Review Article

Trichoderma Species and their Biological mechanisms

Abstract: In Agriculture, biocontrol agents (BCA) are an important tool for preventing crop losses from plant pathogen infections and for increasing plant food production. Also reducing the need for chemical pesticides and fertilizers, while offering an eco-friendlier and more sustainable alternative. The fungus genus *Trichoderma* is one of the most commonly used and studied organisms for biocontrol applications due to its numerous biocontrol traits, including parasitism, antibiosis, secondary metabolite production and induction of plant defense systems. It is well known that there are several species of *Trichoderma* that are mycoparasites. However, some of those species can antagonize other organisms such as nematodes and plant pests, making this fungus a very versatile BCA. Bioformulations containing *Trichoderma* species or other plant-beneficial microbes, such as plant growth-promoting bacteria (PGPB), have been used in agriculture. The purpose of this review shows recent literature regarding biocontrol studies about six of the most widely used *Trichoderma* species highlighting their biocontrol traits and the use of these fungal genera in *Trichoderma*-based formulations to control or prevent plant diseases, and their importance as a substitute for chemical pesticides and fertilizers

Keywords: *Trichoderma,* biocontrol agent, secondary metabolites, mycoparasitism

1. Introduction

Global population growth is placing tremendous pressure on agricultural production systems due to the increased demand for food. Thus, it is necessary to expand open-field cultivation areas, in addition to increasing efficiency and investment in growing fruits and vegetables under greenhouse conditions. Chemical fertilizers have been used to increase plant growth to the limit of the plant's innate capacity.

In contrast, all agricultural systems are susceptible to potential pathogens, such as viruses, bacteria, fungi, and other microorganisms [48], causing serious economic losses every year. This is why chemical pesticides are the first choice for many agricultural producers. There is no doubt that pesticides are known for their immediate use and solution to problems. Fertilizers and pesticides can cause collateral damage to the environment, as well as to human and animal health [44,30,60]. Chemical pesticides also induce resistance in pathogens, making them difficult to control after years of use [35]. Many countries, mostly in North America and Europe, and some Asian countries are trying to regulate and reduce its use. A similar trend is taking place among consumers, who are shifting from conventional to organic production, ignoring the large size and appearance of fruits and vegetables. There are similar issues in other developing countries.

Plant diseases can be controlled or managed effectively through sustainable agriculture practices. There are several genera of fungi that are effective biocontrol agents against fungal phytopathogens, such as *Alternaria, Penicillium, Pichia, Aspergillus* and *Trichoderma.* As far as the field is concerned, *Trichoderma* is most effective [70,77]. *Sclerotium rolfsii* disease symptoms were reduced by *Trichoderma sp.* Efficacious biocontrol agents were produced by accumulating Salicylic and Jasmonic acids in Sunflower plants [77]. Under greenhouse conditions, ten endophytic fungi, including *Penicillium* sp., *Guignardia mangiferae, Hypocrea* sp., *Neurospora* sp., *Eupenicillium javanicum, Lasiodiplodia theobromae,* and *Trichoderma* sp., inhibited *Fusarium oxysporum* f.sp. *cucumerinum,* the disease-causing agent of Cucumber stem. Of 32 fungal isolates from *Brugmansia aurea, A. aculeatus* inhibited the growth of *F. solani* and *A. fumigatus*, showing potential as BCA [10].

A fungal BCA can also kill insects and nematodes. Insects that affect significant crops such as *Tetranychus urticae* and other have been demonstrated to be controlled by several *Trichoderma* species [54]. Due to their positive effects on plant growth promotion, Arbuscular mycorrhizal fungi (AMF) have been extensively studied; however, they are also effective against phytopathogens, such as *Meloidogyne incognita* and other nematodes [54]. Another potential BCA for pathogens is *Arthrobotrys oligospora*, which forms adhesive structures to capture nematodes.

Abiotic stresses, including high temperatures, can be mitigated by fungi biocontrol agents [34,35]. Their ability to induce systemic resistance makes them useful as plant defense enhancers as well. Plant yields are increased by this protection against several pathogens. The role of fungi in crop production and plant growth is thus significant [55]. *Trichoderma, Aspergillus, Fusarium, Penicillium, Piriformospora, Rhizoctonia, Colletotrichum, Gliocladium, Phoma,* and others induce plant growth [28,25]. A fungus called *Acremonium* sp. enhanced root and shoot length of *Allium tuberosum* plants and was antifungal against *Botryiosphaeria dothidea* and *Botrytis cinerea* [37]. *Alternaria* species, *Phomopsis* species and *Cladosporium* species increased biomass in Tobacco plants, suggesting they could be used as plant growth promoters [86]. *T. virens* and *T. atroviride* can enhance secondary root system development and biomass production of *Arabidopsis* and Tomato plants [11,62], being one of the most used genera as plant growth promoters.

Agricultural production systems must shift towards sustainability due to the damage caused by chemical fertilizers and pesticides. To achieve this, they should minimize the use of synthetic fertilizers and pesticides. As a low-cost, eco-friendly alternative, fungi of the genus Trichoderma promote plant growth and provide protection against pests and pathogens. Bioinoculants containing Trichoderma as an antagonistic agent are one of the most active biological control strategies in various countries. A substantial portion of the global market for biological control agents (BCAs) is based on *Trichoderma* species [72,36]. A number of fungal and oomycete pathogens are controlled by *Trichoderma*-based biopesticides, including *Acremonium cucurbitacearum*, *Alternaria* species, *Aphanomyces cochlioides*, *Aspergillus* species, *Lasiodiplodia theobromae*, *Botrytis cinerea*, *Botrytis* species, *Collisletotnicios* species, *Collisletnicios* species, *Diplodia natalensis, Fusarium* species and *Gaeumannomyces graminis tritici*, *Lasiodiplodia theobroma*, *Phoma betae*, *Rhizoctonia solani, Rhizopus oryzae*, *Pythium* spp., *Serpula* spp., *Sclerotium* spp., *Verticillium dahliae*, among others [72].

Trichoderma is a genus of filamentous fungi commonly found in soil, rhizospheres, and endospheres of plants. In addition to controlling pathogens such as fungi and nematodes, these fungi have attracted our attention [54]. These beneficial aspects of various *Trichoderma* species are discussed in this study, showing different modes of action that are beneficial for many sustainable agricultural production systems.

2.Mode of actions of *Trichoderma* species

Trichoderma has been characterized as a biocontrol agent and plant growth promoter by over 200 species [15,6], leading to numerous studies to discover their mechanisms of action, focusing on mycoparasitism and competition [74,59], the production of antagonistic secondary metabolites [54] and the induction of systemic resistance in plants.

A number of Trichoderma species have been registered, including *Trichoderma harzianum*, *T. asperellum*, *T. atroviride*, *T. longibrachiatum*, *T. viride*, and *T. virens* are the most sampled ones [39]. The first three species are among the most common biocontrol agents used to control fungal phytopathogens by mycoparasitism and competition. Meanwhile, species such as *T. virens*, *T. longibrachiatum*, and *T. viride* use antibiosis as a strong mechanism of action against several plant pathogens [51,59,49,83].

2.1 *Trichoderma atroviride*

A filamentous fungus, *Trichoderma atroviride* is normally isolated from soil in temperate regions, where it grows most efficiently at 25°C, exhibiting hyaline spores with inconspicuous aerial hyphae and gray or dark green conidia within two to seven days [54]. It has a characteristic coconut smell due to the production of the volatile compound 6-pentyl-2H-pyran-2-one, or 6-PP, which also acts as a biocontrol agent against several plant pathogens, including *Cylindrocarpon destructans*, *Macrophomina phaseolina*, *Phytophthora* sp., as well as stimulating plant growth and enhancing systemic resistance.

2.1.1 Competition

Competition for space and nutrients occurs when T. *atroviride* inhibits *Phytophthora* growth and zoospore synthesis. The interaction between *T. atroviride* and Tomato plants enhances their resistance to disease caused by this oomycete [45]. In addition, T. *atroviride* competes and antagonizes *Fusarium avenaceum* and *Fusarium culmorum,* key Maize pathogens [10], and *Neofusicoccum parvum,* a Grapevine pathogen. Dual culture assays reveal that *T. atroviride* can parasitize *Neofusicoccum batangarum, Neofusicoccum pervum, Phytophthora nicotianae, Penicillium digitatum, Neococcus volvulus. P. commune, P. roqueforti, P. verrucosum, Aspergillus steynii, Fusarium proliferatum, F. verticilloides*, *F. sporotrichoides* and *F. poae* [69].

2.1.2 Secondary metabolites

Biocontrol traits can be tested in whole fungal cultures or extracts. Individual components may also be tested, or a combination of components identified from an extract as a whole may be tested. As a result, whole fungal cultures (soluble metabolites) from the local *T. atroviride* strain BC0584 and its volatile organic compounds (VOCs) suppress *F. avenaceum*. Conversely, both soluble metabolites and VOCs failed to inhibit F. *culmorum.* However, both pathogens are controlled by *T. atroviride* BC0584 [10]. VOCs are produced by *Trichoderma* species, and 6-PP is the most characterized VOC produced by species that synthesize this compound, such as *T. atroviride* [54]. Higher amounts of 6-PP are synthesized under dark conditions. As a result, T. *atroviride* P1 and IMI 206,040 strains acts against *R. solani* and *F. oxysporum* [47]. Certain metabolites, like antibiotics are obtained from fermented cultures after several days of growing the fungus in a liquid medium [54]. Fermented cultures from *T. atroviride* CCTCCSBW0199 could inhibit *B. cinerea* growth in an in vitro assay to 73% [43], indicating an antibiosis mechanism to control the pathogen.

During a broad-range pathogen study, found that both ethyl acetate extract and fungal filtrate from *Trichoderma* are cytotoxic and inhibit growth of 25 pathogens, including seven *Penicillium species,* six *Aspergillus species,* six *Fusarium species,* two *Neofusicoccum species,* two *Colletotrichum species,* and two *Phytophthora species*[69]. There are several physiological processes occurring in the *Trichoderma* velvet complex, including the synthesis of secondary metabolites [83]. In a study to unravel the role of *vel1*, a member of the velvet complex in *T. atroviride* T23, Karuppiah and collaborators [54,33] found that the fungal extract of the wild-type strain and the *vel1* overexpressing strain, both alone and in the co-culture with *Bacillus amyloliquefaciens* 1841, inhibit the growth of the Wheat pathogen *F. graminearum*, and decrease the disease severity in plants treated with those strains; the authors also note that the co-cultures have a better inhibition rate over the pathogen, and induce a stronger plant resistance than the single cultures [54].

It has been shown that some secondary metabolites produced by T. *atroviride* can induce plant resistance against the pathogen, for instance, fermented cultures of *T. atroviride* CCTCCSBW0199 alone or in combination with brassinolide can significantly increase peroxidase (POD) and superoxide dismutase (SOD) activity in tomato plants, which can subsequently increase plant resistance and reduce the symptoms caused by *B. cinerea* [43].

A swollenin is a protein similar to an expansin in plants that regulates cell wall remodelling and colonization. TaSWO1, a swollenin produced by T. *atroviride, induces resistance in Capsicum annum plants against A. solani* and *R. solani*, reducing symptoms caused by these pathogens [63]. A LysM effector identified as Tal6 in T. *atroviride* IMI 206,040 binds fungal chitin, preventing the plant from sensing the BCA, allowing it to establish a beneficial interaction, and enhancing *T. atroviride* mycoparasitic activity against *B. cinerea, Sclerotium cepivorum, Colletotrichum lindemutianum* and *R. solani* AG2 [61].*T. atroviride* is capable of producing a wide range of volatile and non-volatile secondary metabolites that are indicative of its ability to control different types of phytopathogens, making it an effective BCA in a wide variety of agricultural environments.

2.1.3 Defence induction and priming

Induction of plant defence by *T. atroviride* is one of the most important mechanisms of action of this BCA. It is due to the fact that it is capable of controlling a wide range of plant pathogens, compared to direct mechanisms, such as mycoparasites, which may be limited. It is still possible to use indirect mechanisms to supplement it in some instances. Therefore, *T. atroviride* is an effective antagonist of several fungal, oomycete, insect, and other plant pathogens.

Various plant defense responses can be induced when *Trichoderma* colonizes a plant's roots; for example, *T. atroviride* SC1 induces a SA-mediated defense response within grapevine Tempranillo cultivar, enhancing the protection of the plant against *Neospora parvum*, which is also inhibited when it is grown in dual cultures with *T. atroviride* [42]. When *Trichoderma* species colonize a plant, they alter its transcriptome, modifying genes that are involved in plant defense responses, such as *T. atroviride* P1, which modifies gene transcripts related to plant defense, and induces plant-defense related VOCs to attract the aphid-predatory wasp *Aphidius ervi*. A more effective defense mechanism can be found in tomato plants against the aphid Macrosiphum euphorbiae and the moth *Spodoptera littotalis* [13], showing that *T. atroviride* may control pathogens indirectly, modulating the physiology of plants. Besides modifying plant defense genes, colonization of plants by *T. atroviride* also induces *Arabidopsis*'s sRNA-mediated gene silencing, leading to an increase in gene expression of JA and SA-mediated pathways, which in turn results in priming and increases resistance against *B. cinerea* [57].

2.2 *Trichoderma harzianum*

T. harzianum grows best in temperate climates, with optimal growth at 30 ^{o}C; conidia appear at day 2 in concentric zones on Petri dishes, changing from green to brown; unlike *T. atroviride*, *T. harzianum* has no distinctive odour. It can be found in several substrates, such as soil, other fungi, decaying plant material and as an endophyte of several plants. As a biocontrol agent, it combats soil-borne diseases. As one of the active ingredients in commercial products used to control crop diseases and promote plant growth and yield [54], it has been widely used in agriculture.

2.2.1 Competition

The fungus T. *harzianum* suppresses mycotoxin-producing fungi as well as *Fusarium solani* through competition and antibiosis [8,17]. In an in vitro assay of *F. oxysporum* f.sp. *lycopersici* in confrontation with five *Trichoderma* species, all the species inhibited the pathogen's growth, both *T. harzianum* strains tested, BHU-BOT-RYRL4 and MTCC936, inhibited growth the most (83.17% and 72.13%, respectively). A rhizosphere colonization study showed that *T. harzianum Tr904, as well as T. gamsii* and *T. afroharzianum* competed with *Fusarium pseudograminearum* for space and nutrients, preventing the disease caused by this pathogen.

In the dual confrontation of *T. harzianum* and *Fusarium sudanense*, the BCA parasites the pathogen by degrading its hyphae and inhibiting its growth by competing for nutrients and space [41]. In vitro, *T. harzianum* also showed antagonistic activity against *Alternaria cerealis*, resulting in its growth being limited [46], and *T. harzianum* T-soybean showed mycoparasitic activity against *F. oxysporum*, reducing its growth by 45.45% [54].Dual confrontation assays were performed with two strains of T. *hazianum*, CMML20-26 and CMML20-27, respectively. Asserted strong antimicrobial activity against and *Fusarium ipomeae, Fusarium oxysporum, F. solani*, *Penicillium citrinum*, *P. rotoruae*, *Aspergillus wentii*, *Mucor variicolumellatus* and *M. phaseolina* [53]. *T. harzianum* MRI001 parasitizes *F. oxysporum*, *A. alternata*, *Aspergillus carbonarius*, and *A. flavus.* This will overgrow the pathogens and reducing the production of the mycotoxins ochratoxin and aflatoxin B1, produced by *A. carbonarius* and *A. flavus* respectively [8].

In a confrontational assay, *T. harzianum* competes for space with *Colletotrichum truncatum,* inhibiting its growth [79]. Several Egyptian *T. hazianum* strains were mycoparasitic against *F. graminearum*, *M. phaseolina*, and *F. solani. The* strain *T. harzianum* Th6 was most effective against all three pathogens [24,23].

2.2.2 Secondary metabolites

T. harzianum produces secondary metabolites with important biological properties. In maize roots, *T. harzianum* induces VOCs and exogenous application of 6-PP reduces damage caused by *Phyllophaga vetula* [12], suggesting that the fungus' volatiles cause resistance in the plant, despite not observing direct biocontrol of the pest. The ThMBF1 transcriptional coactivator of T. *harzianum T34* is involved in secondary metabolite synthesis. Regulation of BCA is vital to maintain biocontrol ability over *B. cinerea* and *F. oxysporum, since its* overexpression significantly reduces BCA's ability to inhibit pathogen growth and confer resistance.

Peptaibols are secondary metabolites from Trichoderma species with antibiosis activity against several pathogens [54]. Three peptaibols from *T. harzianum* HK-61, named trichorzins HA II, HA V, and HA VI, reduced Vigna sesquipedalis lesions by 90% (trichorzin HA V). Secondary metabolites can be antibacterial or antimicrobial. A fungal extract of *T. harzianum* CCTCC-RW0024 showed antibiotic activity against *F. gramineraum*, inhibiting pathogen growth by 96.3% [64]. A culture filtrate of T. *harzianum* T-soybean has antifungal activity against *F. oxysporum,* which confers resistance in soybean to *F. oxysporum* [54]. Culture filtrate from *T. harzianum* inhibits the bean pathogen *Pythium ultimum. A* combination of this filtrate and chamomile extract reduces disease symptoms in *Phaseolus vulgaris* seeds [19]. Cell-free culture filtrates showed fungal growth inhibition against *Dematophora necatrix*, *F. solani*, *F. oxysporum* and *Pythium aphanidermatum*, at a concentration of 25% of the filtrate.

2.2.3 Defence induction and priming

Besides, *T. harzianum* can also induce resistance to nematodes and other pathogens. *T. harzianum* inhibits the growth of *Meloidogyne incognita* in tomato plants. In plants, it induces the expression of PR1, PR5, JERF3, and ACO, which are related to SA- and JA/Et-mediated defense responses. *T. harzianum* induces plant defense systems against insects, such as *Nezara viridula*, which feeds on plants. Aphids can also be controlled with it by inducing the plant's defense system against them [54]. Affected Tomato plants inoculated with *T. harzianum* T22 also expressed more loxD and PIN2 genes related to the JA-mediated defense pathway [1]. *T. harzianum* T22 also stimulates strong VOC priming in tomato plants, attracting the parasite *A. ervi*, so the plants can defend themselves against the aphid *M.* euphorbiae [54], reprogramming transcription factors and metabolites to support induction of JA, Et, and ISR defense pathways, and increasing isoprenoid biosynthesis to combat *M. euphorbiae* [54].

Among the defense responses of a plant, ROS production can be induced by beneficial microbes, such as *T. harzianum* inducing the accumulation of H_2O_2 and other defense-related enzymes, such as SOD, in Tomato plants after infection by *F. oxysporum* f.sp. *lycopersici* [82] to protect against it. *T. harzianum* colonizes cucumber roots and reduces ROS and reactive nitrogen species (RNS). Pathogen-induced amplification, redox homeostasis, and antioxidant enzymatic activity enhance plant protection [9]. *T. harzianum* induced priming, defense-related enzyme activity (PAL, POX, PPO), as well as antioxidant enzyme activity in chili pepper plants. In addition, *C. truncatum* reduces symptoms caused by pathogens and ROS accumulation, thus protecting the plant from them.

2.3 *Trichoderma asperellum*

T. asperellum has a wide range of temperatures, ranging from 25°C to 30°C, and is a cosmopolitan species that occurs in agriculture and undisturbed soils [54], and has lifestyles ranging from saprotrophy to biotrophy. After 5 days, dark green conidia form at the center of the colony in Petri dishes [78].

2.3.1 Competition

Along with *T. atroviride*, *T. asperellum* plays a significant role in pathogenic fungus control through competition, hyperparasitism or antibiosis, inducing plant resistance [79,80,54]. Among several strains of *Trichoderma*, in dual culture with *Fusarium camptocerus*, *Fusarium oxysporum*, *A. alternata*, *F. solani*, *Colletotrichum gleosporoides*, *Ganoderma applanatum*, *B. cinerea* and *Cytospora chrysosperma*. The *Trichoderma* strain TaspHu1, identified as *T. asperellum*, exhibited better biocontrol traits, inhibiting the growth of the pathogens by showing mycoparasitic activity and competition for space and nutrients [81]. A dual confrontation assay shows that T. *asperellum* inhibits the growth of *Colletotrichum truncatum* [79] of chilli.

Besides parasitizing other fungi, *T. asperellum* GDFS1009 is capable of parasitizing the moth *Ostrinia furnacalis*, a Maize pest, when it ingests the BCA conidia, and when inoculated in Maize plants. *T. asperellum* GDFS1009 induces POD, SOD, proline, protease, and PPO activities, increasing defense against the moth and the co-inoculation with the well-known entomopathogen *Beauveria bassiana* has a better protection effect in the plants [4].

2.3.2 Secondary metabolites

The enzyme VEL1 is involved in secondary metabolite synthesis. Overexpression in T. *asperellum* induces the expression of defense-related genes in maize plants, which confers resistance against *Cohilohorus herostrophus & Fusarium verticilloides*; co-cultivation of *T. asperellum* and *B. amyloliquefaciens* provides better protection against pathogens [33].Secondary metabolites from *T. asperellums* that evoke defense responses include Epl1-Tas, which induces the expression of genes related to SA-mediated defense pathways (NPR1, TGA, and PR1), JA-mediated defense pathways (COI1, JAZ, MYC2, and ORCA3), and auxin signaling (TIR1 and ARF1). PdPap increases defense-related enzyme activity, conferring over 90% more resistance to *A. alternata* [80]. The expression in plants of the class II hydrophobin HFBII-4 from *T. asperellum* ACCC30536 in

PdPap plants alters the expression of genes related to auxin signaling, SA and JA defense pathways, and defense-associated enzymatic activity (PAL, POD, PPO enzymes), reducing ROS accumulation and diminishing lesion area caused by *A. alternata* [84]. TaspHu1 makes tomato plants more resistant to *A. alternata* by inducing plant defense pathways, as indicated by increased expression of JAR1, MYC2, NPR1, PR1, and GH3.2 genes [81].

2.3.3 Defense induction and priming

Pisum sativum plants induced by *T. asperellum* T42 show enhanced antioxidant activities and lignin accumulation after infection by *Erysiphe pisi*, and co-culture with *Pseudomonas fluorescens* increases HR strength [52]. *T. asperellum* induces priming, defense-related enzymatic activity, and antioxidant activity in chili pepper plants upon infection with *C. truncatum*, reducing the symptoms and conferring resistance. A root dip with *T. asperellum* T1 increases β-1,3-glucanase, chitinase, POX, and phenol oxidase activity in lettuce, conferring resistance to *C. cassiicola* and *C. aeria* [3].

2.4 *Trichoderma virens*

It is a ubiquitous fungus that is isolated from soil and plants. There are two strains that can be distinguished by their secondary metabolite production in nature. The Q strain produces gliotoxin, dimethylgliotoxin, and viridiol. In contrast, P strains produce gliovirin, heptelidic acid, viridiol, and viridin [26].

Glyotoxin and gliovirin are two of the most important metabolites produced by this fungus. It has been reported that they exhibit strong toxic activity and play a role in the establishment of beneficial interactions with plants as well as pathogenic interactions with plant pathogens [54]. The use of secondary metabolites by this fungus as a primary biocontrol mechanism makes sense, given its strong reliance on secondary metabolites. As a result, mycoparasitism is also significant for *T. virens'* biocontrol capacity, as it also induces plant defense responses in order to protect plants from different pathogens by promoting plant defenses.

2.4.1 Competition

As an effective mycoparasite and antagonist, *T. virens* can inhibit the growth of several plant and fungal pathogens, including *F. oxysporum* f.sp. *physalia*. Dual confrontation with *T. virens* Gl006 and *Bacillus velezensis* Bs006 supernatant inhibits its growth. The major reduction in pathogen growth occurs when confronted with BCA alone (above 70%) [29]. Dual confrontation assays showed mycoparasitic activity over *R.* solani, penetrating the pathogen hyphae [20], inhibiting its growth. Its mycoparasitic abilities have been known for several decades, when it was first observed as coiling hyphae around *R. solani in* 1932 [51].

2.4.2 Secondary metabolites

T. virens IMI 304061 is a strain of *T. virens* that has a better antibiosis effect when it comes to *Pythium aphanidermatum.* It also confers increased protection in *Cicer arietinum* plants against *Sclerotium rolfsii* [54]. Gliotoxin from *T. virens* T23 controls *S. rolfsii*, damaging the pathogen's hyphae [27]. The volatile and non-volatile SMs from *T. virens* ZT05 inhibited the growth of *R. solani* at 80.1% and 63.32% respectively. The non-volatile SMs repressed defense-related enzymatic activity in *R. solani*, indicating that BCA could regulate the pathogen's defense mechanism against the mycoparasite [20]. Chitinase and cellulase protein activity are significant traits in BCA. Several *T. virens* mutant strains with enhanced chitinase and cellulase activities inhibited *R. solani* growth in dual confrontation assays than the *T. virens* wild-type strain [54].

Cell-free supernatants, such as *T. virens* Gl006 used alone or in combination with cells or cell-free supernatants from *B. velezensis* Bs006, can be used to test secondary metabolites produced by microorganisms. The culture filtrates from *T. virensis* have antagonistic activity against *F. oxysporum* f.sp. *physalia,* decreasing disease severity in plants of this species.

2.4.3 Defense induction and priming

T. virens induces plant defenses, conferring resistance to different pathogens. For example, *T. virens* IARI-P3 increases PR10 expression in susceptible and resistant *Vigna radiata* plants when infected with *R.*

solani, resulting in a significant reduction in disease symptoms [16]. *T. virens* increases the expression of two oxylipin genes in Maize plants, 12-OPDA (12-Oxo-10(Z),15(Z)-phytodienoic acid) and 9,10-KODA (10-oxo-9-hydroxy-12(Z), 15(Z)-octadecadienoic acid), thus conferring resistance to the pathogen *Colletotrichum graminicola* [75,76].

T. virens TriV_JSB100, or the fungus, induce priming in Tomato plants upon infection with *F. oxysporum* f.sp. *lycopersici*, diminishing the symptoms caused by the pathogen [31]. *T. virens* inoculation induced the JA-mediated defense pathway in the plant. In contrast, the fungal culture filtrate primarily triggers the SA-mediated defense pathway, resulting in overall resistance to the pathogen.

2.5 *Trichoderma longibrachiatum*

Agricultural soils, mushrooms, and marine environments are common habitats for *T. longibrachiatum*, which can cause cardiac and pulmonary mycoses in immunocompromised individuals [58,18,21]. Although it is reported to exert parasitism and induce plant defense systems, it has also been reported to produce several significant secondary metabolites.

2.5.1 Competition

According to the dual confrontation assays, *T. longibrachiatum* EF5 exhibited mycoparasitic activity against *M. phaseolina*, hyphal entanglement was observed between both fungi [68] and mycelia modifications showed antagonistic effects against *M. phaseolina* and *S. rolfsii*.

Mycoparasites of *T. longibrachiatum* (TG1) coil around *Fusarium pseudograminearum* in a mycoparasitic interaction. Wheat plants under salt stress conditions, the BCA reduces disease symptoms. Under field conditions, *T. longibrachiatum* T7407 competed with the pathogen *Magnaporthiopsis maydis* in soil, protecting Maize plants and reducing disease incidence. In addition to being a mycoparasite, *T. longibrachiatum* T7407 also protected maize plants from this pathogen. There is evidence that *T. longibrachiatum* T6 parasitizes *Heterodera avenae* eggs and second-stage juveniles, reducing their viability.

2.5.2 Secondary metabolites

A crude fungal extract containing peptaibols from *T. longibrachiatum* has antibacterial activity against *M. luteus* [54]. *Pyricularia oryzae* is a Rice pathogen and synthetic analogy to the peptaibol Trichogin GA IV from *T. longibrachiatum* are effective antagonistic compounds to inhibit it. It has been shown that synthetic analogy can reduce disease symptoms in Barley and Rice plants [66], which suggests that they can serve as biocidal compounds rather than chemicals. In contrast to chemical compounds, crude fungal extracts containing peptaibols from *T. longibrachiatum* IRAN 3067C inhibited several plant pathogens, notably *R. solani* and *A. solani* [54].

2.5.3 Defense induction and priming

A novel strain of *T. longibrachiatum* H9 colonized cucumber roots and induced JA/ET and SA defense signaling pathways, which conferred resistance to *B. cinerea* [54]. As well as increasing flavonoid and lignin content, *T. longibrachiatum* T6 also induced defense-related enzymatic activity in wheat roots, conferring resistance to *H. avenae* [85].

2.6 *Trichoderma viride*

The optimal growth temperature is 25°C; the isolate can be separated from soil and organic matter. Some strains have a faint coconut smell. Conidia can be observed after two days in some strains. It is one of the most common species of soil plants.

2.6.1 Competition

Due to its mycoparasitic ability, *T. viride* has been used as a biocontrol agent, particularly in the control of fungal pathogens like *F. moniliforme, Cryphonectria parasitica,* and *Schizophyllum commune*. The use of commercial enzymes derived from *T. viride* causes damage to the silkworm *Bombix mori* [5], suggesting that this fungus may degrade chitin from insects causing plant diseases. In dual culture experiments, *T. viride* competed for nutrients and space against *Sclerotinia sclerotiorum*, presenting an inhibitory zone in the culture plates after day 4 of interaction, indicating an antibiosis mechanism exerted by the agent. On day 6, *T. viride* inhibited the pathogen by 67.284% [40]. The growth of *Fusarium solani*, *R. solani*, and *S. rolfsii* was limited by *T. viride* in dual confrontation assays [2].

2.6.2 Secondary metabolites

T. viride produces antifungal SM. It was found that crude mycelial extract and ethanolic extract from this fungus had antifungal activity against *Candida albicans, Fusarium solani, Fusarium oxysporum, R. solani*, and *Pythium ultimum*. In addition, it had antibacterial activity against *Bacillus subtilis*, *Escherichia coli*, and *Pseudomonas fluorescens*, with a clear indication of inhibition zones. Antibacterial activity was found in *T. viride* VOCs against *B. subtilis* and *E. coli* also *antifungal activity against C. albicans, F. solani*, and *R. solani* [2].

The inoculation of *T. viride* alone or in combination with *Trichoderma erinaceum* suppressed *Sclerotinia sclerotiorum* disease in *Phaseolus vulgaris* cv. Anupama plants under glasshouse conditions. However, the combination of BCAs showed better results [40]. Also discovered that plants treated with either *Trichoderma* species or their combination reduced ROS accumulation induced by the pathogen increasing antioxidant activity.

3.Conclusion

Biocontrol agents are considered an environmentally friendly alternative to commercial pesticides and fertilizers due to their detrimental effects on human and environmental health. There are different biocontrol traits in *Trichoderma*, which makes it one of the most effective organisms studied against various plant pathogens, not only controlling fungi and oomycetes, but also insects and nematodes, either by limiting their growth by competition, antibiosis, or parasitism, or by enhancing plant defense against them, making this fungus an effective control option for a variety of phytopathogens.

To understand its interactions with the plant microbiome and its biocontrol characteristics, much work remains to be done regarding the application of *Trichoderma*-based formulations in field conditions and interaction with soilborne microorganisms. Further research is needed in this field.

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