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REVIEW ARTICLE **Open Access**

Trichoderma: a beneficial antifungal agent and insights into its mechanism of biocontrol potential

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Abstract

Background: Agriculture is an indispensable part of any country to feed the millions of people but it is under constant threat of pests. To protect the crops from this huge yield loss recently, chemical pesticides are used. Though chemical pesticides have shown effective results in killing the crop pests, it causes negative impact on the environment as well as humans. So to find an eco-friendly alternative, biological control methods are being used.

Main body: Biological control is a great renaissance of interest and research in microbiological balance to control soil-borne plant pathogens and leads to the development of a better farming system. In biological control, genus *Trichoderma* serves as one of the best bioagents, which is found to be effective against a wide range of soil and foliar pathogens. Genus *Trichoderma* is a soil inhabiting green filamentous fungus, which belongs to the division Ascomycota. The efficacy of *Trichoderma* depends on many abiotic parameters such as soil pH, water retention, temperature and presence of heavy metals. The biocontrol potential of *Trichoderma* spp. is due to their complex interaction with plant pathogens either by parasitizing them, secreting antibiotics or by competing for space and nutrients. During mycoparasitic interactions, production of hydrolytic enzymes such as glucanase, chitinase and protease and also signalling pathways are initiated by *Trichoderma* spp. and the important ones are Heterotrimeric G protein, MAP kinase and cAMP pathway. G protein and MAPK are mainly involved in secretion of antifungal metabolites and the formation of infection structures. cAMP pathway helps in the condition and coiling of *Trichoderma* mycelium on pathogenic fungi and inhibits their proliferation.

Short conclusion: *Trichoderma* being an efficient biocontrol agent, their characteristics and mechanisms should be well understood to apply them in field conditions to restrict the proliferation of phytopathogens.

Keywords: *Trichoderma* spp., Plant pathogens, Biocontrol, Mode of action, Signalling pathway

Background

Plant diseases caused by fungi and bacteria result in severe losses to agriculturally important crops. Plant disease control by chemical methods has many unwanted health, safety and environmental risks. Biological control is a potent mean of reducing the damage caused by plant pathogens and is environmentally non-hazardous. Many species in this genus can be characterized as opportunistic virulent plant symbionts (Harman et al. 2004). *Trichoderma* taxonomy has been classified based on the differences in its morphological characters and sporulation. The species of *Trichoderma* uses several mechanisms to control the growth and proliferation of harmful pathogens such as parasitism, competition and antibiosis. Biocontrol agent like *Trichoderma* has been an integral part of Integrated Pest Management (IPM) to control the pests and diseases in an environmentally friendly manner (Monte, 2001).

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Main text

Insights on *Trichoderma* and its biocontrol mechanism

Taxonomy

The first description of the genus *Trichoderma* was in 1794 by Persoon, and Tulasne and Tulasne suggested the sexual state of a *Hypocrea* species in 1865. Cook and Baker (1983) described genus *Trichoderma* as a common soil inhabitant and the conidiophores are terminating in phialides. Doi and Doi (1986) recognized 63 species under this genus and included some anamorphs of genus *Hypocrea* that were previously placed under genera *Verticillium* and *Gliocladium*, where each having irregularly branched conidiophores and elongated phialides. Bissett (1984) worked on subgrouping the species under genus *Trichoderma* into 5 sections, i.e., *Trichoderma*, *Longibrachiatum*, *Saturnisporum*, *Pachybasium* and then the fifth new section of *Hypocreanum* arose.

For more species identification, other criteria have also been used. Zamir and Chet (1985) applied enzyme electrophoresis for *Trichoderma harzianum* identification and isozyme polymorphism was demonstrated. Another diagnostic approach known as scanning electron microscope (SEM) was used (Hashioka, 1973), which revealed the presence of sheath material with epispore scars. Schlick et al. (1994) firstly used randomly amplified PCR fingerprinting (RAPD) to distinguish between gamma irradiated mutants and wild strains of *T. harzianum* that was found to be the most effective tool. Kindermann et al. (1999) used the nucleotide sequences of the internal transcribed spacer region one of rDNA to investigate phylogenetic relation among *Trichoderma* species of the section Pachybasium, which was found to be nonmonophyletic.

The different species of the genus, *Trichoderma/Hypocrea* were difficult to be distinguished morphologically. It was even proposed to reduce taxonomy to only a single species, *T. viride* (Schuster and Schmoll, 2010). Nowadays, new species can be easily identified due to the development of TrichOKEY, where an oligonucleotide barcode and TrichoBLAST became a search tool. These are easily available online at www.isth.info (Druzhinina et al. 2005; and Kopchinskiy et al. 2005). Recently, according to Kamala et al. (2015) *Trichoderma* species belongs to the division Ascomycota, subdivision Pezizomycotina, class Sordariomycetes, subclass Hypocreomycetidae, order Hypocreales and family Hypocreaceae. Chaverri et al. (2015) have reidentified the ubiquitous *Trichoderma harzianum* into 14 new species with various characteristics.

Morphology

Rifai (1969) and Domsch et al. (1980) described colonies of *Trichoderma* spp. in culture to be floccose, tufted green, growing rapidly and sporulate well under incandescent light than otherwise, often producing spores in bands. Phialides of *Trichoderma* spp. are sterile hyphae creeping septate forming a flat, firm, tuft conidiophores erect arising from a short branch. In *T. viride*, conidia have double-layered walls consisting of an electron dense rough outer layer (epispore) and a moderate electron dense inner layer. Around the conidia and hyphae, a distinct mucilaginous substance is present (Hashioka et al. 1996). Majumdar (1993) and Sengupta (1995) stated that chlamydospores are formed late in cultural media, intercalary or rarely terminal, round and double-walled function as resting spores during unfavourable conditions. Recently, micromorphology of *Trichoderma reesei* has been studied by confocal laser scanning microscope to see the branching pattern of the fungus which produces cellulolytic enzymes (Novy et al. 2016).

Characteristics

Trichoderma spp. are often found wherever decaying plant materials are available mainly of cellulosic materials (Kubicek et al. 2009 and Jaklitsch, 2009). *Trichoderma* spp. are mainly characterized by branched conidiophore-bearing bright green conidia (Gams and Bissett, 1998). Figure 1 demonstrates the conidiophores containing phialides and phialospores of *T. harzianum*. According to Shah et al. (2012), the light green conidia of *T. harzianum* are globose to subglobose, while those of *T. viride* are globose. Small pale green conidia were observed in *T. pseudokoningii*.

Trichoderma as a bioagent

The use of microorganisms as bioagents is a less hazardous method for controlling plant pathogens. Almost 20 species of the genus *Trichoderma* act as bioagents against many soil-borne as well as foliar plant pathogens. *T. harzianum*, *T. koningii*, *T. viride*, *T. atroviride*, *T. pseudokoningii*, *T. longibrachiatum*, *T. hamatum*, *T. polysporum* and *T. reesei* are the most important species, which act as potential antagonists (Monaco et al. 1991). Antagonism of *Trichoderma* against different pathogens has been reported for several times like *Sclerotium rolsfii* (Mukherjee and Tripathi, 2000), *Fusarium ciceris*, *Macrophomina phaseolina*, *Rhizoctonia solani* (Mukhopadhyay and Pan 2012a) and plant parasitic nematodes (Spiegel and Chet, 1998). Mukherjee and Raghu (1997) observed that *Trichoderma* species and *Gliocladium virens* were highly effective in suppressing *S. rolsfii* on ginger rhizomes and on several vegetables in storage. Li et al. (2018) showed that 4 species of *Trichoderma* restricted *Fusarium oxysporum* growth by producing volatile compounds.

Influence of environmental factors on biocontrol potential of Trichoderma strains

Among the *Trichoderma* species, the optimum temperature for the growth is different (Samuels, 1996),

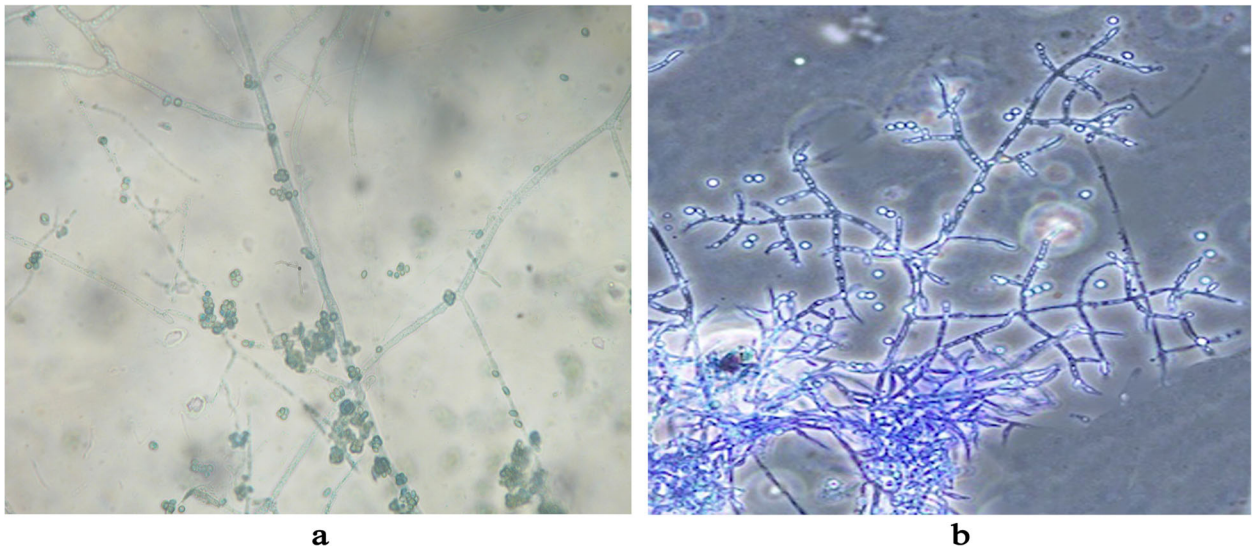

Fig. 1 Phialides and phialospores of **a** *Trichoderma harzianum* and **b** *Trichoderma viride* (taken from the Université de Bretagne Occidentale website)

but mostly they are mesophilic. Water conditions have been shown to strongly effect on *Trichoderma* activities, most particularly spore germination, germ tube growth (Magan, 1988), mycelial growth (Lupo et al. 2002), the interaction with other fungi (Badham, 1991) and on enzyme production (Grajek and Gervais, 1987). At higher water potential, optimum secretion of cellobiohydrolase and NAGase enzymes were observed, while the maximum activities of secreted glucosidase, xylosidase and chymotrypsin-like protease enzymes occurred at lower water potential values than those optimal for growth. Some examined *Trichoderma* strains were able to grow in a wide range of pH from 2.0 to 6.0 with an optimum at 4.0. Mycelial growth of *Trichoderma* strains was also affected by the presence of heavy metals. Zehra et al. (2017) tested *Trichoderma* spp. against *Alternaria alternata*, *F. oxysporum* in different environmental conditions such as salt, temperature and pH and found *T. harzianum* to be most effective

Biocontrol mechanisms of Trichoderma spp.

The main three mechanisms of biocontrol of *Trichoderma* spp. are mycoparasitism, antibiosis, and competition for nutrients or space among others which may operate independently or together to suppress plant pathogens.

Mycoparasitism

Haran et al. (1996) proposed the mycoparasitic activity (hyperparasitism) of *Trichoderma* as one of the major mechanisms involved in their antagonistic activities against phytopathogenic fungi. The importance of *Trichoderma's* mycoparasitism in the biological control of wood decay fungi was discussed by Kumar et al. (1998), who investigated the hyperparasitism of *T. harzianum* by forming appressoria over the pathogenic hyphae of *F. solani* by lightly coiling around them within 95 h of contact. They added that within 6 days, the fungus was completely inhibited, while *T. harzianum* was multiplied by conidiogenesis. *T. gamsii* showed mycoparasitic activities as well as antibiosis against phytopathogens (Chen et al. 2016). In Fig. 2a and b, the microscopic observations on hyphal interaction showed that antagonist, sometimes, grew parallel to the hyphae of the tested pathogen, coiled around and penetrated into the hyphae of the pathogen by producing hook or knob-like structure (appresorium) (Mukhopadhyay and Pan, 2012a).

Antibiosis

Antibiosis is one of the important attributes in deciding the saprophytic ability of the fungus. A range of antibiotics produced by species of *Trichoderma* and *Gliocladium*, which has been suggested as a mode of action of both fungi against plant pathogens was reported by Weindling (1934). Manibhusanrao et al. (1989) reported that antibiotics like trichodermin, suzukacillin and alamethicin produced by *T. harzianum* influence morphological or physiological sequences leading to its successful penetration. *Trichoderma* spp. and *Gliocladium* spp. inhibited the growth of broad range of soil-borne fungi viz. genera of *Fusarium*, *Macrophomina*, *Pythium*, *Phytophthora*, *Rhizoctonia*, *Sclerotinia*, *Sclerotium* and *Verticillium* (Zaher et al. 2013; Ragab et al. 2015 and Chen et al. 2016). do Nascimento Silva et al., (1998) demonstrated the in vitro antagonistic potential of 3 *Trichoderma* spp. against *Colletotrichum gloeosporioides* on passion fruit. *Trichoderma* spp. antagonistic to a range of pathogenic

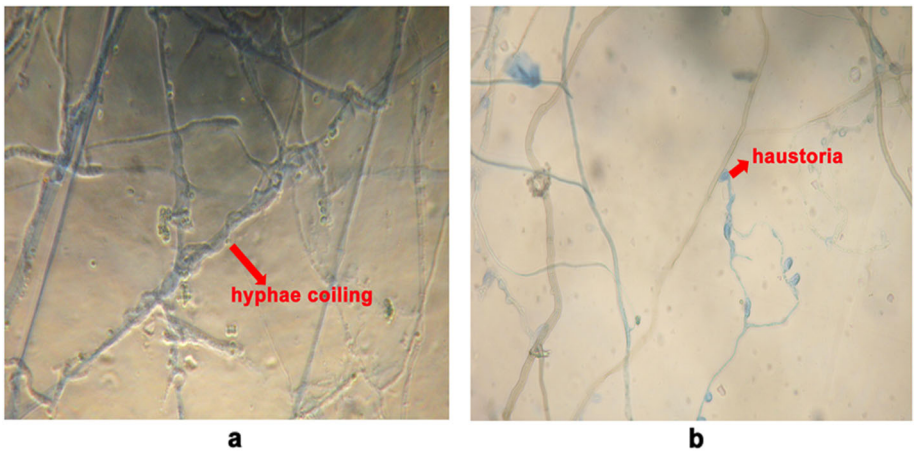

Fig. 2 Mycoparasitism by *Trichoderma* hyphae **a** coiling around the hyphae of *Rhizoctonia solani* and **b** producing haustoria to inhibit growth of *Macrophomina* sp.

fungi was reported to be producing volatile and non-volatile antibiotics (Mukhopadhyay and Kaur, 1990). Studies on the production of volatile and non-volatile antibiotics revealed that *T. harzianum* and *T. viride* were highly effective in reducing the radial growth of *S. rolfsii* (Rao and Kulkarni, 2003). Mukhopadhyay and Pan (2012a) stated that *T. viride* was the most potential antagonist based on volatile and non-volatile antibiotics. Five local isolates of the bioagents, *T. harzianum*, *T. viride*, *T. aureoviride* and *G. virens* isolated from ginger rhizosphere were evaluated in vitro to assess their mode of antagonism against *R. solani*, infecting *Capsicum annuum* and *C. frutescens*. It was observed that the non-volatile antibiotics were more effective than the volatile antibiotics (Bunker and Mathur, 2001).

Bhagat and Pan (2010) screened 12 isolates of *Trichoderma* spp. in vitro against *R. solani* Kuhn. causing root and collar rot of French bean (*Phaseolus vulgaris* L.) by dual culture tests and production of volatile and non-volatile antibiotics and it was found that all the isolates significantly inhibited the mycelial growth of *R. solani*.

Competition

Bioagents compete for nutrients and space with pathogens and, thus, it is the injurious effect of one microorganism to another due to the utilization or removal of some resources from the environment. Competition between iron containing siderophore of *Trichoderma* and wood decay Basidiomycetes fungi was investigated by Srinivasan et al. (1995).

Biopriming and field evaluation of Trichoderma spp.

The biocontrol fungi, *Trichoderma* spp., are not only able to control the pathogens causing plant disease, but can also induce seed germination, seedling emergence and promote plant growth. Vinale et al. (2004) reported that in greenhouse and field trials, *T. harzianum* and *T. atroviride* improved the growth of lettuce, tomato and pepper plants and productivity was increased up to 300% than the untreated control. Similarly, several scientists have got positive results of disease control and increased plant growth and yield in vivo and under field conditions (Harman et al. 2003, Dubey et al. 2007; Bhagat and Pan, 2008; Joshi et al. 2010 and Mukhopadhyay and Pan, 2012b). Seed treatment with bioagents for protection of seeds and control of seed borne diseases offers effective biocontrol agents that have been developed for the control of seed and seedling pathogens such as *Pythium* spp., *R. solani*, *S. rolfsii*, *M. phaseolina* and *Fusarium* spp., which offer the farmers alternative means to chemical fungicides (Dubey et al. 2007 and Nirmalkar et al. 2017).

The efficacy of biological seed treatment can be affected by moisture, temperature and inoculums densities of the pathogen (Mathre et al. 1994) and also by soil pH and iron concentration (Weller, 1988). Efficacy can also be controlled by inoculum density of the bioagents on the seed adjunct treatment such as priming formulation and additives that enhance the activity and survival of the bioagent in the formulated product, crop and pathogen specificity of the bioagent and compatibility with other microbial inoculants. Precolonization provides the bioagent with a competitive advantage over seed attacking pathogens and often provides superior seed protection when compared to seed coating (Harman et al. 1989). Bioagents are effective as a seed treatment, since they colonize roots, increase root mass, health and consequently frequently provide yield increases (Mukhopadhyay et al. 2012b).

Molecular approaches of genus Trichoderma and its benefits

Lytic enzymes and biocontrol An insight into the characters of genus *Trichoderma* at the molecular level would help in developing *Trichoderma* strains with excellent biocontrol properties. Several hundreds of genes and their products might be involved, which give genus *Trichoderma* its properties of biocontrol and plant growth enhancement. Hydrolytic enzymes such as glucanase, chitinase and protease are the key players that give *Trichoderma* the mycoparasitism properties (Haran et al. 1996). 1,4-β-N-acetylglucosaminidases, endo and exochitinases were reported to be secreted by *Trichoderma* spp. that help the fungus to improve its biocontrol potential. β-glucanase produced by *Trichoderma* spp. degrades β-glucan the structural component of the attacking pathogen. 1,3-β glucosidase purified from *T. harzianum* by Lorito et al. (1994), which inhibited germ tube elongation and spore germination of *Botrytis cinerea*. Proteinase from *Trichoderma* spp. is also involved in mycoparasitism. PRA1, a trypsin protease purified from *T. harzianum* CECT 2413 strain showed nematicidal effects by destroying the hatched eggs of *Meloidogyne incognita* (Suarez et al. 2004). Chitinase and protease activity produced by *Trichoderma* spp. helped to control *Sclerotium rolfsii* pathogen in groundnut (Parmar et al. 2015).

Signalling pathways involved in biocontrol mechanism

G protein signalling Neer in 1995 showed that G protein signalling is basically heterotrimeric and constitutes of 3 parts: a G protein-coupled receptor (GPCR), a heterotrimeric G protein (α, β, γ subunits) and an effector. Heterotrimeric G proteins are signal transducers that couple cell surface receptors to cytoplasmic effector proteins and transmit the signal to the MAPK and cAMP signalling pathways (Fig. 3). In fungi, G proteins help during sexual and pathogenic development, secondary metabolism and virulence of the pathogens. *T. atroviride* subgroup I Gα subunit Tga1 was analysed by *tga1* gene over-expression and silencing which showed that it is involved in both coiling and condition (Rocha-Ramirez et al. 2002). Reithner et al. (2005) characterized the Tga1 mutant and showed that the G protein subunit affects processes involved in *Trichoderma* biocontrol like chitinase formation and production of antifungal metabolites which are important for biocontrol by *Trichoderma*. He also proved that Δ*tga1* mutant was not able to overgrow and lyse the host fungi such as *B. cinerea*, *R. solani* and *S. sclerotiorum*. Homologue of Tga1 of *T. atroviride*, i.e., TgaA and TgaB did not show such effects in *T. virens* and also showed different effects in controlling pathogenic fungi such as *R. solani* and *S. sclerotiorum* (Mukherjee et al. 2004). Zeilinger et al. (2005) showed that Tga3 protein of *T. atroviride* is involved in controlling vegetative growth and conidiation and thus Δ*tga3*

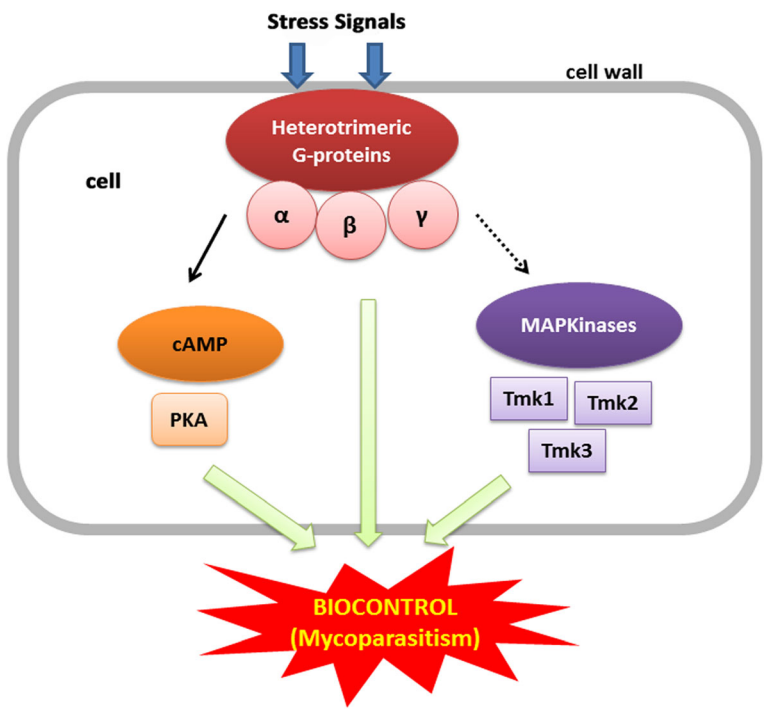

Fig. 3 Schematic representation of signalling pathways involved in mycoparasitism

knockout mutants produced significantly lesser intracellular cAMP levels in comparison to the parental strain. According to experiments done by do Nascimento Silva (2009), intracellular cAMP levels increased at several folds in *T. reesei*, since it carries an activated allele of the subgroup III G*α* protein-encoding Tga3 homologue gna3. TBRG-1 which bears the domain of RasGTPase helps in conidiation of *Trichoderma* but its lack causes positive effects on antibiosis mechanism (Castro et al. 2020).

Mitogen-activated protein kinases

MAPK cascades are found in all eukaryotes and are organized in a 3 kinase architecture comprising of a MAPK, MAPK kinase or MEK and MEK kinase or MEKK or MAPK kinase kinase. In *Trichoderma*, the best observed MAPKs are yeast and fungal extracellular-related kinases (YERK1), and also MAPKs such as Fmk1 from *Fusarium oxysporum*, Pmk1 from *Magnaporthe grisea*, Ubc3/Kpp2 from *Ustilago maydis*, or Bmp1 from *B. cinerea* (Zeilinger et al. 2007). The MAPKs in different species of *Trichoderma* are more or less similar as described by Reithner et al. (2007). According to his findings, there is almost 98% similarity in MAPKs of *T. atroviride* (Tmk1) and *T. virens* (TmkA/Tvk1).

MAPK signalling is important in *Trichoderma* to induce full systemic resistance in plants. TmkA MAPK loss-of-function mutants of *T. virens* can colonize the roots of cucumber plants against *Pseudomonas syringae* pv. *lacrymans* but cannot induce systemic resistance against the pathogen (Viterbo et al. 2005). MAPK cascades traduce signals by sequential phosphorylation of kinases. Inactivation of MAP kinase gene tvk1 in mutant line of *Trichoderma* showed increased mycoparasitism and decreased the growth of the fungus *R. solani* (Mendoza-Mendoza et al. 2003). Esquivel-Naranjo et al. (2016) showed that in *T. atroviride*, the mutants lacking the MAPKK gene Pbs2 and the MAPK Tmk3 were found to be highly sensitive towards cellular stress such as cell wall damage, osmotic and oxidative stress, UV irradiation and high temperature.

cAMP pathway

cAMP signalling in fungi helps in many cellular processes such as the sexual development, virulence, control of differentiation, monitoring of the nutritional status and stress. But the most important function of cAMP signalling is regulation of transcription and cell cycle. In eukaryotes, almost all the effects of cAMP are due to stimulation of cAMP-dependent protein kinases (PKA) (Dickman and Yarden, 1999). Functional PKA is found to be involved in plant pathogenic fungi, processes like growth, morphogenesis and virulence (Xu and Hamer, 1996). The process of sporulation is the main mechanism for survival and spread of *Trichoderma* in the environment. These processes are induced by environmental factors. cAMP plays a pivotal role in signalling during sporulation as investigated in *T. viride* and *T. atroviride* by Casas-Flores et al. (2006). cAMP along with the activators of G protein-mediated signal induce the mycoparasitic behaviour of *T. harzianum* by increasing the coiling behaviour of hyphae (Omero et al. 1999). Nogueira et al. (2015) observed that in *T. reesei* cAMP regulates cellulase expression depending on carbon source. The *cel7a* and *cel6a* genes were expressed in higher amounts in sporophose which increased cAMP levels and regulated secretion of cellulolytic enzymes.

Conclusion

Trichoderma can be an important component in IPM strategies. Biocontrol mechanisms of various species of *Trichoderma* have been isolated and studied. They restrict the growth and proliferation of the pathogens by parasitism and antibiosis as well as molecular approaches are being done. Different signalling pathways are being studied to gain further insights in the biocontrol mechanism of *Trichoderma*.

Abbreviations

MAPK: Mitogen activated protein kinase; cAMP: Cyclic adenosine monophosphate; PRA1: pH-regulated antigen

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RM designed and approved the manuscript and DK substantively revised the manuscript. All authors have read and approved the manuscript.

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Consent for publication

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There are no competing interests.

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