Harnessing Trichoderma in Agriculture

Subjects: Agronomy

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Increased agricultural activities driven by rising food demand have led to environmental problems mostly arising from the high levels of external inputs and resources that are required. Additionally, environmental changes, such as global warming, can lead to various biotic and abiotic stresses, which have negative impacts on crop production. Numerous solutions and agricultural strategies have been introduced to overcome these problems. One of the ways to improve plant production as well as to increase resistance towards biotic and abiotic stresses is by utilizing beneficial microbes as soil inoculants. A better understanding of the ability of Trichoderma to enhance crop production and the mechanisms that are involved are important for deriving maximum benefits from their exploitation. These versatile fungi hold great promise for the development of viable commercial products that can be used widely in agriculture for increasing crop productivity in a more sustainable way.

Trichoderma | growth promoter fungi | sustainable agriculture | stress tolerance | biocontrol

1. Introduction

Continuous growth in the world's population has led to a corresponding increase in food demand, which has necessitated the mass production of agricultural products [1]. By 2050, the population to be fed will be over 9 billion people. Not only do we have to increase food availability, but we also must ensure that supplies are sustainably produced by not compromising the services that nature is able to provide [2]. Intensive large-scale industrial agriculture requires high-external input and resources, and these ultimately cause environmental problems such as water shortages, destruction of biodiversity, a decline in soil fertility, and elevated levels of greenhouse gases, leading to an increase in biotic and abiotic stresses, which threaten agricultural productivity and food security [3][4].

Beneficial microbes employ various mechanisms of action that increase plant productivity through the promotion of plant growth and health, such as (a) colonizing soil and/or plant parts, thereby occupying space and limiting the proliferation of phytopathogens; (b) producing enzymes, antibiotic substances, and volatile organic compounds that suppress the phytopathogens; (c) facilitating nutrient and water uptake; (d) producing phytohormone; (e) inducing local or systemic resistance responses in plants; and (f) improving various physiological and molecular processes [5][6][7]. *Trichoderma* is among the most widespread fungi in the world and is a plant symbiont that resides in varying habitats, including the rhizosphere and plant tissue (as an endophyte). *Trichoderma* is also widely used as biocontrol agent against phytopathogenic microorganisms. For example, *Trichoderma* was found to endophytically colonize *Brassica oleracea* (kale) and activated the systemic resistance of kale plants against the bacterial pathogen, *Xanthomonas campestris* [8]. Some of the mechanisms involved in promoting plant growth and disease protection by means of endophytic fungi include increasing access to nutrients (nitrogen, phosphorus, potassium, zinc, iron, etc.), the production of antibiotics, the production of plant hormones, a reduction in ethylene, or an increase in water acquisition rate [9].

Numerous studies have been conducted to elucidate the mechanisms by which *Trichoderma* confers resistance to plant pathogens and resilience against various kinds of biotic and abiotic stresses [10][11]. Over the years, scientists and agricultural practitioners have focused on the search for environmentally friendly options for the management of cropping systems. Finding the best method for improving crop production is crucial in order to achieve a sufficient food supply for the continuously rising population. Agroecology has been a prominent way of redesigning food systems to achieve greener agriculture approaches with higher sustainability [12][13]. One important agroecological approach for maximizing root and rhizosphere efficiency is the application of beneficial microbes, including *Trichoderma* [14][15]. This strategy can lead to improved crop productivity and better nutrient use efficiency while providing a friendlier option for human health and the environment [16][17].

2. Roles of *Trichoderma* in Sustainable Crop Production

The effects of root inoculation by *Trichoderma* are not restricted to the site of colonization but exist throughout the entire plant system. Colonization involves a complex system whereby the fungus is able to invade plant cells but can only live symbiotically without killing the plant. *Trichoderma* resides at the outermost layer of the roots and does not penetrate into the inner vascular tissue [18]. In *Trichoderma* studies with arabidopsis, the plants were seen to restrict the invasion of *Trichoderma* in the vascular bundle through the presence of metabolites such as salicylic acid (SA) and glucosinolates (GSLs) [19][20]. A successful *Trichoderma*–plant interaction results in improved plant growth and crop yield upon the cumulative positive effects induced by the fungus that subsequently improve nutrient uptake and transport in plants [21][22]. For instance, composted kitchen wastes comprising *T. harzianum* showed considerable promise as a biofertilizer for tomato plants with yield increases of up to 336.5% [23]. In a chickpea study, *Trichoderma* spp. caused an increase in the growth and yield parameters of the treated plants compared to the uninoculated controls. This result was found to be caused by the enhanced solubilisation and uptake of phosphate [24]. Furthermore, a maximum yield of chilies (69.55 q/ha) was recorded when the seeds were pre-treated with *T. harzianum* together with its foliar sprays.

Nutrient solubility and availability are induced by the acidification of soils by plant roots upon inoculation with the fungus. The process occurs through the secretion of some organic acids such as gluconic, citric, and fumaric acids [25]. In the case of sugarcane, both *T. harzianum* and *T. viride* were significantly effective in enhancing the uptake of phosphorus as well as other micronutrients, thereby improving germination, tiller population, millable canes output, and commercial cane sugar yield (CCS t/ha) [26]. In tomato plants, shoot and root growth attributes as well as chlorophyll content were significantly increased when sown in *Trichoderma*-fortified soil. Mineral contents in both shoot and root were higher compared to control plants [27]. Upon the application of *T. virens*, the efficiency of nitrogen uptake in lettuce and rocket plants was greater with enhanced crop yield and quality. Those acids reduce soil pH, subsequently allowing better nutrients solubility and uptake [28]. Other than acidification, the induction of root growth by the fungus and the increase in root biomass contributed to better nutrient absorption. It was observed that the single inoculation of broccoli plants with *T. viride* significantly increased the above-ground fresh weight, root length, chlorophyll *b*, head diameter, root phosphorus content, and shoot nitrogen content compared to uninoculated control plants [29].

Trichoderma sp. also secretes secondary metabolites that play important roles in elevating plant growth and yield. For example, *T. harzianum* and *T. atroviride*, with their main secondary metabolites harzianic acid (HA) and 6-pentyl-α-pyrone (6PP), respectively, were observed to improve grape plant growth, yield, and quality [30]. Vinale et al. [31] showed that the 6PP produced by *Trichoderma* has an auxin-like mechanism of action that is involved in plant growth improvement. Further study demonstrated that 6PP is responsible for promoting plant growth and regulating root architecture, inhibiting primary root growth, and inducing lateral root formation [32]. This study showed that 6PP modulated the expression of *PIN* auxin-transport proteins in a specific and dose-dependent manner in primary roots. Other than that, *T. harzianum* was found to release a metabolite called harzianolide, which is a plant growth regulator that is responsible for improving the growth of tomato seedlings [33]. This study revealed that harzianolide enhances root length and tips as well as induces the expression of genes involved in the salicylic acid (PR1 and GLU) and jasmonate/ethylene (JERF3) signaling pathways that are related to the plant defence mechanism. In arabidopsis, *T. virens* and *T. atroviride* were found to secrete indole acetic acid (IAA) and auxin-related substances; these metabolites are important for root development [34]. Studies have shown that rice plants inoculated with *T. asperellum* produced better plant architecture, higher panicle number, longer panicle length, and increased plant height [35][36][37]. This is in agreement with previous study on the application of *T. harzianum* on maize plants. When applied to the soil or directly to the seeds, the fungus caused an increase in all of the measured parameters, including growth parameters and levels of chlorophyll, starch, nucleic acids, total protein, and phytohormones of the plants [38].

Numerous studies have been conducted to elaborate the mechanisms by which *Trichoderma* promotes plant growth and development [30][31][39][40][41]. Some of these mechanisms can be explained by the upregulation of photosynthesis-related proteins resulting in a better photosynthetic rate, plant nitrogen use efficiency [39], and enhancement of plant nutrient uptake [42]. While molecular studies on *Trichoderma* effects are still in a nascent stage, some are showing promising results. For example, a large portion of the genes related to carbohydrate metabolism, stress modulation, and photosynthesis were up-regulated in maize plants upon inoculation with *Trichoderma* [43]. Similarly, in rice, the presence of *T. asperellum* was found to be correlated with the up-regulation of different genes, some of which have been identified to be involved in photosynthesis and chlorophyll biosynthesis. The up-regulation of genes related to CO_2 fixation, response to light, and stomatal complex development indicated an enhancement of the plant's efficiency in photosynthesis [44]. **Table 1** summarizes the genes reported to be up-regulated in various plants upon *Trichoderma* inoculation.

Table 1. Up-regulated genes in some plants upon *Trichoderma* inoculation.

Plants	*Trichoderma* Species	Genes	Observed Effects	References
Arabidopsis, cucumber	*T. asperelloides*	MDAR	Increased osmo-protection/oxidative stress.	[45]

Plants	*Trichoderma* Species	Genes	Observed Effects	References
Arabidopsis	*T. atroviride*, *T. virens*	AtERD14	Mitigated cold stress effects.	[46]
Rapeseed	*T. parareesei*	NCED3, ACCO1, ERF1 and PYL4	Improved tolerance to drought and salinity.	[47]
Wheat	*T. longibrachiatum*	SOD, POD, and CAT	Seedlings were protected from salinity.	[48]
Tomato	*T. harzianum*	TAS14 and P5CS	Improved tolerance to cold.	[49]
Potato	*T. harzianum*	Lox and GST1	Induction of plant disease resistance.	[50]
Poplar	*T. asperellum*	PdPapARF1	Promoted growth and defence responses.	[51]

3. Roles of *Trichoderma* in Sustainable Plant Disease Management

Since the 1920s, the very common, soil-inhabiting fungi, *Trichoderma* spp. have been recognized for their capability to act as biocontrol agents against many phytopathogens based on their abilities to parasitize other fungi and to produce antibiotics [42][52]. Later, their principal mechanism of action for plant protection was known to be based on the induction of disease resistance. *Trichoderma* has been documented to control many pathogenic microorganisms that affect plants, including bacteria (*Pseudomonas* and *Xanthomonas*), other fungi (e.g., *Fusarium*, *Curvularia*, *Colletotrichum*, *Alternaria*, *Rhizoctonia*, and *Magnaporthe*), the oomycetes (*Pythium* and *Phytophthora*), and at least one virulent virus (green mottle mosaic virus on cucumber) [42].

3.1. Trichoderma as Biocontrol Agents against Plant Pathogenic Bacteria

Plant diseases caused by bacteria are relatively difficult to control. However, the most common methods used to effectively control these diseases include plant breeding and cultural, chemical, biological, and physical control measures. Biocontrol agents are effective in controlling bacterial pathogens and are safer for the environment than chemical bactericides/pesticides. The excessive application of chemicals and consumer acceptance towards resistant cultivars can be very complex, which makes the use of biocontrol agents an attractive alternative [22].

Trichoderma showed an inhibitory effect on the growth and survival of the pathogenic Gram-negative bacterium, *Ralstonia* spp., in tomato plants, which was attributed to the secretion of various compounds such as lysozyme, viridin, and [illegible] [53]. Moreover, bacterial wilt caused by the soilborne bacterium *R. solanacearum* was inhibited by the application of *T. asperellum*, and the disease incidence was subsequently decreased with concomitant improvement in plant growth and yield under field conditions. This was achieved through the induction of a maximum level of defence enzyme activities, such as POX, PPO, and PAL, β-1,3-

References

1. Raza, A.; Razzaq, A.; Mehmood, S.; Zou, X.; Zhang, X.; Lv, Y.; Xu, J. Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. Plants 2019, 8, 34.
2. Grafton, R.Q.; Daugbjerg, C.; Qureshi, M.E. Towards food security by 2050. Food Sec. 2015, 7, 179–183.
3. Pandey, P.; Irulappan, V.; Bagavathiannan, M.V.; Senthil-Kumar, M. Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits. Front. Plant Sci. 2017, 8, 537.
4. FAO. The 10 Elements of Agroecology. 2020. Available online: http://www.fao.org/3/i9037en/i9037en.pdf (accessed on 18 May 2020).
5. Saba, H.D.; Vibhash, M.; Manisha, K.S.; Prashant Farham, H.; Tauseff, A. Trichoderma—A promising plant growth stimulator and biocontrol agent. Mycosphere 2012, 3, 524–531.
6. Poveda, J. Beneficial effects of microbial volatile organic compounds (MVOCs) in plants. Appl. Soil Ecol. 2021, 168, 104118.
7. Harman, G.E.; Doni, F.; Khadka, R.B.; Uphoff, N. Endophytic strains of Trichoderma increase plants' photosynthetic capability. J. Appl. Microbiol. 2021, 130, 529–546.
8. Poveda, J.; Zabalgogeazcoa, I.; Soengas, P.; Rodríguez, V.M.; Cartea, M.E.; Abilleira, R.; Velasco, P. Brassica oleracea var. acephala (kale) improvement by biological activity of root endophytic fungi. Sci. Rep. 2020, 10, 20224.
9. Poveda, J.; Eugui, D.; Abril-Urías, P.; Velasco, P. Endophytic fungi as direct plant growth promoters for sustainable agricultural production. Symbiosis 2021, 85, 1–19.
10. Singh, A.; Shukla, N.; Kabadwal, B.C.; Tewari, A.K.; Kumar, J. Review on plant-Trichoderma-pathogen interaction. Int. J. Curr. Microbiol. Appl. Sci. 2018, 7, 2382–2397.

glucanase, and total phenolic contents in plants [54]. Other examples of biocontrol of bacterial phytopathogens include the induction of resistance by *Trichoderma* conferred protection to tomato plants against *Xanthomonas euvesicatoria* (the causative agent of bacterial spot) and [55] cucumber plants grown in the presence of *Trichoderma* exhibiting greater protection against *Pseudomonas syringae* pv. *lachrymans* infection. *T. harzianum* activated separate metabolic pathways in cucumber that are involved in plant signaling and biosynthesis. Plant protection may be conferred by a combination of several modes of action provided by *Trichoderma*, such as phytoalexins biosynthesis, lignification, and the accumulation of pathogenesis related proteins and antimicrobial secondary metabolites [56].

3.2. Trichoderma as Biocontrol Agents against Phytopathogenic Fungi

Other than bacterial infections, fungal diseases are often associated with damage to crops, causing major losses in agricultural activities and food production. Thus, finding the best option to eradicate this problem is crucial. *Trichoderma* was found to have the ability to eliminate phytopathogenic fungi through a mechanism known as mycoparasitism. This involves the suppression of other microorganisms at the same site, thereby making it the dominant organism at the location [15][57].

Mycoparasitism by *Trichoderma* species involves an attack on the pathogen's cell or structures [58]. It was reported that *T. koningii* did not invade healthy tissues but colonized infected or damaged onion root tissues as a secondary colonizer, where it reduced *Sclerotium cepivorum* infection by destroying the hyphae [59]. On the other hand, *T. virens* not only parasitized the hyphae of many pathogenic fungal species, but also penetrated and destroyed some of the resting structures of these fungi, thereby reducing their inoculum potential in soil [60]. The pre-emergence of damping-off diseases in cotton seedlings caused by *Rhizopus oryzae* was observed to be controlled upon *T. virens* treatment. This fungus metabolized the pathogen propagule germination stimulants that emanated from the germinating cotton seed [61].

Several species of *Trichoderma* also produce volatile and non-volatile antibiotics and enzymes, which have shown antagonistic effects towards phytopathogenic fungi [62]. Protease, endochitinases, β-glucosidases, mannosidases, and phosphatases released by *T. harzianum* were found to be involved in the biocontrol of various pathogens, including *Guignardia citricarpa* (the causative agent of citrus black spot). These enzymes are involved in the degradation of pathogen cell wall membranes and proteins [63]. *Trichoderma* also releases metabolites that are capable of diminishing or antagonizing pathogenic microbes [64]. Fungal terpenoids (desoxyhemigossypol, hemigossypol, and gossypol) synthesized in cotton roots by *T. virens* were found to be involved in combating *R. solani*-incited cotton seedling [65]. The application of *Trichoderma* on *R. solani*-infected chilies improved plant growth and yield. This was attributed to the reduction of the damping-off disease of seedlings as well as to reducing root and stem rot in chilies [66].

In another report, inoculation of *T. harzianum* inhibits *R. solani* growth by the induction and expression of lipoxygenase (Lox) and glutathione S-transferase (GST1) genes in the roots of potato plantlets that have been simultaneously inoculated with both organisms [50]. The Lox gene product is crucial for lipid peroxidation processes during plant defence responses to pathogen infection [67]. On the other hand, GST1 is a defence gene that is

11. Hidangmayum, A.; Dwivedi, P. Plant responses to Trichoderma spp. and their tolerance to abiotic stresses: A review. J. Pharmacogn. Phytochem. 2018, 7, 758–766.

12. Altieri, M.; Nicholls, C.; Montalba, R. Technological approaches to sustainable agriculture at a crossroads: An agroecological perspective. Sustainability 2017, 9, 349.

13. Altieri, M.; Nicholls, C. Agroecology and the reconstruction of a post-COVID-19 agriculture. J. Peasant Stud. 2020, 4, 881–898.

14. Baez-Rogelio, A.; Morales-García, Y.E.; Quintero-Hernández, V.; Muñoz-Rojas, J. Next generation of microbial inoculants for agriculture and bioremediation. Microb. Biotechnol. 2016, 10, 19–21.

15. Harman, G.; Khadka, R.; Doni, F.; Uphoff, N. Benefits to plant health and productivity from enhancing plant microbial symbionts. Front. Plant Sci. 2021, 11, 610065.

16. Finkel, O.M.; Castrillo, G.; Herrera Paredes, S.; Salas González, I.; Dangl, J.L. Understanding and exploiting plant beneficial microbes. Curr. Opin. Plant Biol. 2017, 38, 155–163.

17. Mahato, D. Trichoderma's contribution in environmentally friendly plant disease management. Biotica Res. Today 2021, 3, 591–594.

18. Poveda, J.; Eugui, D.; Abril-Urias, P. Could Trichoderma Be a Plant Pathogen? Successful Root Colonization. In Trichoderma, Rhizosphere Biology; Sharma, A., Sharma, P., Eds.; Springer: Singapore, 2020; pp. 35–59.

19. Alonso-Ramírez, A.; Poveda, J.; Martín, I.; Hermosa, R.; Monte, E.; Nicolás, C. Salicylic acid Prevents Trichoderma harzianum from entering the vascular system of roots. Mol. Plant Pathol. 2014, 15, 823–831.

20. Poveda, J. Glucosinolates profile of Arabidopsis thaliana modified root colonization of Trichoderma species. Biol. Control 2021, 155, 104522.

21. Imadi, S.R.; Shazadi, K.; Gul, A.; Hakeem K.; R. Sustainable Crop Production System. In Plant, Soil and Microbes; Hakeem, K.; Akhtar, M.; Abdullah, S., Eds.; Springer: Cham, Switzerland, 2016; pp. 103–116.

22. Al-Ani, L.K.T. Trichoderma: Beneficial Role in Sustainable Agriculture by Plant Disease Management. In Plant Microbiome: Stress Response. Microorganisms for Sustainability; Egamberdieva, D., Ahmad, P., Eds.; Springer: Singapore, 2018; pp. 105–126.

23. Molla, A.H.; Haque, M.M.; Haque, M.A.; Ilias, G.N.M. Trichoderma-enriched biofertilizer enhances production and nutritional quality of tomato (Lycopersicon esculentum Mill.) and minimizes NPK fertilizer Use. Agric. Res. 2012, 1, 265–272.

24. Rudresh, D.L.; Shivaprakash, M.K.; Prasad, R.D. Tricalcium phosphate solubilizing abilities of Trichoderma spp. in relation to P uptake and growth and yield parameters of chickpea (Cicer

involved in the detoxification of toxic substances by their conjugation with glutathione, the attenuation of oxidative stress, and participation in hormone transport [68]. Biotic stresses can induce plants to produce higher levels of damaging reactive oxygen species (ROS). The excessive production of ROS causes oxidative stress resulting in the damage of cellular components, consequently leading to the death of plant cells [69]. A study conducted by Herrera-Téllez et al. [70] found that tomato plants pre-treated with *T. asperellum* and that were subsequently challenged with two fungal pathogens, *Fusarium oxysporum* and *B. cinerea*, experienced less severe wilting and stunting symptoms compared to non-treated plants due to the ROS modulation by *Trichoderma*.

Besides their direct antagonistic effects against fungal and bacterial plant pathogens, *Trichoderma* species have also been found to induce resistance against various plant diseases. This resistance induction can be either localized or systemic. The effects of systemic resistance induced by *Trichoderma* were recorded using a model rhizobacterium. For example, *T. virens* successfully induced plant systemic resistance in maize against *Colletotrichum graminicola* [71]. Other than that, *T. virens* was capable of inducing localized resistance against *R. solani* infection of cotton roots through the stimulation of terpenoid synthesis by the plant [65]. The mechanisms involved in these inductions are associated with different kinds of changes at the biochemical and molecular levels in the plants [72].

The capability of *Trichoderma* to protect plants against different bacterial and fungal pathogens is summarized with examples in **Table 2**.

Table 2. *Trichoderma* species and their biotic stress regulation mechanisms.

Plants	*Trichoderma* Species	Phytopathogens	Observed Effects	References
Tomato	*T. harzianum*	*Clavibacter michiganensis*	Prevented the incidence of bacterial canker.	[73]
Tomato	*T. harzianum* and *T. longibrachiatum*	*X. euvesicatoria*, *Alternaria solani*	Reduced bacterial spots, triggering systemic acquired resistance (SAR) or induced systemic resistance (ISR).	[55]
Tomato	*T. harzianum*	*Ralstonia* spp.	*Trichoderma* spp. AA2 inhibited the growth and survival of *Ralstonia* spp.	[53]
Tomato	*T. asperellum*	*R. solanacearum*	Delayed wilt development,	[54]

arietinum L.). Can. J. Microbiol. 2005, 51, 217–222.
25. Kumar, A. Effect of Trichoderma spp. in plant growth promotion in chilli. Int. J. Curr. Microbiol. Appl. Sci. 2019, 8, 1574–1581.
26. Srivastava, S.N.; Singh, V.; Awasthi, S.K. Trichoderma induced improvement in growth, yield and quality of sugarcane. Sugar Tech 2006, 8, 166–169.
27. Azarmi, R.; Hajieghrari, B.; Giglou, A. Effect of Trichoderma isolates on tomato seedling growth response and nutrient uptake. Afr. J. Biotechnol. 2011, 10, 5850–5855.
28. Fiorentino, N.; Ventorino, V.; Woo, S.L.; Pepe, O.; De Rosa, A.; Gioia, L.; Romano, I.; Lombardi, N.; Napolitano, M.; Colla, G.; et al. Trichoderma-based biostimulants modulate rhizosphere microbial populations and improve N uptake efficiency, yield, and nutritional quality of leafy vegetables. Front. Plant Sci. 2018, 9, 743.
29. Tanwar, A.; Aggarwal, A.; Kaushish, S.; Chauhan, S. Interactive effect of AM fungi with Trichoderma viride and Pseudomonas fluorescens on growth and yield of broccoli. Plant Prot. Sci. 2013, 49, 137–145.
30. Pascale, A.; Vinale, F.; Manganiello, G.; Nigro, M.; Lanzuise, S.; Ruocco, M.; Marra, R.; Lombardi, N.; Woo, S.L.; Lorito, M. Trichoderma and its secondary metabolites improve yield and quality of grapes. Crop Prot. 2017, 92, 176–181.
31. Vinale, F.; Sivasithamparam, K.; Ghisalberti, E.L.; Marra, R.; Barbetti, M.J.; Li, H.; Woo, S.L.; Lorito, M. A novel role for Trichoderma secondary metabolites in the interactions with plants.

Plants	*Trichoderma* Species	Phytopathogens	Observed Effects	References
			effectively decreased disease incidence, increased fruit yield, and improved plant growth promotion.	
Tomato	*T. asperellum*	*F. oxysporum*, *B. cinerea*	Inhibited ROS production.	[70]
Arabidopsis thaliana	*T. asperelloides*	*P. syringae*	Lesser necrotic lesions surrounded by extensively spreading chlorosis.	[74]
Radish, lettuce, tomato	*T. hamatum*	*X. campestris*	Lowered bacterial population and disease severity (bacterial leaf spot).	[75]
Rice	*T. harzianum*	*X. oryzae*	Bacterial leaf blight severity was reduced while plant growth was improved.	[76]
Cucumber	*T. asperellum*	*P. syringae* pv. *lachrymans*	Transcript accumulation of biosynthetic defence related genes and accumulation of phenolic compounds (antimicrobial activity).	[56]
Citrus	*T. harzianum*	*G. citricarpa*	The involvement of protease affecting the germination of *G. citricarpa* conidia,	[63]

salinity and drought due to a chorismate mutase. Agron. 2020, 10, 118.

Plants	*Trichoderma* Species	Phytopathogens	Observed Effects	References
			able to deactivate the pathogen’s hydrolytic enzymes that are responsible for plant tissues necrosis.	
Onion	*T. koningii*	*S. cepivorum*	Destroyed the hyphae, making it detached at septa, cell walls dissolved, and many hyphal apices burst.	[59]
Cotton	*T. virens*	*R. solani*	Induced terpenoid synthesis, toxic to the pathogen.	[65]
Cotton	*T. virens and T. longibrachiatum*	*R. oryzae*	Metabolized pathogen propagule germination stimulants that emanate from the germinating cotton seed.	[61]
Cotton	*T. virens*	*R. solani*	Penetrated and destroyed some of the resting structures of the pathogen.	[60]
Sunflower	*T. koningii*, *T. aureoviride*, *T. longibrachiatum*	*S. sclerotiorum*	Head rot incidence was significantly reduced, delayed epidemic onset.	[77]
Wheat	*T. harzianum*, *T. aureoviride*, *T. koningii*	*Pyrenophora triticirepentis*	Pathogen mycelium on the leaf surface collapsed or disintegrated.	[78]

58. Brand, A. Hyphal growth in human fungal pathogens and its role in virulence. Int. J. Microbiol. 2012, 2012, 517529.

59. Metcalf, D.A.; Wilson, C.R. The process of antagonism of Sclerotium cepivorum in white rot affected onion roots by Trichoderma koningii. Plant Pathol. 2001, 50, 249–257.

Plants	*Trichoderma* Species	Phytopathogens	Observed Effects	References
Rambutan	*T. harzianum*	*Botryodiplodia theobromae*, *Colletotrichum gloeosporioides*, *Gliocephalotrichum microchlamydosporum*	Reduced the occurrence of the three postharvest diseases, also retained the overall quality and colour of the fruits.	[79]
Chickpea	*T. atroviride*, *T. koningii*, *T. harzianum*, *T. hamatum*	*F. oxysporum*, *Ascochyta rabiei*	Suppressed fungal infections by mycoparasitism, antibiosis, and competition for space and/or nutrients.	[80]
Arabidopsis, Rapeseed	*T. harzianum*	*B. cinerea*	Induction of systemic defence, mediated by jasmonic acid.	[81]

…ing plant protection against insect pests and parasitic nematodes. Based on previous studies on the mode of action of *Trichoderma* as the mycoparasite fungus, *Trichoderma* species can act directly as an entomopathogen through parasitism, and the production of insecticidal secondary metabolites, antifeedant compounds and repellent metabolites. On top of that, this versatile fungus can act indirectly as a mycoparasite through the activation of systemic plant defensive responses, the attraction of natural enemies, or the parasitism of insect-symbiotic microorganisms [82]. For example, *T. longibrachiatum* that was formulated into a biopesticide was reported to be able to control the insect pest *Leucinodes orbonalis* in brinjal plants as well as increasing crop yield by 56.02% [87]. Moreover, under laboratory conditions *T. harzianum* exhibited an inhibitory activity of around 70-80% towards *Xylotrechus arvicola* (an important pest in vineyards) and *Acanthoscelides obtectus* (a causal agent of severe post-harvest losses in the common bean) [88].

The application of *T. gamsii* to the roots of *Arabidopsis thaliana* decreased the feeding behaviour of herbivore *Trichoplusia ni* through the modulation of the metabolome as well as affecting the content of phytohormones in plant leaves. *T. gamsii*-inoculated plant leaves recorded higher levels of amino acids and abscisic acid and lower concentrations of sugars compared to untreated plants [89]. Maize plant roots associated with *T. atroviride* recorded higher resistance against the insect herbivore *Spodoptera frugiperda* compared to untreated plants. Further examination indicated that there was a significant increase with regards to the emission of volatile terpenes and the accumulation of jasmonic in roots of inoculated rice plants. Chemical analyses revealed that *T. atroviride* produced the volatiles 1-octen-3-ol and 6-pentyl-2H-pyran-2-one, which were believed to have an important role in reducing the consumption of the foliar tissue of maize plants by *S. frugiperda* [90].

66. [illegible] Management of seedling rot of chilli (Capsicum annuum L.) using Trichoderma spp. and fluorescent pseudomonads (Pseudomonas fluorescens). J. Trop. Agric. 2006, 44, 79–82.

67. Hwang, I.S.; Hwang, B.K. The pepper 9-lipoxygenase gene CaLOX1 functions in defense and cell death responses to microbial pathogens. Plant Physiol. 2010, 152, 948–967.

68. Gullner, G.; Komives, T.; Király, L.; Schröder, P. Glutathione S-transferase enzymes in plant-pathogen interactions. Front. Plant Sci. 2018, 9, 1836.

69. Xie, X.; He, Z.; Chen, N.; Tang, Z.; Wang, Q.; Cai, Y. The roles of environmental factors in regulation of oxidative stress in plant. BioMed Res. Int. 2019, 2019, 9732325.

70. Herrera-Téllez, V.I.; Cruz-Olmedo, A.K.; Plasencia, J.; Gavilanes-Ruíz, M.; Arce-Cervantes, O.; Hernández-León, S.; Saucedo-García, M. The protective effect of Trichoderma asperellum on tomato plants against Fusarium oxysporum and Botrytis cinerea diseases involves inhibition of reactive oxygen species production. Int. J. Mol. Sci. 2019, 20, 2007.

71. Djonović, S.; Vargas, W.A.; Kolomiets, M.V.; Horndeski, M.; Wiest, A.; Kenerley, C.M. A Proteinaceous elicitor Sm1 from the beneficial fungus Trichoderma virens is required for induced systemic resistance in maize. Plant Physiol. 2007, 145, 875–889.

72. Nawrocka, J.; Małolepsza, U. Diversity in plant systemic resistance induced by Trichoderma. Biol. Control 2013, 67, 149–156.

The inoculation of *T. atroviride* in tomato plants induced plant resistance to the insects *Spodoptera littoralis* and *Macrosiphum euphorbiae*. These protection capacities were attributed to a plant response induced by *T. atroviride* that was linked with molecular and biochemical changes in tomato plants. *T. atroviride* also produced alterations in plant metabolic pathways leading to the production and release of volatile organic compounds (VOCs) that are involved in the attraction of the aphid *Aphidius ervi* (a parasitoid with activity against many pests), thus reinforcing indirect plant defence barriers [91]. The insecticidal efficacy of *T. harzianum* with natural protectants was also found to be an acceptable approach for the management of stored product damage resulting from the insects *Callosobruchus maculatus* and *C. chinensis* in cowpea seeds. The *T. harzianum*-based biofungicide formulation caused complete insect mortality and inhibited progeny production. Thus, this eco-friendly product can be an effective strategy for the management of both insects on stored cowpea seeds [92].

73. Utkhede, R.; Koch, C. Biological treatments to control bacterial canker of greenhouse tomatoes. BioControl 2004, 49, 305–313.

74. Brotman, Y.; Lisec, J.; Méret, M.; Chet, I.; Willmitzer, L.; Viterbo, A. Transcript and metabolite analysis of the Trichoderma-induced systemic resistance response to Pseudomonas syringae in Arabidopsis thaliana. Microbiology 2012, 158, 139–146.

75. Aldahmani, J.H.; Abbasi, P.A.; Sahin, F.; Hoitink, H.A.J.; Miller, S.A. Reduction of bacterial leaf spot severity on radish, lettuce, and tomato plants grown in compost-amended potting mixes. Can. J. Plant Pathol. 2005, 27, 186–193.

76. Jambhulkar, P.P.; Sharma, P.; Manokaran, R.; Lakshman, D.K.; Rokadia, P.; Jambhulkar, N. Assessing synergism of combined applications of Trichoderma harzianum and Pseudomonas fluorescens to control blast and bacterial leaf blight of rice. Eur. J. Plant Pathol. 2018, 152, 747–757.

77. Escande, A.R.; Laich, F.S.; Pedraza, M.V. Field testing of honeybee-dispersed Trichoderma spp. to manage sunflower head rot (Sclerotinia sclerotiorum). Plant Pathol. 2002, 51, 346–351.

78. Perelló, A.; Mónaco, C.; Simón, M.R.; Sisterna, M.; Bello, G.D. Biocontrol efficacy of Trichoderma isolates for tan spot of wheat in Argentina. Crop Prot. 2003, 22, 1099–1106.

79. Sivakumar, D.; Wijeratnam, R.S.; Wijesundera, R.L.; Marikar, F.M.; Abeyesekere, M. Antagonistic effect of Trichoderma harzianum on postharvest pathogens of rambutan (Nephelium lappaceum). Phytoparasitica 2000, 28, 240–247.

80. Poveda, J. Biological control of Fusarium oxysporum f. sp. ciceri and Ascochyta rabiei infecting protected geographical indication Fuentesaúco-Chickpea by Trichoderma species. Eur. J. Plant Pathol. 2021, 160, 825–840.

81. Poveda, J.; Hermosa, R.; Monte, E.; Nicolás, C. The Trichoderma harzianum Kelch protein ThKEL1 plays a key role in root colonization and the induction of systemic defense in Brassicaceae plants. Front. Plant Sci. 2019, 10, 1478.

82. Poveda, J. Trichoderma as biocontrol agent against pests: New uses for a mycoparasite. Biol. Control 2021, 159, 104634.

83. Nicol, J.M.; Turner, S.J.; Coyne, D.L.; den Nijs, L.; Hockland, S.; Tahna Maafi, Z. Current nematode threats to world agriculture. In Genomics and Molecular Genetics of Plant-Nematode Interactions; Jones, J., Gheysen, G., Fenoll, C., Eds.; Springer Science + Business Media: Dordrecht, The Netherlands, 2011; pp. 21–43.

84. Moosavi, M.R.; Askary, T.H. Nematophagous fungi-commercialization. In Biocontrol Agents of Phytonematodes; CABI Publishing: Wallingford, UK, 2015; pp. 187–202.

85. Harman, G.E.; Uphoff, N. Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. Scientifica 2019, 2019, 1–25.

86. Reddy, P.P.; Rao, M.S.; Nagesh, M. Management of citrus nematode, Tylenchulus semipenetrans, by integration of Trichoderma harzianum with oil cakes. Nematol. Mediterr. 1996, 24, 265–267.

87. Ghosh, S.K.; Pal, S. Entomopathogenic potential of Trichoderma longibrachiatum and its comparative evaluation with malathion against the insect pest Leucinodes orbonalis. Environ. Monit. Assess. 2016, 188, 37.

88. Rodríguez-González, Á.; Mayo, S.; González-López, Ó.; Reinoso, B.; Gutierrez, S.; Casquero, P.A. Inhibitory activity of Beauveria bassiana and Trichoderma spp. on the insect pests Xylotrechus arvicola (Coleoptera: Cerambycidae) and Acanthoscelides obtectus (Coleoptera: Chrisomelidae: Bruchinae). Environ. Monit. Assess. 2017, 189, 12.

89. Zhou, D.; Huang, X.F.; Guo, J.; dos-Santos, M.L.; Vivanco, J.M. Trichoderma gamsii affected herbivore feeding behaviour on Arabidopsis thaliana by modifying the leaf metabolome and phytohormones. Microb. Biotechnol. 2018, 11, 1195–1206.

90. Contreras-Cornejo, H.A.; Macías-Rodríguez, L.; del-Val, E.; Larsen, J. The root endophytic fungus Trichoderma atroviride induces foliar herbivory resistance in maize plants. Appl. Soil Ecol. 2018, 124, 45–53.

91. Coppola, M.; Cascone, P.; Lelio, I.D.; Woo, S.L.; Lorito, M.; Rao, R.; Pennacchio, F.; Guerrieri, E.; Digilio, M.C. Trichoderma atroviride P1 colonization of tomato plants enhances both direct and indirect defense barriers against insects. Front. Physiol. 2019, 10, 813.

92. Gad, H.A.; Al-Anany, M.S.; Atta, A.A.; Abdelgaleil, S.A. Efficacy of low-dose combinations of diatomaceous earth, spinosad and Trichoderma harzianum for the control of Callosobruchus maculatus and Callosobruchus chinensis on stored cowpea seeds. J. Stored Prod. Res. 2021, 91, 101778.