



Revolutionary Role of Trichoderma in Sustainable Plant Health Management: A Review

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This work was carried out in collaboration among all authors. Authors AKS and RS conceived the presented idea about the topic selection for the review paper and wrote the paper. Authors AK and RS collection of data. Authors SM, ML, VS performed computer simulations and contributed to paper writing. Authors BK and PSD performed text mining analysis and reviewed the paper. Ethical and informed consent for data use: The information provided in the article related to the topic that helpful for readers. Data availability and access: The data available in the article is freely available. All authors read and approved the final manuscript.

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ABSTRACT

The use of chemical pesticides in agricultural practices has led to significant concerns related to health and the environment in the last few decades. Consequently, there has been a growing interest in finding alternative approaches for controlling pests and diseases that are effective and environmentally friendly. Among these alternatives, *Trichoderma harzianum* has gained attention due to its remarkable ability to combat various crop pathogens in sustainable form. Biocontrol agents have gained prominence as eco-friendly substitutes for conventional chemical pesticides in disease management and crop improvement. *T. harzianum*, a common filamentous fungus, has emerged as a promising biocontrol agent due to its multifaceted strategies for suppressing diseases and promoting crop growth. *T. harzianum* fosters plant growth by aiding nutrient absorption, improving soil structure, and generating growth-promoting substances like auxins and cytokinins. Field studies have substantiated the efficacy of *T. harzianum* in managing a wide array of plant diseases caused by fungi, bacteria, and nematodes whether used as a seed treatment, soil application, or foliar spray, *T. harzianum* establishes a beneficial presence early in the plant's life cycle, providing enduring protection. In conclusion, *T. harzianum* holds immense potential as a biocontrol agent to sustainably safeguard crops. *Trichoderma* species play a pivotal role in managing plant diseases due to their versatile mechanisms. As global agriculture seeks alternatives to chemical pesticides, leveraging *T. harzianum*'s potential offers a valuable avenue toward resilient and environmentally safe crop production.

Keywords: *Trichoderma*; biotic factors; fungi; nematode; antibiosis; mycoparasitism; management.

1. INTRODUCTION

Trichoderma spp. is regarded as one of the most effective fungal biocontrol agents for controlling various plant diseases as well as stress brought on by abiotic factors, as has been highlighted in a number of scientific communications and publications to date. *Trichoderma* spp. is frequently used as soil applications, seed treatments, and seedling root dips to manage various plant diseases, promote plant growth, and increase crop output [1-3]. The ability of *Trichoderma* to reduce abiotic stresses and the exact mechanisms involved, as well as its capacity to manage various plant stresses like osmotic, salinity, chilling, and heat stress, have all been the subject of recent publications. *Trichoderma* can withstand physiological stress, such as low seed quality brought on by seed aging [4]. Under challenging conditions, one common detriment to plants is the accumulation of harmful reactive oxygen species (ROS). *Trichoderma* possesses the capacity to ameliorate the damage caused by ROS accumulation in stressed plants. For instance, when seedlings undergo osmotic stress, treating seeds with *Trichoderma* reduces lipid peroxidation. Enhancing plant resilience to abiotic stressors is a notable positive outcome of the *Trichoderma*-plant interaction, gaining increased attention due to the potential insight into its underlying mechanisms that could advance crop production techniques. Recent studies have revealed that select *Trichoderma*

strains could potentially be harnessed for industrial purposes, producing diverse enzymes, growth hormones, and valuable secondary metabolites. In genetic engineering, *Trichoderma* is now employed for transgenic development. This review encompasses the advancements in understanding how these antagonistic fungi and their metabolites interact with plants, yielding substantial plant improvements to guard against various threats. There are more than 370 *Trichoderma* spp. including *T. harzianum*, *T. viride*, *T. asperellum*, *T. hamatum*, *T. atroviride*, *T. koningii*, *T. longibrachiatum*, and *T. aureoviride* are reported to date [5,6]. There are several species of *Trichoderma* has been used as biocontrol agent including *T. harzianum*, *T. hamatum*, *T. longibrachiatum*, *T. koningii*, *T. viride*, *T. polysporum*, *T. asperellum* [7]. It has been mentioned in several studies that most *Trichoderma* spp. can produce bioactive substances and have antagonistic effects on plant-pathogenic fungi and plant-pathogenic nematodes [8]. A number of bioactive substances, including secondary metabolites and cell wall-degrading enzymes, can effectively improve crop resistance, reduce plant diseases, and promote plant growth [9].

2. MECHANISMS OF TRICHODERMA ACTION

2.1 Competitive Interaction

A fundamental facet of biological control, competition transpires when multiple

microorganisms for limited resources. The establishment of an introduced antagonist in the presence of native microflora can pose long-term challenges [10,11]. *Trichoderma* spp. possess enduring conidia and a wide range of substrate utilization, potent contenders for resources [12].

2.2 Nutrient and Space Competition

Trichoderma spp. are rapidly proliferating fungi with persistent conidia and a broad substrate utilization capacity. They present robust competition for nutrients and space against other microorganisms that contribute to plant diseases [13]. Weaker competitors among microorganisms often perish due to starvation. *Trichoderma*'s competition for nutrients has been identified as a biocontrol mechanism against various plant pathogens. These fungi produce siderophores that sequester iron, hindering pathogenic microorganism growth by rendering iron inaccessible once chelated. Importantly, *Trichoderma* strains, also, compete for space and essential exudates from seeds and roots that trigger the germination of propagules of plant pathogenic fungi in soil. Moreover, they possess the capability to utilize a wide array of substrates including herbicides, fungicides, and phenolic compounds. The ability of *Trichoderma* to reduce abiotic stresses and the exact mechanisms involved, as well as its capacity to manage various plant stresses like osmotic, salinity, chilling, and heat stress, have all been the subject of recent publications. *Trichoderma* is now used in genetic engineering for the creation of transgenics. This study includes a compilation of the most current developments and advances in our understanding of the various roles played by these antagonist fungi and their metabolites in interactions with plants, as well as how these alterations result in significant improvements for plants that help defend them from various threats. *Trichoderma* species have been recognized as capable of harming other fungi for more than 60 years. Additionally, researchers are aware of them as potential biological control agents [14,15]. Some studies have discovered that *Trichoderma* species can eliminate plant diseases and promote plant growth [16,17]. Besides, *Trichoderma* spp. has been proven able to detoxify toxic compounds and fasten the degradation of organic material [18,19]. *Trichoderma* speeds up growth, takes up

nutrients, and alters the rhizosphere under field conditions all contributing to their success in the soil ecosystem and their function as natural decomposers. Additionally, the potential to withstand adverse conditions and have tremendous effectiveness against plant pathogenic diseases [20,21]. According to Halifu et al. [22], *Trichoderma* spp. exude cell wall-degrading enzymes such as cellulase, xylanase, and glucanases, which interfere with microbial cells' ability to assimilate nutrients in the rhizosphere. This review gives insights into various mechanisms used by *Trichoderma* to alleviate the stresses with special emphases on how it induces resistance and various uses of *Trichoderma* in plant disease management.

2.3 Root Colonization

Trichoderma spp. play a pivotal role in enhancing the uptake of macro- and micronutrients by plants in agricultural fields. This enhancement is achieved by solubilizing nutrients and ensuring the availability of essential elements such as phosphorus (P) and micronutrients like iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn). *Trichoderma* employs four distinct mechanisms to achieve nutrient solubilization: enzymatic hydrolysis facilitated by phytase, redox reactions mediated by ferric reductase, chelation through siderophores, and acidification using organic acids. This array of mechanisms allows *Trichoderma* to solubilize various minerals including phytase, CuO, and metallic Zn. Analytical techniques such as high performance liquid chromatography (HPLC) have revealed the presence of organic acids such as lactic acid, citric acid, tartaric acid, and succinic acid in *Trichoderma* cultures. Furthermore, *Trichoderma*-treated plants demonstrate significant increases in both plant biomass dry matter (92%) and copper uptake (42%) compared to untreated controls. Notably, specific *Trichoderma* isolates display an enhanced ability to solubilize insoluble tricalcium phosphate, particularly in chickpeas. *T. harzianum* has been found to augment phosphorus uptake in treated plants. Additionally, the secretion of gluconic and citric acids by *Trichoderma* contributes to soil acidification, promoting the solubilization of phosphates, micronutrients, and mineral components, including iron, magnesium, and manganese [23,20,24].



Fig. 1. Various modes of action used by Trichoderma

2.4 Mycoparasitism

The process of mycoparasitism involves the antagonist fungus parasitizing other fungi responsible for causing plant diseases. The role of *Trichoderma* spp. as a biocontrol agent was first recognized by Weindling [25], who also observed mycoparasitic behavior in *Trichoderma*. Moreover, in 1988, Wells documented instances where *T. lignorum* (*viride*) hyphae coiled around and terminated *R. solani* growth. A specific *Trichoderma* species exhibits chemotropic growth towards its target hosts, attaching to them, enveloping their hyphae, and subsequently infiltrating the points of contact. Recent ultrastructural and histochemical analyses propose that *Trichoderma* hyphae, entwined at interaction sites with their hosts, undergo localized cell wall degradation. Investigations using electron microscopy have demonstrated that the antagonist, *Trichoderma* spp., enzymatically degrades host cell walls during interactions with *Sclerotium rolfii* or *Rhizoctonia solani*. As indicated by studies by Ghasemi *et al.*, [26], Abdel-Rahim and Abo-Elyousr [27], and Mukherjee *et al.*, [28] mentioned that *Trichoderma* spp. release extracellular enzymes including α -(1,3)-glucanases, chitinases, lipases, and proteases when cultured on the cell walls of pathogenic fungi. Additionally, predominant *Trichoderma* species generate a variety of

secondary metabolites, such as non-ribosomal peptides, terpenoids, pyrones, and indole-derived compounds. *Trichoderma* has the ability to produce hundreds of antimicrobial secondary metabolites, including trichomycin, gelatinomycin, chlorotrichomycin, antibacterial peptides, and many more [29]. Within the rhizosphere, reciprocal signaling occurs between *Trichoderma*, and plants, leading to alterations in physiological and biochemical processes in both entities. For instance, the presence of fungal auxin-like compounds prompts various *Trichoderma* strains to stimulate root branching, thereby increasing shoot biomass through cellular processes like proliferation, expansion, and differentiation.

2.5 Antibiosis

In the context of antibiosis, *Trichoderma* spp. emit volatile compounds that exhibit toxicity towards surrounding pathogenic microorganisms. These volatile substances exert a lethal impact on the pathogenic entities, either preventing disease occurrence or repressing its progression. *Trichoderma* generates secondary metabolites that confer a competitive advantage against diverse microorganisms. These volatile metabolites yield benefits encompassing symbiosis, metal transport, and differentiation, among others [30,31]. Antibiotic agents,

constituting volatile lytic enzymes or toxins, selectively target and dismantle the pathogens. Notably, *Trichoderma* spp. generate a repertoire of volatile substances, including lactones, alcohols, terpenes, and specific compounds such as Trichodermin, Viridin, Viridiol, Gliotoxin, and Gliovirin [4]. These volatile compounds collectively undermine the viability of adjacent pathogenic microorganisms, thereby mitigating disease incidence.

2.6 Induction of Plant Resistance by *Trichoderma* spp

Numerous investigations [30,32,33] elucidate that *Trichoderma* spp. elevate the expression of plant genes associated with chitinase, glucanase, and peroxidase production, augmenting the plants' defense mechanisms against pathogenic bacteria. Biopriming of seeds with *Trichoderma* enhances plants' resilience against pathogenic assaults [21]. The rapid proliferation and spore production of *Trichoderma*, coupled with its strategic timing of invasion [34,35], facilitate effective disease management. By secreting antibiotics and possessing cell wall-degrading enzymes like cellulases, chitinases, and glucanases, *Trichoderma* spp. establish competitive dominance [26,11]. Furthermore, pretreatment of plants with *Trichoderma* species triggers a hypersensitive response, systemic acquired resistance (SAR), and induced systemic resistance (ISR) [36,20,24]. For instance, exposure to *Trichoderma* induced substantial physiological modifications in tomato plants, ultimately enhancing their resistance to diseases

([37]. Preconditioning cucumber plants with *Trichoderma* spp., as reported by Yedidia et al. [32], prompted systemic responses involving defense genes expressing phenylalanine and hydroperoxides lyase, alongside the systemic accumulation of phytoalexins combating *Pseudomonas syringae* pv. *lachrymans*. This priming led to a hypersensitive reaction and the elicitation of SAR and ISR mechanisms [36,20,11]. Such interactions exemplify *Trichoderma*'s capacity to protect its ecological niche by competitively outmaneuvering microbial competitors, thereby positioning it as an effective adversary against pathogenic fungi and a promising biocontrol agent [38,11,39].

2.7 *Trichoderma*'s Defense Activation through Gene Regulatory Mechanisms

Several strains of *Trichoderma* have displayed the ability to initiate defense responses in plants by activating various signaling pathways such as mitogen-activated protein kinase (MAPK) cascades, the cAMP pathway, and other pathways related to gene expression modulation that contribute to plant disease suppression and mycoparasitism inhibition [40,41]. A key player in this process is the MAP-kinase TVK1, which has been identified in *T. virens* [42] as well as its counterparts in *T. asperellum* [43] and *T. atroviride* [44]. This kinase is pivotal in regulating signaling transduction pathways, thereby influencing output pathways that are vital for effective biocontrol. Interaction between *T. virens*, *T. asperellum*, and plant roots against *R. solani* has been observed to increase the activity

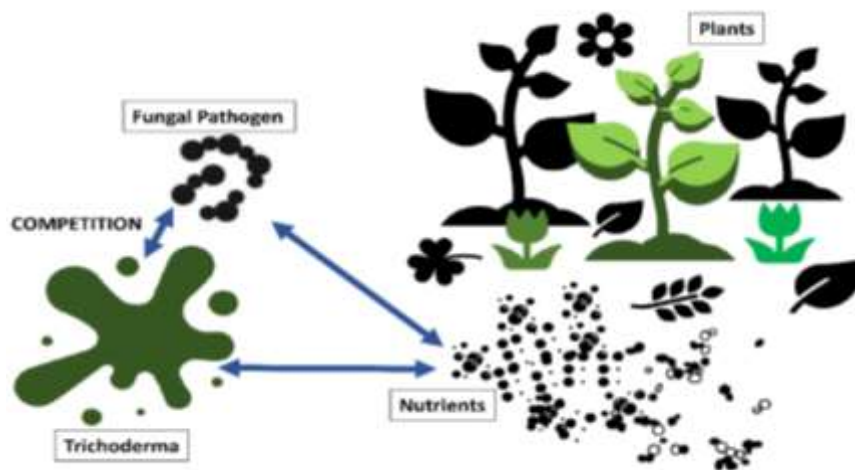


Fig. 2. Mechanism of action by competition

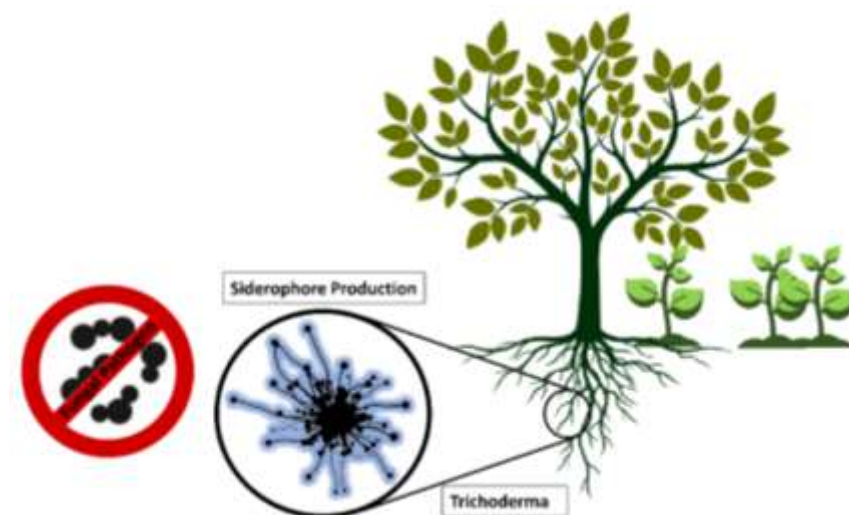


Fig. 3. Induction of resistance by Trichoderma

of genes linked to plant disease suppression [45,43]. Although deletion of these specific genes leads to reduced mycoparasitism efficiency, mutant strains exhibit enhanced biocontrol abilities. Notably, *Trichoderma* species possess genes such as TGA1 (*T. atroviride*), TGA A (*T. virens*), TGA3 (*T. atroviride*), and GNA3 (*T. reesei*) that have been extensively investigated for their involvement in biocontrol potential. TGA1 induces the production of antifungal compounds and facilitates coiling around host hyphae, contributing to effective antagonism; the absence of TGA1 leads to inhibited growth of host fungi [46]. Another gene, Tga A, has been found to activate MAP-kinases, and its deletion results in the emergence of avirulent strains, highlighting its role in biocontrol [47]. Similarly, TGA3's presence is crucial for *Trichoderma*'s biocontrol capacity [48]. GNA3's constitutive activation in *T. reesei* is associated with favorable effects on mycoparasitism, thus contributing to effective disease reduction.

2.8 Secondary Metabolites

In addition to enzymatic strategies, fungi possess a potent chemical repertoire that aids their survival and competition within their ecological niches [49,11]. Numerous strains of *Trichoderma* spp. have been identified as producers of various secondary metabolites, including mycotoxins and potential antibiotics like peptaibols, along with over 100 metabolites exhibiting antibiotic activity such as polyketides, pyrones, terpenes, metabolites derived from amino acids, and polypeptides [50]. The peptide antibiotic paracelsin was the initial characterized

secondary metabolite in *Trichoderma* spp. [51]. A novel class of peptaibols was subsequently discovered in *Trichoderma* [52]. Importantly, the presence of mycotoxin-producing *Trichoderma* species like *T. brevicompactum*, *T. arundinaceum*, *T. turrialbense*, and *T. protrudens* does not pose a risk to biocontrol efforts. These species are distantly related to those used in biocontrol, indicating that mycotoxins are not pivotal in defense mechanisms against pathogens. *Trichoderma* spp., like other fungi, known to emit a variety of volatile organic compounds, garnering increased attention recently [53,54]. The biosynthesis of peptaibols in *Trichoderma* spp. is regulated by various factors, particularly environmental conditions such as light, pH, nutrient availability, starvation, and mechanical damage. The production of conidia is intertwined with effective peptaibol synthesis [49,55]. Moreover, *Trichoderma*-treated plants have exhibited increased production of plant growth hormones, including cytokinin-related molecules like zeatin and gibberellin, fostering growth in terms of root and shoot length as well as biomass and leaf expansion [56].

2.9 The Role of Trichoderma in Managing Plant Diseases

The utilization of living organisms to curtail pest populations is referred to as biocontrol. *Trichoderma* spp., as highlighted by Hajek and Eilenberg in 2018, stands out as the most widely employed biocontrol agent against various root, shoot, and post-harvest diseases, earning them recognition for their eco-friendliness. According

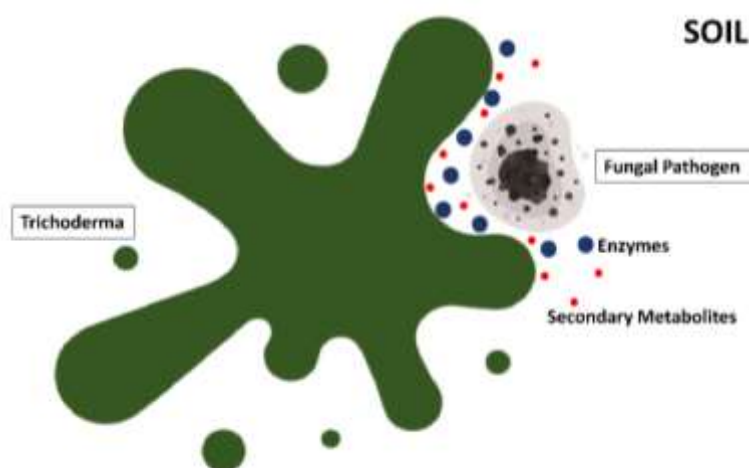


Fig. 4. Mechanism of action by secondary metabolites

to Siemering *et al.*'s findings in 2016, *Trichoderma* primarily establishes itself along root surfaces and within the upper layers of root cells, with roots serving as their primary habitat. The introduction of *Trichoderma* involves a successful application to plant roots during seeding, as demonstrated by Gava and Pinto in 2016 and Siddaiah *et al.* in 2017. Several researchers assert that treating seeds has proven effective in ensuring the colonization of *Trichoderma* spp. on roots, facilitating plant benefits. At present, *Trichoderma* species adopt three primary mechanisms for biological control against pathogens: (i) recognizing and infiltrating plant pathogenic fungi-like species by disrupting their cell walls and absorbing released nutrients, a strategy known as mycoparasitism; (ii) promoting plant disease resistance by altering root architecture during interactions with pathogens; and (iii) combating root-knot and cyst nematodes. Their impact on crops generally aligns, there are instances of species-specific and strain-specific relationships. Commercially available products typically contain one or more *Trichoderma* species, such as *T. viride*, *T. virens*, and *T. harzianum*. The effectiveness of products containing different species or strains can vary under similar field and climatic conditions. The prevalent forms of *Trichoderma* spp. products are wettable powders or granules. Approximately ninety percent of various *Trichoderma* strains are applied to crops to counter plant diseases due to their antagonistic properties against phytopathogens.

The evaluation of their performance as biocontrol agents (BCAs) considers input costs within the field and crop productivity. Comparatively, the

input costs and applications related to BCA and crop productivity demonstrate cost-effectiveness when pitted against synthetic inputs. Despite their cost advantage, excessive use of synthetic inputs like fertilizers and pesticides can lead to reduced profitability for farmers, if the balance between input costs and crop productivity is skewed. *Trichoderma* species not only minimize crop losses but also increase yields, bolstering profitability. Imran *et al.*'s observations in 2020 underscore how the judicious application of *Trichoderma*, along with compost, can offer an economical alternative to pricey chemical fertilizers. The utilization of *Trichoderma* is an effective sustainable approach to maintaining soil health. Research indicates that *Trichoderma* species effectively suppress plant pathogenic organisms like *Pythium arrhenomanes*, *Rhizoctonia solani*, *Fusarium oxysporum*, *etc.* *T. harzianum*, widely distributed worldwide and found across various substrates, features prominently in agricultural practices for its natural disease-suppressing abilities. Table 1 shows various bicontrol agents and their use in disease management.

In the *T. harzianum* species complex, consisting of closely linked members with minimal morphological differences, substrate, and origin play a pivotal role in defining ecological notions of species. Variations in functional goals, such as the secretion of secondary metabolites, growth conditions, target phytopathogens, host ranges, and geographic distribution, arise within this complex. Ahluwalia *et al.*'s 2015 study revealed distinct variations in secondary metabolites and antifungal activity between two *T. harzianum* strains (T-4 and T-5) from different geographical

regions in the Himalayas, reflecting the impact of environmental conditions. Moreover, studies by Napitupulu *et al.*, in 2019 demonstrated differences in antagonistic efficacy among ten *T. harzianum* strains isolated from diverse sources across Java, Indonesia. These strains exhibited varying degrees of antagonism against *Fusarium oxysporum* f.sp. *cubense*. Trichoderma's potential in bacterial disease management merits exploration.

2.10 Trichoderma spp. for Bacterial Disease Management

Trichoderma spp.'s inhibitory effects on various plant pathogens, encompassing fungi and plant parasitic nematodes, are well-documented. Evidence substantiates their effectiveness against plant pathogenic bacteria, both in laboratory settings and in mitigating bacterial disease severity in controlled environments and fields.

In field conditions, different isolates of *T. asperellum* demonstrated their effectiveness in reducing disease occurrence, delaying bacterial wilt symptoms in tomatoes caused by *R. solanacearum*. The application of *T. asperellum* was observed to amplify activities like peroxidase (POX), phenylalanine ammonia-lyase (PAL), polyphenol oxidase (PPO), -1,3-glucanase, and total phenol after the pathogen was introduced in the field, consequently fortifying systemic acquired resistance in tomato plants [71]. Additionally, when *T. asperellum* was applied to the root system, it exhibited systemic resistance against angular leaf spot (*Pseudomonas syringae* pv. *lachrymans*) in cucumbers, leading to a decrease in disease intensity. *T. hamatum* has consistently demonstrated protection against the bacterial leaf spot of tomatoes induced by *Xanthomonas euvesicatoria*, by influencing plant physiology and disease resistance through systemic gene expression adjustments related to stress and metabolism [37].

Table 1. Fungal strains as biocontrol agents against various plant pathogens

Fungal strains	Targeted disease	Target pathogen	Reference
<i>Aspergillus fumigates</i>	Cocoa/black pod	<i>Phytophthora Palmivora</i>	Adebola and Amadi [57]
<i>Paecilomyces lilacinus</i>	Tomato/Root-knot disease	<i>Meloidogyne javanica</i>	Hanawi [58]
<i>Penicillium oxalicum</i>	Tomato/Root-knot disease	<i>Fusarium oxysporum</i> f. sp. <i>Lycopersici</i>	Sabuquillo et al. [59]
<i>Penicillium</i> sp. EU0013	Tomato and cabbage/wilt	<i>Fusarium oxysporum</i>	Alam et al. [60]
<i>Pochonia chlamydosporia</i>	Carrot/Root knot disease	<i>Meloidogyne incognita</i>	Bontempo et al. [61]
<i>Purpureocillium lilacinum</i>	Vigna radiata/Root-knot disease	<i>Meloidogyne incognita</i>	Khan et al. [62]
<i>Purpureocillium lilacinum</i>	Pineapple/Root knot disease	<i>Meloidogyne javanica</i>	Kiriga et al. [63]
<i>Trichoderma hamatum</i>	Cabbage	<i>Sclerotinia sclerotiorum</i> apothecia	Jones et al. [64]
<i>Trichoderma asperellum</i>	Beans	<i>S.sclerotiorum</i> apothecia	Geraldine et al. [65]
<i>Trichoderma asperellum</i>	Onion	<i>Sclerotium cepivorum</i>	Rivera-Méndez et al. (2020)
<i>Trichoderma atroviride</i>	Beans	<i>Botrytis cinerea</i>	Brunner et al. [66]
<i>Trichoderma harzianum</i>	Rice/brown spot	<i>Bipolaris oryzae</i>	Khalili et al. [67]
<i>Trichoderma harzianum</i> T-22	Soya bean	Suppressive effect on <i>S. sclerotiorum</i>	Zeng et al. [68]
<i>Trichoderma</i> spp.	Tobacco/root rot	<i>Rhizoctonia solani</i>	Gveroska and Ziberoski [69]
<i>Trichoderma virens</i>	Okra/Root-knot disease	<i>Meloidogyne incognita</i>	Tariq et al. [70]

(Source:- Kumar et al. [2])

In an *in-vitro* dual culture technique, the effectiveness of five *Trichoderma* species *i.e.*, *Trichoderma viride*, *T. hamatum*, *T. harzianum*, *T. lignorum*, and *T. koningii* against bacterial blight of cotton triggered by *Xanthomonas axonopodis* pv. *malvacearum* was assessed. Except for *T. viride* and *T. lignorum*, all *Trichoderma* species were found to hinder the growth of *X. axonopodis* pv. *malvacearum* after a three-day incubation. Interestingly, *T. harzianum* demonstrated strong antagonistic activity against the plant pathogen *Xanthomonas in-vitro*, sourced from ten varied agro-climatic regions in Karnataka, restricting its growth [72]. Utilizing the well diffusion method and post-harvest storage tests, *T. harzianum* was determined to counteract the bacteria leading to soft rot in vegetable and tuber crops, notably those triggered by *Erwinia carotovora* (Rashid *et al.*, 2013).

2.11 Utilizing *Trichoderma* Spp. in the Control of Nematode Diseases

Plant parasitic nematodes pose a major threat to a variety of crops, both within greenhouses and in the fields. They can either directly cause diseases in plants through parasitism or act as carriers for other harmful pathogens like fungi, bacteria, or viruses. Their subterranean feeding habits make controlling them a formidable challenge. Many nematicides have been banned due to their high residual toxicity, posing significant health and environmental risks. Moreover, these chemicals often fail to penetrate deep enough into the soil to effectively control nematode populations, leading to increased resistance. Using biological means like *Trichoderma* spp. is becoming increasingly relevant for managing these pests. This fungus stands out among biocontrol agents for its antagonistic properties against a wide range of plant pathogens. *Trichoderma* not only coils around nematodes, restricting their movement but also produces spores that attach to nematodes. Additionally, *Trichoderma* releases secondary metabolites, including toxins and antibiotics, which can incapacitate these pests. Studies have revealed that applying specific strains of *Trichoderma*, like *T. harzianum* and *T. viride*, can reduce nematode-related damage in crops such as tomatoes. Various experiments have shown that different *Trichoderma* strains can inhibit the growth and activities of several nematodes. For example, *Trichoderma longibrachiatum* showed potential in controlling nematodes like *Scutellonema* sp. and

Helicotylenchus. Some strains even produce enzymes that help in breaking down the nematode body cuticle. *Trichoderma* also parasitizes nematodes by conidia which are attached to nematodes. The gelatinous matrix of nematodes plays an important role in the attachment of conidia and the parasitization process by forming carbohydrate-lectin-like interactions. *Trichoderma* also produces many secondary metabolites like toxins and antibiotics like malformin, gliotoxin, viridian, and penicillin, which might contribute to the toxicity along with inactivity and immobility of plant parasitic nematodes. The root-knot nematode, *M. incognita*, was found to have significantly fewer galls, egg masses, eggs per egg mass, and reproductive factors after *T. harzianum* and *T. viride* were applied to tomato crops [73]. The hatching of *M. javanica* eggs was shown to be inhibited by *T. harzianum* culture filtrates when they were tested at various concentrations, and this inhibition grew stronger with increasing culture filtrate concentration. *T. harzianum* showed direct parasitism of *M. javanica* eggs and decreased nematode pathogenicity by reducing the number of galls, egg masses, eggs, and gall width under field conditions [74]. Culture filtrates derived from various *Trichoderma* species, including *T. harzianum*, *T. viride*, *T. koningii*, *T. reesei*, and *T. hamatum*, demonstrated the ability to impede the reproductive and developmental processes of reniform nematodes (*Rotylenchus reniformis*) and root-knot nematodes in laboratory settings. This effect was attributed to the presence of harmful metabolites. Moreover, under greenhouse conditions, these filtrates suppressed the mobility and activity of nematodes from both genera by thwarting their infiltration and growth, as observed by their inhibited penetration and development stages [75].

T. longibrachiatum (TL6) exhibited inhibition of eggs and second-stage juveniles (J2s) of *Heterodera avenae* in wheat crops. This was achieved through the parasitization of nematode eggs, characterized by the formation of dense mycelium coverings, breakdown of egg contents, and penetration by numerous hyphae that led to deformities in the J2s. Consequently, greenhouse trials involving wheat seedlings treated with TL6 resulted in reduced *H. avenae* infestations and enhanced plant growth due to the suppression of nematode cysts and juveniles in the soil [76]. *T. longibrachiatum* displayed the ability to inhibit *Scutellonema* sp. and *Helicotylenchus* by creating an appressorium-like

structure that made direct contact with the nematode. This structure produced penetration holes in the nematode's cuticle, causing the cuticle to disintegrate and leading to the collapse of the nematode due to loss of turgor. In contrast, *T. viride* and *T. harzianum* induced excessive coiling of their mycelium around the anterior and head regions of the nematodes, likely related to the extraction of the nematode's bodily contents and suppression of its cuticle. *T. koningii* utilized endo and exochitinases to facilitate hyphal penetration through the nematode's cuticle. Strains of *T. virens*, *T. atroviride*, and *T. rossicum* displayed remarkable efficiency in reducing the population of *Xiphinema index*, and the application of *T. viride* led to a decline in the population of the Potato cyst nematode (*Globoderarosto chinensis*) in soil [77,78].

3. CONCLUSION

Trichoderma species exhibit numerous characteristics that hold significant potential for their utilization in agriculture. These qualities encompass the mitigation of abiotic stresses, enhancement of physiological stress responses, facilitation of nutrient uptake in plants, improvement of nitrogen utilization efficiency in diverse crops, and contribution to heightened photosynthetic efficiency. The global utilization of this genus has expanded, encompassing roles as general plant protectants and growth promoters, in addition to industrial applications. Whereas unscientific and unusual use of chemical pesticides has caused serious hazards to the environment and enhanced pathogens' resistance unscientific and unusual use of chemical pesticides has caused serious hazards to the environment and enhanced pathogens' resistance. to chemical pesticides. Several experiments have proven that *Trichoderma* has good biological control effects and can reduce the use of chemical pesticides [79-85].

The genomes of *Trichoderma* species encompass a plethora of valuable genes, enabling these fungi to adapt to challenging environments such as soil, water, decaying matter, and within plants themselves. The metabolic pathways within *Trichoderma* species are exceptionally intricate, particularly in the context of secondary metabolite production. Nonetheless, the integration of advanced molecular and proteomic techniques offers the possibility of uncovering novel pathways with extensive agricultural applications. The mapping of *Trichoderma* species proteomes and their

interactions has enabled the development of novel products founded on synergistic combinations of the living fungus and its secreted metabolites [86-90]. These innovative formulations are deemed more effective than their predecessors and exhibit efficacy against a broader spectrum of pathogens. The dual capacity of these fungi to induce resistance against biotic stresses such as diseases and abiotic stresses like drought and salinity, coupled with their ability to enhance nutrient utilization efficiency, positions them as immensely valuable tools. Through their application, plant productivity can be notably elevated, contributing to food security and environmental preservation. Importantly, the ability of these fungi to curb the production of compounds from surplus fertilizers can reduce the application of nitrogen fertilizers, thereby mitigating nitrate pollution in soil and water bodies, as well as curtailing air pollution [91-96]. With their antagonistic properties, *Trichoderma* species have proven successful in managing onion diseases such as white rot, pink rot, Fusarium basal rot, onion smudge, and damping off. Their introduction to the root zones of crops like cucumber, bell pepper, and strawberry has led to significant yield increases. Additionally, *Trichoderma* species exhibit resilience against an array of stubborn pollutants including heavy metals, pesticides, and polyaromatic hydrocarbons. This versatility positions *Trichoderma* as a potent biological tool for disease management in plants while concurrently fostering agricultural and environmental sustainability.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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