Review Article

*Trichoderma*Species and theirBiological mechanisms

ABSTRACT: Biocontrol agents (BCA) are an important tool for preventing crop losses and increasing plant food production in agriculture. Providing an eco-friendly and more sustainable alternative to chemical pesticides and fertilizers. A number of biocontrol applications are often conducted on the fungus *Trichoderma*, which is one of the most widely used and studied organisms in the field due to its numerous biocontrol traits, including parasitism, secondary metabolite production, antibiosiswhich induced plant defense mechanisms. It is well known that several *Trichoderma* species act as mycoparasites. Certain species within this group also possess the ability to oppose many organisms, including nematodes and plant pests, hence exhibiting their versatility as a biological control agent. The utilization of bioformulations incorporating *Trichoderma* species or other beneficial microbes for plants, such as plant growth-promoting bacteria (PGPB), has gained significant traction in the agricultural industry. The present review provides a comprehensive summary of the biocontrol studies conducted on six commonly utilized *Trichoderma* species. It focuses on elucidating their biocontrol attributes and explores the potential of incorporating these fungal genera into *Trichoderma*-based formulations for safeguarding against plant diseases. Furthermore, it discusses the viability of *Trichoderma* as a substitute for chemical pesticides and fertilizers.

Keywords:*Trichoderma*sp.,biocontrolagent,parasitism, antibiosis, secondary metabolites and chemical pesticides.

1. INTRODUCTION

The increase in food demand is placing tremendous pressure on agricultural production systems due to global population growth. In addition to increasing efficiency and investment in greenhouse gardening, open-field cultivation must be expanded. Plant growth has been enhanced to its innate capacity with chemical fertilizers. Agriculture, on the other hand, faces serious financial losses due to pathogens, including viruses, bacteria, fungi, and other microorganisms [48]. Many agricultural producers use chemical pesticides because of their immediate use and ability to solve problems. Fertilizers and pesticides can have collateral impacts on the environment, as well as on human and animal health [73,58,56]. In several countries, especially northern countries and western Europe, as well as some eastern countries, chemical pesticides are being regulated to decrease the use of pathogens that become resistant over time. The trend is also occurring among consumers, who are switching from conventional to organic food production, while ignoring the large size and appearance of the vegetables and fruits, which is very similar to what is happening in other developing nations as well.

A variety of biocontrol agents are currently accessible for combating fungal phytopathogens, including as *Alternaria*, *Penicillium*, *Aspergillus*, and *Trichoderma*. *Trichoderma* has been identified as the most efficacious biocontrol agent in field conditions, as supported by previous studies [21,7]. The incidence of symptoms associated with *Sclerotium rolfsii* disease has been mitigated with the application of *Trichoderma* sp. There exists empirical evidence indicating that sunflower plants possess the capacity to accumulate salicylic and jasmonic acids, so enabling them to generate biocontrol agents that exhibit significant efficacy [7]. The fungal taxa comprising this assemblage include *Penicillium* sp., *Guignardiamangiferae*, *Hypocrea* sp., *Neurospora* sp., *Eupenicilliumjavanicum*, *Lasiodiplodiatheobromae* and *Trichoderma* sp. During the process of greenhouse cultivation, it was observed that the growth of *Fusarium oxysporum*f.sp. *cucumerinum* was impeded. A study conducted on 32 isolates of *Brugmansiaaurea* found that *A. aculeatus* shown inhibitory effects on both *F. fumigatus* and *F. solani*. These findings suggest that *A. aculeatus* has the potential to be used as a biological control agent (BCA) [37].

Fungal biological control agents (BCAs) have the potential to effectively eliminate insects and nematodes as well. Multiple species of *Trichoderma* have demonstrated efficacy in managing crop-damaging insects, including *Tetranychusurticae* [50]. Arbuscular mycorrhizal fungi (AMF) have been the subject of thorough investigation due to their significant impact on plant growth. Nevertheless, it is worth noting that they also possess strong phytopathogenic properties, particularly against nematodes such as *Meloidogyne incognita* [50]. *Arthrobotrysoligospora*, a bacterium known for its ability to capture nematodes, is a promising candidate as a biological control agent (BCA) against many infections. Fungi biocontrol agents have been found to have the potential to reduce abiotic challenges, such as high temperatures [10,35]. By eliciting systemic resistance,

UNDER PEER REVIEW

these agents have the potential to augment the plant's defense mechanisms. The implementation of this protective measure results in enhanced plant yields by mitigating the impact of several diseases. The significance of fungus in crop yield and plant growth has been well-documented [64]. *Trichoderma, Aspergillus, Fusarium, Penicillium, Piriformospora, Rhizoctonia, Colletotrichum, Gliocladium, Phoma*, and various other microorganisms have been reported to elicit plant growth [45,13]. The application of *Acremonium* sp., a type of fungus, resulted in the promotion of both root and shoot growth in Allium tuberosum plants. Additionally, it exhibited antifungal properties against *Botryiosphaeriadothidea* and *Botrytis cinerea* [14]. The biomass of Tobacco plants was seen to increase when exposed to *Alternaria* species, *Phomopsis species* and *Cladosporium* species, indicating their potential as plant growth boosters [61]. The genera *T. virens* and *T. atroviride* have been found to have the ability to improve the establishment of secondary root systems and increase biomass output in *Arabidopsis* and Tomato plants. These genera are widely recognized and utilized as plant growth promoters [64,38].

To mitigate the negative impacts of synthetic fertilizers and pesticides, it is imperative for agricultural production systems to transition towards sustainable practices. It is feasible to cultivate plants and safeguard them against pests and infections by the utilization of fungus belonging to the Trichoderma genus, presenting a cost-effective and environmentally sustainable alternative. Numerous nations employ bioinoculants using Trichoderma as a biological control agent. *Trichoderma* species constitute a significant proportion of the worldwide market for biological control agents (BCAs) [18,47]. *Trichoderma*-based biopesticides have been found to effectively control various fungal and oomycete pathogens. These pathogens include *Acremonium cucurbitacearum, Alternaria species, Aphanomyces cochlioides, Aspergillus species, Diplodianatalensis, Fusarium* species, *Gaeumannomycesgraministritici, Lasiodiplodiatheobroma, Phomabetae, Rhizoctonia solani, Lasiodiplodiatheobromae, Botrytis cinerea, Botryti*s species, *Collisletotnicios* species, *Collisletnicios* species *Rhizopusoryzae*, *Pythium* spp., *Serpula* spp., *Sclerotium* spp., and *Verticilliumdahliae*, among others (18).

The genus *Trichoderma* is a type of filamentous fungi that is frequently encountered in the soil, rhizospheres, and endospheres of many plants. In addition to exerting control over fungus and nematodes, these fungi have garnered significant interest [50]. This research presents a comprehensive analysis of the advantageous characteristics exhibited by different species of *Trichoderma*. It highlights the diverse methods via which these species contribute to the enhancement of sustainable agricultural production systems.

2. Mode of actions of*Trichoderma* species

Over 200 species of *Trichoderma* have been identified and studied as biocontrol agents and plant growth promoters [61,6]. As a result, extensive research has been conducted to investigate the processes by which *Trichoderma* exerts its effects, with particular emphasis on mycoparasitism and competition [22,44]. The synthesis of antagonistic secondary metabolites and the stimulation of systemic resistance in plants have been documented [50]. Several species of Trichoderma have been documented, such as *Trichoderma harzianum, T. asperellum, T. atroviride, T. longibrachiatum, T. viride,* and *T. virens*, which have been extensively studied [43]. The initial three species are widely employed as biocontrol agents for the management of fungal phytopathogens through mechanisms such as mycoparasitism and competition. Species such as *T. virens, T. longibrachiatum* and *T. viride* employ antibiosis as a mechanism of defense against many plant diseases [25, 44, 59, 63].

2.1*Trichoderma atroviride*

Trichoderma atroviride, a filamentous fungus, is commonly found in soil in temperate climates. It thrives best at a temperature of 25°C and typically develops hyaline spores with inconspicuous aerial hyphae. Within a span of two to seven days, it produces gray or dark green conidia [50]. The distinct aroma of coconut is attributed to the synthesis of a volatile compound known as 6-pentyl-2H-pyran-2-one (6-PP). This compound not only imparts the characteristic scent but also serves as a biocontrol agent against various plant pathogens such as *Cylindrocarpondestructans, Macrophominaphaseolina*, and *Phytophthora* sp. Additionally, it exhibits properties that promote plant growth and augment systemic resistance.

2.1.1 Competition

The phenomenon of competition for resources, specifically space and nutrients, arises as a result of the inhibitory effects exerted by *T. atroviride* on the growth of Phytophthora and the synthesis of zoospores. The symbiotic relationship between *T. atroviride* and Tomato plants results in an increased level of resistance to the disease produced by this particular oomycete [28]. Moreover, *T. atroviride* engages in competitive interactions

UNDER PEER REVIEW

and antagonistic activities against *Fusarium avenaceum* and *Fusarium culmorum*, which are significant pathogens of maize, as well as *Neofusicoccum parvum*, a disease affecting grapevines [8]. The results of dual culture assays demonstrate that *T. atroviride* is capable of parasitizing a range of fungal and oomycete species, including *Neofusicoccumbatangarum, Phytophthora nicotianae*, *Penicillium digitatum, P. roqueforti, P. verrucosum, Aspergillus steynii, Fusarium proliferatum, F. verticilloides, F. sporotrichoides*, and *F. poae* [60].

2.1.2 Secondary metabolites

The evaluation of biocontrol characteristics can be conducted using intact fungal cultures or extracts. It is also possible to test individual components or test a combination of components derived from an extract as a whole. Consequently, the whole fungal cultures including soluble metabolites derived from the indigenous *T. atroviride* strain BC0584, as well as its volatile organic compounds (VOCs), exhibit inhibitory effects on *F. avenaceum*. In contrast, neither soluble metabolites nor volatile organic compounds (VOCs) exhibited inhibitory effects in *F. culmorum*. Nevertheless, the control of both diseases is achieved with the utilization of *T. atroviride* BC0584 [8]. Volatile organic compounds (VOCs) are generated by many *Trichoderma* species. Among these compounds, 6-PP has been extensively studied and is considered the most well-characterized VOC produced by species capable of synthesizing this particular molecule, such as *T. atroviride* [50]. Increased quantities of 6-PP are produced in the absence of light. The strains *T. atroviride* P1 and IMI 206,040 have been found to have antagonistic effects against *R. solani* and *F. oxysporum* [30]. Metabolites, such as antibiotics, are acquired from fermented cultures following a multi-day cultivation of the fungus in a liquid medium [50]. The growth of B. cinerea was inhibited by 73% in an in vitro study using fermented cultures derived from *T. atroviride* CCTCCSBW0199, suggesting the presence of an antibiosis mechanism for controlling the pathogen [67].

In the course of a comprehensive investigation on pathogens, it was observed that the ethyl acetate extract and fungal filtrate derived from *Trichoderma* exhibit cytotoxic properties and hinder the growth of 25 different pathogens. These pathogens encompass seven species of *Penicillium*, six species of *Aspergillus*, six species of *Fusarium*, two species of *Neofusicoccum*, two species of *Colletotrichum*, and two species of *Phytophthora* [69]. The *Trichoderma* velvet complex encompasses various physiological processes, one of which involves the production of secondary metabolites [63]. In a research investigation, the function of vel1, a constituent of the velvet complex in *T. atroviride* T2, was examined. Another analysis revealed that the fungal extract derived from the wild-type strain was discovered. According to the authors, the strain that overexpresses vel1, when used alone or in co-culture with *Bacillus amyloliquefaciens* 1841, demonstrates inhibitory effects on the growth of the Wheat pathogen *F. graminearum* and reduces the severity of disease in treated plants. The authors also suggest that co-cultures exhibit superior inhibitory effects on the pathogen and enhance plant resistance compared to individual cultures [50,32].

Trichoderma atroviride has the ability to elicit plant resistance against pathogens through the production and release of secondary metabolites. The activity of peroxidase (POD) and superoxide dismutase (SOD) can be enhanced in plants through the fermentation of cultures of *T. atroviride* CCTCCSBW0199, either alone or in combination with brassinolide. This enhancement can lead to an increase in plant resistance and a reduction in symptoms induced by *B. cinerea* [68]. A swollenin is a protein that bears resemblance to a plant expansin, and it plays a role in the regulation of cell wall remodeling and colonization. The swollenin TaSWO1, which is synthesized by the fungus *T. atroviride*, has been found to elicit a defensive response in *Capsicum annum* plants, leading to increased resistance against the diseases *A. solani* and *R. solani*. Consequently, the presence of TaSWO1 results in a reduction of symptoms induced by these particular pathogens [63]. In *T. atroviride* IMI 206,040, a LysM effector known as Tal6 has been discovered. This effector has the ability to bind to fungal chitin, thereby inhibiting the plant's ability to detect the biological control agent (BCA). Consequently, Tal6 facilitates the establishment of a mutually beneficial interaction and enhances the mycoparasitic activity of T. atroviride against various pathogens, including *B. cinerea, Sclerotium cepivorum, Colletotrichum lindemutianum* and *R. solani* AG2 [55]. *Trichodermaatroviride* exhibits the capacity to synthesize a diverse array of volatile and non-volatile secondary metabolites, which serve as markers of its efficacy in managing various phytopathogens. Consequently, *T. atroviride* emerges as a potent biological control agent (BCA) with broad applicability across diverse agricultural settings.

2.1.3 Defence induction and priming

The activation of plant defense mechanisms by *Trichoderma atroviride* is considered to be a highly significant mechanism of action for this biological control agent. The efficacy of indirect mechanisms, such as the use of fungicides, in managing a diverse array of plant diseases surpasses that of direct mechanisms, such as

UNDER PEER REVIEW

mycoparasites, which may exhibit limitations in their effectiveness. In certain cases, indirect procedures can still be employed to complement it. Hence, *Trichoderma atroviride* demonstrates efficacy as an antagonist against several pathogens, including fungi, oomycetes, insects, and other plant pathogens.When *Trichoderma* colonizes the roots of a plant, it can trigger different defense responses. For instance, the colonization of grapevine Tempranillo cultivar by *T. atroviride* SC1 induces a defense response mediated by salicylic acid (SA). This response enhances the plant's ability to protect itself against *Neospora parvum*. Furthermore, the growth of *Neospora parvum* is inhibited when it is cultured alongside *T. atroviride*. This information is supported by reference [34]. The colonization of a plant by *Trichoderma* species results in the alteration of its transcriptome, leading to modifications in genes associated with plant defensive responses. One such example is *T. atroviride* P1, which modulates gene transcripts associated with plant defense mechanisms and generates volatile organic compounds (VOCs) that serve to attract *Aphidiuservi*, a wasp species known for preying on aphids. Tomato plants possess a heightened defense mechanism against the aphid *Macrosiphum euphorbiae* and the moth *Spodoptera littotalis*, which is more efficacious in nature. This finding demonstrates that *T. atroviride* has the potential to indirectly regulate infections by influencing plant physiology [35]. In addition to the alteration of plant defense genes, the presence of *T. atroviride* in plants triggers a process known as Arabidopsis's small RNA-mediated gene silencing. This phenomenon ultimately leads to an upregulation of gene expression in the jasmonic acid (JA) and salicylic acid (SA)-mediated pathways. Consequently, this priming effect enhances the plants' resistance to *B. cinerea*, a pathogenic fungus [36].

2.2*Trichoderma harzianum*

Trichoderma harzianum exhibits optimal growth in temperate regions, particularly at a temperature of 30 degrees Celsius. Conidia of *T. harzianum* manifest on petri dishes in concentric zones, transitioning from a green hue to a brown coloration by the second day. In contrast to *T. atroviride, T. harzianum* lacks any discernible olfactory characteristics. It is present in several substrates, including soil, other fungus, decomposing plant matter, and as an endophyte within multiple plant species. In its capacity as a biocontrol agent, it effectively mitigates the incidence and spread of soil-borne illnesses. One of the active constituents found in commercial solutions utilized for the purpose of managing agricultural diseases and enhancing plant development and productivity has been identified [50].

2.2.1 Competition

The fungus *Trichoderma harzianum* exhibits the ability to inhibit the growth of mycotoxin-producing fungi, including *Fusarium solani*, through mechanisms such as competition and antibiosis [8, 38]. In a laboratory experiment examining the interaction between *F. oxysporum*f.sp. *lycopersici* and five *Trichoderma* species, it was shown that all of the Trichoderma species had inhibitory effects on the growth of the pathogen. Among the *Trichoderma* species examined, both strains of *T. harzianum*, namely BHU-BOT-RYRL4 and MTCC936, demonstrated the highest degree of growth inhibition, with percentages of 83.17% and 72.13% respectively. The findings of a rhizosphere colonization investigation revealed that *T. harzianum* Tr904, along with *T. gamsii* and *T. afroharzianum*, engaged in competitive interactions with *Fusarium pseudograminearum* in terms of resource utilization and spatial occupancy, hence impeding the development of the disease produced by this particular pathogen.

In the context of the interaction between *T. harzianum* and *Fusarium sudanense*, the biological control agent (BCA) parasitizes the pathogen by breaking down its hyphae and suppressing its growth through competition for resources and physical space [39]. In laboratory conditions, it was observed that *T. harzianum* exhibited antagonistic effects against *Alternaria cerealis*, leading to a restriction in its growth [72]. Additionally, *T. harzianum* T-soybean demonstrated mycoparasitic activity against *F. oxysporum*, resulting in a reduction of its growth by 45.45% [50]. The experimental procedure involved conducting dual confrontation experiments using two strains of *T. hazianum*, namely CMML20-26 and CMML20-27, respectively. The study reported significant antibiotic efficacy against various fungal strains, including *Fusarium ipomeae, Fusarium oxysporum, F. solani, Penicillium citrinum, P. rotoruae, Aspergillus wentii, Mucor variicolumellatus*, and *M. phaseolina* [41]. *Trichoderma harzianum* MRI001 has parasitic behavior towards *Fusarium oxysporum, Alternaria alternata,Aspergillus carbonarius*, and *Aspergillus flavus*. The proliferation of pathogens will be induced, leading to a decrease in the generation of mycotoxins ochratoxin and aflatoxin B1, which are synthesized by *A. carbonarius* and *A. flavus*, respectively [8]. *T. harzianum* engages in competitive interactions with *Colletotrichum truncatum*, resulting in the inhibition of the latter's growth [42]. Multiple strains of *T. hazianum* originating from Egypt exhibited mycoparasitic activity against *F. graminearum, M. phaseolina*, and *F. solani.* The efficacy of *T. harzianum* Th6 was observed to be highest against all three infections [43,44]. Th6 was

UNDER PEER REVIEW

discovered to exhibit efficacy against *Pythium aphanidermatum*, *Alternaria brassicicola*, and *Botrytis cinerea* as well. Furthermore, it has been observed that the application of Th6 has the potential to promote the growth of plants, raise the productivity of crops, and bolster their ability to withstand both biotic and abiotic stressors.

2.2.2 Secondary metabolites

Trichoderma harzianum is capable of synthesizing secondary metabolites that possess significant biological properties. In the context of maize roots, it has been observed that *T. harzianum* triggers the production of volatile organic compounds (VOCs). Additionally, the application of 6-PP externally has been found to mitigate the harm inflicted by *Phyllophagavetula*, indicating that the volatiles released by the fungus confer resistance to the plant. However, it is important to note that direct biocontrol of the pest has not been observed in this particular study [45]. The ThMBF1 transcriptional coactivator of *Trichoderma harzianum* T34 has a role in the biosynthesis of secondary metabolites. The regulation of biological control agents (BCAs) is of utmost importance in order to effectively maintain their ability to limit the growth of Botrytis cinerea (B. cinerea) and *Fusarium oxysporum*. Overexpression of BCAs has been shown to have a major negative impact on their ability to inhibit pathogen growth and confer resistance.

Peptaibols, which are secondary metabolites derived from various *Trichoderma* species, exhibit antibiosis efficacy against multiple pathogens [50]. Three peptaibols derived from *Trichoderma harzianum* HK-61, specifically referred to as trichorzins HA II, HA V, and HA VI, exhibited a significant reduction in *Vigna sesquipedalis* lesions by around 90%, with trichorzins HA V being particularly effective in this regard. Secondary metabolites possess the capacity to exhibit antibacterial or antimicrobial properties. The antibiotic activity of a fungal extract derived from *T. harzianum* CCTCC-RW0024 was seen to limit the development of *F. graminerium*, resulting in a significant reduction of pathogen growth by 96.3% [46]. The antifungal activity of a culture filtrate derived from *Trichoderma harzianum* T-soybean has been observed against *Fusarium oxysporum*. This activity has been found to provide soybean plants with resistance against *F. oxysporum* [50]. The culture filtrate derived from *Trichoderma harzianum* exhibits inhibitory effects against the bean pathogen *Pythium ultimum*. The symptoms of disease in *Phaseolus vulgaris* seeds are reduced when a combination of the filtrate and chamomile extract is employed [47]. The cell-free culture filtrates exhibited antifungal activity against *Dematophoranecatrix, F. solani, F. oxysporum*, and *Pythium aphanidermatum* when applied at a concentration of 25% of the filtrate.

2.2.3 Defence induction and priming

In addition, *T. harzianum* has the ability to elicit resistance against nematodes and other diseases. *Trichoderma harzianum* exhibits inhibitory effects on the growth of *Meloidogyne incognita* in tomato plants. In the context of plant biology, it has been observed that the aforementioned genes, namely PR1, PR5, JERF3, and ACO, are upregulated as a result of certain stimuli. These genes are known to be associated with defense responses mediated by salicylic acid (SA) and jasmonic acid/ethylene (JA/Et). *Trichoderma harzianum* elicits plant defense mechanisms against herbivorous insects, such as *Nezaraviridula*, which is known to consume plant tissues. Aphids can also be managed by the activation of the plant's defensive mechanisms against them [9]. Tomato plants that were subjected to inoculation with *T. harzianum* T22 exhibited an increased expression of loxD and PIN2 genes, which are associated with the defense pathway mediated by jasmonic acid (JA) [1]. *T. harzianum* T22 has been observed to induce significant volatile organic compound (VOC) priming in tomato plants, which in turn attracts the parasite *A. ervi*. This interaction enables the plants to initiate a defense response against the aphid *M. euphorbiae.* The mechanism involves the alteration of transcription factors and metabolites to facilitate the activation of jasmonic acid (JA), ethylene (Et), and induced systemic resistance (ISR) defense pathways. Additionally, there is an increase in isoprenoid biosynthesis, which aids in combating the presence *of M. euphorbiae*[50].

One of the defense mechanisms exhibited by plants involves the generation of reactive oxygen species (ROS), which can be triggered by helpful microorganisms like *T. harzianum*. This microbial induction leads to the buildup of hydrogen peroxide (H2O2) and other defense-related enzymes, including superoxide dismutase (SOD), in Tomato plants following infection by *F. oxysporum*f.sp. *lycopersici*. These defense responses serve to protect the plants against the harmful effects of the pathogen [49]. *Trichoderma harzianum* exhibits colonization of cucumber roots and exhibits the ability to mitigate the presence of reactive oxygen species (ROS) and reactive nitrogen species (RNS). The enhancement of plant protection is facilitated by pathogen-induced amplification, maintenance of redox equilibrium, and increased activity of antioxidant enzymes (source: [50]). *Trichoderma harzianum* elicited priming in chili pepper plants, resulting in the activation of defense-related enzymes such as

UNDER PEER REVIEW

phenylalanine ammonia-lyase (PAL), peroxidase (POX), and polyphenol oxidase (PPO), as well as enhanced activity of antioxidant enzymes. Furthermore, *C. truncatum* exhibits the ability to mitigate symptoms induced by pathogens and the formation of reactive oxygen species (ROS), hence conferring protective effects on the host plant.

2.3*Trichoderma asperellum*

T.asperellum exhibits a broad thermal tolerance, spanning from 25°C to 30°C. This species is cosmopolitan in nature, being found in both agricultural and undisturbed soil environments [50]. Moreover, *T. asperellum* demonstrates a diverse variety of lifestyles, encompassing both saprotrophic and biotrophic modes of existence. Following a period of five days, the formation of dark green conidia may be observed at the central region of the colony within the petri dishes [62].

2.3.1 Competition

In addition to *T. atroviride*, *T. asperellum* plays a substantial role in the control of pathogenic fungi through mechanisms such as competition, hyperparasitism, antibiosis, and the induction of plant resistance [42, 57, 50]. In the present study, various strains of *Trichoderma* were examined in a dual culture setup with *Fusarium camptocerus, Fusarium oxysporum, Alternaria alternata, Fusarium solani, Colletotrichum gleosporoides*, *Ganoderma applanatum*, *Botrytis cinerea*, and *Cytosporachrysosperma*. The *Trichoderma* strain TaspHu1, which was identified as *T. asperellum*, demonstrated superior biocontrol characteristics by effectively suppressing pathogen growth through mycoparasitic activity and competitive interactions for resources [53]. The findings of a dual confrontation experiment indicate that *T. asperellum* exhibits inhibitory effects on the growth of *Colletotrichum truncatum,* a pathogenic fungus affecting chili plants [42].

In addition to its ability to parasitize other fungi, *T. asperellum* GDFS1009 demonstrates the capacity to parasitize the moth *Ostriniafurnacalis*, a known pest of Maize, through the ingestion of BCA conidia. This parasitic behavior has also been observed when T. asperellum GDFS1009 is introduced into Maize plants. *T. asperellum* GDFS1009 elicits the activities of peroxidase (POD), superoxide dismutase (SOD), proline, protease, and polyphenol oxidase (PPO), hence enhancing the plant's defense mechanisms against the moth. Additionally, the co-inoculation of *T. asperellum* GDFS1009 with the widely recognized entomopathogen *Beauveria bassiana* has a more pronounced protective impact on the plants [56].

2.3.2 Secondary metabolites

The enzyme VEL1 has a role in the biosynthesis of secondary metabolites. The overexpression of *T. asperellum* in maize plants leads to the activation of defense-related genes, resulting in enhanced resistance against *Cohilohorusherostrophus* and *Fusarium verticilloides*. Additionally, the co-cultivation of *T. asperellum* and *B. amyloliquefaciens* offers improved protection against pathogens, as reported in a previous study [32]. The secondary metabolites derived from Trichoderma asperellum have been found to elicit defense responses. One such metabolite, Epl1-Tas, has been observed to stimulate the activation of genes associated with salicylic acid (SA)-mediated defense pathways, including NPR1, TGA, and PR1. Additionally, Epl1-Tas has been shown to induce the expression of genes involved in jasmonic acid (JA)-mediated defense pathways, such as COI1, JAZ, MYC2, and ORCA3. Furthermore, Epl1-Tas has been found to impact auxin signaling by upregulating the expression of TIR1 and ARF1 genes. The application of PdPap has been found to enhance the activity of defense-related enzymes, resulting in a significant increase of over 90% in resistance against A. alternata [57]. The upregulation of the class II hydrophobin HFBII-4 from *T. asperellum* ACCC30536 in PdPap plants induces changes in the expression of genes associated with auxin signaling, SA and JA defense pathways, and defense-related enzymatic activity (PAL, POD, PPO enzymes). This alteration leads to a decrease in reactive oxygen species (ROS) accumulation and a reduction in the size of lesions caused by *A. alternata* [84]. TaspHu1 enhances the resistance of tomato plants against *A. alternata* by stimulating the activation of plant defense mechanisms, as evidenced by the upregulation of JAR1, MYC2, NPR1, PR1, and GH3.2 genes [53].

2.3.3 Defense induction and priming

The strain *T. asperellum* T42 exhibits heightened antioxidant activity and increased lignin buildup during infection by *Erysiphe pisi*. Additionally, when co-cultured with *Pseudomonas fluorescens*, it enhances the hypersensitive response (HR) strength in *Pisum sativum* plants [57]. *Talaromycesasperellum* elicits priming,

UNDER PEER REVIEW

activates defense-related enzymes, and enhances antioxidant activity in Capsicum annuum plants following infection with *Colletotrichum truncatum*, resulting in symptom reduction and the acquisition of resistance. The application of a root dip containing *T. asperellum* T1 has been found to enhance the activity of β-1,3-glucanase, chitinase, peroxidase (POX), and phenol oxidase in lettuce. This increase in enzymatic activity contributes to the plant's resistance against the pathogens *C. cassiicola* and *C. aeria* [58].

2.4*Trichoderma virens*

This fungus is commonly found in various environments, including soil and plants. In nature, two strains can be differentiated based on their secondary metabolite production. The Q strain is known to generate gliotoxin, dimethylgliotoxin, and viridiol. On the other hand, P strains have been found to synthesize gliovirin, heptelidic acid, viridiol, and viridin [59].Glyotoxin and gliovirin represent two prominent metabolites synthesized by the aforementioned fungus. According to reports, these organisms demonstrate significant toxicity and contribute to the formation of mutually beneficial relationships with plants, as well as antagonistic relationships with plant pathogens [50].The utilization of secondary metabolites as a main biocontrol mechanism by this fungus is logical, considering its significant dependence on secondary metabolites. Consequently, mycoparasitism plays a crucial role in enhancing the biocontrol efficacy of *T. virens*, since it elicits plant defense mechanisms aimed at safeguarding plants against diverse diseases through the stimulation of plant defense responses.

2.4.1 Competition

T. virens demonstrates efficacy as a mycoparasite and antagonist, effectively impeding the proliferation of several plant and fungal diseases, such as *F. oxysporum*f.sp. *physalia*. The growth of *T. virens* Gl006 and *Bacillus velezensis* Bs006 is inhibited by the dual confrontation with their respective supernatants. The primary decrease in pathogen proliferation is observed when exposed just to biological control agents (BCA), with a reduction rate above 70% [60]. The results of dual confrontation experiments demonstrated the mycoparasitic activity of the tested organism against *R. solani*. This activity was observed through the penetration of the pathogen's hyphae and subsequent inhibition of its growth [61]. The mycoparasitic capabilities of this organism have been recognized for numerous years, dating back to its initial observation of coiling hyphae around *R. solani* [25].

2.4.2 Secondary metabolites

The strain T. virens IMI 304061 exhibits enhanced antibiosis against *Pythium aphanidermatum* compared to other strains of *T. virens*. Furthermore, it has been observed that the application of this treatment provides enhanced defense mechanisms in *Cicer arietinum* plants, resulting in heightened resistance against the pathogenic effects of *Sclerotium rolfsii* [50]. The control of *S. rolfsii* by gliotoxin derived from *T. virens* T23 is achieved by the damage inflicted on the hyphae of the pathogen [63]. The growth of *R. solani* was suppressed by 80.1% and 63.32% with the application of volatile and non-volatile secondary metabolites (SMs) derived from T. virens ZT05, respectively. The non-volatile secondary metabolites (SMs) were found to inhibit the enzymatic activity associated with defensive mechanisms in *R. solani*, suggesting that biological control agents (BCAs) have the potential to govern the pathogen's defense response to the mycoparasite [61]. The activity of chitinase and cellulase proteins is considered to be of great importance in the context of biological control agents (BCA). In dual confrontation experiments, it was observed that certain mutant strains of T. virens exhibited increased chitinase and cellulase activities, resulting in a greater inhibition of *R. solani* growth compared to the wild-type strain of *T. virens* [50]. The utilization of cell-free supernatants, specifically T. virens Gl006 in isolation or in conjunction with cell-free supernatants or cells derived from *B. velezensis* Bs006, presents a viable approach for assessing the secondary metabolites synthesized by microorganisms. The culture filtrates derived from *T. virensis* exhibit antagonistic properties against *F. oxysporum*f.sp. *physalia*, resulting in a reduction in disease severity in plants belonging to this particular species.

2.4.3 Defense induction and priming

Trichoderma virens elicits plant defense mechanisms, hence imparting resistance against several diseases. As an illustration, the strain *T. virens* IARI-P3 has been seen to enhance the expression of PR10 in both susceptible and resistant Vigna radiata plants upon infection with *R. solani*. This subsequently leads to a noteworthy decrease in disease symptoms, as reported in a previous study [64]. T. virens induces the

UNDER PEER REVIEW

upregulation of two oxylipin genes, namely 12-OPDA (12-Oxo-10(Z),15(Z)-phytodienoic acid) and 9,10-KODA (10-oxo-9-hydroxy-12(Z), 15(Z)-octadecadienoic acid), in Maize plants. This upregulation leads to the development of resistance to the parasite *Colletotrichum graminicola* [65,69].

T. virens TriV_JSB100, also known as the fungus, has been seen to elicit priming in Tomato plants when they are infected with *F. oxysporum*f.sp. *lycopersici*, resulting in a reduction of the symptoms induced by the pathogen [67]. The inoculation of T. virens resulted in the activation of the jasmonic acid (JA)-mediated defense system in the plant. On the other hand, the fungal culture filtrate predominantly induces the defense mechanism mediated by salicylic acid (SA), leading to a general increase in resistance against the pathogen.

2.5*Trichoderma longibrachiatum*

T. longibrachiatum is frequently found in agricultural soils, mushrooms, and coastal settings, serving as homes for this organism. In patients with weakened immune systems, *T. longibrachiatum* has the potential to induce cardiac and pulmonary mycoses [58,18,21]. While there are reports of its parasitic nature and ability to trigger plant defense mechanisms, it has also been documented to synthesize various noteworthy secondary metabolites.

2.5.1 Competition

Based on the findings from the dual confrontation experiments, it was revealed that *T. longibrachiatum* EF5 shown mycoparasitic activity against *M. phaseolina*. The interaction between the two fungi resulted in hyphal entanglement, and alterations in the mycelia of *T. longibrachiatum* EF5 exhibited antagonistic effects against both *M. phaseolina* and *S. rolfsi*i [68].

The mycoparasites of *Trichoderma longibrachiatum* (strain TG1) exhibit a coiling behavior around *Fusarium pseudograminearum* during a mycoparasitic contact. Under conditions of salt stress, the use of beneficial microorganisms, known as biocontrol agents (BCAs), has been found to mitigate disease symptoms in wheat plants. In a field setting, the fungus *T. longibrachiatum* T7407 engaged in competitive interactions with the pathogenic organism *Magnaporthiopsis maydis* within the soil environment. As a result of this competition, the presence of *T. longibrachiatum* T7407 led to the protection of Maize plants and a subsequent decrease in the occurrence of disease. Furthermore, *T. longibrachiatum* T7407 exhibited mycoparasitic properties and demonstrated its ability to provide protection to maize plants against the aforementioned disease. There exists empirical evidence indicating that *T. longibrachiatum* T6 exhibits parasitic behavior towards the eggs and second-stage juveniles of *Heteroderaavenae*, resulting in a notable reduction in their overall viability.

2.5.2 Secondary metabolites

The antibacterial activity of a fungal extract derived from *T. longibrachiatum*, consisting of peptaibols, has been shown against *M. luteus* [50]. *Pyriculariaoryzae* is a pathogenic organism that only affects rice plants. In the context of combating this pathogen, it has been observed that synthetic analogues of the peptaibol Trichogin GA IV, derived from the fungus *Trichoderma longibrachiatum*, exhibit significant efficacy as antagonistic chemicals to suppress the growth and proliferation of *Pyriculariaoryzae*. Previous research has demonstrated that the application of synthetic analogy has the potential to alleviate disease symptoms in Barley and Rice plants [69]. This finding implies that synthetic analogy may function as biocidal agents, offering an alternative to conventional chemical treatments. In comparison to chemical substances, the crude fungal extracts that consist of peptaibols derived from *T. longibrachiatum* IRAN 3067C shown inhibitory effects on various plant pathogens, particularly *R. solani* and *A. solani* [50].

2.5.3 Defense induction and priming

In a recent study, it was observed that a novel variant of the *T. longibrachiatum* H9 species successfully established itself on the roots of cucumber plants. This colonization led to the activation of the jasmonic acid/ethylene (JA/ET) and salicylic acid (SA) defensesignaling pathways. Consequently, the cucumber plants exhibited enhanced resistance against the pathogenic fungus *B. cinerea* [50]. In addition to augmenting the levels of flavonoids and lignin, the application of *T. longibrachiatum* T6 also stimulated the enzyme activity associated with defense mechanisms in the roots of wheat plants, thereby providing protection against *H. avenae* [70].

UNDER PEER REVIEW

2.6*Trichoderma viride*

The preferred temperature for growth is 25°C, and the organism can be extracted from soil and organic substances. Certain strains exhibit a subtle aroma reminiscent to coconut. In certain strains, the presence of conidia can be seen within a span of two days. This particular species is widely prevalent across various soil types and plant varieties.

2.6.1 Competition

T. viride has been employed as a biocontrol agent due to its mycoparasitic capacity, namely in the management of fungal infections such as *F. moniliforme*, *Cryphonectriaparasitica*, and *Schizophyllum commune*. The utilization of commercial enzymes obtained from *T. viride* has been observed to result in adverse effects on the silkworm *Bombix mori*. This observation implies that this particular fungus may possess the capability to destroy chitin found in insects, hence potentially contributing to the occurrence of plant diseases [5]. In the context of dual culture experiments, it was seen that T. viride engaged in a competitive interaction with *Sclerotinia sclerotiorum*, for both nutrients and physical space. This competition resulted in the formation of an inhibitory zone on the culture plates, which became apparent after the fourth day of interaction. This observation suggests that *T. viride* employs an antibiosis mechanism to exert its inhibitory effects on *Sclerotinia sclerotiorum*. On the sixth day, *Trichoderma viride* exhibited a 67.284% inhibition of the pathogen, as reported in reference [72]. In dual confrontation tests, it was shown that the development of *Fusarium solani, R. solani*, and *S. rolfsii* was constrained by the presence of *T. viride* [73].

2.6.2 Secondary metabolites

Trichoderma viride is capable of synthesizing antifungal secondary metabolites. The study revealed that the crude mycelial extract and ethanolic extract derived from this particular fungus had antifungal properties against *Candida albicans*, *Fusarium solani, Fusarium oxysporum, R. solani*, and *Pythium ultimum*. Furthermore, it exhibited antibacterial efficacy against *Bacillus subtilis, Escherichia coli,* and *Pseudomonas fluorescens*, as evidenced by the presence of distinct zones of inhibition. The study reported the presence of antibacterial activity in the volatile organic compounds (VOCs) of *T. viride* against *B. subtilis* and *E. coli*. Additionally, antifungal activity was seen against *C. albicans, F. solani*, and *R. solani* [73].

Under controlled settings in a glasshouse, the application of *T. viride* alone or in conjunction with *Trichoderma erinaceum* effectively mitigated the incidence of *Sclerotinia sclerotiorum* disease in *Phaseolus vulgaris* cv. Anupama plants. However, the amalgamation of biological control agents (BCAs) yielded more favorable outcomes (40). It was also observed that plants subjected to treatment with either Trichoderma species or a combination thereof exhibited a decrease in the formation of reactive oxygen species (ROS) caused by the pathogen, while simultaneously enhancing antioxidant activity.

3.Conclusion

Biocontrol agents are regarded as a more ecologically sustainable substitute for conventional pesticides and fertilizers, primarily because of their adverse impacts on human and environmental well-being. Trichoderma possesses diverse biocontrol characteristics, rendering it a highly efficacious organism in combatting a wide range of plant pathogens. Its effectiveness extends beyond fungi and oomycetes, encompassing insects and nematodes as well. This is achieved through mechanisms such as growth inhibition via competition, antibiosis, or parasitism, as well as by bolstering plant defenses against these pathogens. Consequently, *Trichoderma* emerges as a potent control alternative for various phytopathogens. Further research is required to gain a comprehensive understanding of the interactions between *Trichoderma*-based formulations and the plant microbiome, as well as the biocontrol features of *Trichoderma*. This research should specifically focus on the use of *Trichoderma*-based formulations in field circumstances and their interactions with soilborne microorganisms. Additional investigation is required within this particular domain.

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