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Review

Trichoderma: A Review of Its Mechanisms of Action in Plant Disease Control

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Abstract: *Trichoderma* has been widely studied for its potential as a biocontrol agent against plant pathogenic organisms. *Trichoderma*'s biological control mechanisms include competition, modification of environmental conditions, antibiosis, induction of plant defensive mechanisms, and mycoparasitism. *Trichoderma* species are known to produce a variety of secondary metabolites that have antifungal activity. These metabolites include peptaibols, gliotoxin, and trichokonins. *Trichoderma* also produces chitinases and β -1,3-glucanases that can degrade the cell walls of fungal pathogens. In addition to direct antagonism against fungal pathogens, *Trichoderma* can also induce systemic or localised resistance in plants, which is achieved through the production of elicitors such as chitin oligosaccharides and β -glucans that activate plant defence responses. *Trichoderma* can also form mutualistic associations with plants. In these associations, *Trichoderma* colonises the roots of plants and promotes plant growth by increasing nutrient uptake and inducing systemic resistance. Using *Trichoderma* as a biocontrol agent has several advantages over conventional crop protection techniques based on applying synthetic pesticides.

Keywords: *Trichoderma*; fungi; pathogen; mode of action; plant diseases; biocontrol; microbe-associated molecular pattern (MAMPs)

1. Introduction

Plant diseases are one of the most critical factors impacting food production, significantly lowering physical and economic output [1–3]. The pathogenic microorganisms known to cause plant diseases include bacteria, fungi, viruses, and nematodes, which can cause mild to severe physiological and morphological conditions [4]. These microbial agents are incredibly damaging and can cause widespread plant disease [2].

Plant diseases are responsible for more than 30% of crop losses, resulting in global economic problems [5–7]. Despite the arrays of synthetic chemical interventions provided, plant disease control that significantly improves agricultural productivity and ensures consumer food security remains a challenge [8]. Pesticides are chemical compounds used in various agricultural (agronomic) activities to eradicate or limit the spread of pests, insects, weeds, and pathogenic microorganisms [9]. Pesticides such as fungicides, bactericides, and nematocides control agricultural pathogenic microorganisms such as fungi, bacteria, and nematodes [10]. Tina *et al.* [11] and Pooja *et al.* [4] submitted that resistance to pesticides, natural microbiota modification or eradication, distortion of the natural habitats of plants, soil contamination, and plant bioaccumulation of hazardous chemicals are some of the negative impacts recorded due to the use of conventional pesticides. As a result, reliance on the use of synthetic pesticides for plant disease management must be discouraged.

Nonetheless, plant disease control has seen significant progress with the employment of other integrated plant disease management (IPDM) strategies, which involve the applications of physical,

cultural, biotechnological, and biological control agents [12]. Some biological control agents (BCAs) (fungi and bacteria) have been identified as essential biocontrol agents for plant disease control because they are environmentally safe and may be cost-efficient [13–15]. Among the identified BCAs is *Trichoderma*, a soilborne fungus that has proven effective in controlling pathogenic microorganisms in plant tissues and rhizosphere using various mechanisms [16–18]. They are highly tolerant of soil contaminants, alter the rhizosphere to improve plant performance, use available soil micronutrients, maintain efficiency in severe conditions, and promote plant growth [19].

However, *Trichoderma* is under-exploited for managing plant diseases, especially in Africa, due to a lack of innovation strategies, financial constraints, technological limitations, and technical assistance [12], despite its efficient control level of plant pathogens [20]. Therefore, there is a need to explore *Trichoderma*'s mechanisms of action against plant pathogenic microorganisms to enhance both the researchers' and farmers' knowledge [21].

2. *Trichoderma* as a Biocontrol Agent

Biological control is the process by which one or more organisms reduce the density of inoculums or the disease-causing activities of a pathogen or parasite in a dynamic or static state. This can be done naturally or by changing the environment, the host, or the antagonist [22].

Microorganisms have a long history of being used as biocontrol agents to control plant diseases caused by pathogenic fungi, bacteria, and nematodes. Biofungicides are natural, non-toxic and ecologically friendly compounds [2]. According to history, farmers' traditional and cultural values were linked to preparing and using plant-protection crops to boost food production before the advent and widespread of synthetic fungicides.

Synthetic fungicides have long been employed to control plant diseases caused by plant pathogenic fungi, even though this practice has been criticised for various reasons [23]. The overuse and incorrect management of synthetic fungicides can harm humans, the environment, and non-target creatures, ultimately leading to resistance and declining biodiversity [24–26] and negatively impacting the ozone layer [27]. In addition to ozone layer depletion, component molecules of synthetic fungicides have been associated, in either ingestion or exposure scenarios, with chronic human, animal, and aquatic biodiversity disorders due to their low and prolonged biodegradability and high tendency to persist in the environment [28].

However, advances in research and technology have helped improve safe plant disease management strategies by introducing Plant-incorporated protectants (PIPs), biochemical pesticides, and biofungicides [2]. Biofungicides are safer for human and animal health and have a lower environmental impact than synthetic fungicides, making them suitable for organic farming. Biofungicides can also lower the risk of pathogen resistance by acting against the pathogen in various ways, both directly and indirectly [12,28].

Trichoderma species is one of the most dominant species of soil fungi used as BCAs [29]. Due to their tremendous reproductive potential, ability to thrive in severe conditions, capacity to enhance plant growth, and ability to parasitise phytopathogens, *Trichoderma* are used as bioagents [30]. *Trichoderma* wards off pathogenic microfungi through mycoparasitism, antibiosis, resource competition, induction of resistance in plants, and the synthesis of cell wall-degrading enzymes such as glucanases and chitinases [31,32].

3. Mechanism of Action of *Trichoderma*

Trichoderma uses various biocontrol strategies, alone or combined, to inhibit plant diseases explicitly or implicitly. It is widely known that indirect processes cause morphological and biochemical changes in the host plant, which boost root development and increase systemic resistance, increasing plant tolerance to stressors [33]. The antagonist releases lytic enzymes, antibiotics, and several other toxic compounds during direct processes to combat diseases, which work to antagonise the pathogen. Biocontrol agents (BCAs) show most of these abilities to control the target disease effectively [34]. The following paragraphs provide a complete description of *Trichoderma*'s strategies to defend against plant pathogens.

3.1. Mycoparasitism

In mycoparasitism, fungal plant pathogens are inhibited by beneficial fungi possessing biocontrol ability. The parasitising fungus (bio-agent) gains entry into the tissue of the plant pathogenic fungus using the hyphae and then releases metabolic substances, which result in structural compromise and nutrient absorption from the host (pathogenic) fungus [35]. Oyesola *et al.* [15] reported the *in vitro* efficacy of *Trichoderma koningii* (biocontrol agent) in inhibiting the mycelia growth of *Aspergillus niger*, *A. nidulans*, and *A. flavus* isolated from rotting tomato fruits, which suggested the possible application of *Trichoderma* in managing post-harvest diseases caused by pathogenic fungi. Several other researchers have also reported that *Trichoderma* have been effectively employed for the control of fungal plant pathogens due to their ability for rapid hyphal elongation, resulting in the overgrowth of the pathogenic fungi hyphae [20–22,36].

Trichoderma's ancestral mode of life is depicted by mycoparasitism, according to a comparative study of the genomes of three species of the fungus that are commonly utilised as biocontrol agents: *T. virens*, *T. reesei*, and *T. atroviride*. *Trichoderma* interacts with plants' roots, colonising them due to the increased quantity of fungal pathogens in the rhizosphere and the generation of nutrient-rich exudates [37]. Accordingly, their mode of operation changed from mycoparasitism to a more generalist plant-related one [35].

In order to initiate the formation of specialised structures and produce enzymes, *Trichoderma* mycoparasitism depends on several biochemical signals. *Trichoderma* initiates chemotropic growth by identifying oligochitins in the pathogen's cell wall. *Trichoderma* hyphae coil around the pathogen's hyphae upon contact, releasing enzymes that break down the cell wall, such as chitinases and β -1,3-glucanases. *Trichoderma* exploits the pores created by the breakdown of the fungal cell wall to draw nutrients from its meal [31,38,39].

3.2. Mycovirus-Mediated Cross-Protection (MMCP)

Biocontrol fungi employ mycovirus-mediated cross-protection (MMCP) to shield plants against disorders resulting from fungal infections [40]. MMCP is one of the five biocontrol techniques employed by helpful fungi, along with mycoparasitism, antibiosis, induced systemic resistance (ISR), and competition for resources and space with pathogens [41]. Mycoviruses, such as *Cryphonectria parasitica* hypovirus 1 (CHV1), are transferred from one fungal strain to another during MMCP, which causes the recipient strain to become less virulent. Due to the identical virulence pathways shared by different fungal pathogens, this weakening may result in cross-protection [37,41].

3.3. Synthesis of Cell Wall Degrading Compounds (CWDCs)

The generation of Cell Wall Degrading Compounds (CWDCs) is a crucial aspect of mycoparasitism's final phase [41]. Chitin, 1,6 -glucans, mannan, chitosan, galactomannan, and most fungal cell walls comprise proteins [38]. *Trichoderma* are well known for their ability to create a suite of extracellular enzymes that hydrolyse essential cell components, such as chitinases [(1,3;1,6)- β -glucanases] and proteases [42]. Chitinases are the lytic enzymes produced by *Trichoderma* that hydrolyse glycosidic bonds between the C1 and C4 carbons of two different molecules [43]. The glycoside hydrolase, the 18 (GH18) family of fungus chitinases, has 20 to 90 kDa of molecular weight [44]. The presence of genes in encoding chitinase synthesis, a vast range of binding biocontrol active against various fungal phytopathogens, results in *Trichoderma* chitinolytic activity [41].

Exo-glucanases and endo-glucanases are two glucanase enzymes that destroy the cell walls of pathogenic fungi [38]. When comparing the genetic properties of *Trichoderma* with other closely related fungi, the genes coding for synthesising their secondary metabolites are likely to be solely associated with the *Trichoderma* genome [45]. Excessive exposure to the gene encoding β -1,3-glucanase at the early stages of mycoparasitism was discovered during the expression of *T. harzianum* and *Fusarium solani* transcriptome interaction [38]. The capacity to regulate bio-*T. virens* by *Pythium ultimum* is also reduced when the Tv bgn-3-gene encoding the enzyme β -1,6-glucanase is removed [46]. *Trichoderma* soluble in fluid cultures having a wall of lyophilised cells of the pathogenic *Fusarium*

culmorum strain as the only carbon source has been reported to have increased chitinolytic and glucanolytic activity [47]. *Trichoderma* displays intense enzymatic activity in chitin and the S-cell wall [41]. In fungal diseases, this shows increased hydrolytic enzyme synthesis [48,49].

Proteolytic enzymes enhance the hydrolysis of peptide bonds in proteins and play a significant part in mycoparasitism [50]. The *Prb1* protease bound by *Trichoderma* was demonstrated to play an important role in biodiversity regulation. For example, cotton seedlings exposed to the *T. virens* gene, *tvsp1*, recorded enhanced resistance against fungi pathogens by 15-32% compared to the wild type. *T. harzianum*'s aspartic protease considerably lowers the incidence of fruit grey fungus that inhibits seed germination and growth of the plant [51]. Proteases generated by the *Trichoderma* gene are hypothesised to control the expression or activity of other hydrolytic enzymes implicated in mycoparasitism [51].

3.4. Production of Antibiotics and Other Antifungal Compounds

Antibiosis is how biocontrol agents produce antimicrobial substances inhibiting phytopathogen growth and reproduction. Antibiosis was observed in *Trichoderma*, which synthesises a variety of antagonistic compounds that break down the cell wall, e.g. pectinase, xylanase, cellulase, lipase, amylase, glucanase and protease, as well as other flexible metabolites or volatile compounds (VOCs) like antibiotics such as trichodermin, gliotoxin, viridin, peptaibols [46]. These and several other secondary metabolites have been isolated and characterised, with over 370 belonging to different groups of potent antagonists [41,52].

Many *Trichoderma* species produce these VOCs, with peptaibols and polyketides being the most prevalent [53]. *Trichoderma* is rich in peptaibols, with over 80% stored in the "Peptaibiotics Database" [54]. Peptaibols are polypeptide antibiotics with molecular weights ranging from 500 to 2200 Da with high protein-free amino acids, particularly isovaline and alpha-aminoisobutyric acid. They are identified by acylated N-terminal and amino alcohols in the residual C-terminal end [55,56]. These antibiotics are produced in numerous *Trichoderma* strains. For example, *T. longibrachiatum* produces a variety of new peptaibols, most of which are related to trichobrachsins, suzukacillins, trichoaureocins, and longibrachsins [57]. Acylated N-termini and amino alcohols in the residual C-terminal region distinguish these biochemicals [58]. In *Trichoderma*, non-ribosomal peptide synthetases (NRPSs) generate peptaibols [45]. These peptaibols are produced in *Trichoderma* species such as *T. citrinoviride*, *T. longibrachiatum*, *T. koningi* and *T. pseudokoningi*, which produce Trichorzins, harzianins, trichotoxin, and trichokindins. These have also been implicated in *T. harzianum* [58]. *T. atroviride* also produces peptaibols like atroviridins A–C and neoatroviridins A–D, whereas *T. viride* produces trichotoxins A and B, trichodecenin, trichocellins and trichorovins [38].

Trichoderma produces polyketides (PKs), a class of architecturally varied biochemical compounds found in bacteria, fungi, and plants [59,60]. Polyketide synthases (PKSs) make PKs from basic units like acetyl-CoA and malonyl-CoA [61]. However, *Trichoderma* is implicated in high PKs encoding genes and polyketide biosynthesis; they have received minimal research attention. Most PKs are found in fumonisin and represent orthologs in *T. reesei*, *T. virens*, and *T. atroviride* [62,63]. In addition, the *T. reesei* gene PKs 4 is essential for the composite cell wall's green colour and stability and its resistance to other fungi [64,65].

Secondary metabolites generated by *Trichoderma* include anthraquinones, pyrones, epipolythiodioxopiperazines (ETPs) and terpenoids [65]. Tetracyclic diterpenes, sesquiterpenes and triterpene viridin are among the terpenoids in *Trichoderma* [66]. *T. asperellum* generates 6-phenyl-a-pyrone (6PAP), effectively controlling *Fusarium oxysporum* [66]. Importantly, *T. harzianum*, *T. aureoviride* and *T. viride* produce anthraquinone pigment compounds such as pachybasin and emodin, which have high antifungal activities and mediate mycoparasitic fungi [21,67,68].

Gliotoxin is the most well-known ETP with immunosuppressive properties, and its antifungal activity also plays an essential role in biological control [69,70]. In addition, *Trichoderma*, particularly *T. harzianum*, synthesises harzianic acid with several properties, including antifungal, plant growth enhancing, and irrigation abilities [47,71].

3.5. Competition for Vital Nutrients and Space

Trichoderma possess effective strategies for colonising plants. *Trichoderma* competes for space and nutrition with pathogenic microorganisms by invading their natural habitats, such as the plant tissues, rhizospheres, or the phyllosphere [72,73]. Their rapid growth pattern significantly enhances their competition with plant pathogens for space and nutrition by producing biochemical substances to eliminate pathogens [74,75]. However, sugar and sucrose levels are high in *Trichoderma* [40] and are utilised as a carbon source [34]. *Trichoderma* has superior competition and nutrient absorption ability compared to other fungi genera [46]. This process is linked to gluconic, citric, and fumaric acid production, which reduces soil pH and increases phosphate and microelement (iron, manganese, and magnesium) synthesis [76].

Siderophores is a low molecular weight (less than 10 KDa) chelator with high iron affinity (Fe). It is formed under the stress of iron deficit and significantly impacts the competition process in *Trichoderma* [77,78]. Fe ions, a cofactor, aid the development and growth of many fungal pathogens [79]. Microbial siderophores' chemical composition and iron-binding characteristics are commonly separated into catecholate, hydroxamate and carboxylate [80]. Coprogens, ferrichrome, and fusarinines are hydroxamate siderophores widely found in fungi and have a standard architectural arrangement of N5-acyl-N5-hydroxyornithine [81,82]. Figure 1 explains how siderophores bind to Fe^{3+} and convert it to Fe^{2+} , a soluble form that plants and microbes may easily absorb [83].

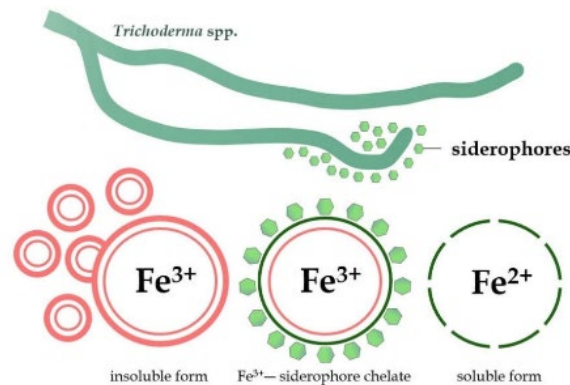


Figure 1. The insoluble iron (Fe^{3+}) transformation into a soluble and easily assimilated (Fe^{2+}) form. *Trichoderma* releases molecules called siderophores. These siderophores bind to the insoluble iron (Fe^{3+}), forming a siderophore chelate complex. The chelate makes the iron soluble, converting it into Fe^{2+} [83].

Trichoderma inhibits the mycelia growth of soil pathogens by depleting iron from their natural sources [84,85]. A report from an *in vitro* experiment carried out by Oyesola *et al.* [2] showed that *T. koninggi* inhibited the mycelia growth of *Aspergillus niger*, *A. flavus* and *A. nidulans*, while *T. harzianum* controlled the growth of *Fusarium acuminatum*, *Alternaria infectoria* and *Alternaria alternata* [86]. In addition, one of the significant abilities of *Trichoderma* as a biocontrol agent is metal ion absorption [34]. *Trichoderma* has also been shown to compete effectively with complex carbon substrates and phytopathogens such as *Colletotrichum*, *Botrytis*, *Verticillium*, and *Phytophthora*. *Trichoderma*'s decisive inhibitory action in *Botrytis cinerea*, *Macrophomina phaseolina* and *Fusarium graminearum* pathogens was also attributed to enzymes-mediate nutrient competition and environment [87,88].

3.6. Induction of Plant Resistance

The evolution of specific pattern recognition receptors to identify microbial-based signals called microbe-associated molecular patterns (MAMPs) or plant-associated molecular patterns (PAMPs) induced during pathogen invasion are examples of plant resistance molecules [41,89].

Trichoderma, a rhizosphere fungus, interacts with plant roots to induce resistance against diseases in the host plants. They indirectly induce plants' local or systemic immune systems for

resistance against pathogens [38,59]. Plant resistance develops because of the activity of multiple elicitors from microbial cells (exoelicitors) and plant tissues (endoelicitors). There are two types of elicitors: race-specific elicitors that only promote gene-to-gene type defence in a variety of host cultivars, and gene-to-gene elicitors produced by pathogenic and non-pathogenic variants that activate non-race specific defences in both the host and pathogen [90,91].

Elicitors generate physical, chemical, and biological changes in plants, such as ion flow and the formation of reactive oxygen species (ROS), which operate as a barrier to limit phytopathogen spread and the production of numerous immunological chemicals such as phytoalexins, enzymes, and phytohormones [92,93]. In the presence of the non-pathogenic fungus *Trichoderma*, various monocotyledonous and dicotyledonous plant species display increased immunological activity [94]. The recognition of stored domains, such as microbe-related molecular patterns (MAMP) or pathogen-related molecular patterns (PAMP), is the foundation of plant defence [95].

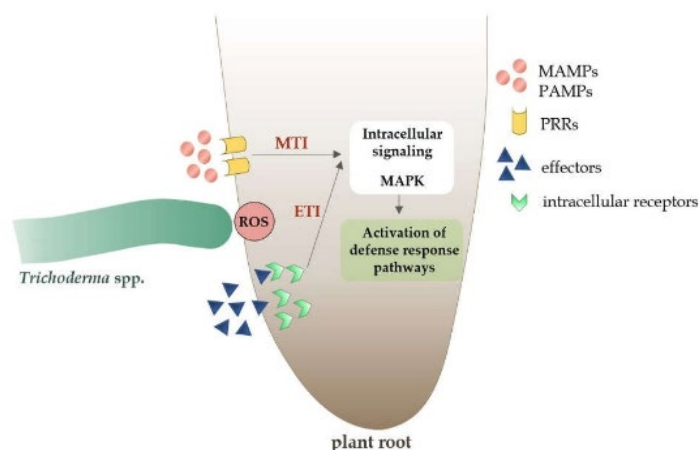


Figure 2. Plant defence response to the microbe-associated molecular pattern (MAMPs) molecules and effectors. MTI (MAMP-Triggered Immunity): This is activated when the plant detects specific molecules (MAMPs/PAMPs) from the fungus. ETI (Effector-Triggered Immunity): Triggered by the presence of fungal effectors. Intracellular signalling MAPK: Part of the process leading to defence response activation [96].

MAMP/PAMP and effector-triggered immunity (ETI) molecules are detected by both transmembrane pattern recognition receptors (PRRs) and intracellular receptors (IR), resulting in MTI/PTI (the microbe-associated molecular pattern (MAMPs)-triggered immunity/pattern-triggered immunity) or local ETI diseases, as depicted in Figure 3 [96]. An ETI-type immune response is usually more effective than MTI/PTI and results in systemic cell death due to hypersensitivity response (HR) activation [97]. Mitogen-activated protein kinases (MAPKs) convey information from receptors to plant cells, triggering a chain of immunological reactions throughout the body [97].

Trichoderma activation of the MTI and ETI immunological pathways results in systemic acquired resistance (SAR) against biotrophic diseases, induced systemic resistance (ISR) against necrotrophic diseases, and induced resistance (IR), which is an efficient defence against biotrophic and necrotrophic diseases and some abiotic stress factors [98].

The expression of pathogenesis-associated protein components (PR) and the generation of salicylic acid (SA) as a signalling molecule describe SAR [94]. Next, significant chemicals targeting the ISR type include jasmonic acid (JA) and ethylene (ET). Aminobutyric acid activates the IR defence, which uses abscisic acid (ABA) as a signalling molecule [99].

Increased enzymes and metabolites indicate the stimulation of signalling systems for the plant's immune response due to *Trichoderma* elicitor action. Introducing *Trichoderma* into host plants significantly boosts the activity of phenylalanine, tyrosinase, catalase, guaiacol peroxidase, glucanase and chitinase [40]. In a study, *Capsicum annum* treated with *T. harzianum* and *T. asperellum* species showed antifungal abilities to control fungal disease caused by *Colletotrichum truncatum*

[100,101]. In another study, *T. longibrachiatum* was linked to cucumber plant resistance to *B. cinerea* challenge through signalling pathways related to plant hormones [102].

Trichoderma's role in efficiently controlling various diseases of plants is made possible by their different mechanisms of action against disease-causing organisms [103].

3.7. Plant Growth Promotion

The capacity of biocontrol agents (BCAs) to stimulate plant growth makes them beneficial to plants. Due to their inherent compatibility, plant growth-promoting fungi, such as *Trichoderma*, can provide this advantage through their endophytic interactions with the plant roots [104,105]. *Trichoderma* are rhizospheric organisms that are prominent in boosting plant growth [106]. *Trichoderma* use several methods to promote plant development; these include.

3.7.1. Mineral Solubilisation

Many microorganisms, particularly those connected to roots, can boost the development and yield of plants. It has been proposed in a few instances that this impact entails the solubilisation of mineral nutrients that would otherwise be inaccessible. The soil's microflora could determine the intricate dynamic balance of solubilisation and insolubilisation that macro- and micronutrients go through in soil, determining how easily plant roots can absorb the nutrients [107].

Thus, it is well known that microbial interactions with plant roots significantly impact the nutritional condition of plants and their resistance to pathogens [108]. *Trichoderma* species are among the most researched biocontrol microorganisms because they enhance plant development [109].

One of the earliest *in vitro* studies to investigate the mineral solubilisation ability of *Trichoderma* was conducted by Altomare et al. [107]. The result of the study revealed that *Trichoderma harzianum* solubilised Rock phosphate, MnO₂, Zn, and Fe₂O₃ by chelation and reduction, which play a significant role in the biocontrol of plant pathogens. Li et al. [110] investigated the relationship between *Trichoderma harzianum* and tomato plant roots for phosphate and micronutrient solubilisation. The result of the experiment showed the capability of the *Trichoderma* strain (SQR-T037) to solubilise phytate, Fe₂O₃, CuO, and metallic Zn. In other experiments by Tandon et al., Bononi et al., Boat Bedine et al., and Song et al., [111–114] *Trichoderma* displayed the capability to solubilise sparingly soluble and insoluble soil micronutrients, which are of immense benefits to the economic plants with effect on biomass accumulation.

3.7.2. Biological Nitrogen Fixation

The biochemical process known as biological nitrogen fixation (BNF) involves particular bacteria (diazotrophs) that have the nitrogenase enzyme converting atmospheric N₂ into ammonia. Nitrogen fixation is carried out by several "free-living," "associative," or "symbiotic" diazotrophs [115,116]. *Trichoderma* enhances photosynthetic carbon fixation capacity, increases nitrogen usage efficiency, and accelerates nitrogen absorption, assimilation, and buildup, significantly affecting plant development and protection against diseases [117].

3.7.3. Phytohormone Level Control

Plant development and defence stimulation are closely linked to *Trichoderma*'s role in synthesising phytohormone [106].

Trichoderma and phytohormones have a complex relationship essential for improving plant health and preventing diseases. The phytohormones produced by these fungi include auxin (indole-3-acetic acid: IAA), gibberellins (GA), abscisic acid (ABA), salicylic acid (SA), and cytokinins (CK). Auxin seems to be especially important in promoting plant development in conjunction with *Trichoderma* [118].

The enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase in *Trichoderma* is significant because it modulates the plant's ethylene biosynthesis and reduces the effects of ethylene-induced stress [119,120]. *Trichoderma* increases plant resistance to diseases caused by fungi, bacteria,

and viruses by modulating phytohormone levels [121]. Applying *Trichoderma* cultures has been linked to higher plant biomass accumulation, excellent water stress resistance, and improved antioxidant machinery. These fungi also cause systemic resistance, activating defensive systems in plants such as the hypersensitive response (HR) and pathogenesis-related (PR) proteins. *Trichoderma*'s capacity to control phytohormones plays a significant role in plant disease management, making it an essential microfungi for crop management and sustainable agriculture [122].

3.7.4. Modification of Plant's Environmental Conditions

Trichoderma modifies soil pH to generate an environment that helps plants defend against diseases. *Trichoderma* lowers the pH of the soil by solubilising minerals and releasing organic acids, which inhibits the growth of pathogens and increases the availability of nutrients for plants. Further impeding the growth of pathogens, this acidic environment also initiates the synthesis of antibiotic chemicals [123]. Additionally, plant growth-promoting actions strengthen plant defence systems, whereas *Trichoderma*'s mycoparasitic activity and resource competition weaken pathogens. This makes plants more disease-resistant and improves the soil ecosystem's balance, lessening the need for artificial fungicides and encouraging sustainable agricultural methods [124]. In addition, *Trichoderma*'s capacity to alter the soil pH enhances soil structure, retains more water, and harbours beneficial microbes, all of which contribute to creating a soil environment that promotes plant protection and development [125]. We can create novel, environmentally friendly methods of managing plant diseases by utilising *Trichoderma*, which will help to ensure a more sustainable future for both the environment and agriculture.

4. Prospects of *Trichoderma* in Plant Disease Control

The prospect of *Trichoderma* is vast and multifaceted, holding great promise for sustainable agriculture and disease management, as this versatile fungus employs a range of modes to protect plants and promote their growth, including mycoparasitism, whereby it parasitises and kills plant pathogens, antibiosis, which involves the production of antibiotics to inhibit pathogen growth, competition, where it out-competes pathogens for resources, induced resistance, which triggers plant defence mechanisms, and plant growth promotion, through the production of plant hormones and nutrients [126,127].

These mechanisms collectively create a robust defence system against pathogens, enhance soil fertility and structure, and boost plant productivity and resilience, making *Trichoderma* an attractive biocontrol agent and plant growth promoter with potential applications in integrated pest management strategies, organic farming, and environmental remediation [128,129].

Further research into its mechanisms of action is likely to uncover even more innovative and effective ways to harness its benefits, such as developing novel formulations and delivery systems, elucidating its role in soil microbiome engineering, and exploring its potential in mitigating the impacts of climate change on agriculture, ultimately leading to a more sustainable food future and a reduced reliance on chemical pesticides.

5. Conclusions

Trichoderma, which has several modes of action via which it exerts biological control against fungi pathogens, is a potential biocontrol agent. The mode of control mechanisms includes competition for resources and space, alteration of environmental factors, antibiosis, activation of plant defence systems, mycoparasitism, and phytohormone synthesis modulation. These mechanisms collectively create a robust defence system against plant pathogens, enhance soil fertility and structure, and promote sustainable agricultural practices. As a biocontrol agent, *Trichoderma* offers several benefits over the conventional crop protection methods that rely on synthetic pesticides. It relies heavily on generating spore-based biopesticides through fermentation procedures and formulation development. However, more study is required to maximise its effectiveness as a biocontrol agent.

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