

# Trichoderma and its role in biological control of plant fungal and nematode disease.

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**Abstract-** Trichoderma is mainly used to control soil-borne diseases as well as some leaf and panicle diseases of various plants. Trichoderma can not only prevent diseases but also promotes plant growth, improves nutrient utilization efficiency, enhances plant resistance, and improves agrochemical pollution environment. Trichoderma spp. also behaves as a safe, low-cost, effective, eco-friendly biocontrol agent for different crop species. In this study, we introduced the biological control mechanism of Trichoderma in plant fungal and nematode disease, including competition, antibiosis, antagonism, and mycoparasitism, as well as the mechanism of promoting plant growth and inducing plant systemic resistance between Trichoderma and plants, and expounded on the application and control effects of Trichoderma in the control of various plant fungal and nematode diseases. From an applicative point of view, establishing a diversified application technology for Trichoderma is an important development direction for its role in the sustainable development of agriculture.

**Keywords:** Trichoderma, plant diseases, biological control, growth promotion, action mechanism



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## Introduction

In the traditional crop cultivation process, the excessive use of pesticides and chemical fertilizers, as well as the long-term large-scale planting of a single crop, has led to the destruction of the farmland ecological environment, plant diseases, insect pest problems, crop pesticide residues, and soil and water environment pollution (Bardin et al., 2015). With green agricultural development, people are urgently seeking safe, effective, and environmentally friendly plant disease control measures. Biological control is mainly used to control harmful organisms in plants through beneficial organisms and their products to control plant diseases and effectively reduce the application of chemical fertilizers and pesticides (Harman et al., 2021). Trichoderma, a biological fungus widely used for plant pest control, mainly exists in the soil, air, plant surface, and other ecological environments and can effectively control a variety of plant diseases. Trichoderma is mainly used to control soil-borne diseases in various plants and some leaf and spike diseases. Trichoderma can prevent disease, promote plant growth, improve nutrient utilization efficiency, enhance plant resistance, and repair agrochemical pollution.

Trichoderma belonging to Eumycota, Deuteromycotina, Hyphomycetes, Hyphomycetales, and Moniliaceae (Kubicek et al., 2019). Its sexual stage includes the Ascomycota, Sordariomycetes, Hypocreales, Hypocreaceae, and Trichoderma ssp. (Sun et al., 2012). 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* (Sánchez-Montesinos et al., 2021; Sun et al., 2022). Trichoderma has been used in biological control research, including *T. harzianum*, *T. hamatum*, *T. longibrachiatum*, *T. koningii*, *T. viride*, *T. polysporum*, and *T. asperellum* (Di Marco et al., 2022). Many studies have shown that most Trichoderma spp. can produce bioactive substances and have antagonistic effects on plant-pathogenic fungi and plant-pathogenic nematodes (Druzhinina et al., 2018). These bioactive substances, including secondary metabolites and cell wall-degrading enzymes, can effectively improve crop resistance, reduce plant diseases, and promote

plant growth (Kubicek et al., 2019). This study systematically and comprehensively elaborated on the research progress on *Trichoderma* spp. and its role in plant disease control, its application as a biological control and its mechanism, as well as preliminarily discussed the problems and prospects of *Trichoderma* as a biological control agent, providing a reference for future research and application.

## **Application and mechanism of action of *Trichoderma* in plant fungal disease control**

### **Application of *Trichoderma* in biological control of plant fungal diseases**

*Trichoderma* is a biocontrol fungus widely distributed worldwide. *Trichoderma* has a huge application value and potential in the field of biological control of plant diseases (Tyśkiewicz et al., 2022). Research on the use of *Trichoderma* to control plant diseases has been reported worldwide. *T. viride* and *T. harzianum* have different degrees of inhibitory effects on 29 species of plant pathogenic fungi belonging to 18 genera, including *Botrytis*, *Fusarium*, and *Rhizoctonia*. *Trichoderma* has control effects on a variety of plant pathogenic fungi, such as *Rhizoctonia solani*, *Pythium ultimum*, *Fusarium oxysporum*, *Sclerotinia sclerotiorum*, *Botrytis cinerea*, *Pseudocercospora* spp. and *Colletotrichum* spp. *Trichoderma* has been widely used for the biological control of cotton verticillium wilt, crop gray mold, tomato gray mold, melon wilt, potato dry rot, tobacco root rot, and other plant diseases. *T. longibrachiatum* T6 biocontrol agent has a good control effect on pepper damping off and can effectively control the spread of pepper disease (Girma, 2022). The control effect was up to 54.8%, which is 12.5% higher than that of the chemical pesticide carbendazim. *T. harzianum* has a good control effect on pepper and potato *Phytophthora* blight. It can inhibit the growth of *Phytophthora* blight in soil, reduce the number of pathogenic fungi, and effectively reduce the rate of dead seedlings and disease index of plants. The control effect of 50× *T. asperellum* fungal fluid on apple canker reached 88.24%, which was significantly higher than that of benziotiazolinone. *T. asperellum* has different effects on different pathogenic fungi, among which its inhibitory effect on the pathogen causing corn leaf spot is the best, at up to 77.91%, followed by *Pythium* and *Fusarium*; and the worst inhibition effect is on corn sheath blight. Therefore, using *Trichoderma* to prevent and control plant diseases can not only inhibit the growth of pathogenic fungi, which is conducive to plant growth but can also reduce the use of chemical pesticides, which is conducive to protecting the ecological environment.

### **Storage resistance and processing technology of *Trichoderma* products**

The commercial application of biocontrol *Trichoderma* depends to a large extent on the stress resistance (such as high temperature, drying, ultraviolet radiation, etc.) and storage resistance (more than 1 year at normal temperature) of the *Trichoderma* preparation. At present, there are two main technologies: on the one hand, reducing acidity and regulating oxygen utilization to induce *Trichoderma* to produce stress-resistant chlamydospores; on the other hand, some chemical additives (such as copper) are added to the preparation. Monfil and Casas-Flores (2014) increased the resistance of *Trichoderma* to high temperature (35~40°C) and ultraviolet radiation by adding trehalose to *Trichoderma*. Monfil and Casas-Flores (2014) added glycerin to the *Trichoderma* preparation as a humectant to prolong its shelf life. Special packaging design, vacuum drying, and low-density polyethylene packaging materials can extend the shelf-life to 15 months. In the field of *Trichoderma* preparation form processing, Chen et al. (2021) developed the *Trichoderma* conidia powder agent and obtained a patented technology for inducing *Trichoderma* to produce chlamydospores. With the increasingly mature biological control technology, the types of commercial preparations for *Trichoderma* spp. are also becoming diverse. There are four main categories: (1) Wettable powders, which are made by mixing conidia powder, powdery carriers, and humectant. (2) Granules are made by mixing and stirring conidia and carrier. (3) A mixture consisting of spore powder and chemical fungicides mixed in proportion on a suitable carrier. (4) Suspenso-emulsion is prepared by suspending conidia in a lotion composed of vegetable oil, mineral oil, emulsifier, etc. In the current market for *Trichoderma* biological agents, *T. Harzianum* is the largest, followed by *T. viride* and *T. koningii*. *Trichoderma* agents widely used in plant disease control mainly include *Trichodex* a commercial preparation of *T. harzianum* T-39; *RootShield*, a commercial preparation of *T. harzianum* T-22; *Binab TF*, a mixed-agent of *T. harzianum* and *T. polyspora*; *Sentinel* (*Novozymes, Denmark*), a commercial preparation of *T. atrovilide*; And *Supervivit* (*Borregaard Bioplant, Denmark*), a commercial preparation of *T. harzianum*.

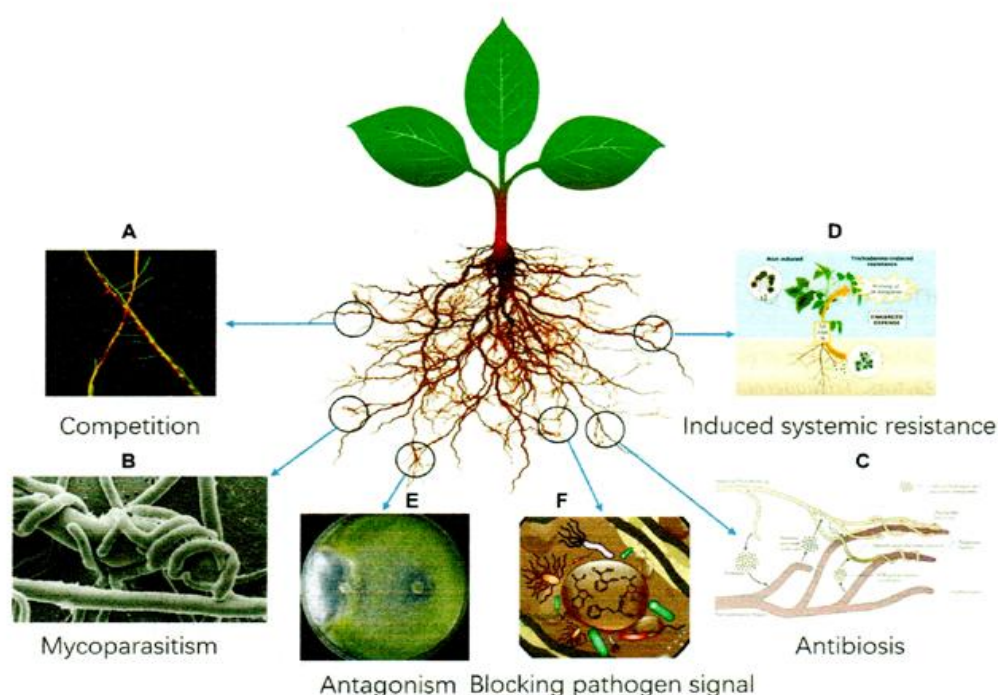
## Mechanism of Trichoderma-induced endophytic microbiome synergistically stimulating plant immune response

### Competitive role of Trichoderma

Trichoderma are saprophytic fungi with fast mycelial growth and strong adaptability to the environment. It can seize the invasive part of the pathogenic fungi in the root of a plant, thus hindering the invasion of the pathogen fungi. It can also rapidly absorb the nutrients required for the growth of the pathogen fungi, resulting in nutrient deficiency and inhibiting the growth and reproduction of the pathogen fungi. Trichoderma has strong adaptability to the environment (Köhl et al., 2019; Morán-Díez et al., 2019; Pescador et al., 2022). Through its rapid growth and reproduction, it can seize nutrients and space near the plant rhizosphere, consume oxygen in the air, and weaken the growth of plant pathogenic fungi (BasińskaBarczak et al., 2020; Oszust et al., 2020; Panchalingam et al., 2022). The growth rate of Trichoderma is much faster than that of plant pathogenic fungi; therefore, it can effectively inhibit the growth of plant pathogenic fungi (Mohiddin et al., 2021). After entering the soil for 24h, Trichoderma can quickly adsorb to the roots of crops for propagation, and the hyphae quickly wrap the roots of crops to form a protective layer, protect the roots of crops from the invasion of pathogens, and kill the nearby pathogens. Risoli et al. (2022) found that the growth rate of *T. harzianum* was 2.0 to 4.2 times faster than that of *B. cinerea*. Trichoderma mycelium competed with *Fusarium graminearum* by clinging, twining, inter-penetration, and other mechanisms, which caused the mycelium of *F. graminearum* to deform and eventually disappear (Dugassa et al., 2021). Trichoderma can capture water and nutrients, occupy space, and consume oxygen, etc. through rapid growth and reproduction, to weaken and exclude the gray mold pathogen in the same habitat (Herrera-Téllez et al., 2019).

### Mycoparasitism of Trichoderma

Mycoparasitism is one of the important mechanisms in the biological control of Trichoderma (Figure 1B). Trichoderma can parasitize about 18 genera of *Pythium*, *Phytophthora*, *Rhizoctonia*, and *Peronospora*. They directly invade or wound the mycelium, causing the pathogen cells to expand, deform, shorten, become round, shrink the protoplasm, and break the cell wall. Trichoderma TM can invade the hyphae of *Sclerotinia sclerotiorum*, attach to and wrap around the hyphae of pathogenic fungi, and break the hyphae of *S. sclerotiorum* until it disintegrates (Shaw et al., 2016). Risoli et al. (2022) found that Trichoderma can form putrescence in a specific environment, which has a mycoparasitic effect on *Botrytis cinerea*. It forms a large number of branches and sexual structures after entering the host hyphae, thus inhibiting the appearance of grape *B. cinerea* symptoms. Trichoderma can degrade the cell wall of pathogenic fungi by secreting chitin-degrading enzymes, so as to better invade the interior of pathogenic fungi.



**Figure 1(A-F)** Schematic diagram of the mechanism of action of Trichoderma in plant fungal disease control (Martinez – Medina et al., 2013; Ladman et al., 2015; Moran –Diez et al., 2020; Manzar et al., 2022; Tanizi et al., 2022)

Trichoderma mycelium hyperparasitized *Fusarium graminearum* by clinging, twining, inter-penetration, and other mechanisms, which caused the mycelium of *F. graminearum* to deform and eventually disappear.

Chitinase secreted by *T. harzianum* plays an important role in promoting cell wall dissolution, mycelial autolysis, chitin assimilation, fungal parasitism, and inhibiting spore germination, mycelial growth, and spore formation (Saravanakumar et al., 2017). *T. koningiopsis* can invade the hyphae of *Sclerotinia sclerotiorum*, attach to and wrap around the hyphae of pathogenic fungi, and break the hyphae of *S. sclerotiorum* until it disintegrates (Shaw et al., 2016).

### **Antibiosis effect of Trichoderma**

Antibiosis mainly refers to the ability of Trichoderma to inhibit the growth of plant pathogenic fungi by secreting antagonistic substances. Trichoderma can produce hundreds of antimicrobial secondary metabolites, including trichomycin, gelatinomycin, chlorotrichomycin, and antibacterial peptides (Maruyama et al., 2020). These secondary metabolites can act as antibacterial agents, promote plant growth, and provide rich materials for the development of agricultural antibiotics (Nawrocka et al., 2018). Naglot et al. (2015) found that the metabolites of *T. viride* had a significant inhibitory effect on the wilt-specific form of *F. oxysporum*, with an inhibition rate of 54.81%. Manganiello et al. (2018) found that the volatile secondary metabolites secreted by *T. viride* TG050 609 can cause the mycelium of *P. nicotianae* to grow irregularly, break, or even dissolve, proving that *T. viride* has an antibiosis effect on *P. nicotianae*. In addition, most Trichoderma strains can produce antimicrobial substances such as pentaibols, which can inhibit a variety of plant pathogenic fungi and can also cooperate with cell wall-degrading enzymes on pathogenic fungi to effectively inhibit their growth. Some studies have shown that some Trichoderma spp. can produce volatile metabolites, which can inhibit the growth of colonies to varying degrees, and some of them can inhibit the growth of colonies by more than 80%.

In recent years, research on the genome, transcriptome, proteome, and metabolome of Trichoderma has developed rapidly (Zhang Y. et al., 2022). Genome and EST sequencing, and microarray and microarray based expression profiling have become important tools for exploring Trichoderma genes and studying the mechanism of action (Tamizi et al., 2022). In genomics research, a cDNA library of *T. harzianum* EST has been constructed, and multiple new genes have been identified (Ferreira Filho et al., 2020). The researchers completed the genome sequencing of *T. reesei*, *T. virens*, and *T. atroviride*. Rubio et al. (2014) used high-density oligonucleotide (HDO) microarray technology and bioinformatics analysis to detect and analyze: after 20h of interaction between *T. hamatum* T7 and tomato, there were 200 differentially expressed genes, of which 166 were up-regulated and 34 were down-regulated; 43.14% of genes are related to molecular function, 56.86% are related to biological processes, and 32.0% are related to cell component formation. Shores and Harman (2010) identified the changes of 27 endochitinase genes and 4 exochitinase genes in maize after interaction between *T. harzianum* T22 and maize using proteomic methods and EST libraries and discovered a new specific chitinase. Chen et al. (2021) used proteomic techniques to identify proteins related to resistance to root rot in maize, among which chitinase, SOD, isoflavone reductase, and PR protein are associated with resistance to root rot in maize seedlings.

### **Induced systemic resistance of Trichoderma**

Trichoderma can induce host plants to produce defense responses. While inhibiting the growth and reproduction of pathogenic fungi, it can also induce crops to produce self-defense systems to obtain local or systemic disease resistance (Figure 1D). Trichoderma-induced plant disease resistance is achieved through two approaches: one is to regulate the plant disease resistance response by regulating elicitors or effectors; second, the cell wall-degrading enzyme produced by Trichoderma releases oligosaccharides that can induce plant resistance (Gomes et al., 2015). At present, there are more than 10 elicitors of Trichoderma that induce plant resistance, including Sm1, QID74 hydrophobic protein, chitin-degrading enzyme, MRSP1, xylanase, cellulase, endopolygalacturonase, sucrase, and antibacterial peptides. These substances are mainly derived



from five *Trichoderma* species: *T. asperellum*, *T. viride*, *T. atroviride*, and *T. harzianum* (Karimi Aghcheh et al., 2013; Lamdan et al., 2015; Ngo et al., 2021; Matas-Baca et al., 2022; Zaid et al., 2022; Zhu et al., 2022). Saravanakumar et al. (2016) found that the activities of peroxidase (POD) and phenylalanine ammonia lyase (PAL) of corn seeds coated with *Trichoderma* increased significantly, and the plants were resistant to *curvularia* leaf spot of corn.

### **Antagonism of *Trichoderma***

The antagonism of *Trichoderma* is often considered the result of simultaneous or sequential action of more than two mechanisms (Saravanakumar et al., 2016; Sui et al., 2022; Figures 1E,F). Based on multiple mechanisms, *Trichoderma* has synergistic capabilities. Jogaiah et al. (2018) found that the synergistic use of *T. harzianum* and fungicides can effectively inhibit tomato gray mold, and the inhibition rate was higher than that of both fungicides alone. Zhang et al. (2017) found that the fermentation metabolites of *T. viride* CCTCC-SWB0199 and brassinolide in a certain proportion had a higher effect on the control of tomato gray mold than when the two were applied separately. Jogaiah et al. (2018) found that the biocontrol effect of *Trichoderma* spp. against plant pathogens fungi are often the result of a combination of multiple mechanisms, and different strains have different emphasis on biocontrol mechanisms. Monfil and CasasFlores (2014) used transcriptology and metabolomics to study the tripartite interactions of *Arabidopsis*, *Trichoderma*, and *Pseudomonas syringae* tomato varieties. The results showed that the treatment of *Arabidopsis* roots with *Trichoderma* for 48h induced more than 300 gene expression changes in the roots, but the changes in leaf genes were different from those in the roots (Monfil and Casas-Flores, 2014). *Trichoderma* induces the differential expression of host plant genes, mainly at the level of quantity. A metabolomics study found that 27 compounds were related to induced resistance in *Arabidopsis thaliana* (Monfil and Casas-Flores, 2014). The biocontrol effect of *Trichoderma* on plant pathogenic fungi is often the result of multiple mechanisms, and different strains have different biocontrol mechanisms (De Zotti

### **Application and mechanism of action of *Trichoderma* in plant nematode disease control**

Application of *Trichoderma* in the control of plant nematodes At present, the reported *Trichoderma* with nematicidal activity mainly includes *T. longibrachiatum*, *T. viride*, *T. harzianum*, *T. Hamatum*, *T. atroviride*, and *T. koningii* (Zhu et al., 2022). The fermentation broth of *T. longibrachiatum* T6 has a strong lethal effect on the eggs and second-instar larvae of cereal cyst nematodes in wheat (Zhu et al., 2022). The relative inhibition rate of the two concentrated fermentation broths on egg hatching was 46.47%, and the corrected mortality rate for the second-instar larvae was 44.45% (Sokhandani et al., 2016). Microscopic observation showed that the fermentation liquid of *T. longibrachiatum* T6 could digest the contents of nematode eggs and body cavities of the second instar larvae (Zhu et al., 2022). Khan et al. (2020) used inducers to make *T. koningiopsis* UFSMQ40 produced fermentation broth containing a large amount of chitinase, and its lethal rate to root-knot nematodes of South China and Java was 90.4 and 63.2%, respectively. Baazeem et al. (2021) analyzed the transcriptional activity of *chi18-5* and *chi18-12* genes of *T. harzianum* FB10 in *Trichoderma* egg parasitism. Compared to the control, the expression of *chi18-5* and *chi18-12* genes during parasitism increased significantly, indicating that the chitinase content increased, which could provide favorable conditions for egg cleavage (Baazeem et al., 2021).

### **Mechanism of *Trichoderma* resistance to nematode disease**

The mechanism by which *Trichoderma* inhibits nematode disease remains unclear. Some studies suggest that the serine protease *pr1* of *Trichoderma* has similar biochemical characteristics to the protein *Pr1* of nematicidal fungi, so it has a certain nematode inhibition effect (Forghani and Hajihassani, 2020). The antimicrobial peptides produced by *Trichoderma* also have nematicidal effects (Fan et al., 2020).

### **Mycoparasitism effect of *Trichoderma***

*Trichoderma* mycoparasitism is an important mechanism for controlling nematodes and includes identification, contact, entanglement, penetration, and parasitism (Li et al., 2020; Figure 2). *Trichoderma* mycelium penetrates the eggshell or cuticle of larvae and adults of nematodes, colonizes, absorbs nutrients from nematodes, and causes nematode death (Marraschi et al., 2019). *Trichoderma* mycoparasitic nematode processes involve the production and co-secretion of various degrading enzymes (Moo-Koh et al., 2022). The

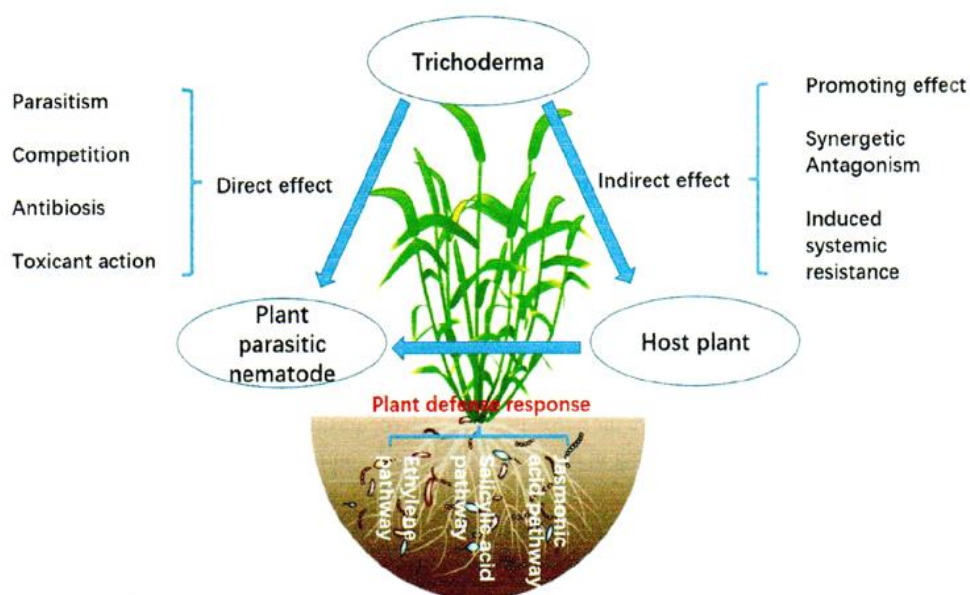
induction of *Trichoderma* activities of  $\beta$ -1, 3-glucanase, chitinase, and protease are increased, which can enhance the immunity of plants to nematodes (Poveda et al., 2020). The hyperparasitic process is mainly regulated by heterotrimeric G protein, cAMP, and MAPK motif signals, and secretes extracellular chitinase, glucanase, xylanase, cellulase, and protease, among which chitinase and protease are particularly important and can degrade the cyst, egg, larva, and adult body wall of nematodes (Li et al., 2020). *Trichoderma* secretes glucosidases NAG1 and NAG2, which act on the extracellular and self-cell walls, respectively, and their main function is to degrade chitin so that they can protect their cell walls from degradation during the process of hyperparasitism (Poveda et al., 2020).

### **Antibiosis effect of *Trichoderma***

*Trichoderma* can inhibit the growth and reproduction of nematodes by secreting antagonistic substances (Moo-Koh et al., 2022). *Trichoderma* produces a variety of secondary metabolites, including trichomycin, gliotoxin, viridin, antibacterial peptide,  $\beta$ -1, 3-glucanase, chitinase, polypeptides, polyketones, butyrolactones, sesquiterpene heptadecarboxylic acid, terpenes, and some volatile substances (hydrocarbons, alcohols, furans, aldehydes, alkanes, olefins, esters, aromatic compounds, heterocyclic compounds, and various terpenoids) (Kappel et al., 2020). Contina et al. (2017) reported for the first time that *T. harzianum* ThzID1-M3 labeled with GFP significantly inhibited the reproduction of potato cyst nematodes, with a cyst decline rate of 60%. The inhibition rates of the fermentation broth of *T. hamatum* HZ-9 and *T. virens* HZ-L9 on the hatching of soybean cyst nematode eggs were 80.6 and 79.4%, respectively (Contina et al., 2017). The secondary metabolites produced by the same *Trichoderma* species in different media have different effects on nematode resistance (Forghani and Hajihassani, 2020). The inhibition rate of *T. viride* secondary metabolites on wheat medium and solid medium on egg hatching of southern root knot nematode was 71.6 and 67.3%, respectively (Baazeem et al., 2021). Baazeem et al. (2021) detected and analyzed the *T. hamatum* FB10 secondary metabolite nematocidal active ingredient; thirteen kinds of chemical substances were obtained, including 6-amyl- $\alpha$ -pyranone. The inhibition rate of egg hatching of *Meloidogyne incognita* was 78.26%.

### **Toxicity effect of *Trichoderma***

*Trichoderma* produces toxic secondary metabolites that directly come into contact with nematodes, which is an important direct biological control mechanism (Khan et al., 2020). It has been found that the toxic secondary metabolites produced by *Trichoderma* are divided into two categories, one is small molecules and volatile substances, including aromatic compounds, polyketides, butenolactones, and terpenoids, etc.; the other is macromolecular metabolites, including peptides, enzymes, etc. (Khan et al., 2020). It has been reported that the main nematocidal substances isolated from *Trichoderma* are trichodermin, acetic acid, gliotoxin, and peptide cyclosporin A (Fan et al., 2020). Meanwhile, Moo-Koh et al. (2022) used GC-MS to detect and analyze the nematocidal active components of *Trichoderma* TUV-13 strain and obtained more than 40 chemical components, among which of which the main alkanes are the most, in addition to organic acids, esters, ketones, steroids, and other organic compounds. Li et al. (2020) summarized and analyzed the secondary metabolites and activities of 20 species of *Trichoderma*, including *T. aureoviride*, *T. arundinaceum*, *T. brevicompactum*, *T. citrinoviride*, *T. gamsii*, *T. polysporum*, *T. saturnisporum*, *T. spirale*, *T. cremeum*, *T. pseudokoningii*, and *T. lignorum*. There were 390 non-volatile secondary metabolites, among which wickerol A, harziandione, trichodermin, and cyclonerodiol exhibited nematocidal activity (Khan et al., 2020). The *T. virens* B3 fermentation broth has strong toxic activity against cereal cyst nematodes, and the killing rate is as high as 86.2% (Forghani and Hajihassani, 2020). The fermentation broth can maintain good stability for a long time. The fermentation broth of *T. citrinoviride*, *T. harzianum*, *T. acroviride*, and *T. koningiopsis* had a strong toxic effect on the southern root-knot nematode J2, with a mortality rate of more than 85% (Du et al., 2020).



**Figure 2** Schematic diagram of the mechanism of action of Trichoderma in plant nematode disease control

### Induced resistance effect of Trichoderma

Induced resistance is the response of plants to stress, which is stimulated by external factors. Trichoderma-colonized plant roots cause physiological and metabolic changes and produce a variety of secondary metabolites that act as elicitors (Al-Hazmi and TariqJaveed, 2016). At present, there are more than 20 elicitors produced by Trichoderma that induce plant resistance, including antitoxins, polypeptides, lipopeptides, cellulases, hydrophobic proteins, non-toxic gene proteins, terpenoids, phenol derivatives, glycosidic ligands, and flavonoids (Pocurull et al., 2020). These secondary metabolites induce plant defense responses and promote plant growth. The interaction between Trichoderma and plants increases the synthesis of defense-related enzymes and substances. *T. hamatum* can induce the activities of phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and peroxidase (POD), which are related to tobacco defense reaction, to increase significantly (Al-Hazmi and TariqJaveed, 2016). In tomatoes treated with *T. harzianum*, the control effect against *M. incognita* was 61.88%. Further studies have shown that the levels of reactive oxygen species (ROS), superoxide ( $O_2^-$ ), hydrogen peroxide ( $H_2O_2$ ), and malondialdehyde (MDA) in tomatoes were significantly increased, and the defense-related genes PAL, C4H, 4CL, CAD, LPO, CCOMT, Tpx1, and G6PDH were upregulated, thus inducing the defense response of tomatoes to *M. incognita* (Pocurull et al., 2020). Plant-induced resistance mainly involves signal transduction pathways such as those of salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). In the interaction between Trichoderma and Arabidopsis, tomato, and cucumber, JA, SA, and ET contents increased to varying degrees, indirectly improving plant resistance (Hinterdobler et al., 2021). This process is also related to activating chitinase and glucanase activities and inhibiting the plant antioxidant enzyme system. The expression of ETR1 and LOX1 genes of jasmonic acid and the ethylene signal pathway increased significantly in *T. asperellum* DQ-1 irrigated tomato, which enhanced tomato resistance (Agbessenou et al., 2022). Some volatile secondary metabolites of Trichoderma are important elicitors that induce plant resistance (Al-Hazmi and TariqJaveed, 2016). The volatile substances produced by *T. harzianum* and *T. asperellum* act as elicitors to stimulate the up-regulated expression of Arabidopsis-induced resistance-related transcription factor MYB72, which triggers a JA-regulated defense response (Agbessenou et al., 2022). At present, the interaction mechanisms and signal transduction pathways between Trichoderma volatile secondary metabolites and plants have not been thoroughly studied. The active substances produced by Trichoderma are recognized by plants, thus activating the signal transduction pathway and inducing the production of plant system resistance. The microbial determinants recognized by microorganisms are called microbe-associated molecular patterns (MAMPs) (Baazeem et al., 2021). After Trichoderma infects plant roots, it releases a variety of MAMPs to activate immune response (MTI), thus

inducing plant systemic resistance (ISR) (Li X. et al., 2022). Abdelkhalek et al. (2022) showed that *T. hamatum* strain Th23 promotes tomato growth and induces systemic resistance against tobacco mosaic virus.

### **Application of Trichoderma in promoting plant growth and repairing environment**

Trichoderma can produce plant growth stimulators, such as indoleacetic acid (IAA) and harzianolide, to promote the development and growth of plant roots by secreting phytase and ferritin to promote the absorption of P and Fe by plants; decomposes soil organic matter; increases the supply of soil nutrients; improves crop photosynthetic efficiency; improves plant height, stem diameter, and other agronomic traits; and increases production (Lombardi et al., 2020a). Many studies have shown that most *Trichoderma* spp. can produce bioactive substances and have antagonistic effects on plant-pathogenic fungi and plant-pathogenic nematodes. Bioactive substances, including secondary metabolites and cell wall-degrading enzymes, can effectively improve the resistance of crops, reduce plant diseases, and promote plant growth.

Trichoderma can improve soil nutrient availability and utilization efficiency. The aboveground biomass of cucumber seedlings inoculated with *Trichoderma* MF-2 increased by 39.07%, with a significant growth-promoting effect, and an increased number of beneficial microorganisms in the soil (Singh et al., 2019; Ye et al., 2020). Different *Trichoderma* strains had different degrees of antagonism to *F. oxysporum*, and the combination of *Trichoderma* wettable powder treatment significantly increased banana yield (Samuelian, 2016; Bubicic et al., 2019; Damodaran et al., 2020). Li et al. (2020) found that the biocontrol agent *Trichoderma* GYXM-1p1 strain had a strong growth-promoting effect through pot cultivation. After treatment with this strain, the root length, plant height, root fresh weight, dry weight, total fresh weight, and total dry weight of cabbage plants were significantly improved compared to the water control ( $p < 0.05$ ), and the total fresh weight and total dry weight of cabbage plants were increased by 417.60% and 762.69%, respectively, compared with water control. Ruan et al. (Intana et al., 2021; Nuangmek et al., 2021) found that the application of nitrogen fertilizer with *Trichoderma* promoted the quality of muskmelon. After the application of *Trichoderma*, the soluble sugar content of muskmelon fruit increases significantly, improving the quality of muskmelon. The application of *Trichoderma* can increase the SPAD value of chlorophyll in peanut leaves, improve the main agronomic traits of peanuts, significantly increase the activity of protective enzymes in peanut roots, stems, and leaves, and reduce the content of MDA (Kovács et al., 2021; Al-Askar et al., 2022). When 1.5kg/666.7m<sup>-2</sup> was applied, the number of pods per plant, pod weight, seed kernel weight, 100 fruit quality, 100 fruit kernel quality, and yield per plant of peanut increased by 24.63, 20.22, 14.10, 4.86, 7.63, and 12.85%, respectively, compared with the control (Al-Askar et al., 2022).

### **Mechanism of Trichoderma in promoting plant growth and repairing environment**

Trichoderma can promote plant growth, produce substances that can promote plant growth, improve the solubility of nutrients in the soil, and improve plant rhizosphere microecology, thereby promoting plant absorption and growth (Karuppiyah et al., 2019a; Kakabouki et al., 2021; Marra et al., 2021; Figure 3). *Trichoderma* plant interactions can not only induce resistance but also improve the resistance of plants to abiotic stress factors (salt, high temperature, UV). Treatment of cucumber seeds with *T. asperellum* T203 improved the plant's salt tolerance, and the activities of Mn/Cu SOD and catalase (CAT), and significantly reduced ascorbic acid in the plant (Illescas et al., 2022). *Trichoderma* can significantly enhance the Na<sup>+</sup> efflux from the root system of *Lycium barbarum* and its transport to the upper ground, ensure K<sup>+</sup> absorption and maintain the ion balance in the plant, thus reducing the damage of PSII caused by ion toxicity and oxidative stress, protecting photosynthetic pigments, maintaining the photosynthetic performance of *L. barbarum* under salt stress, and reducing biomass loss (Brotman et al., 2013).

The synthesis of plant growth hormones, such as IAA, ABA, ET, GA, and CK is the main mechanism of *Trichoderma* (Karuppiyah et al., 2019b; Wang et al., 2021; Degani et al., 2021b; Agbessenou et al., 2022). *T. asperellum* induced cucumber to produce IAA, GA, and ABA to promote growth (Liu H. et al., 2022). The height, stem diameter, soluble sugar content, and absorption rate of available nitrogen of tomato seedlings treated with *T. asperellum* were significantly increased, and the expression of tomato hormone signal transduction-related genes JAR1, MYC2, NPR1, PR1, and GH3 was significantly increased (Rawal et al., 2022). Another study showed that *T. asperellum* can upregulate the expression of xylanase genes in poplar and has a significant growth-promoting effect (Karuppiyah et al., 2019b). *T. harzianum* regulates tricarboxylic acid cycle (TAC) and hexose monophosphate pathway (HMP) to promote tomato growth by enhancing



succinate dehydrogenase and glucose-6-phosphate dehydrogenase activities (Manganiello et al., 2018). *Trichoderma* produces acidic substances that can dissolve insoluble trace elements in soil and provide more nutrition to plants (Samuelian, 2016). *T. asperellum* can transform insoluble phosphate in the soil into effective phosphorus and promote the absorption and utilization of cucumbers (Karuppiyah et al., 2021; Figure 3). *T. koningiopsis* can produce organic acids that dissolve insoluble tricalcium phosphate under high alkaline stress and can also produce alkaline phosphatase under drought stress to solubilize phosphorus and improve the utilization of nutrients by plants (You et al., 2022). Many experiments have verified that *Trichoderma* promotes plant growth (Mayo et al., 2015; Bononi et al., 2020; Lombardi et al., 2020b; Swain et al., 2021; Velasco et al., 2021; Bridžiuvienė et al., 2022; Joo and Hussein, 2022; Li X. et al., 2022); under complex field production conditions, the mechanism by which *Trichoderma* promotes plant growth requires more systematic research.

### Conclusion and future perspectives

At present, chemical control is the main method used for plant disease control and is achieved by spraying pesticides and fungicides. Although the effect of chemical control is good and helpful in increasing agricultural production, the unscientific use of chemical pesticides has caused serious pollution to the environment and enhanced pathogens' resistance to and chemical pesticides. Several experiments have proven that *Trichoderma* has good biological control effects and can reduce the use of chemical pesticides. However, there are still few biocontrol agents against *Trichoderma* on the market, and more effective and suitable strains need to be found to join the biocontrol team (Nieto-Jacobo et al., 2017; Fiorentino et al., 2018; López et al., 2019; Nawrocka et al., 2019; Poveda et al., 2019; CabralMiramontes et al., 2022).

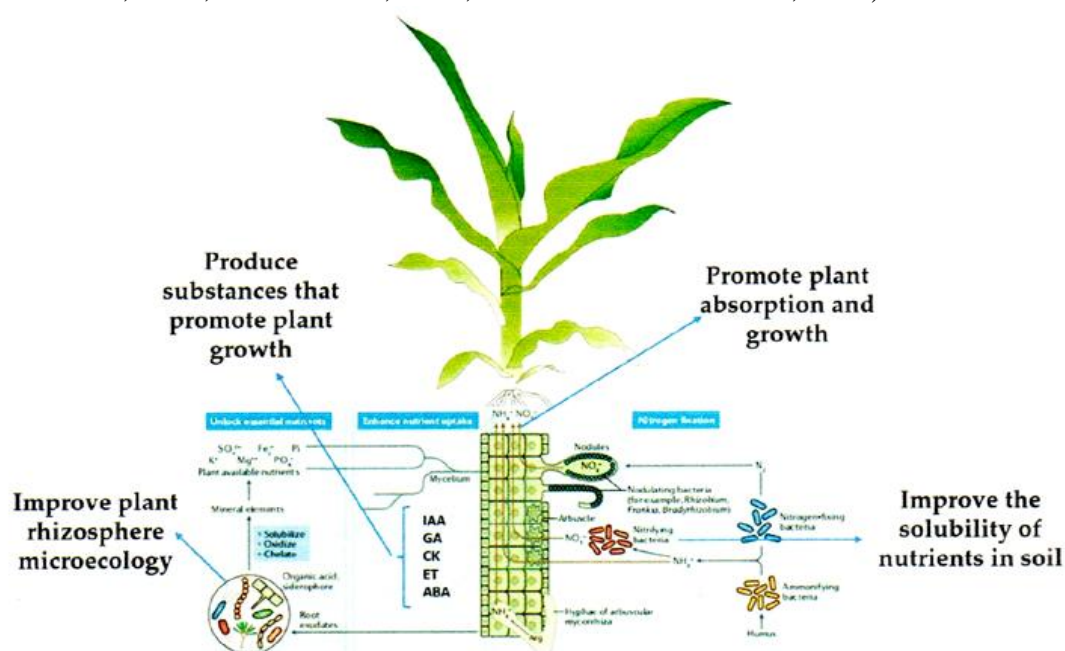


Figure 3

*Schematic diagram of the mechanism of action of Trichoderma in promoting crop growth and repairing the environment*

Although *Trichoderma* has great prospects for agricultural applications, there are still some problems in the development and utilization of *Trichoderma*. Because the spore preparation of *Trichoderma* is generally a living fungal preparation, which is often affected by various natural factors such as humidity, temperature, soil acidity, alkalinity, and the soil microbial community when it is applied in the field, the field test performance is unstable, and the biological control effect is weakened. In addition, the shelf life of biological control agents is relatively short, and some microorganisms must be stored at low temperatures to ensure the concentration of live microorganisms when they are applied. There are still several problems to be solved in the application of *Trichoderma* in the biological control of plant diseases. The first is to explore and produce efficient strains, which can be screened through genetic engineering technology to produce *Trichoderma*

biocontrol-engineered strains that are resistant to chemical pesticides and low temperatures. At the same time, it is necessary to develop effective *Trichoderma* agents suitable for use with various application methods to enhance the control effect and improve the processing technology of *Trichoderma* agents to extend the shelf life of biological control agents. Second, exploring the combined effects of *Trichoderma* spp. and other microorganisms is necessary. The development of Pesticides with volatile and non-volatile secondary metabolites secreted by *Trichoderma* as the main active ingredient will be the focus of future research and the development of new Pesticides. To improve the quality of *Trichoderma* biopesticides, in addition to monitoring traditional indicators such as pH, dissolved oxygen, and temperature in the fermentation process, it is also necessary to monitor its correlation with the yield of antagonistic substances at the level of the cell metabolic flow, genome, proteome, and metabolome (Mulatu et al., 2021). However, it is necessary to establish more scientific quality standards for *Trichoderma* products in vivo, such as increasing the content of antagonistic substances or activity indicators (Niu et al., 2020). The development of new dosage forms, such as cell microcapsules, water-in-oil emulsions, and other protective dosage forms, should be strengthened, and the molecular mechanism of chlamydospore production should be further studied (Table 1). With further study of transgenic *Trichoderma*, a prospective study on the biological and environmental safety of transgenic *Trichoderma* should be conducted (Li et al., 2021). At present, the balance regulation of *Trichoderma* colonizing host and plant immune response, long-distance and trans-growth period transduction mechanism of systematically induced plant disease resistance and its defense signals, identification of *Trichoderma* elicitors to recognize plant targets or receptors, and mechanism of *Trichoderma*-induced plant endophytic microbiome to synergistically stimulate plant immune response has become an international research topic of interest. Studies on miRNA regulation of *Trichoderma* colonization host process and plant immune response, and the regulation mechanism of cross-border miRNA transduction between *Trichoderma*, plants, and pathogenic microorganisms are emerging. The combination design or co-culture technology of *Trichoderma* and other microorganisms has become key for tapping new metabolites with specific functions of microorganisms, broadening the target spectrum of microbial metabolites, and developing new biopesticides and biostimulants based on metabolites (Wang Y. et al., 2022). It is expected to become a new direction for the development of macromolecular biopesticides by molecular construction or modification of the *Trichoderma* multi-stimulator fusion protein and the development of new plant immune-activating protein pesticides. At present, it is urgent to reveal the synergistic interactions among *Trichoderma*, plants, and pathogenic microorganisms in induced disease resistance on a cross-genome scale, develop *Trichoderma* and other microbial symbiotic agents that can cure both diseases and pests, and develop new biostimulator products based on *Trichoderma* metabolites.

**TABLE 1 The main biological function of common species of *Trichoderma*.**

<b>Name of species</b>	<b>Major function</b>	<b>Reference</b>
T. harzianum	Induced systemic resistance to fungi disease and increased plant productivity; Nematode resistance; Improved plant growth and root architecture.	Saravanakumar et al. (2016), Poveda et al. (2019), Coppola et al. (2019)
T. asperellum	Antifungal activities; Plant growth promotion; Stress resistance; Enrich soil fertility	Wang H. et al. (2022), AL-Askar et al. (2021), Degani et al. (2021b)
T. asperelloides	Antifungal activities; Plant growth promotion; Stress resistance	Ruangwong et al. (2021a), Phoka et al. (2020), Rawal et al. (2022)
T. atroviride	Fungistatic activity, plant growth promotion; Antifungal and antibacterial activities; Plant growth promotion and nutrient assimilation; Induced systemic defense responses; Stress resistance	Coppola et al. (2019), Zhang C. et al. (2022), González-López et al. (2021), Leal et al. (2021), Nawrocka et al. (2019)
T. hamatum	Nematode resistance; Increased plant productivity; Antibacterial and antifungal activities; Plant growth promoting	Li X. et al. (2022), Velasco et al. (2021), Baazeem et al. (2021)

T. virens	Antifungal activities; Plant growth promotion Jogaiah et al. (2018), Halifu et al. (2020) T. viride Antifungal activities; Enhanced root development; Nematode resistance; Stress resistance	Al-Hazmi and TariqJaveed, (2016), Naglot et al. (2015), He et al. (2020)
T. longibrachiatum	Antifungal activities; Improve salt resistance; Nematode resistance; Plant growth promotion; Induced systemic defense responses	Ngo et al. (2021), Boamah et al. (2021), AL-Askar et al. (2022), Degani et al. (2021b), Yuan et al. (2019)
T. ghanense	Plant growth promotion; Enrich soil fertility Bridžiuvienė et al., 2022 T. tomentosum Plant growth promotion; Enrich soil fertility	Bridžiuvienė et al. (2022)
T. volatiles	Induced systemic resistance Pescador et al. (2022) T. velutinum Plant growth promotion	Mayo-Prieto et al. (2019)
T. phayaoense	Antifungal activities; improve plant growth and root architecture Nuangmek et al. (2021) T. koningiopsis Antifungal activities; Plant growth promotion	Ruangwong et al. (2021b), You et al. (2022)
T. citrinoviride	Antifungal activities; Nematode resistance Park et al. (2019), Fan et al. (2020) T. reesei Antifungal activities	Hinterdobler et al. (2021)
T. gamsii	Antifungal activities; Affected herbivore feeding behaviour	Alukumbura et al. (2022), Zhou et al. (2018), Di Marco et al. (2022)
T. aggressivum	Fungal diseases biological control	Sánchez-Montesinos et al. (2021)
T. atrobrunneum	Nematode resistance	Hernández et al. (2018) T. afroharzianum Plant growth promotion Kappel et al. (2022)
T. bissettii	Antifungal activities	Chung et al. (2022)
T. parareesei	Improve plant quality	Rubio et al. (2014)
T. lignorum	Nematode resistance	Daza et al. (2019)
T. taxi	Antifungal activities	Chen et al. (2021)
T. strigosellum	Nematode resistance; Plant growth promotion	Batista et al. (2021)
T. hebeiensis	Antifungal activities; Plant growth promotion	Swain et al. (2021)
T. erinaceum	Antifungal activities; Plant growth promotion	Swain et al. (2021)

Compared with single-life biocontrol fungi, compound biocontrol fungi can better avoid the problems of weak adaptability to the environment, narrow range of disease resistance, and insufficient control effect. At present, there are many preparations containing different kinds of Trichoderma, which are being used in sustainable agricultural crops, but the application of these preparations is still expensive, and not available to all farmers. The application of compatible or affinity multiple microorganisms for compounding has become a trend in the development of biocontrol agents. Trichoderma can form alliances with a variety of microorganisms such as bacteria and fungi to directly or indirectly improve the ability of plants to prevent and control diseases. The following aspects may be the main research focus of Trichoderma as a biocontrol fungus in the future: the molecular mechanism of the specific interaction between Trichoderma and plants; Molecular basis of plant immunity induced by Trichoderma; Improvement of Trichoderma fermentation process; Establishing diversified application technology models of Trichoderma. The commercial application of biocontrol

Trichoderma depends largely on the stress resistance (such as high temperature, drying, ultraviolet radiation, etc.) and storage resistance (more than 1 year at normal temperature) of the Trichoderma agent. At present, there are two main technologies. One is to reduce the acidity and regulate the utilization of oxygen to induce Trichoderma to produce stress-resistant chlamydospores, and the other is to add some chemical additives (such as copper) to the inoculum. How the effectors produced by Trichoderma interact with plant cell receptors has become the key to revealing the mechanism of Trichoderma inducing plant immunity. With the deepening of the research on transgenic Trichoderma, prospective research on the biological and environmental safety of transgenic Trichoderma should be carried out.

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