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Unlocking the Potential of *Trichoderma*: Exploring Its Role as a Beneficial Pesticide Agent and Unraveling the Intricacies of Signalling Pathways

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Abstract:

In agricultural systems, insects are the primary pest, which results in considerable reductions in crop productivity and storage. Chemical insecticides are extremely hazardous to humans as well as to the environment and have been extensively used to manage insects during the past few decades. It is necessary to introduce an effective and eco-friendly alternative to minimize the usage of chemical insecticides. *Trichoderma* species are widely studied and used as a biocontrol agent in agriculture systems due to their direct and indirect mechanisms involved in pest control. Direct and indirect pest management is mainly associated with mycoparasitism and activation of systemic plant defensive responses respectively. As mycoparasitic interactions are not merely a contact response, it is evident that *Trichoderma* recognizes signals from the host fungus and triggers the transcription of genes relevant to the biocontrol processes. Recent studies on the signalling pathways underlying *Trichoderma* biocontrol have revealed that heterotrimeric G-proteins, mitogen-activated protein (MAP) kinases and cAMP pathways have a crucial impact on processes that are involved in biocontrol. This review summarises the effect and the signalling pathways of *Trichoderma* as a biocontrol agent against pests.

Keywords: *Trichoderma*, biocontrol, mycoparasitism, G-proteins, Mitogen-Activated Protein Kinases, cAMP

1. Introduction

In today's global outlook, with the steady growth of the world's population, and the effects of climate change, securing high and quality harvests necessitates the implementation of feasible and efficient solutions. To attain these goals, it is vital to understand the functions of insects in our farming systems.

Insects are important in biological processes such as seed dissemination, nutrient cycling, bioturbation, pollination and pest control [1]. In the case of herbivorous insects, the insect-plant interaction is a complicated and highly diverse process involving both biotic and abiotic elements. The insect has to first identify specific chemical signals from the host plant. Consequently, the plant builds various morphological structures and produces defence chemical substances to fend off herbivore attacks [2,3]. On this matter, herbivorous insects have developed to surpass plant resistance and to uptake nutrients from various parts of plants, just as plants were able to develop more specialized and potent defence mechanisms [4,5]. Additionally, the microbiota of each site plays a fundamental role in insect-plant interactions. Plant-associated microorganisms are capable of activating broad defensive mechanisms in response to herbivore attacks, while insect endosymbionts assist in the detoxification of plant defensive secondary chemicals [2,6,7]

The main cause for the low crop yield in agricultural products intended for human consumption and feed for animals is due to the damage caused by insect pests [8]. Losses can take place both in the field as well as in storage (post-harvest) [9]. Insect pests account for 70% of the agricultural output losses tropically and between18% to 25% globally. The most significant damages are connected with food deficient areas with rapidly rising communities, and frequently with emerging or re-emerging pests [10,11].

Synthetic pesticides were first introduced to agricultural lands in the 1920s, to decrease the damage caused by insect pests in agriculture. In the 1960s, the first adverse environmental impact on birds was reported by using chemical pesticides with organochlorine dichlorodiphenyltrichloroethane (DDT). Subsequently, many disorders and deaths of fish species, crustacean neonates and bees were reported due to the use of organophosphate insecticides, carbamate insecticides and synthetic pyrethroids and neonicotinoids. Although the use of pesticides had reduced the effect of insect pests significantly, chemical treatment has many harmful environmental implications on many species and various environmental compartments [12,13].

The need to look for innovative alternatives in pest management is evident given the agricultural losses brought on by insect pests and the substantial negative environmental impact resulting from the widespread use of chemical insecticides. Alternatives that are both efficient and environmentally beneficial have come along in recent years, including the utilization of microorganisms [14,15].

2. Discussion

2.1 Fungi as biological insect pest controllers

Fungi are a ubiquitous and diverse group of microorganisms with a wide range of biotechnological applications. Among many other uses, they are used for producing biofertilizers, antibiotics, anticancer medicines, industrial enzymes and pest and disease management for plants [16]. Due to the need for innovative alternatives to chemical pesticides, the usage of mycopesticides in agriculture has been one of the most developed applications in recent decades. They hold major potential for limiting production loss, lowering energy use, and restoring agroecosystems' efficiency [17,18].

Microorganisms known as entomopathogenic fungi target and usually kill insects and other arthropods [19]. There is no single monophyletic group of entomopathogenic fungi. There have been recorded cases of 12 *Oomycetes* species, 65 *Chytridiomycota* species, 238 *Basidiomycota* species, 339 *Microsporidia* species, 474 *Entomophtoromycota* species, and 476 *Ascomycota* species of entomopathogenic fungi [20]. Various biopesticides based on organisms from the genera *Beauveria*, *Metarhizium*, *Verticillium*, *Lecanicillium*, *Hirsutella*, *Paecilomyces* have been commonly used all over the world. These fungi have a broad range of activities, allowing them to infect a wide range of arthropod species [21,22]. Entomopathogenic fungi typically infect insects by directly penetrating their cuticles [23]. Proteases, chitinases, and other hydrolytic enzymes are expressed, along with specialized structures, e.g., appressoria or penetrant tubes; and secondary and other metabolites to aid in the spore germination and development of the fungus across the host surfaces. Subsequently, numerous biochemical processes take place in the fungus and insect host, promoting the infection by suppressing the host immune system and facilitating sporulation on the dead host due to antibiotic action against invading saprophytes. To complete their life cycle, entomopathogenic fungi need to produce a wide range of insecticidal secondary metabolites during the process [24,25].

In addition to controlling insect pests, their remarkable capacity to colonise plants and exist as fungal endophytes, expand their role in agricultural production and integrated pest management [26,27]. Endophytic fungi have been discovered to live on plants from more than 100 different families specifically from wheat [28], common bean [29], sorghum [30], tomato [31], cotton [32], corn [33] and in numerous other economically essential crops. Numerous studies have been conducted regarding the mechanisms of endophytic fungi-induced host protection against pests and pathogenic organisms [32,34,35,36]. One of the most referred mechanisms is that these fungal endophytes produce bioactive compounds, which improve plant resistance to pathogens and pests as well as increase plant uptake of nutrients, tolerance to biotic and abiotic stressors and overall plant growth [37].

Analysing the potential harm caused to natural enemies is crucial when employing mycopesticides against insect pests in agriculture. Utilising various biological approaches, such as microbes, predators, and/or parasitoids are necessary for the advancement of integrated pest management (IPM). It has been noted that entomopathogenic fungi, including *Beauveria bassiana* or *Metarhizium anisopliae*, can greatly lessen the activity of predatory insects and parasotoids [38].

2.2 *Trichoderma*: A highly advantageous mycoparasite fungus in agriculture

Genus *Trichoderma* belongs to the Hypocreaceae family, consisting of more than 100 species and extensively researched, owing to its properties such as rapid growth, capacity to use a variety of substrates, and tolerance to toxic agents [39,40]. Its primary economic importance is centred on its usage as an agent of biocontrol in agriculture and as a provider of enzymes for various biotechnological industries [41,42]. Currently, *Trichoderma* species are sold as the active components of bio-pesticides, growth promoters, biofertilizers and resistance stimulants due to its capacity to enhance soil nutrition as well as to promote vegetative growth and plant protection [43].

Various *Trichoderma* spp. grow in the rhizosphere and have the ability to penetrate and colonize plant roots [44]. The above facultative/opportunistic symbiosis is fuelled by *Trichoderma*'s capacity to obtain sucrose or additional nutrients from plants in exchange for enhancing plant defences against pathogens while boosting photosynthetic capacities [45,46]. A coordinated transcriptome, proteomic and metabolomic response is elicited in the plant when *Trichoderma* is present in the rhizosphere [45,47,48]. This plant alteration is frequently advantageous, enhancing growth, yield, and pathogenic resistance [49]. *Trichoderma* spores can be applied to crops in a variety of ways such as pre-planting applications to seeds or breeding materials, integration into the soil during seeding or transplanting, irrigation watering or application as a root drench or dip. Direct application to seeds and roots has shown to be the most effective method for colonization [43].

A comparative investigation of the genomes of three species of *Trichoderma* that are often used as biocontrol agents in agriculture (*T. virens*, *T. reesei*, and *T. atroviride*) has showed that the mycoparasitism is an ancient life style and an innate feature of *Trichoderma*. *Trichoderma* eventually interacts with the roots and colonizes them as a result of the presence of more fungal pathogens in the rhizosphere and the formation of nutrient-rich exudates [50]. In this way, their gene evolution pattern has shaped the nutritional expansions and environmental generalism [51].

Trichoderma has an increased level of chitinases and -1,3-glucanases than other fungi, which indicates the need to break down the primary barrier - cell wall. Particularly *T. virens* and *T. atroviride* have the highest number of chitinolytic enzymes of all reported fungi, which belongs to the GH18 of CAZy glycoside hydrolases family. In liquid cultures, chitinase gene expression is increased by substances like fungal cell walls, colloidal chitin, or the chitin monomer N-acetylglucosamine [52]. The N-acetylglucosaminidase-encoding gene, nag1 in *T. atroviride* has a significant role on the induction by chitin of other chitinases [53].

2.3 *Trichoderma: Direct management of insects*

Trichoderma has the ability to actively parasitize insect hosts and use their bodies as a source of nutrition for the growth of its conidia. Conidia frequently stick to the cuticle or secrete adhesive mucus as the conidium swells during pre-germination [54]. Enzymes including chitinases, glucanases, and proteases are released by *Trichoderma* species as a result of interactions with the cell walls of phytopathogenic fungi [55,56]. The production and secretion of metabolites have a significant role in the effects of *Trichoderma* species on other organisms. The genes involved in the production of secondary metabolites frequently form in clusters comprising core enzymes such as non-ribosomal peptide synthetases (NRPSs), polyketide synthases (PKSs) or terpene synthases/cyclases and accessory enzymes (eg. cytochrome P450s, oxidoreductases, methyl transferases, etc.). Environmental signals, as well as transcriptional and epigenetic modulators, control these clusters [57,58,59]. Some studies on the direct management of insects by *Trichoderma* are compiled in Table 1.

Table 1. Direct management of insects by *Trichoderma*

***Trichoderma* Species**	**Antagonistic molecules**	**Effect/Mode of action**	**Target pest**	**Reference**
Trichoderma viride	Chitinase	Affecting the integrity of the peritrophic matrix of the insect midgut by chitinolytic enzymes	*Bombyx mori* (Domestic silk moth)	[60]
	Chitinase	Decrease growth rate and larval weight	*Corcyra cephalonica* (Rice Moth)	[61]
	Trichoderma viride mediated synthesis of titanium dioxide nanoparticles (TDNPs)	Larvicidal, antifeedant and pupicidal effect	*Helicoverpa armigera* (Cotton Bollworm)	[62]
	Secondary metabolite(s)	Act as an oviposition attractant	*Culex quinquefasciatus*	[63]
Trichoderma harzianum	Secondary metabolites	Secondary metabolite toxicity	*Periplaneta americana* (American cockroach)	[64]
	Fungal spores	Parasitism	*Cimex hemipterus* (Tropical bed bugs)	[65]
	Secondary metabolites	larvicidal and pupicidal effect	*Aedes aegypti L*	[66]
	Fungal spores	Secondary metabolite toxicity	*Schizaphis graminum*	[67]
	Fungal spores and extracts	Secondary metabolite toxicity	*Pectinophora gossypiella* (Pink bollworm)	[68]
	Fungal spores and extracts	Secondary metabolite toxicity	*Earias insulana* (Egyptian stemborer)	[68]
	Fungal spores	Secondary metabolite toxicity	*Tenebrio molitor* (Mealworm)	[69]
Trichoderma asperellum	Secondary metabolite 6-pentyl-α-pyrone (6PP)	Secondary metabolite toxicity	*Tetranychus urticae* (Red spider mite)	[70]
Trichoderma longibrachiatum	Fungal spores	Parasitism	*Leucinodes orbonalis* (Eggplant fruit shoot borer)	[71]
	Fungal spores	Parasitism	*Bemisia tabaci* (Silverleaf whitefly)	[72]
Trichoderma citrinovirid	Metabolite with antifeedant activity	Influenced the feeding preference	*Schizaphis graminum*	[73]
	Fungal spores	Parasitism	*Acanthoscelides obtectus* (Bean weevil)	[74]

Trichoderma album	Fungal spores	Parasitism	*Rhyzopertha dominica* (American wheat weevil)	[75]
Trichoderma sp.	Secondary metabolites	Secondary metabolite toxicity	*Locusta migratoria* (Migratory locust)	[76]

2.4 Trichoderma: Indirect management of insects

Trichoderma can act in an indirect manner by inducing the plant defence system, so the plant can protect itself from its pathogens (eg. generation of a mixture of volatiles that attracts natural predators of the herbivores [77,78].

Plant defence responses mediated by the jasmonic acid (JA) or salicylic acid (SA) signalling pathways are activated in response to fungal root colonization or the recognition of soil diffusible secondary metabolites like non-ribosomal peptides or volatiles produced from *Trichoderma*, which are effective against a variety of shoot and root pathogens [79,80]., And also JA and SA-dependent molecular pathways are activated by chewing insects like caterpillars and phloem-sucking herbivores, respectively [81]. In maize plants, *T. harzianum* inoculation has increased the number of natural pest enemies, meanwhile decreasing the number of arthropod pests. Furthermore, the levels of sucrose, jasmonic acid (which activates defence responses against herbivory) and (Z)-3-hexen-1-ol (a volatile substance that attracts herbivores' natural enemies) were significantly altered after *T. harzianum* inoculation [82]. Similarly, *T. gamsii/T. Asperellum* [83] *T. atroviride* [84], *T. longibrachiatum* [85] and *Trichoderma* sp. have exhibited a significant activation of plant systemic resistance against many insects.

The indirect control by mycoparasitism of insect-symbiotic microorganisms is another strategy used by *Trichoderma* to manage pests. Important phases of this process are prey detection, positive chemotropic growth toward it, chemical and physical attack that ultimately leads to the destruction of fungal prey hyphae and eventually uptake of nutrition [86].

Xylosandrus germanus Blandford, an invasive ambrosia beetle (*Coleoptera: Curculionidae: Scolytinae*), marked as a significant hazelnut pest in Turkey. The females of these insects dig tunnels in the xylem of the trees that serve as their hosts, and they then inoculate those tunnels with spores from the fungi *Raffaelea* and *Ambrosiella*. They need this symbiotic nutritional relationship to thrive because both larvae and adults can only eat these wood-degrading fungi. It has been demonstrated that inoculating hazelnut branches with spores of *T. harzianum*, *T. asperellum*, and *T. atroviride* significantly lowers the numbers of beetles by directly mycoparasitizing the beetle-symbiotic fungus [15]. Similar mycoparasitism exerted by *Trichoderma* sp on *Atta sexdens rubropilosa* (leaf-cutting ants) and their fungal symbiont (*Leucoagaricus)* was noted by Rocha *et al*. [87].

2.5 Signalling pathways involved in the biocontrol mechanism of *Trichoderma*

The role of G protein

Basically, heterotrimeric G protein signalling is made up of three components: an effector, a heterotrimeric G protein (α, β, γ subunits), and a G protein-coupled receptor (GPCR). Ligand interaction to the receptor causes a conformational shift that results in the release of the G protein and the exchange of GDP for GTP on the G α subunit. When GTP-bound, α separates from its ßγ partner. Both signalling components control the actions of downstream effectors [88]. These receptors can be classified into nine groups ; classes I and II are composed of pheromone receptors and are identical to the yeast Ste2p and Ste3p receptors; classes III and V consist of putative carbon source receptors and cAMP-sensors; class IV comprises *Schizosaccharomyces pombe* Stm1p-like nitrogen sensors; class VI, which is similar to filamentous fungi, comprises receptors with an RGS domain downstream of their trans membrane regions; classes VII and VIII have been identified recently and share similarities with some vertebrate receptors; class IX composed of fungal opsins, similar to the bacterial retinal-binding rhodopsin, with *Neurospora crassa* NOP-1 and ORP-1 as important members [89].

Highly conserved heterotrimeric G protein α subunits, which become active upon ligand binding to a specific receptor, are essential for controlling processes like asexual development, sexual reproduction and pathogenicity, in which pathogenic fungi react to signals from their hosts and detect the presence of mating partners through pheromones [90]. It was reported that Tga1 gene of G-protein α subunit influences mycoparasitism-related coiling and light-induced conidiation in *T. atroviride*. [91]. Further studies demonstrated that Tga1 gene mutations can stimulate continuous sporulation, elevate internal steady-state cAMP levels and gene deletion can cause loss of mycoparasitic abilities of *T. atroviride* (Fig. 1) [92]. But, unlike Tga1 gene, which influences development and conidiation in *T. atroviride*, its homologue, TgaA gene of *Trichoderma virens* showed no such effects on these traits [93].

Furthermore, there are three main subgroups of fungi Gα subunits [94].The subgroup I of Gα proteins are similar to the mammalian Gαi subunits. Both proteins contain a consensus sequence for myristoylation (MGXXXS) at the N-terminus and a site for ADPribosylation by pertussis toxin (CAAX) at the C-terminus.[95,96]. Microbial Gα proteins of subgroup I are specifically capable of inhibiting adenylate cyclase enzyme to lower the intracellular cAMP level [97]. Few members of the fungal Gα protein subgroup II, which is distinguished by their lack of the consensus site for pertussis toxin-dependent ribosylation, have been linked to a specific biological process or phenotype and have no homology with any mammalian G-proteins. Their functions are less clear, and their direct effectors have not yet been well discovered. Members of the fungal subgroup III, which are homologues of the mammalian Gs family, have a favourable effect on the internal cAMP level and also control morphological and developmental measures, including germination, conidiation, and the production of secondary metabolites [94]. Mutants of *T. atroviride*, lacking the Tga3 protein of subgroup III of fungal Gα proteins exhibited changes in vegetative growth, conidiation and conidial germination, as well as decreased intracellular cyclic AMP levels. Moreover, structures related to mycoparasitism were not formed, clearly indicating a loss of host recognition [90]. Even though the chitinase-encoding genes ech42 and nag1 were transcribed at a much faster rate than in the wild type, Tga3 mutants displayed a lesser extracellular chitinase activity. Tga3 gene may be capable of altering chitinase secretion, resulting in the observed buildup of chitinolytic enzymes inside the cell and their retention in the cell wall. Exogenous cAMP had no effect on suppressing the altered phenotype or restoring mycoparasitic overgrowth, but it did restore the ability to form infection structures [90].

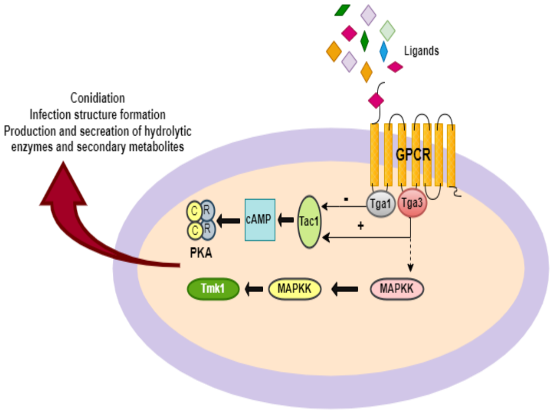

Fig. 1. Schematic representation of Mycoparasitism-relevant signalling pathways of *Trichoderma atroviride* . Tga1, Tga3: subgroup I and III G-protein α subunits; GPCR: G protein-coupled receptor; Tac1: adenylate cyclase; PKA: protein kinase A regulatory (R) and catalytic (C) subunits; Tmk1: MAP kinase

Mitogen-activated protein kinases (MAPK)

All eukaryotes have well conserved MAPK cascades throughout evolution. Mitogen-activated protein kinase cascades transmit a range of signals by sequentially activating serine/threonine protein kinases through phosphorylation, which controls the gene expression necessary for a variety of biological activities in eukaryotes [98,99]. Typically, these cascades have been structured in a three-kinase architecture, composed of MAPK, a MAPK activator (Mitogen-Activated Protein Kinase Kinase = MEK, MKK, or MAPKK), and a MEK activator (MEK kinase = MEKK, or MAPK kinase kinase) [100,101]. When activated, MAPKK (MAP kinase kinase) is initially phosphorylated in this signal transduction cascade, which then phosphorylates and activates MAPKK, followed by the phosphorylation and activation of MAPK for downstream functions [102].

The model fungus, *Saccharomyces cerevisiae* contains six main MAPK pathways, three of which have widespread homologues in filamentous fungi: Hog1-like MAPK pathway, Slt2-like MAPK pathway, and Fus3-like MAPK pathway [103,104]. In *S. cerevisiae*, the Hog1 pathway responds to high osmolarity signals activated by upstream sensors and effectors, which causes a cytoplasmic reaction that affects glycerol and ion transporters, metabolism, and translation [105]. The Slt2 pathway is usually involved in maintaining cell wall integrity and gets activated when the cell surface is stressed, such as during high-temperature growth, hypoosmotic shock, polarized growth, actin disruption, or the presence of substances or mutations that hinder the production of the cell wall [106]. The Fus3/Kss1 pathway is involved in pheromone-induced mating responses and filamentous growth. Although filamentous fungi have a highly conserved Fusp/Kss1 MAPK cascade, they only have a single Fus3/Kss1 orthologue [107].

Contradictory findings have been published about the function of this MAP kinase in the generation of mycoparasitism-related enzymes in various strains of *T. virens*, where tmkA and tvk1 encode the same protein [108]. Chitinase and protease activity increased in Δtvk1 mutants whereas ΔtmkA strains displayed a delay and decreased capacity for clearing a chitin-containing media. The ΔtmkA mutants of *T. virens* exhibited hyperparasitic coiling around the hyphae of *Rhizoctonia. solani* which was similar to the wild type. However, *T. virens* Gv29-8 strain clearly exhibited an increase in the expression level of mycoparasitism-related genes during direct confrontation with *R. solani* [108,109]. Additional research on the function of Tvk1 demonstrated that this MAPK controls conidiation, hydrophobicity and the expression of genes encoding for cell wall proteins during *T. virens* development [110].

T. atroviride (Tmk1) MAPK showed 98% identity with *T. virens* TmkA/Tvk1 which exhibited decreased radial growth and light-independent conidiation [111]. Direct plate confrontation assays using *R. solani* and *B. cinerea* as hosts revealed that Tmk1 affects *T. atroviride*'s host specificity like *T. virens* TmkA, because Δtmk1 mutant was still able to parasitize *R. solani* but was no longer able to outgrow *Botrytis cinerea*, although attachment to and growth alongside *Botrytis* hyphae could still be seen microscopically. Furthermore, extracellular chitinase activity and nag1 and ech42 transcription levels were dramatically increased in Δtmk1 mutants under chitinase-inducing circumstances and the mutants also displayed a deregulation of the synthesis of antifungal metabolites. Additionally, the mutants had an improved capacity to defend bean plants against *R. solani* infection, which is consistent with the discovery that mycoparasitism-related processes (eg. Coiling and metabolite production) are boosted after tmk1 deletion [111]

Under indirect management of pests, *T. virens* ΔtmkA mutants were used to study the role of MAPK signalling in causing plant systemic defence during *Trichoderma*-plant interaction. ΔtmkA mutants of *Trichoderma* were able to colonize cucumber roots, but they were unable to produce full systemic resistance against the pathogenic *Pseudomonas syringae pv. lacrymans*, indicating that *T. virens* requires MAPK signalling in order to produce full systemic resistance in the plants [112].

cAMP signalling in *Trichoderma* biocontrol

The cAMP (Cyclic adenosine 3′5′ monophosphate) signalling pathway is a fundamental signalling course in biocontrol, which involves in fungal physiological traits such as growth, development, differentiation, sporulation, morphology, and the synthesis of secondary metabolites. The relative activity of the degradative enzymes (phosphodiesterases) and the synthesizing enzyme (adenylyl cyclase) determine the level of cAMP in cells [113].

The main components of the cAMP signaling pathway are the G-protein system which includes G-protein coupled receptors (GPCRs) and heterotrimeric G-proteins as well as adenylyl cyclase (AC) and cAMP-dependent protein kinase (PKA) and downstream effectors [114]. The cAMP signalling pathway includes the following steps for extracellular signal transduction; GPCRs carry extracellular signals into cells, and activated heterotrimeric G-proteins stimulate AC, causing it to produce cAMP. After that, cAMP stimulation activates PKA, which then controls the expression activities by phosphorylating downstream proteins like transcription factors, modulating a variety of biological processes [115].

In *T. reesei*, a species with the ability to defend against *Pythium ultimum* and to protect zucchini plants from *P. ultimum* blight in planta, cAMP was found to act as a positive effector of endoglucanase induction by improving the efficacy of the induction process [116,117]. *Trichoderma* survives and disperse mainly by the generation of conidia, which is triggered by environmental conditions like blue light and nutritional stresses. In *T. viride*, the exogenous cAMP increases the development of conidia in both illuminated and dark colonies, where photo induction of conidiation is followed by a sharp temporal rise in the intracellular cAMP level [118,119]. PKA is crucial for the control of light responses in this fungus by cloning and characterizing the gene (pkr-1) that encodes the regulatory subunit of protein kinase A (PKA) from *T. atroviride* [120]. The deletion of the adenylate cyclase-encoding gene (tac1) of *T. virens* reduced the intracellular cAMP levels significantly, did not sporulate in darkness, was unable to outgrow host fungi such as *Sclerotium rolfsii*, *R. solani*, and *Pythium* sp., and produced fewer secondary metabolites. [121].

3. Conclusion

Crop output decline is a prominent issue in agricultural systems as a result of insect pests. Because of this, the use of chemical insecticides to minimize the losses has become crucial, despite the fact that their widespread usage has seriously harmed the ecosystem. Application of novel methods for the management of insect pests, such as the use of biopesticides, is necessary for the development of agriculture that preserves the environment. Today's market has a wide variety of mycopesticides that are useful for controlling insect pests, albeit the market share is still quite limited. It may be challenging to build new alternatives that are more dependent on biological and environmental elements such as biopesticides, because farmers have been using chemical insecticides extensively for the past few decades. Despite this, use of mycopesticide continues to rise meanwhile the use of chemical pesticide declines year after year.

Trichoderma are filamentous fungi and are extensively studied and employed as biocontrol agents in agriculture due to their mechanisms such as mycoparasitism on plant pathogenic fungi. In addition, *Trichoderma* exhibits high persistence in the agrosystems because of their diverse resource acquisition strategies associated with a wide range of crops. Several studies have been conducted on the use of *Trichoderma* as biological control agents for insect pests during the last decades. In this regard, it is important to acknowledge the capacity of *Trichoderma* to control insect pests both directly (parasitism, synthesis of insecticidal secondary metabolites, antifeedant compounds, and repellent metabolites) and indirectly (activation of systemic plant defensive responses, parasitism of insect-symbiotic microbes and attraction of natural enemies). Signalling pathways involving G-protein subunits, mitogen-activated protein kinases and cAMP pathways have been linked in these processes on numerous occasions.

Further research into the biochemical and physiological aspects by which *Trichoderma* spp. acting as a biocontrol agent against numerous insect pests is required for a comprehensive understanding of this multitalented biocontrol agent. Moreover, for this purpose, it is mandatory to understand the molecular mechanisms involved in these beneficial traits. *Trichoderma* genomes can be an exceptionally valuable source of candidate genes for generating transgenic plants that are resistant to both biotic and abiotic stressors. Finally, taking into account all of the facts presented in this review, the usage of *Trichoderma* species should be recommended as a viable alternative to pesticides in the era of a green economy that promotes human health and environmental protection.

Conflict of interests

The authors declare no conflicts of interest.

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