

## Exploring the Role of Volatile Organic Compounds of *Trichoderma* in Plant Health Management

Madhusmita Mahanta<sup>1\*</sup>, Pranab Dutta<sup>2\*</sup>, Tanjil Rahman<sup>3</sup> and Tharringwon Marchang Ningshen<sup>1</sup>

<sup>1</sup>College of PG Studies in Agricultural Sciences, Umiam-793103, CAU (Imphal), Meghalaya

<sup>2</sup>College of Agriculture, Kyrdemkulai-793104, CAU (Imphal), Ri Bhoi, Meghalaya

<sup>3</sup>Faculty of Agricultural Sciences and Technology, Assam down town University, Panikhaiti, Gurwahati-781026, Assam

---

### Abstract

*Trichoderma* (Hypocreales) with promising biocontrol and plant growth promoting activities acts upon the phytopathogens by adopting multifaceted tactics and induction of plant defense responses. *Trichoderma* species having biocontrol potential are often armed with a treasure house of low molecular weight secondary metabolites which help in its antagonistic properties *via* mycoparasitism, antibiosis, competition and by induction of plant defense responses. Broadly, the secondary metabolites are classified into two groups *viz.*, volatile organic compounds (VOCs) and non-volatile organic compounds. The VOCs produced by *Trichoderma* are either gas-phase and/ or carbon-based molecules of both low and high molecular weight with antifungal, antibacterial, nematocidal effects as well as exhibit plant growth promoting properties. VOCs of *Trichoderma* leads to hyphal abnormalities in the phytopathogen such as deformation, swelling/shrinkage, lysis as well as change in hyphal pigmentation. This chapter attempts at a brief explanation on use and scope of VOCs released by *Trichoderma* species in plant health management.

---

**Keywords** Anti-microbial property, plant health management, *Trichoderma*, volatile organic compound

---

### Introduction

In the light of emerging population and decrease in agricultural lands worldwide, ensuring food safety is becoming a challenging job. Despite adoption of different management tactics, the agricultural sector confronts losses due to various biotic and abiotic factors. Amongst them, biotic factors like phytopathogens and insect pests can cause significant yield losses in agricultural crops, thereby posing a threat to the efforts of mankind to increase the overall agricultural production.

With a global change in the perspective of agricultural practices from chemocentric to organic based, biological control agents (BCAs) such

\*Corresponding author's e-mail: madhusmita.mahanta12@gmail.com

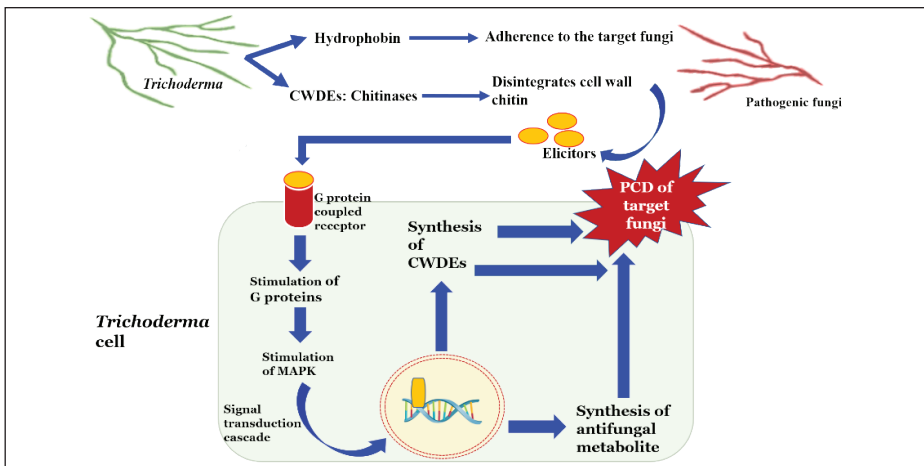
In: Current Trends in the Diagnosis and Management of Plant Diseases. (Eds.) Dutta, P., Upamanya, G.K., Pandey, A.K., 2024. Biotica Publications, Tripura, India.

as *Trichoderma* are welcomed by farming communities for plant disease management. *Trichoderma* (Hypocreales) is a versatile genus of Ascomycetes fungi with promising biocontrol and plant growth promoting activities. The genus was first described by Persoon (1794) and the species belonging to this genus is considered as agriculturally important microbes. *Trichoderma* acts upon the phytopathogens by adopting tactics such as antibiosis, competition, mycoparasitism (Dutta and Das, 1999) and induction of plant defense responses. However, a synchronized combination of all these factors is necessary for *Trichoderma* to confer protections to the host plant against phytopathogens (Dutta *et al.*, 2023).

## Major biological control strategies of *Trichoderma*

### 1. Mycoparasitism

Mycoparasitism can be defined as a complex phenomenon wherein a fungus is preyed upon by another fungus in direct confrontation. Weindling in early 1930s observed the mycoparasitic nature of *Trichoderma lignorum* on *Rhizoctonia solani* (Weindling, 1932). The sequential events of mycoparasitism includes locating the prey fungus, attraction, hyphal attachment followed by hyphal coiling, and release of hydrolytic enzymes by *Trichoderma* to facilitate hyphal penetration which ultimately leads to complete dissolution of the pathogen hyphae (Mukherjee *et al.*, 2012). As the biological control ability of *Trichoderma* was first understood after discovering it as a mycoparasite, therefore, mycoparasitism is also termed as an ancestral trait of *Trichoderma* or its sexual stage i.e., *Hypocrea* (Kubicek *et al.*, 2011). When a prey fungus is in the vicinity, the complex process of mycoparasitism is triggered by different stimuli released by the *Trichoderma* (Fig. 1). A summary of cellular signals/ compounds necessary for mycoparasitism is listed out in table 1.



**Fig. 1:** Mode of action of *Trichoderma* against phytopathogens (abbreviations used: CWDE: cell wall degrading enzymes; MAPK: mitogen activated protein kinase; PCD: Programmed cell death) (adopted from Dutta *et al.*, 2023)

**Table 1: Cellular signals/ compounds of *Trichoderma* for mycoparasitism**

Sl. No.	Events of mycoparasitism	Signal/ compound responsible	References
1.	Sensing the presence of host/ prey fungi	Binding of the cell wall carbohydrates of <i>Trichoderma</i> to the lectins of the prey hyphae	Dutta <i>et al.</i> (2023)
2.	Attraction and attachment to host fungi	Hydrophobins: Known for their high surface activity, hydrophobin proteins with a large exposed hydrophobic area, possesses an ability to form an amphipathic membrane at the interface of hydrophilic and hydrophobic environment. All the mycoparasitic species of <i>Trichoderma</i> are documented to abundantly produce hydrophobin proteins.	Kubicek <i>et al.</i> (2008); Druzhinina <i>et al.</i> (2011),
3.	Hyphal coiling around the prey fungi		
4.	Penetration in to the lumen of the prey hyphae	Penetration is facilitated by development of appressoria by <i>Trichoderma</i> . High concentration of osmotic fluid such as glycerol in the appressoria provides sufficient mechanical pressure necessary to invade the prey hyphal wall (Sood <i>et al.</i> , 2020). -Release of hydrolytic enzymes such as chitinase, cellulase, protease by <i>Trichoderma</i> acts synergistically to help penetration	Dutta <i>et al.</i> (2023)

## 2. Antibiosis

After the historic discovery of mycoparasitism in *Trichoderma*, Weindling (1934) mentioned about some lethal principle released by *Trichoderma* which can inhibit the growth of phytopathogen *R. solani* both *in vitro* and *in vivo* conditions. The lethal principle was later identified as gliotoxin, which is a secondary metabolite of *T. virens*. The process by which the diffusible low molecular weight secondary metabolites interact with other microbes to restrict/ reduce their growth is termed as antibiosis. Therefore, a mycoparasitic *Trichoderma* is armed with a treasury of secondary metabolites to further strengthen its antagonistic abilities. Examples of some secondary metabolite of *Trichoderma* playing significant role in antibiosis are gliotoxin,

viridin, viridiol, pachybasin, harzianic acid, Koniginin *etc.* (Zeilinger *et al.*, 2016).

### 3. Competition

The ability to sequester nutrients from scarce or immobilized state, in a rate faster than other rhizospheric microbes, makes *Trichoderma* an aggressive colonizer of plant roots. They eliminate other micro-organisms from inhabiting their niche by outracing them in the competition for food, space, water/ oxygen (Dutta, 2018). The diversified profile of secondary metabolites released by *Trichoderma* encourage antagonism of other microbes by antibiosis (*i.e.*, competitive capacity) and promotes a faster rate of growth and development for itself and the host plant (*i.e.*, metabolic versatility) (Saravanakumar *et al.*, 2017).

### 4. Induction of plant defense responses

A plant possesses three layers of immunity *viz.*, i) Physical/ morphological barriers such as presence of cuticle, waxy layer, trichomes, stomata *etc.*, ii) Molecular pattern triggered immunity (MTI) by PAMP, MAMP, DAMP recognition receptors present in plant, iii) Effector triggered immunity (ETI) by recognition of effector protein by the resistance protein present in plant. Therefore, infection/ invasion by a foreign organism in to the plant system, triggers the immune response in plants. *Trichoderma* species are predominantly found as a root colonizer of plants. The plant root exudates attract *Trichoderma*, wherein, they interact with plant *via* molecular crosstalk to recognize, adhere and colonize the roots. The colonization process stimulates production of reactive oxygen species in plants that gives rise to immune responses such as MTI and ETI. *Trichoderma*, having metabolic superiority over other microbes, can withstand this toxic environment inside plant, which is otherwise detrimental to other pathogenic microbes (Dutta *et al.*, 2023). Therefore, induction of plant defense response by *Trichoderma* protects the plant from infection and invasion by phytopathogens.

### Secondary metabolites of *Trichoderma*

Secondary metabolites can be defined as low molecular weight, diffusible organic compounds released by an organism which do not have any direct role in their growth, development and/ or reproduction (Keswani *et al.*, 2017). *Trichoderma* produces an array of diverse secondary metabolites *viz.*, azaphilones, 6-pentyl- $\alpha$ -pyrone (6PP), gliotoxin, gliovirin, koniginins, anthraquinones, lactones, trichothecenes, viridin, viridiol, pachybasin, peptaibols, pyridine *etc.* The secondary metabolites of *Trichoderma* can be broadly categorized in to two classes *viz.*, volatile organic compounds and non-volatile organic compounds (Dutta *et al.*, 2022).

Volatile Organic Compounds (VOCs) can be defined as low molecular weight organic compounds such as alcohols, ketones, terpenes, esters, lactones or C<sub>8</sub> which are with a substantive vapor pressure under ambient

conditions (Siddiquee *et al.*, 2012). The VOCs produced by *Trichoderma* are either gas-phase and/ or carbon-based molecules of both low and high molecular weight. They play a significant role in antagonism of phytopathogens, competitions to acquire nutrients as well as promotes plant growth and development. Few of the VOCs released by *Trichoderma* also comes under the class of semio-chemicals owing to the attractant and deterrent property imparted to the different insect pests. Apart from their use in agriculture and plant protection, some of these compounds also has a scope in pharmaceutical industries, food and flavouring industries as well as in cosmetic industries (Keswani *et al.*, 2014). The type and nature of the VOCs produced primarily depends upon four key factors *viz.*, species/ strain and age of *Trichoderma* producing it, specific molecular structure of the compound, presence of other microbes, and the balance between its biosynthesis and biotransformation rates (Vinale *et al.*, 2012; Khan *et al.*, 2020). The VOCs secreted by biocontrol strain of *Trichoderma* include hundreds of compounds which belongs to different classes such as aldehydes, amines, aromatics, esters, ketones, thiols and terpenes. Few examples of VOCs include  $\alpha$ -farnesene,  $\alpha$ -muurolene, benzoic acid,  $\beta$ -bisabolene,  $\beta$ -chamigrene,  $\beta$ -cubeben,  $\beta$ -himachalene,  $\beta$ -sesquiphellandrene, cadinene, calamenene, 2,2-dimethoxy-1,2-diphenyl-ethanone, farnesol, limonene, 6PP, 1,2,3,4,5-pentamethyl-1,3-cyclopentadiene and propanoic acid.

### **Applications of VOCs of *Trichoderma* in plant health management**

The VOCs released by *Trichoderma* are primarily known for their antagonistic effect on the biotic causal agents of plant diseases. They are reported to have antifungal, antibacterial, nematicidal effects as well as exhibit plant growth promoting properties (Salwan *et al.*, 2019). An exposure to the VOCs could cause hyphal abnormalities in the phytopathogen such as deformation, swelling/ shrinkage, lysis as well as change in hyphal pigmentation. The VOCs are preferred over non- VOCs due to their ease of diffusion through pores to a longer distance, and their detrimental effect on phytopathogen without direct contact (Inayati *et al.*, 2019).

#### **i) Role of *Trichoderma* VOCs against phytopathogens**

There are several reports on VOCs released by *Trichoderma* species which are proven to have antimicrobial properties. According to their biochemical nature, VOCs released by *Trichoderma* species perform antibiosis by inhibiting translational pathways to obstruct the process of protein synthesis; encourage mycoparasitism by guiding the penetration to prey hyphae; impede cell wall synthesis, growth, reproduction and sporulation as well as interfere with the nutrient uptake and metabolite production by the prey fungi (Dutta *et al.* (2023). Work conducted by researchers such as Scarselletti and Faull (1994); Poole *et al.* (1998) provided experimental evidence to the antifungal property exhibited by 6PP against phytopathogens *viz.*, *Botrytis cinerea*, *Rhizoctonia solani* and *Fusarium oxysporum*. Volatilome produced by different species of *Trichoderma* are reported to inhibit the growth of major fungal phytopathogens such as by *Sclerotium rolfsii*, *Macrophomina phaseolina*,

*Rhizoctonia solani* and *Colletotrichum gloeosporioides*. Late blight of potato caused by *Phytophthora infestans* can be tackled by the VOCs such as 6PP, isoamyl alcohol and isobutyl alcohol released by *T. Atrioviride* (Razo-Belman and Ozuna, 2023). Similarly, VOCs produced by *T. harzianum*, *T. viride*, *T. virens* such as harzianic acid, harzianopyridone etc. are effective in inhibiting mycelial growth and sclerotial production of a vast number of soil-borne fungal phytopathogens viz. *Alternaria brassicicola*, *B. cinerea*, *C. capsici*, *F. oxysporum*, *Gaumenomyces graminis* var. *tritici*, *Helminthosporium oryzae*, *Leptosphaeria maculans*, *Phytophthora* spp., *Pythium irregulare*, *R. solani*, *S. rolfisii* and, *Sclerotinia sclerotiorum* (Karsli and Sahin, 2021; Dutta et al., 2023). In similar studies, it was demonstrated that *Trichoderma* species such as *T. album*, *T. aureoviride*, *T. hamatum*, *T. harzianum* and *T. viride* reduced the mycelial growth of *Alternaria alternata*, *Alternaria brassicae*, *Alternaria solani*, *Botrytis fabae*, *F. Oxysporum* and *Fusarium solani*. El-Hasan et al. (2009) reported about the antibacterial effect of volatile fraction of viridifungin against *Erwinia amylovora* and *Clavibacter michiganensis*. Volatilome of *T. harzianum*, *T. hamatum*, and *T. virens* was demonstrated to have notable biocontrol activity against *Xanthomonas oryzae* pv. *oryzae* causing bacterial leaf blight of rice (Gangwar and Sinha, 2010). Likewise, Khan et al. (2020) in their study found out that secondary metabolite of *T. pseudoharzianum* and *T. viride* exhibit inhibitory effect against *Ralstonia solanacearum* and *Xanthomonas campestris*.

### ii) Role of *Trichoderma* VOCs against plant parasitic nematodes

The menace caused by plant parasitic nematodes (PPN) are reported to cause 10% yield loss in agricultural sector across the world. The root knot nematode *Meloidogyne* is one of the most dangerous and destructive polyphagous plant parasitic nematode (PPN) which can parasitize over 2000 of agriculturally important plant species. Due to the residual toxicity of synthetic agrochemicals employed to tackle the problem of PPN, there has been regulative restrictions on the use of many such synthetic agrochemicals (Yang et al., 2012). To find an ecofriendly and sustainable alternative, *Trichoderma* spp. has been explored for their nematicidal activity. The information generated through these studies confirms the antagonistic activity of *Trichoderma* species and its volatile bioactive metabolites against *Meloidogyne* spp. causing root knot disease in guava, okra, Indian ginseng, mungbean and tomato (Sonkar et al., 2018). 6PP- a majorly produced VOC with coconut odour was reported to cause more than 85% nematicidal activity against *Caenorhabditis elegans*, *Bursaphelenchus xylophilus*, *Meloidogyne hapla* and *Panagrellus redivivus* (Yang et al., 2012; Deng et al., 2022). Du et al. (2020) reported about the nematicidal activity of Cyclonerane-type sesquiterpenes such as 10-cycloneren-3,5,7-triol, 10(E)-cycloneretriol against *Meloidogyne incognita*.

### iii) Role of *Trichoderma* VOCs as plant growth promoter

Apart from their role in inhibition of phytopathogens and PPN, few of the VOCs released by *Trichoderma* plays remarkable role in plant growth

promotion. 6PP, a VOC produced by *Trichoderma* was amongst the firsts to get characterized. This VOC was initially used in food industry owing to its coconut odour. However, addition of 6PP in greenhouse studies revealed to enhance lateral root development and promote plant growth (Lee *et al.*, 2016). *Trichoderma* species *viz.*, *T. asperellum*, *T. atroviride*, *T. citrinoviride*, *T. hamatum*, *T. harzianum*, *T. koningii* are well known for their ability to produce 6PP (Salwan *et al.*, 2019). VOCs of *Trichoderma* such as ethylene, sesquiterpene isoprenoids, and 6PP when produced in an orchestrated manner, stimulate plant growth (Contreras-Cornejo *et al.*, 2024). A study conducted by Pascale *et al.* (2017) revealed that VOCs from the class pyridone and pyrones promote growth and yield in grape. Pyridone such as harzianic acid and pyrones like 6PP are shown to enhance fruit quality of grape by increasing the total amount of polyphenols and antioxidant activity. Another compound *i.e.*, harzianolide produced by *T. harzianum* was shown to enhance the growth of tomato seedlings by 2.5 folds (Cai *et al.*, 2013).

### Conclusion and future prospects

*Trichoderma* species are well explored and researched for their biocontrol and plant growth promoting properties. Conventional bioformulation of *Trichoderma* species prepared with either spores or whole organism is widely used across the country. However, the study on an integral part behind *Trichoderma*'s antagonistic as well as PGP activities, *i.e.*, its secondary metabolites is still at nascent stage. Despite the fact that the research in this line is challenging but, it is one of the emerging frontier areas of research. In the age of global warming, where climate change is a serious issue to talk about, the agriculturists should be ready with an alternative to tackle any unwanted problems. Although, *Trichoderma*, is a very promising micro-organism from the perspective of plant health, but they might also fail to work under an adverse climatic condition. Therefore, knowledge on the bioactive metabolites of agriculturally important microbes such as *Trichoderma*, coupled with modern omics study might help in future to mine a potential VOC or non-VOC that could be used as an alternative bioformulation.

### References

- Cai, F., Yu, G., Wang, P., Wei, Z., Fu, L., Shen, Q. and Chen, W., 2013. Harzianolide, a novel plant growth regulator and systemic resistance elicitor from *Trichoderma harzianum*. *Plant Physiology and Biochemistry*, 73, 106-113.
- Contreras-Cornejo, H.A., Schmoll, M., Esquivel-Ayala, B.A., González-Esquivel, C.E., Rocha-Ramírez, V. and Larsen, J., 2024. Mechanisms for plant growth promotion activated by *Trichoderma* in natural and managed terrestrial ecosystem. *Microbiological Research*, 127621.
- Deng, X., Wang, X., Li, G., 2022. Nematicidal effects of volatile organic compounds from microorganisms and plants on plant-parasitic nematodes. *Microorganisms*, 10(6), p.1201.

- Druzhinina, I.S., Seidl-Seiboth, V., Herrera-Estrella, A., Horwitz, B.A., Kenerley, C.M., Monte, E., Mukherjee, P.K., Zeilinger, S., Grigoriev, I.V. and Kubicek, C.P., 2011. *Trichoderma*: the genomics of opportunistic success. *Nature reviews microbiology*, 9(10), 749-759.
- Du, F.Y., Ju, G.L., Xiao, L., Zhou, Y.M., and Wu, X. (2020). Sesquiterpenes and cyclodepsipeptides from marine-derived fungus *Trichoderma longibrachiatum* and their antagonistic activities against soil-borne pathogens. *Mar. Drugs*, 18(3), 165. doi: 10.3390/md18030165
- Dutta, P. and Das, B.C., 1999. Effect of seed pelleting and soil application of *Trichoderma harzianum* in the management of stem rot of soybean. *Journal of Mycology and Plant Pathology*, 29(3), 317-322.
- Dutta, P., 2018. Bioformulation of *Trichoderma harzianum* for the management of soil borne plant diseases. paper presented in ICCPP\_2018 at Boston, USA. *Phytopathol.* S1.274. doi: 10.1094/PHYTO-108-10-S1.240
- Dutta, P., Deb, L. and Pandey, A.K., 2022. *Trichoderma*- from lab bench to field application: Looking back over 50 years. *Front. Agron.* 4:932839. doi: 10.3389/fagro.2022.932839
- Dutta, P., Mahanta, M., Singh, S.B., Thakuria, D., Deb, L., Kumari, A., Upamanya, G.K., Boruah, S., Dey, U., Mishra, A.K. and Vanlaltani, L., 2023. Molecular interaction between plants and *Trichoderma* species against soil-borne plant pathogens. *Frontiers in Plant Science*, 14, 1145715.
- El-Hasan, A., Walker, F., Schöne, J., Buchenauer, H., 2009. Detection of viridifungin a and other antifungal metabolites excreted by *Trichoderma harzianum* active against different plant pathogens. *Eur. J. Plant Pathol.* 124, 457-470. doi: 10.1007/s10658-009-9433-3
- Gangwar G.P., Sinha, A.P., 2010. Comparative antagonistic potential of *Trichoderma* spp. against *Xanthomonas oryzae pv. oryzae*. *Annals of Plant Protection Sciences*, 18(2), 458-463.
- Inayati, A., Sulistyowati, L., Aini, L.Q., Yusnawan, E., 2019. Antifungal activity of volatile organic compounds from *Trichoderma virens*. In: *AIP Conference proceedings* (Vol. 2120, No. 1). AIP Publishing.
- Karsli, A., Sahin, Y.S., 2021. The role of fungal volatile organic compounds (FVOCs) in biological control. *Türkiye Biyolojik Mücadele Dergisi*, 12(1), 79-92.
- Keswani, C., Bisen, K., Chitara, M.K., Sarma, B.K. and Singh, H.B., 2017. Exploring the Role of Secondary Metabolites of *Trichoderma* in Tripartite Interaction with Plant and Pathogens. In: *Agro-Environmental Sustainability*. (Eds.) Singh, J.S. and Seneviratne, G. Springer International Publishing. pp. 63-78.
- Keswani, C., Mishra, S., Sarma, B.K., Singh, S.P., Singh, H.B., 2014. Unraveling the efficient applications of secondary metabolites of various *Trichoderma* spp. *Appl. Microbiol. Biotechnol.* 98, 533-544. doi: 10.1007/s00253-013-5344-5.
- Keswani, C.; Mishra, S.; Sarma, B. K.; Singh, S. P. and Singh, H. B. (2014).



- Unraveling the efficient applications of secondary metabolites of various *Trichoderma* spp. *Appl. Microbiol. Biotechnol.* 98: 533–544. doi: 10.1007/s00253-013-5344-5.
- Khan, R.A., Najeeb, S., Mao, Z., Ling, J., Yang, Y, Li, Y. and Xie, B., 2020. Bioactive Secondary Metabolites from *Trichoderma* spp. against Phytopathogenic Bacteria and Root-Knot Nematode. *Microorganisms*, 8, 401; doi:10.3390/microorganisms8030401
- Kubicek, C.P., Baker, S., Gamauf, C., Kenerley, C.M., and Druzhinina, I. S., 2008. Purifying selection and birth-and-death evolution in the class II hydrophobin gene families of the ascomycete *Trichoderma/Hypocrea*. *BMC Evol. Biol.*, 8 (1), 1–16. doi:10.1186/1471-2148-8-4
- Kubicek, C.P., Herrera-Estrella, A., Seidl-Seiboth, V., Martinez, D.A., Druzhinina, I.S., Thon, M., Zeilinger, S., Casas-Flores, S., Horwitz, B.A., Mukherjee, P.K. and Mukherjee, M., 2011. Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome biology*, 12, 1-15.
- Lee, S., Yap, M., Behringer, G., Hung, R., Bennett, J.W., 2016. Volatile organic compounds emitted by *Trichoderma* species mediate plant growth. *Fungal biology and biotechnology*, 3, 1-14.
- Mukherjee, M., Mukherjee, P.K., Horwitz, B.A., Zachow, C., Berg, G. and Zeilinger, S., 2012. *Trichoderma*–plant–pathogen interactions: advances in genetics of biological control. *Indian journal of microbiology*, 52, 522-529.
- Persoon, C.H., 1794. Neuer versucheinersystematische einteilung der schwämme. *Racodium Römer's Neues Magazin der Botanik*. 1, 123.
- Poole, P.R., Ward, B.G., Whitaker, G., 1998. The effects of topical treatments with 6-pentyl-2-pyrone and structural analogues on stem end postharvest rots in kiwi fruit due to botrytis cinerea. *J. Sci. Food Agric.* 77(1), 81–86. doi: 10.1002/(SICI) 1097-0010(199805)77:1<81::AID-JSFA6>3.0.CO;2-5
- Razo-Belman, R., Ozuna, C., 2023. Volatile organic compounds: A review of their current applications as pest biocontrol and disease management. *Horticulturae*, 9(4), 441.
- Salwan, R., Rialch, N., Sharma, V., 2019. Bioactive volatile metabolites of *Trichoderma*: An overview. In: *Secondary Metabolites of Plant Growth Promoting Rhizomicroorganisms: Discovery and Applications*. (Eds.) Singh, H.B. et al. Springer Nature, Singapore. pp. 87-111.
- Saravanakumar, K., Li, Y., Yu, C., Wang, Q., Wang, M., Sun, J., et al. 2017. Effect of *Trichoderma harzianum* on maize rhizosphere microbiome and biocontrol of *Fusarium* stalk rot. *Sci. Rep.* 7, 1771. doi: 10.1038/s41598-017-01680-w
- Scarselletti, R., Faull, J.L., 1994. In vitro activity of 6-pentyl-a-pyrone, a metabolite of *Trichoderma harzianum*, in the inhibition of *Rhizoctonia solani* and *Fusarium oxysporum* sp. *lycopersici*. *Mycol. Res.* 98(10), 1207–1209. doi: 10.1016/S0953-7562(09)80206-2
- Siddiquee, S., Cheong, B.E., Taslima, K., Hossain, K., and Hasan, M.M.,

2012. Separation and identification of volatile compounds from liquid cultures of *Trichoderma harzianum* by GC-MS using three different capillary columns. *J. Chromatogr. Sci.* 50, 358–367.
- Sonkar, S.S., Bhatt, J., Meher, J., Kashyap, P., 2018. Bio-efficacy of *Trichoderma viride* against the root-knot nematode (*Meloidogyne incognita*) in tomato plant. *J. Pharmacogn. Phytochem.* 7, 2010–2014.
- Sood, M., Kapoor, D., Kumar, V., Sheteiwiy, M.S., Ramakrishnan, M., Landi, M., Araniti, F. and Sharma, A., 2020. *Trichoderma*: The “secrets” of a multitasking biocontrol agent. *Plants*, 9(6), 762.
- Vinale, F., Girona, I. A., Nigro, M., Mazzei, P., Piccolo, A., Ruocco, M., et al., 2012. Cerinolactone, a hydroxy-lactone derivative from *Trichoderma cerinum*. *J. Nat. Prod.* 75, 103–106. doi: 10.1021/np200577t
- Weindling, R., 1932. *Trichoderma lignorum* as a parasite of other soil fungi. *Phytopathol.*, 22, 837–845.
- Weindling, R., 1934. Studies on a lethal principle effective in the parasitic action of *Trichoderma lignorum* on *Rhizoctonia solani* and other soil fungi. *Phytopathol.*, 24, 1153–1179.
- Yang Z., Yu, Z., Lei, L., Xia, Z., Shao, L., Zhang, K., Li, G., 2012. Nematicidal effect of volatiles produced by *Trichoderma* sp. *Journal of Asia-Pacific Entomology*, 15(4), 647-650.
- Zeilinger, S., Gruber, S., Bansal, R., Mukherjee, P.K., 2016. Secondary metabolism in *Trichoderma*—chemistry meets genomics. *Fungal Biol. Rev.*, 30, 74–90. doi: 10.1016/j.fbr.2016.05.001.