant death in less or more susceptible chickpea cultivars and can develop at any stage of plant growth, and affected plants may be grouped in patches or appear spread throughout a field (Arafoui *et al.,* 2006, Jiménez-Díaz *et al.,* 2015). Severe wilt symptoms in chickpea plants mostly start to appear 25-30 days after sowing (Kumari *et al.,* 2016). Use of pathogen free planting material, avoiding sowing into high risk soils and choice of cropping are some cultural practices to control the wilt incidence in chickpea crop (Jendoubi *et al.,* 2016). Whereas the most efficient and reliable method of disease control and maximizing crop productivity worldwide to date has been the use of fungicides or resistant cultivars as part of an integrated management approach.

However, the high pathogenic variability and development of resistance in different populations of *F. oxysporum* presents problems for sustainability of resistant cultivars, a major constraint in developing resistant cultivars (Bayraktar and Dolar, 2012). The superiority of chemicals over biocontrol agents in terms of effective and quick disease control is well known however, the ill effects of chemicals on human health and environment are major limitations to application of chemical pesticides in the long run (Sharma, 2011). Moreover the use of agrochemical inputs causes several negative effects such as the development of pesticide resistance to applied agents and also has non-targeted environmental impacts (Gerhardson, 2002).

Demand of an alternate to Chemical pesticides (Fungicides)

Burgeoning of fungicide tolerance in pathogen strains and non-availability of fungicides along with appropriate application technologies to resource indigent farmers further reinforce the need for alternate strategies. Moreover, use of fungicides is expensive and results in accumulation of toxic compounds which adversely affects the soil biota (Jimnenez-Gasco *et al.,* 2004). Thus, rising public concern about harmful environmental effects of agrochemicals constituted the need for greater sustainability in agriculture with alternate disease control strategies.

Plant disease suppression by soil microorganisms is a possibly effective alternative means of reducing the chemical input in agriculture (Compant *et al.,* 2005). Biocontrol of plant pathogenic microorganisms relies on different antagonistic traits including competition for colonization site or nutrients, production of volatile/diffusible antibiotics, enzymes and induction of systemic resistance (ISR) against the pathogens (Raaijmakers *et al.,* 2009; Kumari and Khanna, 2016).

The strategy for control of fungal diseases of plants by the use of potential antagonistic microorganisms has been the focus of intense research throughout world. This approach is popularly known as biological control of phytopathogens and has been demonstrated to be successful in a number of host pathogen systems.

Biological Control

Biological control is an eco-friendly and potentially emerged alternative to chemical control. Soil-borne diseases have been controlled more recently by means of certain beneficial antagonistic bacteria that are indigenous to the rhizosphere of most of the plants (Compant *et al.,* 2005; Reino *et al.,* 2008).

The plant rhizosphere is a remarkable ecological environment as a myriad of microorganisms colonizes in, on and around the roots of growing plants. Distinct communities of beneficial soil microorganisms are associated with the root system of all higher plants (Khalid *et al.,* 2009). These plant growths promoting rhizobacteria (PGPR) can be useful in enhancing the growth and reducing the disease severity in several agricultural crops when applied on to seed or soil (Arafoui *et al.,* 2006; Kumari and Khanna, 2014).

Plant Growth Promoting Rhizobacteria (PGPR)

Plant growth promoting rhizobacteria (PGPR) are a group of bacteria that can be found in the rhizosphere (area under the influence of the roots), rhizoplane (at or along the root surface), in symbiotic (inside the roots) or in close association with roots. A large array of bacteria including species of *Pseudomonas, Azospirillum, Azotobacter, Bacillus, Beijerinckia, Burkhoderia, Klebsiella* and *Serratia* have shown plant growth promoting properties (Govindarajan *et al.,* 2006; Govindarajan *et al.,* 2007; Gyaneshwer *et al.,* 2001). The application of PGPR in agricultural crops, offers an attractive alternative to chemical fertilizers, pesticides, and other supplements (Ashrafuzzaman *et al.,* 2009).

These PGPR strains facilitate growth of plants either directly or indirectly. The direct mechanism of plant growth stimulation involves the production of substances by bacteria and its transport to the developing plants or facilitates the uptake of nutrients from the recipient environment. The direct growth promoting mechanisms of PGPR includes (i) Biological N_2 fixation (Wani *et al.,* 2007) (ii) solubilization of insoluble phosphorus form soil minerals (Khan *et al.,* 2009) (iii) sequestering of iron by production of siderophores as chelating agents (Rajkumar *et al.,* 2006) (iv) production of phytohormones such as auxins, cytokinins, gibberellins and (v) lowering of ethylene concentration to reduce the biotic and abiotic stress (Liu *et al.,* 2007). Indirect stimulation includes the antagonistic potential to reduce the deleterious effects of plant pathogens on crop yield such as suppression of phytopathogens by producing siderophores that chelate iron making it unavailable to pathogen (Pidello, 2003), antibiotics such as Phenazine-1-carboxylic acid (PCA), Di-acety

phloroglucinol (DAPG), Pyaocyanin etc (Chin-A-Woeng *et al.,* 2003). Furthermore indirect mechanism also include the enhancement in the activity of phenolic compounds and pathogenesis related (PR) proteins in plants such as peroxidase (PO), polyphenol oxidase (PPO) that catalyse the formation of lignin, phenylalanine ammonia-lyase (PAL) that involved in formation of phytoalexins and other phenolic compounds by these rhizobacteria. Other enzymes include defense-related proteins such as β-1,3-glucanases and chitinases which degrade the fungal cell wall and cause lysis of fungal cell (Chin-A-Woeng *et al.,* 2003), hydrogen cyanide (HCN), ammonia etc. (Hu *et al.,* 2005; Liu *et al.,* 2006; Glick *et al.,* 2007). Some *Pseudomonas* sp. especially fluorescent pseudomonads have been reported to be used as efficient agricultural biocontrol agents as they can produce large amount of secondary metabolites to protect plants from phytopathogens and stimulate plant growth (Arafoui *et al.,* 2006).Thus, they are being exploited as potential biological control agents to decrease the use of chemical pesticides in agriculture.

General antiphytopathogenic mechanisms of plant growth promoting rhizobateria

Biological control of soil borne pathogens with antagonistic microorganisms has been extensively investigated. Among them, *Pseudomonas* and *Bacillus* sp. are known to increase plant growth due to production of diverse microbial metabolites like siderophore, indole acetic acid, phosphate-solubilization, hydrogen cyanide, ammonia production etc. A few strains of fluorescent *Pseudomonas* are also known to produce antifungal compounds that elicit induced systemic resistance in the host plant or interfere specifically with fungal pathogeniciy factors (Hass and Defago, 2005). Various mechanisms for antagonism have been implicated like cell wall degrading enzymes (pectolytic enzymes, cellulases, xylanases and glycosidic hydrolases), plant hormones (indole acetic acid, ethylene and cytokinin), siderophore which can chelate iron and other metals and contribute to disease suppression by conferring a competitive advantage to the biocontrol agent for the limited supply of essential trace minerals in natural habitats (Deshwal *et al.,* 2003). Microbial siderophore may also stimulate plant growth directly by competitively inhibiting iron uptake system by fungal pathogen (Kravchenko *et al.,* 2002).

Indole acetic acid (IAA), being a plant growth promoting hormone directly promotes the root growth by stimulating plant cell elongation or cell division and indirectly by influencing bacterial 1-aminocyclopropane-1- carboxylic acid (ACC) deaminase activity. ACC is the direct precursor of ethylene an inhibitor of root growth (Siddiqui and Shakeel, 2009). Arafoui *et al.,* (2006) reported effective biocontrol of fusarium wilt of chickpea by using antagonistic *Rhizobium* isolates *in vitro* in dual culture and *in vivo* in field condition. Biocontrol activity and plant growth promotion of bacterial strains was evaluated under greenhouse conditions, in which *P. aeuroginosa* (P10 and P12), *B. subtilis* (B1, B6, B28 and B99) and *P. aeuroginosa* (P12 and B28) provided better control than untreated control in seed treatment and soil-inoculation (Karimi *et al.,* 2012).

Additionally PGPR are also involved in increased uptake of nitrogen, solubilization of minerals such as phosphorus, zinc, potassium etc. (Siddiqui *et al.,* 2009). Application of *Bacillus, Pseudomonas* and *Rhizobium* spp. have been reported to improve the growth of *Fuasrium oxysporum* infected plants by competing with the pathogen and the production of essential nutrients, enzymes, antibiotics and other organic acids to solubilise various soil minerals (Akhtar *et al.,*

2012; Landa *et al.*, 2004). Plant growth promoting rhizobacteria, competitively colonize plant roots and stimulate plant growth and decrease the incident of plant diseases by some indirect mechanisms also. The PGPR mediate biological control indirectly by eliciting induced systemic resistance against a number of plant diseases (Jetiyanon and Kloepper 2002). Implementation of some PGPR strains through seed or seedling bacterization has been effectively found to lead to a state of induced systemic resistance in the treated plants (Kloepper *et al.,* 2004).

Induced resistance is the enhancement of plants' defensive capacity against a broad spectrum of pathogens and pests that is acquired after appropriate stimulation.

The resulting elevated resistance due to an inducing agent is called induced systemic resistance (ISR) or systemic acquired resistance (SAR). Both are different in a way that Induced systemic resistance (ISR) is induced by non-pathogenic rhizobacteria, mediated by a Jasmonic acid (JA) or ethylene-sensitive pathway, whereas systemic acquired resistance (SAR) is induced systemically after inoculation with necrotizing pathogens or application of some chemicals and is mediated by a salicylic acid (SA) dependent process (Zhang *et al.,* 2010). Both SAR and ISR are the activation of latent resistant mechanisms of host plants that are expressed upon subsequent or challenge inoculation with a pathogen mainly (Vallad and Goodman, 2004). The PGPR cause plant cell wall modifications and physiological changes that lead to the synthesis of compounds involved in plant defense mechanisms (Conarth *et al.,* 2001). Carbohydrate polymers, lipids, glycoproteins, lipopolysaccharides, siderophores and salicylic acid secreated or derived from the cell wall of PGPR are major elicitors that mediate induced systemic resistance (Antoun and Prevost, 2005). Most important bacteria studied and exploited as biocontrol agent includes the species of fluorescent *Pseudomonas* and *Bacillus.* Leguminous roots are colonized by numerous rhizospheric microorganisms and these enhance legume nitrogen fixation due to a synergism with rhizobia, thus co-inoculation of rhizobia with plant growth PGPR, is a way to improve nitrogen availability in sustainable agriculture production systems (Rajendran *et al.,* 2012). Stimulation of nodulation and plant growth has also been reported for chickpea using *Pseudomonas* strains that are antagonistic to fungal pathogens (*Aspergillus* sp., *Fusarium oxysporum, Pythium aphanidrematum* and *Rhizoctonia solani*) as co-inoculant with *Mesorhizobium* and this also enhanced nodulation by 68%, compared to *Mesorhizobium* alone (Goel *et al.,* 2002).

Thus, identification of potential bacterial antagonists of *Fusarium oxysporum* and *Rhizoctonia solani* help to reduce the pathogenic effects and chemical inputs and such organisms can also increase the symbiotic effectiveness of *Rhizobium.* Bacterial antagonists isolated from the chickpea rhizosphere are also known to enhance grain yield due to their plant growth promoting potential (Whipps, 2001).

Antagonistic functionality traits of rhizobacteria

Siderophore production

Iron is the fourth most abundant element on earth (Ma 2005), however, in aerobic soils, iron is mostly precipitated as hydroxides, oxyhydroxides, and oxides so that the amount of iron available for assimilation by living organisms is very low, ranging from 10^{-7} to 10^{-23} M at pH 3.5 and 8.5 respectively. Microorganisms have evolved specialized mechanisms for the assimilations of iron,

including production of iron chelating compounds, known as siderophores. Siderophores are low molecular weight (500-1000 Da), high affinity ferric ion chelators, synthesized and secreted by many microorganisms in iron deprivation for acquisition of iron from insoluble forms by mineralization and sequestration (Sarode *et al.,* 2009). The role of siderophores in plant growth promotion and biological control is well established (Hass and Defago, 2005).

Siderophores produced by rhizosphere inhabitants has been studied well and it has been reported that ability to produce siderophores not only improve rhizosphere colonization of producer strain but also play an important role in iron nutrition of plant (Vansuyt *et al.,* 2007) and antagonism against phytopathogens (Chincholkar *et al.,* 2007). Role of siderophores in induced systemic resistance (ISR) in plants is also well appreciated (Zhang *et al.,* 2010). Improvement in plant iron nutrition by soil bacteria is even more important when the plant is exposed to an environmental stress such as heavy metal pollution (Nair *et al.,* 2007).

The iron sequestering siderophores produced by antagonistic PGPR have a higher affinity for iron than produced by fungal pathogens, allowing the microbes to scavenge most of the available iron and thereby reduce its availability for the growth of fungal pathogen (Bashan and Bashan, 2005). The presence of siderophore-producing PGPR in rhizosphere increases the rate of Fe^{3+} supply to plants and therefore enhances the plant growth and productivity of crop. Iron-siderophore complex is used by plants to quench the iron thirst and this constitutes the direct plant growth promotion (Sharma and Johri, 2003). Further, this compound after chelating Fe^{3+}makes the soil Fe^{3+} deficient for other soil microbes and consequently inhibits the activity of competitive microbes (Sivaramaiah *et al.,* 2007, Masalha *et al.,* 2000). Siderophores are usually classified by the ligands used to chelate the ferric iron. The major groups of siderophores include the catecholates (phenolates), hydroxamates and carboxylates (Saharan and Nehra, 2011). Some examples of catecholate siderophores are the siderophore enterobactin produced by *Escherichia coli*, bacillibactin produced by *Bacillus subtilis* and *Bacillus anthracis* and vibriobactin produced by *Vibrio cholera*. Some of the examples ofhydroxamate siderophores are the ferrichromes produced by *Ustilago sphaerogena*, desferrioxamine B (Deferoxamine) by *Streptomyces pilosus* and *Streptomyces coelicolor*, desferrioxamine E by *Streptomyces coelicolor* (Prashant *et al.,* 2009)

The ability of *Pseudomonas* to grow and produce siderophores is dependent on the iron content and the type of carbon sources in the medium. Low-iron concentration in soil stimulates the production and secretion of yellow-green fluorescent iron-binding peptide by *Pseudomonas* isolates and the biosynthesis of siderophores have also been reported to be affected by several other environmental parameters (Manwar *et al.,* 2004). Though siderophores are part of primary metabolism (iron is an essential element), on occasions they also behave as antibiotics which are commonly considered to be secondary metabolites (Haas and Defago, 2005). Suryakala *et al.,* (2004) has reported that siderophores exerted maximum impact on *Fusarium oxysporum* than on *Alternaria* sp. and *Colletotrichum capsici*. The role of microbial siderophores in N-fixation has also been implicated. Gill *et al.,* (1991) demonstrated that mutants of *Rhizobium meliloti* that were unable to produce siderophore were able to nodulate the plants but the efficiency of nitrogen fixation was less as compared to the wild type indicating the importance of iron in nitrogen fixation. Another indirect mode of plant growth

promotion is the ability of siderophore to protect from heavy metal toxicity (Glick, 2003).

Such unequivocal importance of iron in plant growth promotion and biological control encourage screening new PGPR for their ability to produce siderophores.

HCN production

Hydrogen cyanide is a broad-spectrum antimicrobial compound involved in biological control of root diseases by plant associated rhizobacteria (Ramette *et al.,* 2003). Some rhizobacteria, including species of *Alcaligenes, Aeromonas, Bacillus, Pseudomonas* and *Rhizobium* (Devi *et al.,* 2007; Ahmad *et al.,* 2006) are capable of producing HCN (Rezzonico *et al.,* 2007) which is a secondary metabolite that suppresses the growth and development of competing microorganisms (Siddiqui, 2006) as it is a powerful inhibitor of many metal enzymes, especially copper containing cytochrome c oxidases (Hassanein *et al.,* 2009). HCN production is a common trait within the group of *Pseudomonas* present in the rhizosphere, with some studies showing that about 50% of pseudomonads isolated from potato and wheat rhizosphere were able to produce HCN *in vitro* (Bakker and Schippers, 1987; Schippers *et al.,* 1990).

Hydrogen cyanide supply to the cell inhibits the electron transport thereby disrupting energy leading to the death of the pathogenic organism. It inhibits proper functioning of enzymes and natural receptors by reversible mechanism of inhibition. Antifungal activity of *Pseudomonas, Bacillus* and *Azotobacter* may be due to the production of HCN and siderophores or synergistic interaction of these two or with other metabolites (Ahmed *et al.,* 2006). HCN from *Pseudomonas* CHAO strain not repressed by fusaric acid played a significant role in disease suppression of *F. oxysporum* f.sp. *radicis-lycopersici* in tomato (Duffy *et al.,* 2003). Ramettee *et al.,* (2003) reported that HCN is abroadspectrm antimicrobial compound involved in biological control of root disease by many plant associated flourescent pseudomonads.

Among the different mechanisms involved in disease suppression, the production of antimicrobial secondary metabolites such as HCN as well as 2,4-diacetylphloroglucinol by fluorescent *Pseudomonad* is reported to be of significance for effective biocontrol (Hass and Defago 2005).Direct inhibition of fungi by HCN is thought to be the main mechanism of action (Blumer and Hass, 2000), where the effect of bacterium would be comparable to the HCN mediated plant defense mechanisms (Luckner, 1990). It has been reported that strains of *Pseudomonas* producing HCN, suppress plant disease, whereas mutant strains unable to synthesize HCN lose their ability to protect plants from phytopathogens (Sacherer *et al.,* 1994). Siddiqui *et al.,* (2006) found the production of HCN by *Pseudomonas fluorescens* strain CHAO as an antagonistic factor contributing to biocontrol of *Meloidogyne javanica,* a root knot nematode *in situ* and suppression of galling in tomato. Some strains of *Pseudomonas* producing HCN and antagonistic to phytopathogens have also been reported to inhibit the growth of infected plant (Kumar *et al.,* 2005).

Antibiosis

Antibiosis plays an active role in the biocontrol of plant disease and often acts in concert with competition and parasitism. Antibiosis has been postulated to play an important role in disease suppression by rhizobacteria (Mallesh, 2008). Ahmadzadeh *et al.,* (2006) reported that the efficient PGPR strains for antibiotic activity were selected by determining the toxicity of metabolites

produced on pathogen by the PGPR. The synthesis of antibiotics is the mechanism that is most commonly associated with the ability of a PGPR to suppress pathogen development (Whipps, 2001).Antibiotics constitute a wide and heterogeneous group of low molecular weight chemical organic compounds that are produced by a wide variety of microorganisms (Raaijmakers *et al.,* 2002). The antibiotics synthesized by PGPR include kanosamine, oligomycin A, 2,4-diacetylphloroglucinol, oomycin, HCN, phenazines, pyoluteorin, and pyrrolnitrin. Although the main target of these antibiotics are the electron transport chain (phenazines, pyrrolnitrin), metalloenzymes such as copper-containing cytochrome oxidases, membrane integrity (biosurfactants), their mode of action are still largely unknown (Haas and Defago, 2005; Raaijmakers *et al.,* 2009).

The production of antibiotics is considered one of the most powerful and studied biocontrol mechanisms for combating phytopathogens. One of the most efficient antibiotics in the control of plant pathogens is 2,4-DAPG and is produced by various strains of *Pseudomonas* (Fernando *et al.,* 2006; Rezzonico *et al.,* 2007).

The most widely studied group of rhizospheric bacteria with respect to the production of antibiotics is that of the fluorescent Pseudomonads, these are known to reduce fungal growth *in vitro* by the production of one or more antifungal antibiotics that may also have *in vivo* activity (Whipps 2001).A strain of *Serratia marcescens* has been reported to produce antibiotics and has proven to be a useful biocontrol agent against *Scleritium rolfsi* and *Fusarium oxysporum* (Someya *et al.,* 2002).

Volatile antifungal compounds

Plant growth promoting rhizobia can support plant growth by nitrogen fixation, secretion of phytohormones, solubilization of minerals or secretion of antibiotics and antifungal metabolites. Apart from these mechanisms it recently became apparent that microorganisms have developed another potential weapon against phytopathogens. They are capable of releasing functional volatile organic compounds (VOCs) (Kai *et al.,* 2007; Vespermann *et al.,* 2007; Kai *et al.,* 2009).

Volatile organic compounds are low molecular weight compounds (below 300 Da), lipophilic and have relatively low boiling points. Such volatiles are ideal infochemicals as they occur in the biosphere over a range of concentrations and can act over long distances (Wheatley, 2002). Thus, these compounds have an important effect on neighboring organisms and the development of the organisms in the ecosystem. VOCs were shown to be biologically useful in numerous cases i.e. allowing pollinators to localize flowers, to attract predators of herbivores (indirect defense) or to defeat pathogens directly or to cause growth inhibition. As a result, these compounds may act inter or intraspecifically (Piechulla and Pott, 2003).

A wealth of VOCs are produced and released in the microbial world. More than 400 volatiles are known to be emitted from different bacteria (Schulz and Dickschat, 2007). Volatile compounds such as alkanes, alkenes, alcohols, aldehydes, ammonia, esters, ketones, sulfides, and terpenoids known to be produced by a number of rhizobacteria are reported to play an important role in biocontrol (El-Katatany *et al.,* 2003).The biological significance of these microbial volatiles has been investigated. Volatiles of different soil bacteria influence the growth of various fungi (Chuankun *et al.,* 2004; Fernando *et al.,* 2005). Rhizobacterial isolates comprising *Serratia plymuthica, Serratia odorifera, Pseudomonas fluorescens, and Pseudomonas trivialis* synthesize and emit complex blends of volatiles that inhibit growth

of manyphytopathogenic and non phytopathogenic fungi (Kai *et al.,* 2007; Vespermann *et al.,* 2007). Volatile compounds such as ammonia and HCN produced by a number of rhizobacteria were reported to play an important role in biocontrol. Tripathi and Johri (2002) reported that volatiles released by fluorescent *Pseudomonads* had significant antagonistic influence on growth of *C. dematium* and *S. rolfsii.* Furthermore, bacterial volatiles also have an impact on protozoa, metazoa such as nematodes, and *Aedes aegypti* (Kai *et al.,* 2009).

Volatiles also play an important role in the inhibition of sclerotial activity, limiting ascospore production and reducing disease levels. In studies conducted by Hassanein *et al.,* (2009) some toxic volatile metabolites produced by *Pseudomonas aeruginosa* reduced the growth of both *Fusarium oxysporum* and *Helminthosporium* sp. In another report bacteria isolated from soybean plants produced antifungal organic volatile compounds, these compounds inhibited sclerotia and ascospore germination and mycelia growth of *Sclerotinia sclerotium in vitro* and in soil tests (Fernando *et al.,* 2005). *Bacillus* species exhibiting antifungal potential have a wide range of antimicrobial activities that inhibit mycelia growth of *Fusarium oxysporum* with the highest effect in reducing fusarium wilt of onion (Wahyudi *et al.,* 2011). This compound has the ability of degrading cell walls of soil-borne fungal pathogen (El-Tarabily *et al.,* 2000). Bapat and Shah (2000) reported that *Bacillus brevis* which produced an extracellular antagonistic metabolite inhibited germination of conidia and was fungicidal to the vegetative mycelia of *Fusarium oxysporum* sp.*udum.* Yiu-K-wok *et al.,* (2003) emphasized that *Bacillus subtilis* filtrate was active at different dilutions against macroconidium germination and hyphal growth of *Fusarium graminearum* depending on the initial macroconidium density. Interest is focused on the qualitative and quantitative composition as well as on the timing of volatile emissions.

Diffusible antifungal compounds

Endophytic microorganisms have attracted the attention of researchers because of their potential to serve as biocontrol agents as they are able to produce a number of secondary metabolites to inhibit pathogens (Ryan *et al.,* 2008). Antibiotics produced by PGPR include phenazine, pyoluteorin, pyrrolnitrin and cyclic lipopeptides all of which are diffusible (Haas and Defago, 2005). Certain PGPR degrade fusaric acid produced by *Fusarium* sp. causative agent of wilt and thus prevents the pathogenesis. Some PGPR can also produce enzymes that can lyse cells and are diffusible. *Pseudomonas stutzeri* produces extracellular chitinase and laminarinase which could lyse the mycelia of *Fusarium solani* (Isnansetyo *et al.,* 2003).

Phenazine is a potent green pigmented antimicrobial metabolite implicated in antagonism (Tjeerdvan *et al.,* 2004). It is nitrogen containing low molecular weight antimicrobial compound consisting of brightly coloured pigment produced by the bacterial genera pertaining to *Pseudomonas, Burkholderia, Brevibacterium* and *Streptmyces* (Fernando *et al.,* 2005). The ability to produce phenazines is limited almost exclusively to bacteria and has been reported in members of the genera *Pseudomonas, Streptomyces, Nocardia, Sorangium, Brevibacterium* and *Burkholderia* (Mavrodi *et al.,* 2006).

Flourescent *Pseudomonas* and *Bacillus* species play an active role in suppression of pathogenic microorganisms by the secretion of extracellular metabolites that are inhibitory at low concentration such as phenazine derivatives. *Pseudomonas fluorescens*

producing DAPG have been recovered from soil and rhizosphere samples of many crop species as well as from marine environments (Fuente *et al.,* 2004; Isnansetyo *et al.,* 2003). In addition to their antifungal activity, such bacteria have been found to possess some antiviral properties and also inhibit the growth of soft-rotting bacteria and cyst nematodes of potato (Cronin *et al.,* 1997) due to presence of DAPG. Xiang-Tian Yin *et al.,* (2011) isolated *B. amyloliquefaciens* strain PEBA20 from poplar and reported its potential against poplar canker caused by *B. dodhidea*. Sharma and Parihar (2010) reported in their investigations, the ability of extracellular antifungal metabolites of *Actinomycetes* against *Rhizopus stolonifer, Aspergillus flavus, F.oxysporum* and *Alternaria* sp. Even under these low concentrations circumstances if the antibiotic producers are able to control plant diseases it may be due to the involvement of systemic resistance mediated by the antibiotics at very low concentration or due to the interaction of antibiosis with other extra cellular metabolites that may trigger ISR. According to a study by Küçük and Kivanç (2003), avoiding direct contact with an antagonist has given the pathogen an opportunity for greater development. However it has also shown that *T. harzianum* expresses reducing effect over both volatile and diffusible metabolites and have more reducing effect than volatiles ones (Ryan *et al.,* 2008).

Induction of Pathogenesis related (PR) proteins

The utilization of a plant's own defense mechanism is the subject of current interest in the management of pests and diseases. Induction of plant defense genes by prior application of inducing agents is called induced resistance (Saravanakumar *et al.,* 2007).The defense gene products include peroxidase (PO), polyphenol oxidase (PPO) that catalyze the formation of lignin and phenylalanine ammonia-lyase (PAL) that is involved in phytoalexin and phenolics biosynthesis. Other defense enzymes include PR proteins such as *β*-1,3-glucanases and chitinases which degrade the fungal cell wall. Chitin and glucanoligomers released during degradation of fungal cell wall act as elicitors of various defense mechanisms in the plants (Sateesh *et al.,* 2004).Induction of defense enzymes makes the plant resistant to pathogen invasion. Excellent inducers include pathogens, non-pathogenic PGPR, chemicals and plant products (Ramamoorthy *et al.,* 2002). The induced protection by selected strains of non-pathogenic, root–colonizing PGPR has been shown to be capable of inducing disease resistance in addition to promoting plant growth.

Plant growth promoting rhizobacteria, especially *Pseudomonas fluorescens* and *Bacillus subtilis*, are promising candidates of biological control. In a study, *P. fluorescens* (Pf1 and Py15) and *B. subtilis* (Bs16) strains have been developed commercially as a talc-based formulation and tested against several crop diseases (Vivekananthan *et al.,* 2004, Kavino *et al.,* 2007; Thilagavathi *et al.,* 2007). Investigations on mechanisms of disease suppression by plant products and PGPR reveal that these may either act on the pathogen directly (Amadioha, 2000), or induce systemic resistance in host plants resulting in reduction of disease development (Ramamoorthy *et al.,* 2002).

Systemic resistance (ISR) induced by *Bacillus* and *Pseudomonas* sp. activate multiple defense mechanisms that include increased activity of pathogenesis related (PR) proteins like chitinase, β-1,3-glucanase and peroxidase (PO), and also the accumulation of low molecular weight substances called phytoalexins (Vivekananthan *et al.,* 2004). Chitinases and β-1,3-glucanases are a structurally and functionally diverse group of

hydrolytic enzymes involved in defense reactions of plants against pathogens (Rajendran *et al.,* 2007).

As far as chickpea is concerned, different investigations have shown that induced resistance, through the accumulation of various phenolic compounds and phytoalexins, synthesis of pathogenesis-related proteins as well as the activation of different enzymes such as chitinases, ß-1,3-glucanases, peroxidases, polyphenol oxidases and key enzymes in phenylpropanoid and isoflavonoid pathways, may play a crucial role in the biological control of chickpea diseases by antagonistic microorganisms (Arafaoui *et al.,* 2006).

With increasing awareness about the adverse effects of chemical fertilizers and pesticides, it is very important to explore various mechanisms by which plant growth promoting microorganisms can control the phytopathogenic effects in the crop plants. Plant growth promoting rhizobacteria can be used as an effective biofungicide on the condition of their effectiveness under field conditions, against such soil borne fungal phytopathogens. Further investigations need to focus on enhancing the self defence mechanism of plants by these antagonistic rhizobacteria and to evaluate the synergistic potential of antagonists to formulate various combinations of these so as to have better results against such soil borne phytopathogens.

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