



# Biological functions of *Trichoderma* spp. for agriculture applications

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## ABSTRACT

*Trichoderma* spp. have been widely used in agricultural applications due to its well known biological control mechanism. The usage of this microbial inoculant in *Trichoderma*-based products attracts the attention of researchers to discover more on other potential benefits of *Trichoderma* spp. Hence, through research work from worldwide researchers, we present the success of *Trichoderma* spp. relate to plant diseases, plant growth, decomposition process and bioremediation. Plus, their secondary metabolites production in agroecosystem will also be reviewed in this paper. These surprising findings bring enormous advantages to the agriculture industry in order to apply environmentally friendly agriculture practices.

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## 1. Introduction

The future of food production and environmental safety are in jeopardy due to issues in agriculture. The emergence of plant pathogenic microorganisms in a crop plantation caused a pandemic plant diseases phenomenon. Besides, excessive usage of pesticides and synthetic fertilizers expose the living organisms to the high toxicity of chemical compounds. Another issue such as improper management of agricultural waste also pollutes the environment when it has been burned or disposed into water bodies. The best solution to overcome these problems is the application of biological control by using *Trichoderma* spp. in agricultural products. *Trichoderma* spp. significantly suppress the growth of

plant pathogenic microorganisms and regulate the rate of plant growth. Recent works have shown that common plant disease such as root rot disease, damping off, wilt, fruit rot and other plant diseases can be controlled by *Trichoderma* spp. (Begum et al., 2010; El Komy et al., 2015; Howell, 2002; Mbarga et al., 2012). The secondary metabolites secreted by *Trichoderma* spp. have proven its role in suppressing the growth of pathogenic microorganisms and stimulating the plant growth (Contreras-Cornejo et al., 2015a, 2015b; Kubicek et al., 2001; Kullnig et al., 2000). Besides, the interaction between plant and *Trichoderma* spp. successfully regulate root architecture, increase the length of lateral and primary root that result in the effectiveness of nutrient uptake by the plant (Cai et al., 2013; Naseby et al., 2000; Yedidia et al., 2001).

The discovery of *Trichoderma* spp. as natural decomposition agent and biological agent of bioremediation has been reported by several studies. The rate of decomposition process increases when there is the

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inoculation of *Trichoderma* spp. in an agricultural waste substrate such as empty fruit bunches (EFB), palm oil mill effluent (POME) and crop residues (Amira et al., 2011; Sharma et al., 2012). Recent works have shown that the ability of *Trichoderma* spp. to detoxify pesticides and herbicide have been revealed in several findings (Vázquez et al., 2015; Zafra et al., 2015). Both of these potentials give significant advantages to the agriculture industry to overcome pollution-related issues.

Since the challenges in coping with issues in the agriculture industry have grown tremendously, sustainable strategies by using biological control approach are necessary. Thus, the use of *Trichoderma* sp. as a biological agent seems to be an excellent approach. This review presents a compilation of studies and findings that discover the potentiality of *Trichoderma* sp. as a plant growth promoter agent, a biocontrol agent of plant disease, biological agent for bioremediation and natural decomposition agent.

## 2. *Trichoderma* spp.

The genus of *Trichoderma* contributes to a large number of its capabilities among different strains as multifunctional fungi that are found in a large variety of ecosystems. Typically, they are found from forest or agricultural soils. *Trichoderma* strains can be identified by common morphology characteristics which are a bright green conidial pigment, have rapid growth and are repetitively branched, as shown in Fig. 1.

*Trichoderma* is a genus of fungi in the family Hypocreaceae, commonly one of the rhizosphere inhabitants. The difficulties encountered during the identification of *Trichoderma* isolates at the species level become more significant because of the morphological differences are rare and hard to observe. In 1969, Rifai introduced the concept of “species aggregate” and categorized *Trichoderma* strains into nine aggregates based on morphological features (Rifai, 1969). Unfortunately, some of the “species aggregate” consists of two or more morphology that was non-differentiable. In later studies, Bissett (1991) reviewed Rifai's work and attempted to integrate similar forms within the species concept based on morphology, including the characteristics of the conidiophore branching system. As a result, *Trichoderma* was classified into five sections: Saturnisporum, Pachybasium, Longibrachiatum, *Trichoderma* and Hypocreanum.

Generally, morphological features were used to classify the species of *Trichoderma*. Waghunde et al. (2016) stated that species belonging to *Trichoderma* genus have about 10,000 species, most rapidly growing. In the beginning, *Trichoderma* strains appeared white and cottonish, then developing into yellowish-green to deep green compact tufts especially at the centre of a growing spot or in concentric ring-like zones on the agar surface as shown in Fig. 1.

As shown in Fig. 2, conidiophores are repeatedly branched, irregularly arranged in whorls, appear as clusters of divergent, usually asymmetrical bent, flask-shaped/cylindrical to nearly subglobose phialides. The ellipsoidal to globose conidia are generally green, sometimes

hyaline to cluster in aggregates at the terminal of the phialides (Zhu and Zhuang, 2015).

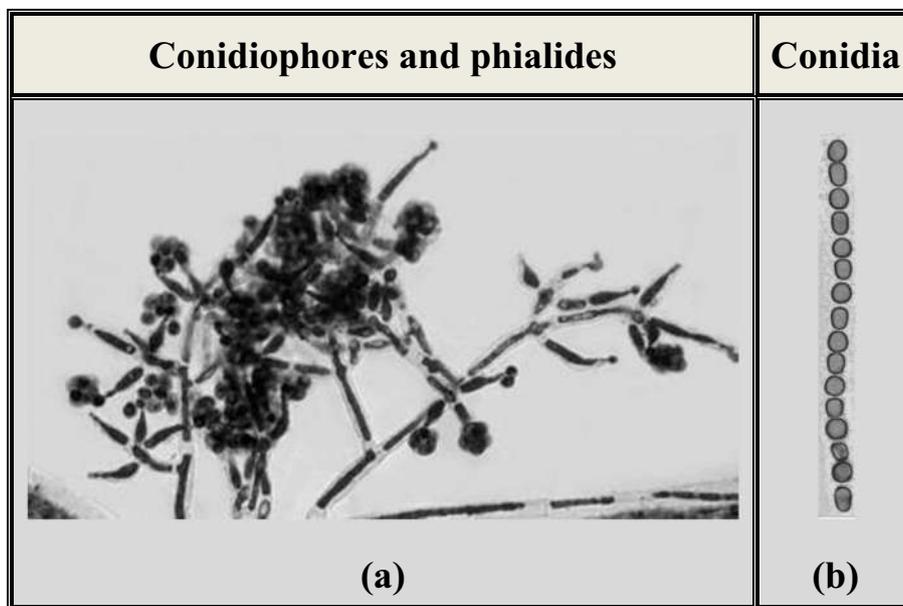
For six decades, *Trichoderma* spp. are known to have the capability of attacking other fungi. Also, they are well known as potential biological control agents among researchers (El Komy et al., 2015; Naher et al., 2014; Sundaramoorthy and Balabaskar, 2013). According to the findings of some researchers, *Trichoderma* spp. can kill plant pathogens and enhance the plant growth (El Komy et al., 2015; Contreras-Cornejo et al., 2015a, 2015b; Garnica-Vergara et al., 2016). Besides, *Trichoderma* spp. have been proven its ability to detoxify toxic compounds and fasten degradation of organic material (Amira et al., 2011; Sharma et al., 2012; Vázquez et al., 2015; Zafra et al., 2015). The success of *Trichoderma* spp. in the soil ecosystem and its role as natural decomposer is due to its ability to hasten the growth, its capability in nutrient uptake and the ability to modify the rhizosphere. It is also able to tolerate unfavourable environment and has powerful destructive capability against plant pathogenic microorganisms (Benítez et al., 2004; Harman, 2006).

Unfortunately, besides from the greatness of the genus on controlling plant diseases, *Trichoderma* species at the same time, cause a big damaging effect on mushroom production houses. Green mold disease on cultivated mushrooms caused by *Trichoderma* spp. are reported by researchers worldwide (Hatvani et al., 2017; Mazin et al., 2018; Aydoğdu et al., 2020). Besides, a current finding also revealed that the 30–80% mortality of Austrian pine seedling in an experiment conducted by Li Destri Nicosia et al. (2015) caused by *T. viride* due to its pathogenic behaviour. Some of these fungi that can act as human pathogens are also producers of mycotoxin. For example, Tijerino et al. (2011) found trichodermin, a mycotoxin in trichothecins group, is secreted by *T. brevicompactum*. Commonly, it contaminates the food source, and consumption of these mycotoxin leads to vomiting and gastroenteritis (Yang et al., 2017). Moreover, *T. longibrachiatum* was reported as an emerging human pathogen in immunocompromised patients, starting from the findings of Munoz et al. (1997) in the pediatric patient until recently found by Sautour et al. (2018) in neutropenic patient with acute leukemia. Thus, the research community need to stay away from publicizing *Trichoderma* species that endangered human health. Consequently, while the studies on effective biocontrol fungal are ongoing, further research to avoid the risk for humans, plants and other organisms contributed by *Trichoderma* spp. also need to be focused.

Commonly, biological control agents may not affect non-target organisms. Unfortunately, *Trichoderma* spp. that characterized as antagonistic strains do not particularly target on pathogenic organisms, but also the other microorganisms (Ros et al., 2017). Several researchers have observed the unintended consequences of *Trichoderma* spp. on soil microbial populations. According to Halifu et al. (2019), secretion of cell wall degrading enzymes such as cellulase, xylanase and glucanases by *Trichoderma* species impairs the microbial cells functions such as nutrient absorption in the rhizosphere. As a result, the structure of the microbial community is disrupted; this is consistent with the



Fig. 1. Three different isolated strains of *Trichoderma* spp.



**Fig. 2.** Conidiophores, phialides and conidia of *Trichoderma* strains; (a) Conidiophores and phialides of *T. rufobrunneum*, (b) Green conidia of *T. rufobrunneum*. (Adapted from Zhu and Zhuang (2015).)

findings of Ros et al. (2017). At the same time, genus *Trichoderma* spp. has some advantage on soil microorganisms as reported by Cai et al. (2015), these fungi can also enhance plant growth by releasing hormone-like compounds that boost up the root development and plant growth. The rapid growth of plant induce microbial populations through the secretion of significant amounts of root exudates, which in turn increases the availability of nutrients for the microbial consumption (Carvalhais et al., 2015).

However, the distinctive species categorized in genus of *Trichoderma* were hardly to differentiate morphologically. Hence, polyphasic approach, the inclusive outcome of various techniques, such as molecular, morphological, genomic, and physiological analysis, are used to discover the characterization of a new species (Badaluddin et al., 2018). For instance, multi-gene phylogeny is one of the molecular methods usually used to identify *Trichoderma* species. Currently, integration of multi-gene phylogeny with morphological characters are used together to determine the description of *Trichoderma* at the species level. As reported by Pandian et al. (2016), identification of *Trichoderma asperellum* strain Ta13 involved the combination of morphology and molecular analysis using genes such as cal, tef1, act, rpb2 and ITS. It was found that *Trichoderma asperellum* strain Ta13 morphologically characterized by a branched and paired conidiophores with radial phialides and globose to sub-globose shaped conidia having a size of  $2.91 \mu\text{m} \times 2.37 \mu\text{m}$ . Meanwhile, detection of the local similarity between sequences in International Society on Thrombosis and Haemostasis (ISTH) database of this strain showed 100%, 99.20%, 99.80%, 98.70% and 99.30% nucleotide similarity for cal, tef1 $\alpha$  intron4 (large), tef1 $\alpha$  intron5 (short), act, rpb2 and ITS1/ITS2 respectively.

A combination of some new genetic tools and physiological activity is used to determine the different functional groups within *Trichoderma* spp. which related to the production of secondary metabolites (Zeilinger et al., 2016). The necessity to identify strains of *Trichoderma* as biological control agents, contributed by these integrated methods. Generally, secondary metabolites secreted by this fungus are not directly involved only in growth, but also in development, signalling and interaction with other organisms. According to a recent genomic tool, various types of metabolites produced by genus of *Trichoderma* is reflected in the genomes of three species (<https://genome.jgi.doe.gov/portal/>). According to Bottacini et al. (2018), each genome consists of a unique gene inventory, which determines the specific phenotype

and interaction with the environment. For instance, 440 genes present in *T. virens* genome, have been identified (Eukaryotic Orthologous Groups; KOG) as connected to several physiological activities such as synthesis of secondary metabolites, transport and catabolism activities. Meanwhile, *T. reesei* and *T. atroviride* contain 262 and 349 genes, respectively. Most of the SM genes present in *T. reesei* are also found in *T. virens* and *T. atroviride* (Kubicek et al., 2011). The source of KOG database come from National Center for Biotechnology Information (NCBI). This orthologous sequences added information to taxonomic classification and phylogenetic studies of *Trichoderma* spp. The pattern of genetic divergence also allows researchers to identify the gene that is responsible for strain diversification within genus of *Trichoderma*.

### 3. *Trichoderma* spp. as a biocontrol agent of plant disease

Biocontrol can be defined as the use of living organisms to depress the pest population. It is nature friendly (Hajek and Eilenberg, 2018). Woo et al. (2014) mentioned that *Trichoderma* spp. are the most commonly used biocontrol agents against a broad spectrum of root, shoot, and postharvest pathogens. Siemering et al. (2016) reported in their article that roots become the main habitat for the fungus, especially along the root surfaces and underneath the outermost layer of root cells. In order to establish the fungus in and on the plant roots, *Trichoderma* is effectively applied during seeding. Several researchers reported that seed treatment had been a successful technique in ensuring the colonization on *Trichoderma* spp. on the root to provide plant benefits (Gava and Pinto, 2016; Xue et al., 2017; Siddaiah et al., 2017).

To date, the primary mechanisms for biological control by *Trichoderma* spp. acting upon the pathogens are (i) recognition and invasion towards plant pathogenic fungal-like species through cell wall disruption and absorption of released nutrients known as mycoparasitism (Bhat, 2017), (ii) induce the resistance of plant towards diseases by root architecture alteration during the interaction with pathogens (Kumar et al., 2019) and (iii) attack the root-knot and cyst nematodes by destroying nematode eggs and second phase juvenile, also some segment of adult nematodes (Heidari and Olia, 2016) as shown in Fig. 3.

These indirect and direct mechanisms may respond effectively during the biocontrol event depending on the *Trichoderma* strain, targeted pathogen, the grown crop, and environmental background that includes

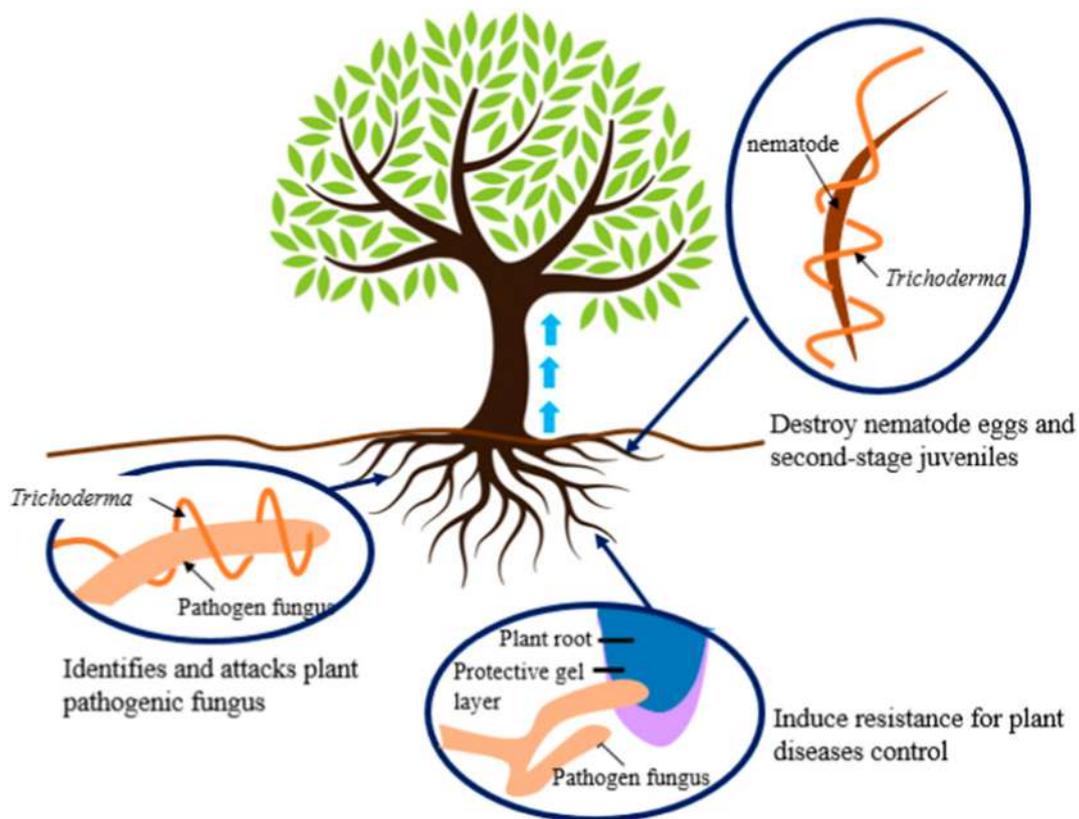


Fig. 3. Plant disease management by *Trichoderma* spp. (Siemering et al., 2016).

pH, temperature, salinity and nutrient availability. Most of their effect on crops are identical; however, there are species-specific and even strain-specific relation. Products that are commercially marketed commonly contain one or more *Trichoderma* species such as *T. viride*, *T. virens*, and *T. harzianum*. The efficiency of products containing various species or strains may act differently within the similar field and climate conditions.

The most widely *Trichoderma* spp. products are formulated in a wettable powder or granules. Ninety percent of various *Trichoderma* strains are applied to crops, with the aim to control plant diseases due to antagonistic characteristic expressed by them against phytopathogen. The impact of their usage as a biocontrol agent (BCA) on the field is evaluated on the input cost and in relation to crop productivity. As a result, it was found that the input cost and crop productivity application of BCA are economical and low cost compared to synthetic inputs (Masso et al., 2016). For some reasons, farmers may use an excessive amount of synthetic inputs (such as synthetic fertilizers and pesticides) that's favorable for being cheaper, do not bring in any higher profits to farmers. Farmers experienced economic losses if the balance between input costs and crop productivity is not right. Not only to cut down the crop losses, *Trichoderma* spp. also boost up the yields (productivity), resulting in an increase in revenue. According to Imran et al. (2020), a proper application of this BCA with compost onto crop field can lower or become an alternative for expensive chemical fertilizers. From the perspective of maintaining the soil health, usage of *Trichoderma* is a great sustainable approach. Researchers have reported that *Trichoderma* spp. suppress the growth plant pathogenic organisms such as *Pythium arrhenomanes*, *Rhizoctonia solani*, *Fusarium oxysporum*, *Alternaria tenuis* and *Botrytis cinerea* as shown in Table 1.

*T. harzianum* is widely distributed over the globe and easily found on all various types of substrates. Perhaps, it is the most frequent name used in agricultural practices related to *Trichoderma* spp., involving suppressing plant disease, naturally. The members of the *T. harzianum*

species complex are very much alike or no morphologically distinction as well as really connected. Numerous researches proposed that *T. harzianum* is a species complex, particularly several cryptic species are named. Recently, Chaverri et al. (2015) isolated *Trichoderma* cultures from four marketed biocontrol brands that claimed to have *T. harzianum*. They recognized nine new species in the *T. harzianum* species complex which were *T. afarasin*, *T. afroharzianum*, *T. atrobrunneum*, *T. camerunense*, *T. endophyticum*, *T. neotropiale*, *T. pyramidale*, *T. rifaii* and *T. simmonsii*.

In ecology, the substrates and origins have a strong correlation with species concepts in the *T. harzianum* complex. According to Chaverri et al. (2015), these may lead to differentiation of functional purposes, such as excretion of secondary metabolites, growth condition, target phytopathogen, host ranges and area distribution, between diversity in the *T. harzianum* species complex. For instance, findings by Ahluwalia et al. (2015) revealed the differentiation of antifungal activity and secondary metabolites secreted from two different strains of *T. harzianum* (T-4 and T-5) originated from two distinctive geographical distribution at Himalayan region with varied environmental conditions. Also, the degree of antagonism of ten *T. harzianum* strains isolated by Napitupulu et al. (2019) from various sources (leaf litter and soil) of samples in different site in Java, Indonesia showed differences against *Fusarium oxysporum* f.sp. *cubense*.

The efficiency of *T. harzianum* and *T. asperellum* in controlling plant diseases are reported by numerous studies shown in Table 1. This is consistent with Mbarga et al. (2012) findings which revealed that *T. asperellum* suppresses the growth of *Pythium myriotylum* by more than 60%. El Komy et al. (2015) stated that cell-wall degrading enzymes, were highly produced by *T. asperellum* isolates, and showed high antagonistic activity against *Fusarium oxysporum* f. sp. *lycopersici* (FOL) isolates. Furthermore, John et al. (2010) found that *T. viride* was identified as an efficient biocontrol agent for soybean root rot disease caused by fungal pathogens, *Fusarium oxysporum* f. sp. *adzuki* and

**Table 1**  
Examples of biocontrol of plant pathogen mediated by beneficial fungi.

Name of disease	Crop	Causal agent	Biocontrol strain	Reference
Root rot disease	Soybean ( <i>Glycine max</i> (L.) Merr. cv)	<i>Pythium arrhenomanes</i> f. sp. <i>adzuki</i>	<i>T. viride</i>	John et al. (2010)
	Corn ( <i>Zea mays</i> )	<i>Fusarium oxysporum</i> f. sp. <i>adzuki</i>		
	Cocoyam ( <i>Xanthosoma sagittifolium</i> )	<i>Pythium myriotylum</i>	<i>T. asperellum</i>	Mbarga et al. (2012)
	Pepper plants ( <i>Capsicum annuum</i> )	<i>Rhizoctonia solani</i>	<i>T. harzianum</i>	Ahmed et al. (2003)
	Eggplant ( <i>Solanum melongena</i> L.)	<i>Macrophomina phaseolina</i>	<i>T. harzianum</i> <i>T. polysporum</i> <i>T. viride</i>	Ramezani (2008)
Damping off	Pepper ( <i>Capsicum annuum</i> )	<i>Phytophthora capsici</i>	<i>T. harzianum</i>	Ezziyyani et al. (2007)
	Cucumber ( <i>Cucumis sativus</i> )	<i>Pythium</i> sp.	<i>T. harzianum</i>	Paulitz et al. (1990)
	Cotton ( <i>Gossypium hirsutum</i> )	<i>Rhizoctonia solani</i>	<i>T. harzianum</i>	Lewis and Papavizas (1987)
	Sugar beet ( <i>Beta vulgaris</i> )		<i>T. hamatum</i>	
	Cotton ( <i>Gossypium hirsutum</i> )	<i>Pythium aphanidermatum</i> <i>Pythium ultimum</i> <i>Rhizopus oryzae</i>	<i>T. virens</i>	Howell (2002)
Wilt	Tomato ( <i>Solanum lycopersicum</i> )	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> (FOL)	<i>T. asperellum</i>	El Komy et al. (2015)
	Melon ( <i>Cucumis melo</i> )	<i>F. oxysporum</i>	<i>T. harzianum</i> T-78	Bernal-Vicente et al. (2009)
Fruit rot	Chili ( <i>Capsicum annuum</i> )	<i>Alternaria tenuis</i>	<i>T. harzianum</i>	Begum et al. (2010)
	Tomato ( <i>Solanum lycopersicum</i> )	<i>Rhizoctonia solani</i>	<i>T. viride</i> <i>T. virens</i> <i>T. harzianum</i>	Amin and Razdan (2010)
Brown spot	Tobacco ( <i>Nicotiana tabacum</i> )	<i>Alternaria alternata</i>	<i>T. harzianum</i>	Gveroska and Ziberoski (2012)
Brown root rot	Peanuts ( <i>Arachis hypogaea</i> )	<i>Fusarium solani</i>	<i>T. harzianum</i>	Rojo et al. (2007)
Anthracnose grey mold	Strawberry ( <i>Fragaria ananassa</i> )	<i>Colletotrichum acutatum</i> <i>Botrytis cinerea</i>	<i>T. hamatum</i> <i>T. atroviride</i> <i>T.</i> <i>longibrachiatum</i>	Freeman et al. (2004)
			<i>T. gamsii</i>	Matarese et al. (2012)
Head blight	Wheat and other small grain cereals ( <i>Triticum aestivum</i> )	<i>Fusarium graminearum</i> <i>Fusarium culmorum</i>		
Sheath blight	Rice ( <i>Oryza sativa</i> )	<i>Rhizoctonia solani</i>	<i>T. harzianum</i>	Naeimi et al. (2010)
Blossom blight	Alfalfa ( <i>Medicago sativa</i> )	<i>Sclerotinia sclerotiorum</i>	<i>T. atroviride</i>	Li et al. (2005)
Web blight	Beans ( <i>Phaseolus vulgaris</i> )	<i>Sclerotinia sclerotiorum</i>	<i>T. viride</i>	Amin and Razdan (2010)
Collar rot	Tomato ( <i>Solanum lycopersicum</i> )	<i>Sclerotium rolfsii</i>	<i>T. virens</i> <i>T. harzianum</i>	

*Pythium arrhenomanes*. This is due to the ability of *Trichoderma* sp. as a parasite on these two pathogenic causing agents and killed them after 120 h of incubation on dual culture assay.

Kant et al. (2017) defined forma specialis as a taxonomic grouping of the pathogen in a particular species with the same host range, that infect only a single or a few plant species. To date, within the species of *Trichoderma*, limited forma specialis have been discovered as this genus are famously known of being biological control agent. A case study conducted by Samuels et al. (2002) reported that aggressive colonization in commercially grown *Agaricus bisporus* was shown exclusively due to two forma specialis of a new *Trichoderma*, viz. *T. aggressivum* f. *europaeum* in Europe and *T. aggressivum* f. sp. *aggressivum* in North America, is supported by Hatvani et al. (2007). The above-cited work indicated that 'forma specialis' issues in *Trichoderma* usually associated as common pathogenic fungi for edible mushrooms.

The mycoparasitism potential of *Trichoderma* sp. to attack and destroy plant pathogenic organisms has been identified (Brotman et al., 2010; Elad et al., 1983). Brotman et al. (2010) found that *Trichoderma* spp. penetrate the host cell wall by forming a hook-like structure during penetration. At the same time, *Trichoderma* spp. grow along the host hyphae. It will mechanically and enzymatically secrete cell wall degrading enzymes during penetration process. Also stated by Harman et al. (2004) and Omann et al. (2012), this phenomenon involves the production of various of biologically active compounds including cell wall degrading enzymes, and secondary metabolites. Eventually, these active compounds could kill the target pathogens.

More recently Baiyee et al. (2019) collected the extracellular metabolites from *T. spirale* T76–1 culture filtrates and evaluated their antibiosis against *Corynespora cassiicola* and *Curvularia aerea*. In the antibiosis study, the strain completely prevented the growth of *Phytophthora*

*capsici* (100% of growth inhibition). The isolates *T. spirale* T76–1 have produce metabolites that inhibited the growth of *C. cassiicola* and *C. aerea* at (84.68%) and (93.03%), respectively. High activities of  $\beta$ -1,3-glucanase ( $10.13 \pm 0.99$  U mL<sup>-1</sup>) and chitinase ( $0.93 \pm 0.09$  U mL<sup>-1</sup>) by *T. spirale* T76–1 degrade chitin, a major component (3–60%) of most fungi. In fact, morphological disruption of *C. cassiicola* and *C. aerea* were observed by scanning electron microscopy when treated with cell-free culture filtrate of *T. spirale* T76–1. Controls of *C. cassiicola* and *C. aerea* were observed as normal cell wall of hyphae, whereas uneven and rough cell-wall surfaces of *C. cassiicola* and shrivel and lysed mycelia in *C. aerea* were discovered.

A similar effect was reported of the growth inhibition *Sclerotium rolfsii*, a causal agent of stem rot disease in groundnut, by as much as 87.91% when treated with *T. virens* NBAll Tvs12 (Hirpara et al., 2017). Besides, particular activity of cell wall-degrading enzymes, chitinase ( $2.126 \mu\text{M}\cdot\text{mg}^{-1}$ ) and  $\beta$ -1,3-glucanase ( $2.670 \text{ mM}\cdot\text{mg}^{-1}$ ) were detected to be the highest among other *Trichoderma* strains tested in the experiment. Thus, the growth inhibition of test pathogen has a definite correlation with chitinase and  $\beta$ -1,3-glucanase activities. Additionally, the biocontrol activity of this strain can be maximized by improving the environmental parameter, for instance, temperature and humidity. As a result, there will be an enhancement of biocontrol agent growth during interaction with phytopathogenic organism under environmental conditions.

Findings showed by several reports found that the components that build up fungal cell walls were hydrolyzed by hydrolytic enzymes (e.g. chitinases and glucanases) secreted by *Trichoderma* spp. (Alias et al., 2011; Qualhato et al., 2013). Furthermore, Zhou et al. (2014) in his study revealed that *Trichoderma* spp. produce koniginins to inhibit the growth of pathogenic microorganisms. This report is supported by Hu et al. (2017) findings which shows koniginins molecules produced

by *Trichoderma* spp. inhibit the growth phytopathogens; *Fusarium flocciferum* and *Fusarium oxysporum*.

According to Nawrocka and Małolepsza (2013), *T. harzianum* released a large number of peptaibols as its secondary metabolism. Peptaibols are a large family of antimicrobial peptides. The production of peptaibols inhibits  $\beta$ -(1, 3) glucan synthase activity in a pathogenic microorganism (Lorito et al., 1996).  $\beta$ -(1, 3) glucan synthase is one of the enzymes that are responsible for synthesizing  $\beta$ -(1, 3) glucan, which is the main component of the cell wall as shown in Fig. 4. Thus, without  $\beta$ -(1, 3) glucan synthase will lead to no construction of the cell wall. As shown in Fig. 4, the effect of the peptaibol on  $\beta$ -glucan synthase is specific and reduced incorporation of uridine diphosphate (UDP) glucose (UDP-Glc), the building blocks for synthesis of cell wall polysaccharides. More recent researches found that these compounds largely produced by *T. virens* and *T. atroviride* also play an important role as plant elicitors (Bisen et al., 2016; Mukherjee et al., 2012; Shi et al., 2012). Spiteller (2008) defined plant elicitors as molecules that stimulate defence responses in plants when there is a pathogen attack.

The genus of *Trichoderma* also acknowledged as endophytic fungi is present on leaf tissue or roots, sapwood and will provide sorts of advantages to their host (Cummings et al., 2016). The symbiotic relationship between *Trichoderma* spp. and plant roots shown by the colonization of root surfaces by this genus and penetration to the root surface establish *Trichoderma* spp. as endophytes. Then, they secrete a number of bioactive secondary metabolites that contribute a beneficial role on their plant host. At the same time, genomic and metabolic modification in plant host are triggered by this endophytic fungi during root establishment (Ghaffari et al., 2016). As a result, the plant defence towards various causal agent of plant diseases and insects increases.

More recently, Contreras-Cornejo et al. (2018) reported of maize (*Zea mays*) resistance against *Spodoptera frugiperda*, an insect herbivore contributed by *T. atroviride*. In that work, it was found that *T. atroviride* boost up the plant growth, decreased herbivory and change insect feeding habit after it was inoculated to maize plant. The stimulation of

defence responses against herbivory contributed by the accumulation of jasmonic acid and the rise of volatile terpenes concentration released by this beneficial fungus, *T. atroviride*. Specifically, the terpenes compounds that were involved in the modification of feeding habit of *S. frugiperda* and reduction of foliar tissue consumption were octenol and 6-amil- $\alpha$ -pyrone.

Plant diseases have a huge impact on agricultural production and food supply. Hence, effective strategies in controlling diseases are crucial to decrease the application of pesticides in agriculture. Therefore, the usage of biological control agents such as *Trichoderma* spp. is one of the best ways to do so.

#### 4. *Trichoderma* spp. as plant growth promoter agent

Hyakumachi and Kubota (2003) describe plant growth-promoting fungi (PGPF) as a microorganism that can stimulate plant growth. The major impacts of these PGPF are commonly shown on the crop growth, quality of the final yield and productivity. Recently, researches have revealed that *Trichoderma* spp. can be an excellent PGPF. Most findings reported that *Trichoderma* spp. improve overall plant health, by creating a favorable environment and production of a large amount of secondary metabolites, as shown in Table 2.

There are a plethora of factors influencing the plant growth, for example, temperature, light intensity, nutrient availability and microbial community. Rhizosphere is the particular zone of soil surrounding plant root that is concentrated with nutrients, due to the great amount of photosynthetic byproducts released from the roots (Yuan et al., 2016). As a consequence, a mass microbial community hold up by rhizosphere can bring benefits, neutral or damage effect towards plant growth. Plant exerts multiplex connection with rhizospheric inhabitants, that is necessary for plant development and nutrient assimilation. Till recently, researches had revealed that *Trichoderma* spp. are directly giving an impact on plant development and crop productivity. *Trichoderma* spp. can be an excellent plant growth promoting fungi

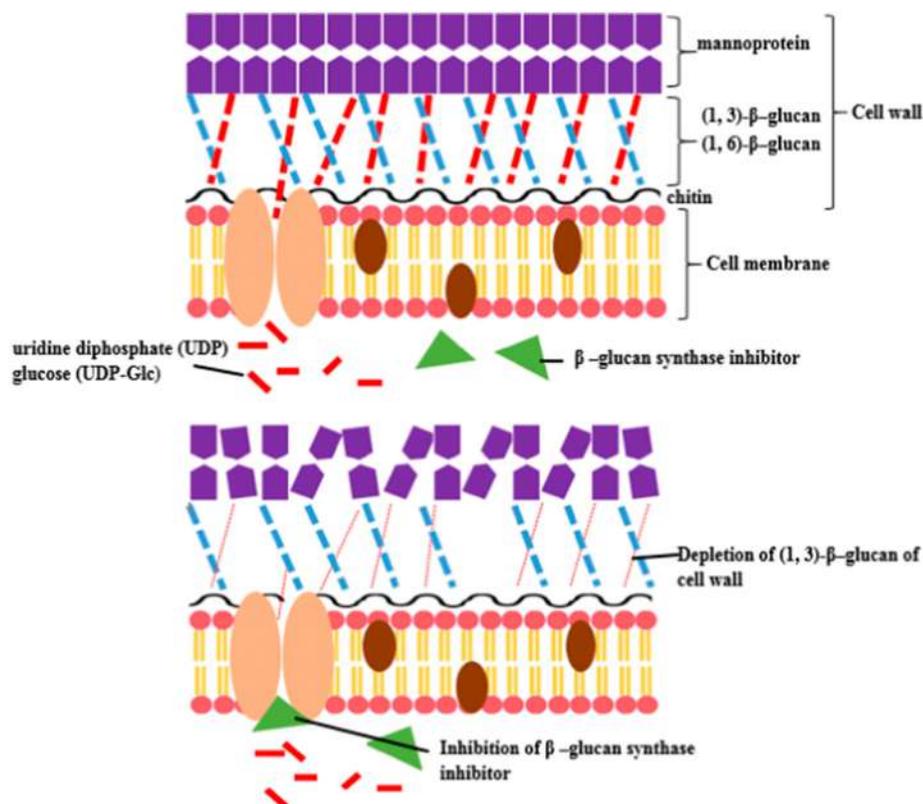


Fig. 4.  $\beta$ -1,3-Glucan synthase inhibition mechanisms by peptaibols (glucan synthase inhibitor).

**Table 2**  
Effect of *Trichoderma* spp. on plant growth and development.

<i>Trichoderma</i> strain	Effect	Crop	References
<i>T. harzianum</i> N47	-Increase the number of lateral root and root length.	Pea ( <i>Pisum sativum</i> )	Naseby et al. (2000)
<i>T. harzianum</i>	-Increase in cumulative root length, root surface area and the number of root tips	Cucumber ( <i>Cucumis sativus</i> )	Yedidia et al. (2001)
<i>T. harzianum</i> strain M10	-Increase germination of tomato seeds and improved the growth of the seedlings	Tomato ( <i>Solanum lycopersicum</i> )	Vinale et al. (2013)
<i>T. harzianum</i> strain SQR-T037	-Produce harzianic acid -Give better root development for the enhancement of root length and tips. promoted tomato seedling growth	Tomato ( <i>Solanum lycopersicum</i> )	Cai et al. (2013).
<i>T. virens</i>	-Produce harzianolide -Produce the auxin-related compounds indole-3-acetic acid, indole-3-acetaldehyde, and indole-3-ethanol.	<i>Arabidopsis thaliana</i>	Contreras-Cornejo et al. (2009)
<i>T. atroviride</i>	-Produce 6-pentyl-2H-pyran-2-one (6-PP), which promoted plant growth and regulated root architecture, inhibiting primary root growth and inducing lateral root formation.	<i>Arabidopsis thaliana</i>	Garnica-Vergara et al. (2016)
<i>T. virens</i> and <i>T. atroviride</i>	-Produce abscisic acid (ABA)	<i>Arabidopsis thaliana</i>	Contreras-Cornejo et al. (2015a, 2015b)

(PGPF) as described by Hyakumachi and Kubota (2003). Interestingly, plants are good to acknowledge and react towards rhizosphere populations and their secondary metabolites such as auxins, ethylene and other volatile organic compounds. Some of *Trichoderma* spp. that have a significant role as PGPF are shown in Table 2. To date, unfortunately, the discovery of synergistic mechanisms as well as the secondary metabolites and plant signals is still an open question.

According to Cai et al. (2013), *T. harzianum* strain SQR-T037 released secondary metabolite named harzianolide. The findings showed that harzianolide significantly induced the tomato seedling growth in either a hydroponic system or soil, at concentrations of 0.1 ppm and 1 ppm. Further results stated that harzianolide had an influence on the early stages of plant growth by enhancement of the root length and root tips. It promotes better root development.

Furthermore, *T. virens* and *T. atroviride* were found to produce indole acetic acid (IAA) and auxin-related substances (Contreras-Cornejo et al., 2014). IAA is a plant hormone of auxin class. It has a crucial part in both root developments. Contreras-Cornejo et al. (2014) reported that the root tip of *Arabidopsis* plant increased when it was inoculated with *Trichoderma* sp. under normal condition. Moreover, Ljung (2013) stated that IAA also empowered in controlling cell enlargement and division, tissue differentiation and responses towards light and gravity.

Yedidia et al. (2001), in his study, revealed that plant that was inoculated with *Trichoderma* spp. contained a high level of iron in shoots and root. These findings showed that transport mechanisms of this element from roots to shoots were also enhanced. It is consistent with studies by Vinale et al. (2013) that discovered harzianic acid synthesized by *Trichoderma* sp. regulates the plant growth due to its Fe(III) binding activity.

Development of root is the common benefit of *Trichoderma* spp. for plant growth as listed in Table 2. This hypothesis is supported by production or control of plant hormones that are responsible for improving the root development such as auxin, harzianic acid and harzianolide by *Trichoderma* spp., that is found in recent studies (Cai et al., 2013; Contreras-Cornejo et al., 2009; Vinale et al., 2013). As studied by Yedidia et al. (2001), plants that were inoculated with *T. harzianum* significantly increased the root area on 28th day. This study also discovered the rising of Cu, P, Fe, Zn, Mn and Na concentration in the inoculated root. The demonstration is shown in Fig. 5. In the same time, it was discovered that concentration of Mn, Zn and P increased by 70%, 25%, and 30%, respectively in the shoot of the plant.

The study supports the hypothesis by Contreras-Cornejo et al. (2016), which stated a large surface area of roots due to inoculation of *Trichoderma* spp. allows the root to explore a bigger region of soil. This enables the plant to uptake more macronutrients and micronutrients in the soil that give advantages to the plant when encounter with

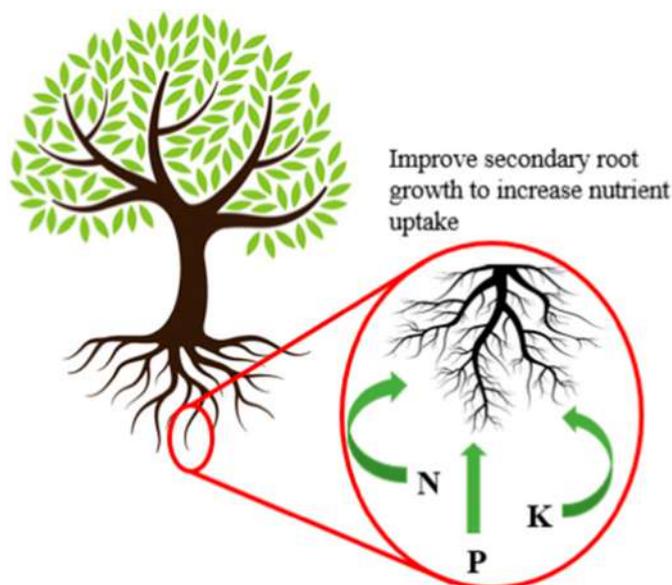
other organisms to compete for the minerals or when minerals are depleted.

The discoveries of *Trichoderma* spp. metabolites may support the application of new biofertilizers instead of the application of synthetic/chemical fertilizer in the agriculture industry. *Trichoderma* spp. may be an effective strategy as biofertilizer with fungal inoculants to improve crop production. Besides, it minimizes the pollution caused by excess usage of synthetic/chemical fertilizer in the agriculture industry.

### 5. *Trichoderma* spp. as natural decomposition agent

Decomposition is defined as the biological process to degrade and break down organic materials into smaller particles that can be used by other organisms. Decomposers/natural decomposition agents such as fungi play a vital role during this process. Nutrient cycling can be achieved by the role played by decomposer in returning nutrients from dead organic matter back into the soil. Eventually, these nutrients will be used by plants to undergo photosynthesis, as shown in Fig. 6.

*Trichoderma* spp. are good natural decomposition agents that enhance the rate of organic matters decomposition process. Amira et al.



**Fig. 5.** *Trichoderma* spp. increase the nutrients uptake by root improvement (Siemering et al., 2016).

(2011), revealed that *Trichoderma* spp. significantly increased the rate of decomposition of empty fruit bunches (EFB) and palm oil mill effluent (POME) from 4–6 months to 21–45 days. Ochoa-Villarreal et al. (2012) stated that the plant cell wall consists of cellulose and hemicellulose that responsible for its rigidity. Both of these components can be broken down by *T. virens* due to its production of cell wall degrading-enzyme. Amira et al. (2011) findings also discovered compost inoculated with *T. virens* has higher xylanase and cellulase activities compared to control. These activities eventually accelerate the degradation of cellulose and hemicellulose that help to reduce the time of the decomposition process.

Haddadin et al. (2009) discovered that the combination of microorganisms such as *T. harzianum* and *Phanerochaete chrysosporium* inoculated in olive pomace compost effectively breaks down its cellulose and lignin in only 50 days. Also, their study revealed that these two fungi combination significantly speed up the rate of decomposition by degrading 71.9% of lignin and 59.25% of cellulose after 30 days. These findings are consistent with Ahmed et al. (2009) who reported *T. harzianum* produce three cellulases, exoglucanase (EXG), endoglucanase (EG) and  $\beta$ -glucosidase (BGL). Cell degrading enzyme production is the key to speed up the rate of decomposition.

*Trichoderma* spp. had been proven that it could increase the rate of decomposition leading to the high availability of nutrients in soil utilized by other organisms. Siddiquee et al. (2017) analyzed the macronutrients percentages found in compost that contain EFB from the oil palm industry inoculated with *Trichoderma* spp. have higher N, P and K composition compared to control. The values are 0.91:2.13:6.68, respectively. Sharma et al. (2012) also supports this hypothesis which the discovery of the degradation crop residues such as cane trash, paddy trash and wheat trash with mixture or urea, cattle dung inoculated with *Trichoderma* spp. have increased N,P,K content. The percentages of N, P and K significantly increase in cane trash (47.56:189:37.2), paddy trash (30.09:188:41.2) and wheat trash (32.47:221:20.3) respectively in 90 days, when compared to the initial value. Robertson and Paul (2000) proposed that the rate of decomposition and nutrients availability vary tremendously. He also stated in his study that the nutrients loss from organic matter could be measured by decomposition.

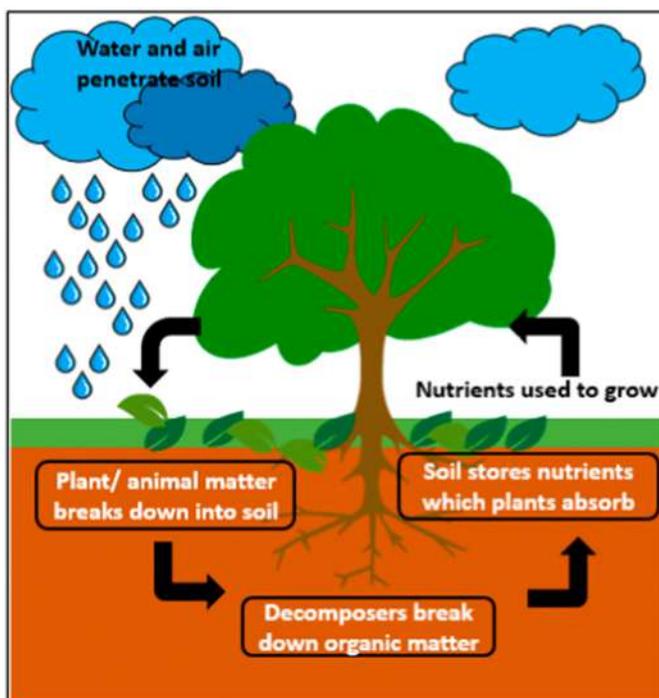


Fig. 6. Role of decomposer in the nutrient cycle.

A great number of researches shows the production of compost inoculated with *Trichoderma* spp. successfully improve the soil nutrients (Haddadin et al., 2009; Siddiquee et al., 2017; Sharma et al., 2012) and increase the growth of crops (Islam et al., 2014). According to Islam et al. (2014), plant height of *Amaranthus lividus* (Amaranth Red Leaf) and *Basella alba* (Malabar spinach) boosted up when the compost inoculated with *T. harzianum* (IES-103) were applied. *Trichoderma* infused-compost also increases the yield of ripe chili fruit by showing the highest percentage (69.30%) compared to chemical fertilizer usage (61.22%). In comparison, the control has the lowest percentage (50.50%) of yield (Hock et al., 2014).

Therefore, *Trichoderma* spp. consider a potential natural decomposing agent that can produce a high quality of compost with aerobic or microaerobic, low oxygen concentration condition but not quite anaerobic (Afrãa et al., 2016). Since most of the agricultural waste does not have systematic and proper steps to dispose of them, an excellent alternative is to turn them into compost. These findings should induce the way of sustainable waste management protocol in the agriculture industry and lower the environmental pollution.

## 6. *Trichoderma* spp. as a biological agent of bioremediation

Excess pesticides and synthetic fertilizer usage in the agricultural industry caused pollution, mainly water pollution and soil pollution. Ahlawat et al. (2010) stated, once the chemicals had been released, the compounds break down at different rates and it depends on the physio-chemical properties. Unfortunately, these chemicals do not degrade instantly, they may be absorbed by crops, leach below the root zone or to water bodies adheres to soil particles or volatilized at atmosphere. Removal of chemical compounds can be accomplished by biological or chemical method (Zin et al., 2019). The term bioremediation referred as biological control, is defined by Atlas and Pramer (1990) as 'the use of biological agents to reclaim soils and waters polluted by substances hazardous to human health and/or the environment'.

*Trichoderma* spp. had been proven their ability to metabolize different types of pesticides recently (Zafra et al., 2015; Vázquez et al., 2015). Pesticides such as mancozeb and carbendazim are used to suppress fungal diseases in field crop including paddy, fruit and vegetables and oilseed (Singh and Sharma, 2018; Didwania et al., 2019). However, excessive and repeated use of these two fungicides become a problem to worry about as they harm living organisms in the surroundings (Tiwari et al., 2016).

Sulfonylurea herbicide is commonly used in the agriculture industry to control the growth of weed. Unfortunately, the toxicity of sulfonylurea gives a huge impact on the microorganism in the soil. According to El-Ghamry et al. (2001) and Pampulha and Oliveira (2006), the sulfonylurea had suppressed the growth of soil microbial biomass consistently with the increasing rate of the herbicides. These findings are supported by Boldt and Jacobsen (1998), which revealed in their research that 76 out of 77 isolated strains of fluorescent pseudomonads had slow growth effect in metsulfuron methyl presence. Also, the researchers reported that the factor that causes growth suppression of microorganisms is inhibition of acetolactate synthase. Acetolactate synthase is responsible in the production of branched-chain amino acids leucine, valine and isoleucine. As stated by Garault et al. (2000), branched amino acids are important in the growth of microorganisms.

Luckily, these problems can be solved by *Trichoderma* spp. as they have the capability to degrade sulfonylurea herbicide. Vázquez et al. (2015) revealed that *T. harzianum* strain successfully detoxify metsulfuron methyl, which is one type of sulfonylurea herbicide. As shown in Table 3, *Trichoderma harzianum* T7 showed the highest (100%) detoxification effect towards metsulfuron methyl followed by *T. harzianum* T6 (92.6%) and no detoxification effect showed by *T. harzianum* T5 at the highest amount of metsulfuron methyl (0.1 mg/mL) application. This finding is consistent with the study done by Yadav and Choudhury (2014), which reported *Trichoderma*

spp. use up of the sulfolphuron as a primary carbon source and detoxify it by destroying sulfonyl urea bridge and sulfonylamide bond.

Besides, the application of insecticide such as dichlorvos (DDVP) is widely used in the agriculture industry, but excessively amount of its residues in soil jeopardize human health and the ecosystems. The exposure of DDVP residues can lead to human death through inhibition of acetylcholinesterase, which controls the neurotransmitter acetylcholine activity. Recently, bioremediation of DDVP is potentially described by *T. atroviride* strain T23 (Sun et al., 2019). The study found that *T. atroviride* strain T23 possess a protein that encodes TaPon1-like, that is involved in efficient biodegradation activity of DDVP. The discovery of TaPon1-like hydrolase is a crucial foundation to an inclusive understanding of organophosphate pesticide degradation mechanism.

Various fungicides have been introduced into the market, effective against diseases affecting vegetables and fruit crops. A systemic fungicide, carbendazim are extensively used to control soil-borne disease caused by numerous phytopathogenic fungi. Unfortunately, it was found as a major contaminant traced in agriculture soil. Sharma et al. (2016) reported that *T. harzianum*, *T. viride*, and *T. atroviride* are excellent bioremediation agent of carbendazim. Within 5 days, 85% of carbendazim were degraded by *T. harzianum*, whereas 20%–50% of carbendazim degraded by the other two species. On the other hand, Linhart et al. (2019) reported a fungicide, called penthiopyrad applied to control some foliar and soil borne fungal diseases in fruit, nut and vegetable crops contaminated the surrounding area. These penthiopyrad residues are risky to human health and biodiversity. To date, a *Trichoderma*-containing product, Zumba Plant showed a maximum degradation of penthiopyrad as much as 20% when it was applied on apple trees of Golden Delicious varieties in Poland (Podbielska et al., 2020). Also, their work found that *T. harzianum* strains in Zumba plant product exhibited the effectiveness of penthiopyrad degradation ranged from 34.2% on 3rd day to 56.9% on 14th day.

One of the most worrying environmental pollutants, due to its toxicant, immobile and bioaccumulative properties is polycyclic aromatic hydrocarbons (PAHs). Synthetic PAHs such as phenanthrene, pyrene, and benzo[a]pyrene are commonly used in pesticides. Recent progress in the bioremediation capability of *T. asperellum* H15 have been discovered by Zafra et al. in 2015, found that *T. asperellum* H15 is an effective PAH biodegrade in soil due to high tolerance towards the high amount of PAHs. The study conducted by Zafra et al. (2015) found this strain degrade benzo[a]pyrene, pyrene, and phenanthrene as much as 81%, 63%, and 74%, respectively in PAHs-contaminated soil. Enzyme activities of catechol 1,2 dioxygenase, laccase, and peroxidase have been detected to play a key role in the degradation of PAHs by *T. asperellum*. However, further researches on the bioremediation of contaminated soil at field scale and the exact mechanism used by *Trichoderma* spp. are compulsory.

The repeated application of pesticides in the soil will soon bring an alarming situation in the world. Hence, *Trichoderma* spp. are proven to be one of the potential biological bioremediation agents in order to reduce the pollution caused by excessive usage of pesticide. Besides, bioremediation by species belonging to genus *Trichoderma* in agriculture industry acts as an excellent and natural way to preserve the fertility of the soil. Healthy soil filled with nutrient and microorganisms is needed to enhance the best of plant growth, leading to high yield of production.

**Table 3**

Spectrophotometric quantification of metsulfuron methyl (MM) transformation by *Trichoderma harzianum* strains (T5, T6 and T7). Source: (Vázquez et al., 2015).

Initial MM (mg/ml)	T5	T6	T7
0.0005	100%	100%	100%
0.005	36%	22%	100%
0.1	0%	92.6%	100%

Note: Table shows the percentage of the transformation of MM after incubation with *T. harzianum* strains.

## 7. Conclusion

In agriculture, the new and established innovations boost up the yield of agriculture produce. Unfortunately, several of these conventional practices give a destructive impact on the environment. The challenge faced by modern farming is to accomplish a great number of yields in an environment-friendly manner. Hence, quick action on finding eco-friendly solutions need to be done.

The success of *Trichoderma* strains as biocontrol agents against different pathogenic microorganisms is well known worldwide. Not only that, current findings revealed that these fungi also enhance plant resistance, plant growth and development, leading to an increase in yield production. Mechanisms that are usually involved are antibiotics, mycoparasitism, competition for nutrients and also stimulation of systemic resistance in plants. Recently, *Trichoderma* spp. are being used to control plant diseases in the sustainable disease management system.

Besides playing its role in reducing diseases and improving plant growth, *Trichoderma* spp. can also be used in waste/organic materials decomposition and polluted area detoxification. The increase of nutrient value in compost degraded by *Trichoderma* strains is discovered in several research papers. Thus, the benefits of *Trichoderma* spp. when combined in a product are being able to control different crop diseases, stimulates plant growth and development, improves the composting process and promises a clean environment towards achieving sustainable agriculture.

## Declaration of competing interest

None.

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## References

- Afrãa, R., Sushant, S., Ali, F., 2016. Assessment of the composting process and compost's utilization. *Vegetos; An Int. J. Plant Res.* 29, 2. <https://doi.org/10.5958/2229-4473.2016.00011.2>.
- Ahluwat, O.P., Gupta, P., Kumar, S., Sharma, D.K., Ahluwat, K., 2010. Bioremediation of fungicides by spent mushroom substrate and its associated microflora. *Indian J. Microbiol.* 50, 390–395.
- Ahluwalia, V., Kumar, J., Rana, V.S., Sati, O.P., Walia, S., 2015. Comparative evaluation of two *Trichoderma harzianum* strains for major secondary metabolite production and antifungal activity. *Nat. Prod. Res.* 29, 914–920.
- Ahmed, A.S., Ezziyani, M., Sánchez, C.P., Candela, M.E., 2003. Effect of chitin on biological control activity of *Bacillus* spp. and *Trichoderma harzianum* against root rot disease in pepper (*Capsicum annuum*) plants. *Eur. J. Plant Pathol.* 109, 633–637.
- Ahmed, S., Bashir, A., Saleem, H., Saadia, M., Jamil, A., 2009. Production and purification of cellulose-degrading enzymes from a filamentous fungus *Trichoderma harzianum*. *Pak. J. Bot.* 41, 1411–1419.
- Alias, N., Mahadi, N.M., Abdul Murad, A.M., Abu Bakar, F.D., Md Illias, R., 2011. Three dimensional structure prediction of recombinant endochitinase from *Trichoderma virens* UKM-1. *J. Agrobiotech.* 2, 83–92.
- Amin, F., Razdan, V.K., 2010. Potential of *Trichoderma* species as biocontrol agents of soil borne fungal propagules. *J. Phytol.* 2, 38–41.
- Amira, R.D., Roshanida, A.R., Rosli, M.I., Zahrah, M.S.F., Anuar, J.M., Adha, C.N., 2011. Bio-conversion of empty fruit bunches (EFB) and palm oil mill effluent (POME) into compost using *Trichoderma virens*. *Afr. J. Biotechnol.* 10, 18775–18780.
- Atlas, R.M., Pramer, D., 1990. Focus on bioremediation. *ASM News.* 56, 352–353.
- Aydođdu, M., Kurbetli, I., Kitapçı, A., Süli, G., 2020. Aggressiveness of green mould on cultivated mushroom (*Agaricus bisporus*) in Turkey. *J. Plant. Dis. Protect.* 127, 695–708.
- Badaluddin, N.A., Jamaluddin, S.N.T., Ihsam, N.S., Sajili, M.H., Khalit, S.I., Mohamed, N.A., 2018. Molecular identification of isolated fungi from Kelantan and Terengganu using internal transcriber spacer (ITS) region. *J. Agrobiotech.* 9, 222–231.
- Baiyee, B., Pornsuriya, C., Ito, S.I., Sunpapao, A., 2019. *Trichoderma spirale* T76-1 displays biocontrol activity against leaf spot on lettuce (*Lactuca sativa* L.) caused by *Corynespora cassicola* or *Curvularia aerea*. *Biol. Control* 129, 195–200.
- Begum, M.F., Rahman, M.A., Alam, M.F., 2010. Biological control of *Alternaria* fruit rot of chili by *Trichoderma* species under field conditions. *Mycos.* 38, 113–117.

- Benítez, T., Rincón, A.M., Limón, M.C., Codon, A.C., 2004. Biocontrol mechanisms of *Trichoderma* strains. *Int. Microbiol.* 7, 249–260.
- Bernal-Vicente, A., Ros, M., Pascual, J.A., 2009. Increased effectiveness of the *Trichoderma harzianum* isolate T-78 against *Fusarium* wilt on melon plants under nursery conditions. *J. Sci. Food Agric.* 89, 827–833.
- Bhat, K.A., 2017. A new agar plate assisted slide culture technique to study mycoparasitism of *Trichoderma* sp. on *Rhizoctonia solani* and *Fusarium oxysporum*. *Int. J. Cur. Microbiol. Appl. Sci.* 6, 3176–3180.
- Bisen, K., Keswani, C., Patel, J.S., Sarma, B.K., Singh, H.B., 2016. *Trichoderma* spp.: efficient inducers of systemic resistance in plants. *Microbial-mediated Induced Systemic Resistance in Plants*. Springer, Singapore, pp. 185–195.
- Bissett, J., 1991. A revision of the genus *Trichoderma*. II. Infrageneric classification. *Can. J. Bot.* 69, 2357–2372.
- Boldt, T.S., Jacobsen, C.S., 1998. Different toxic effects of the sulfonylurea herbicides metsulfuron methyl, chlorsulfuron and thifensulfuron methyl on fluorescent pseudomonads isolated from an agricultural soil. *FEMS Microbiol. Lett.* 161, 29–35.
- Bottacini, F., Morrissey, R., Esteban-Torres, M., James, K., van Breen, J., Dikareva, E., Egan, M., Lambert, J., Limpt, K.V., Knol, J., Motherway, M.O.C., Sinderen, D.V., 2018. Comparative genomics and genotype-phenotype associations in *Bifidobacterium breve*. *Sci. Rep.* 8, 1–14.
- Brotman, Y., Kapuganti, J.G., Viterbo, A., 2010. *Trichoderma*. *Curr. Biol.* 20, R390–R391.
- Cai, F., Yu, G., Wang, P., Wei, Z., Fu, L., Shen, Q., Chen, W., 2013. Harzianolide, a novel plant growth regulator and systemic resistance elicitor from *Trichoderma harzianum*. *Plant Physiol. Bioch.* 73, 106–113.
- Cai, F., Chen, W., Wei, Z., Pang, G., Li, R., Ran, W., Shen, Q., 2015. Colonization of *Trichoderma harzianum* strain SQR-T037 on tomato roots and its relationship to plant growth, nutrient availability and soil microflora. *Plant Soil* 388, 337–350.
- Carvalho, L.C., Dennis, P.G., Badri, D.V., Kidd, B.N., Vivanco, J.M., Schenk, P.M., 2015. Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. *Mol. Plant-Microbe Interact.* 28, 1049–1058.
- Chaverri, P., Branco-Rocha, F., Jaklitsch, W., Gazis, R., Degenkolb, T., Samuels, G.J., 2015. Systematics of the *Trichoderma harzianum* species complex and the re-identification of commercial biocontrol strains. *Mycologia* 107, 558–590.
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., Cortés-Penagos, C., López-Bucio, J., 2009. *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in *Arabidopsis*. *Plant Physiol.* 149, 1579–1592.
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., Alfaro-Cuevas, R., López-Bucio, J., 2014. *Trichoderma* spp. improve growth of *Arabidopsis* seedlings under salt stress through enhanced root development, osmolyte production, and Na<sup>+</sup> elimination through root exudates. *Mol. Plant Microbe Interact.* 27, 503–514.
- Contreras-Cornejo, H.A., López-Bucio, J.S., Méndez-Bravo, A., Macías-Rodríguez, L., Ramos-Vega, M., Guevara-García, Á.A., López-Bucio, J., 2015a. Mitogen-activated protein kinase 6 and ethylene and auxin signaling pathways are involved in *Arabidopsis* root-system architecture alterations by *Trichoderma atroviride*. *Mol. Plant-Microbe Interact.* 28, 701–710.
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., Vergara, A.G., López-Bucio, J., 2015b. *Trichoderma* modulates stomatal aperture and leaf transpiration through an abscisic acid-dependent mechanism in *Arabidopsis*. *J. Plant Growth Regul.* 34, 425–432.
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., del-Val, E., Larsen, J., 2016. Ecological functions of *Trichoderma* spp. and their secondary metabolites in the rhizosphere: interactions with plants. *FEMS Microbiol. Ecol.* 92. <https://doi.org/10.1093/femsec/fiw036>
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., del-Val, E., Larsen, J., 2018. The root endophytic fungus *Trichoderma atroviride* induces foliar herbivory resistance in maize plants. *Appl. Soil Ecol.* 124, 45–53.
- Cummings, N.J., Ambrose, A., Braithwaite, M., Bissett, J., Roslan, H.A., Abdullah, J., Stewart, A., Agbayani, F.V., Steyaert, J., Hill, R.A., 2016. Diversity of root-endophytic *Trichoderma* from Malaysian Borneo. *Mycol. Progress.* 15, 50. <https://doi.org/10.1007/s11557-016-1192-x>.
- Didwania, N., Gupta, K.N., Gupta, S., Bisen, R., 2019. Bio-intensive approaches in the management of fungal diseases of oil yielding crops. In: Khan, M.R., et al. (Eds.), *Bio-intensive Approaches – Application and Effectiveness in Plant Disease Management*. Indian Phytopathological Society, New Delhi, pp. 333–356.
- El Komy, M.H., Saleh, A.A., Eranthodi, A., Molan, Y.Y., 2015. Characterization of novel *Trichoderma asperellum* isolates to select effective biocontrol agents against tomato *Fusarium* wilt. *Plant Pathol. J.* 31, 50–60.
- Elad, Y., Chet, I., Boyle, P., Henis, Y., 1983. Parasitism of *Trichoderma* spp. on *Rhizoctonia solani* and *Sclerotium rolfsii*-scanning electron microscopy and fluorescence microscopy. *Phytopath.* 73, 85–88.
- El-Ghamry, A.M., Huang, C.Y., Xu, J.M., 2001. Combined effects of two sulfonylurea herbicides on soil microbial biomass and N-mineralization. *Int. J. Environ. Sci.* 13, 311–317.
- Ezzuyyani, M., Requena, M.E., Egea-Gilabert, C., Candela, M.E., 2007. Biological control of *Phytophthora* root rot of pepper using *Trichoderma harzianum* and *Streptomyces rochei* in combination. *Int. J. Environ. Sci.* 15, 342–349.
- Freeman, S., Minz, D., Kolesnik, I., Barbul, O., Zveibil, A., Maymon, M., Nitzani, Y., Kirshner, B., Rav-David, D., Bilu, A., Dag, A., 2004. *Trichoderma* biocontrol of *Colletotrichum acutatum* and *Botrytis cinerea* and survival in strawberry. *Eur. J. Plant Pathol.* 110, 361–370.
- Garault, P., Letort, C., Juillard, V., Monnet, V., 2000. Branched-chain amino acid biosynthesis is essential for optimal growth of *Streptococcus thermophilus* in milk. *Appl. Environ. Microbiol.* 66, 5128–5133.
- Garnica-Vergara, A., Barrera-Ortiz, S., Muñoz-Parra, E., Raya-González, J., Méndez-Bravo, A., Macías-Rodríguez, L., López-Bucio, J., 2016. The volatile 6-pentyl-2H-pyran-2-one from *Trichoderma atroviride* regulates *Arabidopsis thaliana* root morphogenesis via auxin signaling and ethylene insensitive 2 functioning. *New Phytol.* 209, 1496–1512.
- Gava, C.A.T., Pinto, J.M., 2016. Biocontrol of melon wilt caused by *Fusarium oxysporum* Schlect f. sp. melonis using seed treatment with *Trichoderma* spp. and liquid compost. *Biol. Control* 97, 13–20.
- Ghaffari, M.R., Ghabooli, M., Khatibi, B., Hajirezaei, M.R., Schweizer, P., Salekdeh, G.H., 2016. Metabolic and transcriptional response of central metabolism affected by root endophytic fungus *Piriformospora indica* under salinity in barley. *Plant Mol. Biol.* 90, 699–717.
- Gveroska, B., Ziberoski, J., 2012. *Trichoderma harzianum* as a biocontrol agent against *Alternaria alternata* on tobacco. *ATI-Applied Tech. Innovations.* 7, 67–76.
- Haddadin, M.S., Haddadin, J., Arabiyat, O.J., Hattar, B., 2009. Biological conversion of olive pomace into compost by using *Trichoderma harzianum* and *Phanerochaete chrysosporium*. *Bioresour. Technol.* 100, 4773–4782.
- Hajek, A.E., Eilenberg, J., 2018. *Natural Enemies: An Introduction to Biological Control*. Second Ed. Cambridge University Press, New York.
- Halifu, S., Deng, X., Song, X., Song, R., 2019. Effects of two *Trichoderma* strains on plant growth, rhizosphere soil nutrients, and fungal community of *Pinus sylvestris* var. mongolica annual seedlings. *Forests* 10, 758. <https://doi.org/10.3390/f10090758>.
- Harman, G.E., 2006. Overview of mechanisms and uses of *Trichoderma* spp. *Phytopathol.* 96, 190–194.
- Harman, G.E., Howell, C.R., Viterbo, A., Chet, I., Lorito, M., 2004. *Trichoderma* species—opportunistic, avirulent plant symbionts. *Nat. Rev. Microbiol.* 2, 43–56.
- Hatvani, L., Antal, Z., Manczinger, L., Szekeres, A., Druzhinina, I.S., Kubicek, C.P., Nagy, A., Nagy, E., Vágvolgyi, C., Kredics, L., 2007. Green mold diseases of *Agaricus* and *Pleurotus* spp. are caused by related but phylogenetically different *Trichoderma* species. *Phytopathol.* 97, 532–537.
- Hatvani, L., Kredics, L., Allaga, H., Manczinger, L., Vágvolgyi, C., Kuti, K., Geösel, A., 2017. First report of *Trichoderma aggressivum f. aggressivum* green mold on *Agaricus bisporus* in Europe. *Plant Dis.* 101, 1052. <https://doi.org/10.1094/PDIS-12-16-1783-PDN>.
- Heidari, F., Olia, M., 2016. Biological control of root-knot nematode, *Meloidogyne javanica*, using vermicompost and fungus *Trichoderma harzianum* on tomato. *Iran. J. Plant Pathol.* 52, 109–124.
- Hirpara, D.G., Gajera, H.P., Hirpara, H.Z., Golakiya, B.A., 2017. Antipathy of *Trichoderma* against *Sclerotium rolfsii* Sacc.: evaluation of cell wall-degrading enzymatic activities and molecular diversity analysis of antagonists. *J. Mol. Microb. Biotech.* 27, 22–28.
- Hock, O., Subramaniam, G., Abdullah, F.B., 2014. Effect of *Trichoderma*-infused compost on yield of chili plants. Presented at International Conference on Advances in Environment, Agriculture & Medical Sciences (ICAEAM'14), 16–17 November 2014. Lumpur, Kuala.
- Howell, C.R., 2002. Cotton seedling preemergence damping-off incited by *Rhizopus oryzae* and *Pythium* spp. and its biological control with *Trichoderma* spp. *Phytopathol.* 92, 177–180.
- Hu, M., Li, Q.L., Yang, Y.B., Liu, K., Miao, C.P., Zhao, L.X., Ding, Z.T., 2017. Koninginins RS from the endophytic fungus *Trichoderma koningiopsis*. *Nat. Prod. Res.* 31, 835–839.
- Hyakumachi, M., Kubota, M., 2003. Fungi as plant growth promoter and disease suppressor. In: Arora, D.K. (Ed.), *Fungal Biotechnology in Agricultural, Food and Environmental Application*. Marcel Dekker, New York, pp. 101–110.
- Imran, A., Arif, M., Shah, Z., Bari, A., 2020. Soil application of *Trichoderma* and peach (*Prunus persica* L.) residues possesses biocontrol potential for weeds and enhances growth and profitability of soybean (*Glycine max*). *Sarhad J. Agric.* 36, 10–20.
- Islam, M.A., Mostafa, M.G., Rahman, M.R., 2014. Conversion of solid organic waste into compost using *Trichoderma* spp. and its application on some selected vegetables. *Int. J. Environ. Waste Manag.* 14, 211–221.
- John, R.P., Tyagi, R.D., Prévost, D., Brar, S.K., Pouleur, S., Surampalli, R.Y., 2010. Mycoparasitic *Trichoderma viride* as a biocontrol agent against *Fusarium oxysporum* f. sp. *adzuki* and *Pythium arrhenomanes* and as a growth promoter of soybean. *J. Crop Prot.* 29, 1452–1459.
- Kant, P., Reinprecht, Y., Martin, C.J., Islam, R., Pauls, K.P., 2017. Disease resistance. *Comprehensive Biotechnology (Third Edition)*. 4, pp. 789–805. <https://doi.org/10.1016/B978-0-12-809633-8.09244-X>.
- Kubicek, C.P., Mach, R.L., Peterbauer, C.K., Lorito, M., 2001. *Trichoderma*: from genes to biocontrol. *J. Plant Pathol.* 83, 11–23.
- Kubicek, C.P., Herrera-Estrella, A., Seidl-Seiboth, V., et al., 2011. Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome Biol.* 12. <https://doi.org/10.1186/gb-2011-12-4-r40>.
- Kullnig, C., Mach, R.L., Lorito, M., Kubicek, C.P., 2000. Enzyme diffusion from *Trichoderma atroviride* (= *T. harzianum* P1) to *Rhizoctonia solani* is a prerequisite for triggering of *Trichoderma ech42* gene expression before mycoparasitic contact. *Appl. Environ. Microbiol.* 66, 2232–2234.
- Kumar, R., Kumari, K., Hembram, K.C., Kandha, L., Bindhani, B.K., 2019. Expression of an *endo-α-1, 3-Glucanase* gene from *Trichoderma harzianum* in rice induces resistance against sheath blight. *J. Plant Biochem. Biotechnol.* 28, 84–90.
- Lewis, J.A., Papavizas, G.C., 1987. Application of *Trichoderma* and *Glodcladium* in alginate pellets for control of *Rhizoctonia* damping-off. *Plant Pathol.* 36, 438–446.
- Li Destri Nicosia, M.G., Mosca, S., Mercurio, R., Schena, L., 2015. Dieback of *Pinus nigra* seedlings caused by a strain of *Trichoderma viride*. *Plant Dis.* 99, 44–49.
- Li, G.Q., Huang, H.C., Acharya, S.N., Erickson, R.S., 2005. Effectiveness of *Coniothyrium minitans* and *Trichoderma atroviride* in suppression of sclerotinia blossom blight of alfalfa. *Plant Pathol.* 54, 204–211.
- Linhart, C., Niedrist, G.H., Nagler, M., Nagrani, R., Temml, V., Bardelli, T., Wilhalm, T., Riedl, A., Zaller, J.G., Clausing, P., Hertoge, K., 2019. Pesticide contamination and associated risk factors at public playgrounds near intensively managed apple and wine orchards. *Environ. Sci. Eur.* 31, 28. <https://doi.org/10.1186/s12302-019-0206-0>.

- Ljung, K., 2013. Auxin metabolism and homeostasis during plant development. *Development* 140, 943–950.
- Lorito, M., Farkas, V., Rebuffat, S., Bodo, B., Kubicek, C.P., 1996. Cell wall synthesis is a major target of mycoparasitic antagonism by *Trichoderma harzianum*. *J. Bacteriol.* 178, 6382–6385.
- Masso, C., Mukhongo, R.W., Thuita, M., Abaidoo, R., Ulzen, J., Kariuki, G., Kalumuna, M., 2016. Biological Inoculants for Sustainable Intensification of Agriculture in Sub-Saharan Africa Smallholder Farming Systems. In *Climate change and multi-dimensional sustainability in African agriculture*. Springer, Cham, pp. 639–658.
- Matarese, F., Sarrocco, S., Gruber, S., Seidl-Seiboth, V., Vannacci, G., 2012. Biocontrol of *Fusarium* head blight: interactions between *Trichoderma* and mycotoxicogenic *Fusarium*. *Microbiol.* 158, 98–106.
- Mazin, M., Andreadis, S.S., Jenkins, N.E., Rajotte, E.G., 2018. The mushroom sciarid fly, *Lycoriella ingenua*, benefits from its association with green mold disease (*Trichoderma aggressivum*) in commercial mushroom production. *J. Pest. Sci.* 91, 815–822.
- Mbarga, J.B., Ten Hoopen, G.M., Kuate, J., Adiobo, A., Ngonkeu, M.E.L., Ambang, Z., Begoude, B.A.D., 2012. *Trichoderma asperellum*: a potential biocontrol agent for *Pythium myriotylum*, causal agent of cocoyam (*Xanthosoma sagittifolium*) root rot disease in Cameroon. *Crop Prot.* 36, 18–22.
- Mukherjee, P.K., Horwitz, B.A., Kenerley, C.M., 2012. Secondary metabolism in *Trichoderma*—a genomic perspective. *Microbiol.* 158, 35–45.
- Munoz, F.M., Demmler, G.J., Travis, W.R., Ogdan, A.K., Rossmann, S.N., Rinaldi, M.G., 1997. *Trichoderma longibrachiatum* infection in a pediatric patient with aplastic anemia. *J. Clin. Microbiol.* 35, 499–503.
- Naemi, S., Okhovvat, S.M., Javan-Nikkhah, M., Vágvolgyi, C., Khosravi, V., Kredics, L., 2010. Biological control of *Rhizoctonia solani* AG1-1A, the causal agent of rice sheath blight with *Trichoderma* strains. *Phytopathol. Mediterr.* 49, 287–300.
- Naher, L., Yusuf, U.K., Ismail, A., Hossain, K., 2014. *Trichoderma* spp.: a biocontrol agent for sustainable management of plant diseases. *Pak. J. Bot.* 46, 1489–1493.
- Napitupulu, T.P., Ilyas, M., Kanti, A., Sudiana, I.M., 2019. In vitro evaluation of *Trichoderma harzianum* strains for the control of *Fusarium oxysporum* f. sp. *cubense*. *Plant Pathol. Quarantine* 9, 152–159.
- Naseby, D.C., Pascual, J.A., Lynch, J.M., 2000. Effect of biocontrol strains of *Trichoderma* on plant growth, *Pythium ultimum* populations, soil microbial communities and soil enzyme activities. *J. Appl. Microbiol.* 88, 161–169.
- Nawrocka, J., Maholepsza, U., 2013. Diversity in plant systemic resistance induced by *Trichoderma*. *Biol. Control* 67, 149–156.
- Ochoa-Villarreal, M., Aispuro-Hernández, E., Vargas-Arispuro, I., Martínez-Téllez, M.Á., 2012. Plant cell wall polymers: function, structure and biological activity of their derivatives. In: Souza Gomes, A. (Ed.), *Polymerization*. IntechOpen <https://doi.org/10.5772/46094>.
- Oman, M.R., Lehner, S., Rodríguez, C.E., Brunner, K., Zeilinger, S., 2012. The seven-transmembrane receptor Gpr1 governs processes relevant for the antagonistic interaction of *Trichoderma atroviride* with its host. *Microbiol.* 158, 107–118.
- Pampulha, M.E., Oliveira, A., 2006. Impact of an herbicide combination of bromoxynil and prosulfuron on soil microorganisms. *Curr. Microbiol.* 53, 238–243.
- Pandian, R.T.P., Raja, M., Kumar, A., Sharma, P.R., 2016. Morphological and molecular characterization of *Trichoderma asperellum* strain Ta13. *Indian. Phytopathol.* 69, 297–303.
- Paulitz, T.C., Ahmad, J.S., Baker, R., 1990. Integration of *Pythium nunn* and *Trichoderma harzianum* isolate T-95 for the biological control of *Pythium* damping-off of cucumber. *Plant Soil* 121, 243–250.
- Podbielska, M., Kus-Liśkiewicz, M., Jagusztyn, B., Piechowicz, B., Sadło, S., Słowik-Borowiec, M., Twarużek, M., Szpyrka, E., 2020. Influence of *Bacillus subtilis* and *Trichoderma harzianum* on penthiopyrad degradation under laboratory and field studies. *Molecules* 25, 1421. <https://doi.org/10.3390/molecules25061421>.
- Qualhato, F.T., Lopes, F.A.C., Steindorff, A.S., Brandão, R.S., Jesuino, R.S.A., Ulhoa, C.J., 2013. Mycoparasitism studies of *Trichoderma* species against three phytopathogenic fungi: evaluation of antagonism and hydrolytic enzyme production. *Biotechnol. Lett.* 35, 1461–1468.
- Ramezani, H., 2008. Biological control of root-rot of eggplant caused by *Macrophomina phaseolina*. *Am. Eurasian J. Agric. Environ. Sci.* 4, 218–220.
- Rifai, M.A., 1969. A revision of the genus *Trichoderma*. *Mycol. Papers* 116, 1–56.
- Robertson, G.P., Paul, E.A., 2000. Decomposition and soil organic matter dynamics. *Methods in Ecosystem Science*. Springer, New York, NY, pp. 104–116.
- Rojo, F.G., Reynoso, M.M., Ferez, M., Chulze, S.N., Torres, A.M., 2007. Biological control by *Trichoderma* species of *Fusarium solani* causing peanut brown root rot under field conditions. *Crop Prot.* 26, 549–555.
- Ros, M., Raut, I., Santísima-Trinidad, A.B., Pascual, J.A., 2017. Relationship of microbial communities and suppressiveness of *Trichoderma* fortified composts for pepper seedlings infected by *Phytophthora nicotianae*. *PLoS One* 12 (e0174069). doi:10.1371/journal.pone.0174069.
- Samuels, G.J., Dodd, S.L., Gams, W., Castlebury, L.A., Petrini, O., 2002. *Trichoderma* species associated with the green mold epidemic of commercially grown *Agaricus bisporus*. *Mycologia* 94, 146–170.
- Sautour, M., Chrétien, M.L., Valot, S., Lafon, I., Basmaciyan, L., Legouge, C., Verrier, T., Gonssaud, B., Abou-Hanna, H., Dalle, F., Caillot, D., 2018. First case of proven invasive pulmonary infection due to *Trichoderma longibrachiatum* in a neutropenic patient with acute leukemia. *J. Mycol. Med.* 28, 659–662.
- Sharma, B.L., Singh, S.P., Sharma, M.L., 2012. Bio-degradation of crop residues by *Trichoderma* species vis-à-vis nutrient quality of the prepared compost. *Sugar Tech.* 14, 174–180.
- Sharma, P.R., Sharma, M., Raja, M., Singh, D.V., Srivastava, M., 2016. Use of *Trichoderma* spp. in biodegradation of carbendazim. *Indian J. Agric. Sci.* 86, 891–894.
- Shi, M., Chen, L., Wang, X.-W., Zhang, T., Zhao, P.-B., Song, X.-Y., Sun, C.-Y., Chen, X.-L., Zhou, B.-C., Zhang, Y.-Z., 2012. Antimicrobial peptaibols from *Trichoderma pseudokoningii* induce programmed cell death in plant fungal pathogens. *Microbiol.* 158, 166–175.
- Siddaiah, C.N., Satyanarayana, N.R., Mudili, V., Gupta, V.K., Gurunathan, S., Rangappa, S., Huntrike, S.S., Srivastava, R.K., 2017. Elicitation of resistance and associated defense responses in *Trichoderma hamatum* induced protection against pearl millet downy mildew pathogen. *Sci. Rep.* 7, 43991. <https://doi.org/10.1038/srep43991>.
- Siddiquee, S., Shafawati, S.N., Naher, L., 2017. Effective composting of empty fruit bunches using tropical *Trichoderma* strains. *Biotechnol. Rep.* 13, 1–7.
- Siemering, G., Ruark, M., Geven, A., 2016. The Value of *Trichoderma* for Crop Production. University of Wisconsin–Extension, Cooperative Extension.
- Singh, D., Sharma, R.R., 2018. Postharvest diseases of fruits and vegetables and their management. *Postharvest Disinfection of Fruits and Vegetables*. Academic Press, pp. 1–52.
- Spiteller, D., 2008. Plant defense strategies. *Encyclopedia of Ecology*. Academic Press, pp. 2798–2811.
- Sun, J., Yuan, X., Li, Y., Wang, X., Chen, J., 2019. The pathway of 2, 2-dichlorovinyl dimethyl phosphate (DDVP) degradation by *Trichoderma atroviride* strain T23 and characterization of a paraoxonase-like enzyme. *Appl. Microbiol. Biotechnol.* 103, 8947–8962.
- Sundaramoorthy, S., Balabaskar, P., 2013. Biocontrol efficacy of *Trichoderma* spp. against wilt of tomato caused by *Fusarium oxysporum* f. sp. *lycopersici*. *J. Appl. Biol. Biotechnol.* 1, 36–40.
- Tijerino, A., Cardoza, R.E., Moraga, J., Malmierca, M.G., Vicente, F., Aleu, J., Collado, I.G., Gutierrez, S., Monte, E., Hermosa, R., 2011. Overexpression of the trichodiene synthase gene tri5 increases trichodermin production and antimicrobial activity in *Trichoderma brevicompactum*. *Fungal Genet. Biol.* 48, 285–296.
- Tiwari, R.K., Singh, S., Pandey, R.S., Sharma, B., 2016. Enzymes of earthworm as indicators of pesticide pollution in soil. *Adv. Enzyme. Res.* 4, 113–124.
- Vázquez, M.B., Barrera, V., Bianchinotti, V., 2015. Molecular identification of three isolates of *Trichoderma harzianum* isolated from agricultural soils in Argentina, and their abilities to detoxify in vitro metsulfuron methyl. *Bot.* 93, 793–800.
- Vinale, F., Nigro, M., Sivasithamparam, K., Flematti, G., Ghisalberti, E., Ruocco, M., Varlese, R., Marra, R., Lanzuise, S., Eid, A., Woo, S.L., Lorito, M., 2013. Harzianic acid: a novel siderophore from *Trichoderma harzianum*. *FEMS Microbiol. Letters.* 347, 123–129.
- Waghunde, R.R., Shelake, R.M., Sabalpara, A.N., 2016. *Trichoderma*: a significant fungus for agriculture and environment. *Afr. J. Agric. Res.* 11, 1952–1965.
- Woo, S.L., Ruocco, M., Vinale, F., Nigro, M., Marra, R., Lombardi, N., Lorito, M., 2014. *Trichoderma*-based products and their widespread use in agriculture. *Open. Mycol. J.* 8, 71–126.
- Xue, A.G., Guo, W., Chen, Y., Siddiqui, I., Marchand, G., Liu, J., Ren, C., 2017. Effect of seed treatment with novel strains of *Trichoderma* spp. on establishment and yield of spring wheat. *J. Crop Prot.* 96, 97–102.
- Yadav, U., Choudhury, P.P., 2014. Biodegradation of sulfosulphuron in agricultural soil by *Trichoderma* sp. *Lett. Appl. Microbiol.* 59, 479–486.
- Yang, Y., Yu, S., Tan, Y., Liu, N., Wu, A., 2017. Individual and combined cytotoxic effects of co-occurring deoxynivalenol family mycotoxins on human gastric epithelial cells. *Toxins* 9, 96. <https://doi.org/10.3390/toxins9030096>.
- Yedidia, I., Srivastava, A.K., Kapulnik, Y., Chet, I., 2001. Effect of *Trichoderma harzianum* on microelement concentrations and increased growth of cucumber plants. *Plant Soil* 235, 235–242.
- Yuan, H., Zhu, Z., Liu, S., Ge, T., Jing, H., Li, B., Liu, Q., Lynn, T.M., Wu, J., Kuzyakov, Y., 2016. Microbial utilization of rice root exudates: <sup>13</sup>C labeling and PLFA composition. *Biol. Fert. Soils.* 52, 615–627.
- Zafra, G., Moreno-Montaño, A., Absalón, Á.E., Cortés-Espinosa, D.V., 2015. Degradation of polycyclic aromatic hydrocarbons in soil by a tolerant strain of *Trichoderma asperellum*. *Environ. Sci. Pollut. Res.* 22, 1034–1042.
- Zeilinger, S., Gruber, S., Bansal, R., Mukherjee, P.K., 2016. Secondary metabolism in *Trichoderma*—chemistry meets genomics. *Fungal Biol. Rev.* 30, 74–90.
- Zhou, X.X., Li, J., Yang, Y.H., Zeng, Y., Zhao, P.J., 2014. Three new koniginins from *Trichoderma neokongii* 8722. *Phytochem. Lett.* 8, 137–140.
- Zhu, Z.X., Zou, W.Y., 2015. *Trichoderma* (Hypocrea) species with green ascospores from China. *Persoonia* 34, 113–129.
- Zin, N.A., Badaluddin, N.A., Awang Jaya, N., Sajili, M.H., Khalit, S.I., Lokman, M.N., 2019. Detection and characterization of cadmium tolerant fungi from Kelantan river. *Malaysia. Biosci. Res.* 16, 2768–2776.