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Sustainable Approaches of *Trichoderma* under Changing Environments for Vegetable Production

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THE world's burgeoning population faces a great challenge concerning food security, which could be achieved through different sustainable agricultural practices. *Trichoderma*, as a ubiquitous fungus, is one of the most promising microorganisms that might offer several avenues for sustainable agriculture. *Trichoderma spp.* may guarantee a better solution for conventional problems in agriculture through several approaches including the protection of cultivated plants from undesirable abiotic and biotic conditions under changing environments and promoting their growth in poor or limited soil nutrients. The promising role of *Trichoderma* for vegetable production as a biocontrol and biofertilizers has been confirmed but its role as a plant pathogen still needs more studies. *Trichoderma* could inhibit or suppress the growth of soil phytopathogens, promoting plant growth and soil health, through activation of many mechanisms including synthesis of antibiotics, mycoparasitism and competition for nutrients and space against plant deleterious microorganisms. The sustainable approaches of *Trichoderma* including biofortification, bio-remediation and phyto-remediation as well as exploring future research opportunities will be also addressed in this work.

Keywords: Abiotic stress, Climate changes, Drought, Salinity, Heat stress.

Introduction

Plants, microorganisms and animals are the common living organisms in terrestrial eco systems, which engage in multiple interactions. These interactions could be classified on their effects on plant's development into neutral, beneficial and deleterious groups (Kare et al. 2020). These interactions also may include both detrimental and beneficial at multiple trophic levels (Kredics et al. 2018). Cultivated plants face a lot of

aggressors including pathogenic microorganisms and herbivorous arthropods, which activate plant corresponding signaling defense mechanisms (Macías-Rodríguez et al. 2020). Under certain circumstances, however, these plants are being a target for multiple aggressors, then some pathways could have profound effects on plant defense and resistance to attack (Macías-Rodríguez et al. 2020). The rhizospheric microorganisms may support the cultivated plants in enabling plants

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cope with different environmental stresses or in counteracting plant invaders (Solanki et al. 2021). Plant beneficial rhizospheric microorganisms have the ability to promote soil health and its quality, the growth of cultivated plants and its development, improve plant nutrient use efficiency, the decomposition of soil organic matter and increase the availability and cycling of nutrients (Meena et al. 2017; Alami et al. 2020). The common rhizospheric microorganisms include bacteria, fungi, actinomycetes, and algae, whereas the *Trichoderma* is considered one of the most important genera of fungi.

Trichoderma, as a genus of fungi belongs to the family of Hypocreaceae, is common in all different soils and presents the most prevalent culturable fungi. Several species in this *Trichoderma* genus (e.g., *T. asperellum*, *T. hamatum*, *T. harzianum*, *T. koningii*) could be characterized as excellent biocontrol agents (biofungicides) enhance plant resistance, biofertilizers promote plant growth and improve soil quality (Saravanakumar and Wang, 2020). Persoon succeeded to isolate *Trichoderma* in 1794 for the first time from decomposing organic matter and soil (Sood et al. 2020). *Trichoderma spp.* are considered rhizosphere inhabitants, universal saprotrophic fungi that dominant in the terrestrial ecosystems and they mediate interactions among plants, other soil microorganisms and arthropods at multiple trophic levels (Macías-Rodríguez et al. 2020). *Trichoderma spp.* also have multiple beneficial attributes, which support their applications as an appropriate tool for establishing the sustainability of agricultural practices (Sachdev and Singh, 2020). The maximum growth of *Trichoderma* species could be achieved when grown at 25-30°, whereas some species can grow well and sporulate at 35°. *Trichoderma* species usually have hyaline, septated and smooth-walled vegetative hyphae as well as highly branched conidiophores could be found (Gorai et al. 2020).

Agriculture sector is the main source that provides the human with the essential foods including the cultivated fruits, vegetables and spices as well as other food plants, which supplement the healthy human diet with essential micronutrients and other nutritional components. Vegetable crops comprise a wide range of genera and species, which consider an important component of the healthy human diet through supply the human with minerals, amino acids, antioxidants, vitamins, fiber and

other health-promoting compounds (Ebert, 2020). The global vegetables, also called the most dominant vegetables, are grown plants in several countries worldwide including cucurbits (squashes, cucumbers, pumpkins and gherkins), tomatoes, spinach, alliums (garlic, onion and shallot), chilies (sweet and hot pepper), brassicas (broccoli, cabbages and rape), eggplants, vegetable legumes, lettuce, turnips, carrots and asparagus (Ebert, 2020). The production of vegetables under supplying with *Trichoderma* may support the production of these vegetables and their resistance to different vegetable pathogens (Rivera-Méndez, 2020).

Therefore, this review is an attempt to provide insight on the functioning of *Trichoderma* under different environmental conditions to increase understanding for their effective use in maintaining the sustainability of different agricultural systems.

***Trichoderma*: General Features**

Trichoderma is considered the largest taxon among the fungicolous fungal genera with many ubiquitously distributed species (Kubicek et al. 2019). *Trichoderma* is a ubiquitous genus, belongs to the Ascomycota division, filamentous saprophytic fungus and is opportunistic plant symbionts, which commonly colonize soils rich in organic matter (Macías-Rodríguez et al. 2020). These fungi typically inhabit several soils including clay and sand and in tropical soils (Bononi et al. 2020). This fungus also could proliferate freely in soils and/or shows symbiotic relation with the roots of cultivated plants and foliar parts (Sachdev and Singh, 2020). The density population of *Trichoderma* have been estimated in the rhizosphere in a range between 10 – 1000 CFU g⁻¹ (Cordier et al. 2007). Some *Trichoderma* strains could colonize the plant roots that cultured in both acidic and alkaline soils and can also subsist in soils containing high levels of cobalt and nickel (Zhang et al. 2018).

More than 254 species of *Trichoderma* have been formerly identified and also more than 71 species of *Trichoderma* between 2015 and 2018 were newly identified (Qiao et al. 2018) as well as a lot of species undoubtedly are awaiting discovery in the future. It is reported that *Trichoderma* has a wide geographical distribution under different climatic zones ranging from tropical climate to polar and could sustain its life under different climatic conditions (Sachdev and Singh, 2020). More than 479 volatile organic compounds

have been identified, which are produced by *Trichoderma* (e.g., alkanes, alcohols, furans, ketones and pyrones). These compounds are strain-specific, which their production depends on the components of the growth media on which they are grown (González-Pérez et al. 2018; Macías-Rodríguez et al. 2020). The most versatile species of the genus *Trichoderma* may include the following :

T. afroharzianum, *T. arundinaceum*, *T. asperellum*, *T. atroviride*, *T. citrinoviride*, *T. cremeum*, *T. crissum*, *T. guizouense*, *T. gamsii*, *T. harzianum*, *T. hamatum*, *T. koningiopsis*, *T. koningii*, *T. longipile*, *T. longibrachiatum*, *T. parareesei*, *T. pseudokoningii*, *T. polysporum*, *T. ovalisporum*, *T. reesei*, *T. saturnisporum*, *T. spirale*, *T. virens* and *T. viride* (Kubicek et al. 2019; Gautam and Naraiian, 2020).

Trichoderma spp. are versatile fungi having multiple beneficial attributes, which make them a promising tool for establishing agricultural sustainability. These attributions may include the potential of *Trichoderma spp.* as biocontrol agents or biological control (Sachdev and Singh 2018), plant growth promoter (Sachdev et al. 2018) and as plant-growth-promoting fungior biofertilizers (Sachdev and Singh, 2020). *Trichoderma spp.* also have a distinguished role in physiological stress mitigation and the bioremediation of polluted soils (Tripathi et al. 2017; Sachdev and Singh, 2020). Several species of *Trichoderma* could reduce the abundance of many microbial phytopathogens in rhizosphere through potent inhibitory molecules (e.g., siderophores and gliovirin). *Trichoderma* also could enhance plant growth and then crop productivity through alleviating of the abiotic stress (Macías-Rodríguez et al. 2020). Such beneficial

effects of *Trichoderma* may be mediated by the activation of endogenous mechanisms controlled by phytohormones (e.g., abscisic acid and auxins) and via the alterations in metabolism of the host plants (Fig. 1). Under stress, *Trichoderma* could mediate early defense responses and stimulate plant immunity by enhancing plant resistance, which regulated by the phytohormones (e.g., ethylene, salicylic and jasmonic acid). Several volatile organic compounds and oxygen or nitrogen heterocyclic compounds also could be released by *Trichoderma*, which serve as signaling molecules, that effect on plant growth, herbivorous insects and phytopathogen levels (Macías-Rodríguez et al. 2020).

***Trichoderma* as Biocontrol**

Biocontrol or biological control means the reducing or controlling of diseases or pests using one or more useful micro-organisms, which have no impacts on the environment and other helpful micro-organisms such as some fungi and bacteria (Gorai et al. 2020). *Trichoderma* as important fungi have many potential biocontrol techniques in different agricultural fields, i.e., they antagonize a wide range of phyto-pathogenic fungi (Fig. 2 - 5). Recently, *Trichoderma* was involved in several commercial products to improve soils, as soil improvements, biopesticides and enhancers for plant growth (Gorai et al. 2020). It is reported that disease incidence by different phytopathogens could be listed as follows: virus (47%), fungus (30%), bacterium (16%), phytoplasma (4%), and nematode (1%) (Tripathi et al. 2020). The background and historical side of biological control in genomic era were listed by Tripathi et al. (2020) as follows :

1986	Demonstration of plant growth promotion by <i>Trichoderma</i>
1987	Successful transformation of <i>T. reesei</i>
1992	Lectin-coated model for <i>Trichoderma</i> /biomimetics
1999	Demonstration of internal colonization of plant roots by <i>Trichoderma</i>
2003	MAPK negatively regulate conidiation in <i>T. virens</i>
2005	Role of <i>Trichoderma</i> MAPK in ISR
2008	First <i>Trichoderma</i> genomes sequenced and published (<i>T. reesei</i>)
2009	Endophytism, <i>Trichoderma</i> imparts biotic and abiotic stress tolerance
2009	First time successful crossing in <i>T. reesei</i> under laboratory condition
2010	Pheromone precursor genes described in <i>Trichoderma</i> comparative genome analysis using NGS of different <i>Trichoderma</i> species
2012	Knock out program in <i>Trichoderma</i>

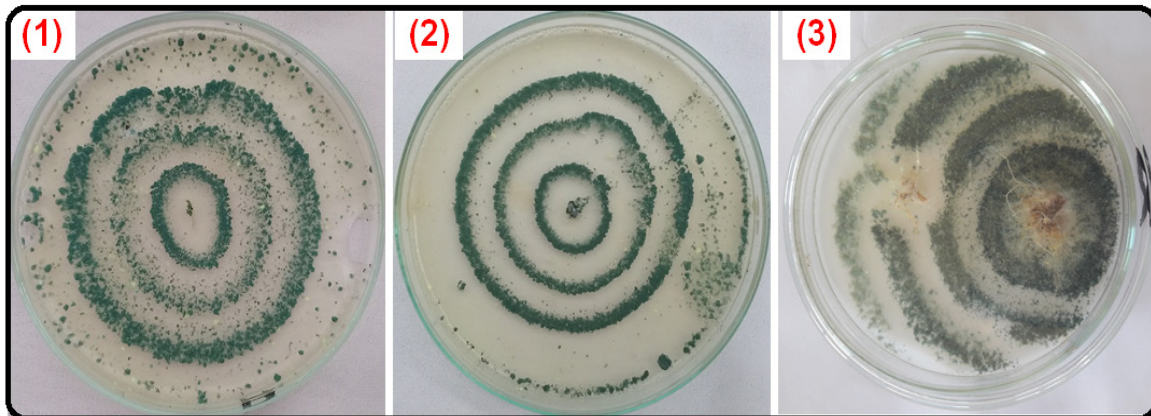


Fig. 1. *Trichoderma* in nature, photos 1 and 2 represent isolated *T. harzianum* from the soil of Kafr El-Sheikh, Egypt and the photo 3 for *T. harzianum*, which was isolated from the roots of tomato infested by *Fusarium* wilt



Fig. 2. The antagonism of *Trichoderma* spp. against *F. oxysporum* f. sp. *cucumerinum*, the casual pathogen of fusarium wilt of cucumber

The mechanisms of biological control are considered significant measures for disease management because chemical fungicides compared to *Trichoderma* adversely impact on other non-target organisms (El Enshasy et al. 2020). *Trichoderma* could cause growth inhibition of different species of phyto-pathogens by establishing a parasitic relationship and/or

impairing their metabolisms. The application of biocontrol agents could stimulate disease suppression under a high doses of chemical fungicide treatments, where about 90% of strains of *Trichoderma* represent fungal biocontrol agents against pathogenic microorganisms (Sood et al. 2020).

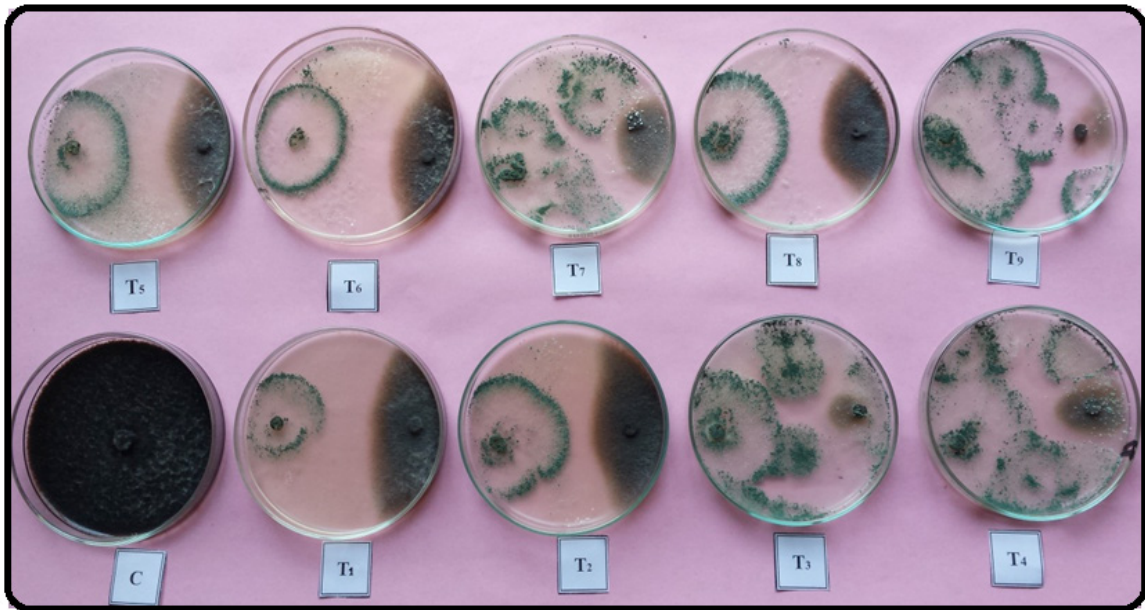


Fig. 3. Two case studies for *Trichoderma* as biocontrol against charcoal rot in *Macrophomina phaseoli*

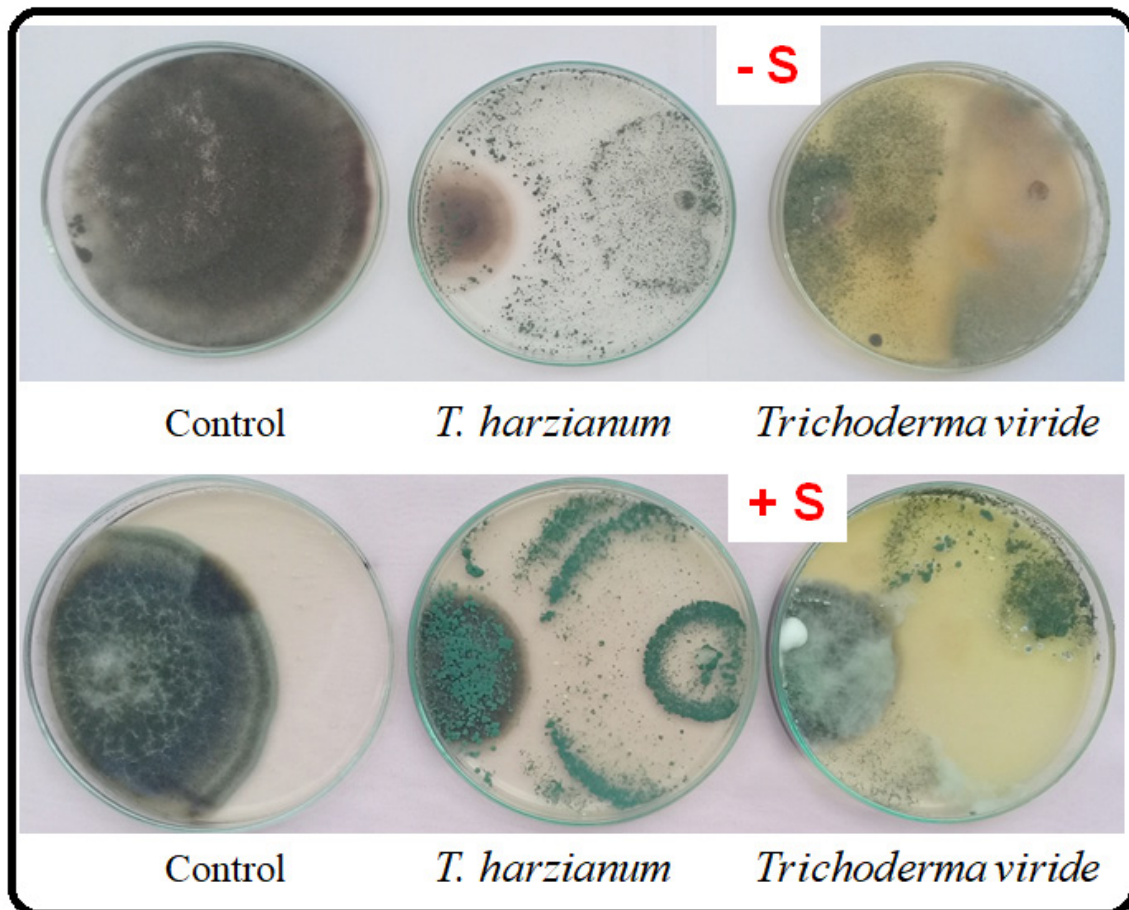


Fig. 4. The highest antagonistic effect of both *T. harzianum* and *T. viride* against *Alternaria porri* in onion in presence or absent (S at 2 g l⁻¹) (Bayoumi et al. 2019)

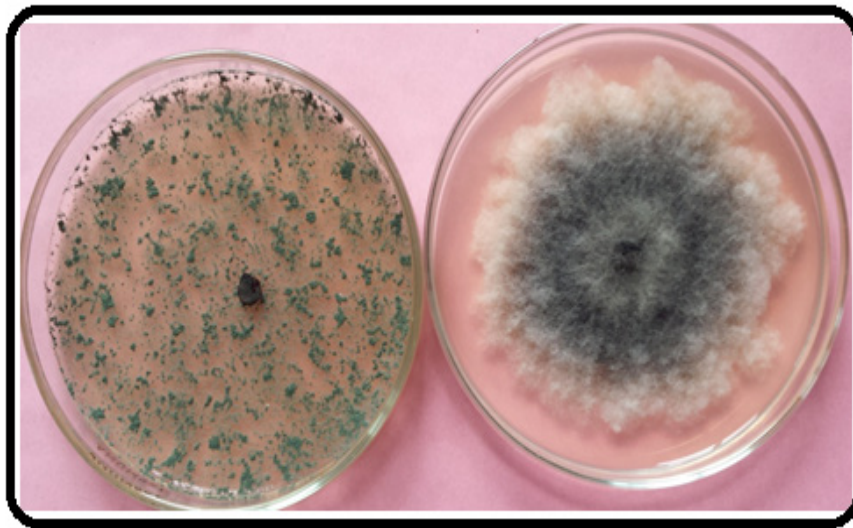


Fig. 5. The antagonism of *Trichoderma asperellium* against charcoal rotin *M. phaseoli*, where the *Trichoderma* inhibited the activity of the phytopathogen of *M. phaseoli* by 100% .

The mechanisms of biological control are considered significant measures for disease management because chemical fungicides compared to *Trichoderma* adversely impact on other non-target organisms (El Enshasy et al. 2020). *T. richoderma* could cause growth inhibition of different species of phyto-pathogens by establishing a parasitic relationship and/or impairing their metabolisms. The application of biocontrol agents could stimulate disease suppression under a high doses of chemical fungicide treatments, where about 90% of strains of *Trichoderma* represent fungal biocontrol agents against pathogenic microorganisms (Sood et al. 2020).

It is confirmed by several researchers that *Trichoderma spp.* are considered promising biocontrol agents against a lot of phyto-pathogensthat attack vegetable crops like tomato (Table 1; e.g., Salas-Marina et al. 2011; Brotman et al. 2012; Suárez-Estrella et al. 2014; de Medeiros et al. 2017; Jogaiah et al. 2018; Herrera-Télez et al. 2019; Chien and Huang 2020; Kashyap et al. 2020; Morán-Diez et al. 2020). *Trichoderma spp.* can also enhance both direct and indirect defense barriers against aphids (*T. harzianum*) and insects (*T.atroviride*) as reported by Coppola et al. (2019 a, b). Concerning the mode of action of *Trichoderma spp.*in destroying pathogenic fungi, *Trichoderma* could release thelytic enzymes in the rhizosphere. These enzymes might catalyze the cell wall damage to target fungi, then, a signaling cascade is activated in *Trichoderma*

cells. This signaling may involve the activation of mitogen-activatedprotein kinase through protein-coupled receptors, then programmed cell death may establish due to changes in gene expression ultimately in pathogenic fungi (Sood et al. 2020). List of plant pathogens that can becontrolled by *Trichoderma spp.* in some vegetable crops including tomato, onion, cucumber and potato is listed in Table 2.

It is worth mention that “Could *Trichoderma* Be a Plant Pathogen? Successful Root Colonization” and this question was asked by Poveda et al. (2020). They mentioned that the root colonization by *Trichoderma* may have two pathways; the first one supposed that the plant defends itself against being colonized by *Trichoderma* with preventing *Trichoderma* from penetration the plant vascular bundle and causing the expected indirect benefits, which include increase plant tolerance against abiotic stresses and resistance against pathogens and/orpests, promote plant growth through improving nutrient acquisition through the roots. The second pathway represents the absence of salicylic acid mediated response, which *Trichoderma* massively colonizes plant roots, penetrating the vascular bundles, producing plant death and may be becoming an opportunistic pathogen (Poveda et al. 2020). The management of infected plants by *Trichoderma* has been investigated by many researchers such as Al-Ani and Mohammed (2020), and Kumari et al. (2020).

TABLE 1. Different *Trichoderma* strains already used against different pathogens for tomato crop

<i>Trichoderma</i> strain	Pathogen	Activity or mechanisms	Reference
<i>Trichoderma asperellum</i>	<i>Xanthomonas perforans</i>	Manage bacterial spot using <i>Bacillus amyloliquefaciens</i>	Chien and Huang (2020)
<i>Trichoderma asperellum</i> and <i>Trichoderma virens</i>	Root-knot nematode (<i>Meloidogyne javanica</i>)	<i>Trichoderma</i> spp. enhance plant growth in enriched with of water-extractable fraction of vermicompost	dos Santos Pereira (2020) et al.
<i>T. longibrachiatum</i> UNS11	Bacterial wilt (<i>Ralstonia solanacearum</i>)	Combined application of <i>Rhizobacteria</i> and <i>Trichoderma</i> strains elicit resistance against bacterial wilt	Konappa et al. (2020)
<i>Trichoderma asperellum</i>	<i>Rhizoctonia solani</i> AG-4	Manage tomato root rot pathogen by increasing total phenol, polyphenol oxidase, peroxidase, proline; reducing sugar, total soluble sugars	Kashyap et al. (2020)
<i>Trichoderma parareesei</i> , <i>T. asperellum</i> , <i>T. harzianum</i>	<i>Pseudomonas syringae</i> pv. Tomato, DC3000,	Phytohormones (e.g., SA, JA, ET and ABA) may support <i>Trichoderma</i> -induced defenses priming against pathogen	Morán-Díez et al. (2020)
<i>Trichoderma asperelloides</i>	<i>Fusarium oxysporum</i> and <i>Alternaria alternata</i>	Reducing the plant disease severity more than 53.8 and 66.7% for each pathogen, res.	Ramírez-Cariño et al. (2020)
<i>Trichoderma harzianum</i>	Root-knot nematode (<i>Meloidogyne javanica</i>)	The combined application of <i>T. harzianum</i> , <i>Glomus mosseae</i> , and <i>Bacillus subtilis</i> promoted the growth of tomato	Sohrabi et al. (2020)
<i>Trichoderma asperellum</i>	<i>Alternaria alternata</i>	Enhancing the resistance of seedlings against pathogen by promoting signal of hormone transduction genes	Yu et al. (2020)
<i>Trichoderma asperellum</i>	<i>Fusarium oxysporum</i> and <i>Botrytis cinerea</i>	By inhibition of ROS production induced by pathogen	Herrera-Téllez et al. (2019)
<i>Trichoderma virens</i>	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Mediating the resistance against <i>Fusarium</i> wilt by involving the salicylic and jasmonic acid pathways	Jogaiah et al. (2018)
<i>Trichoderma atroviride</i>	Root-knot nematode (<i>Meloidogyne javanica</i>)	<i>Trichoderma</i> promote the production of auxin to inhibit ROS as a major defense strategy during plant growth	de Medeiros et al. (2017)
<i>Trichoderma harzianum</i>	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Enhancing the induction of antioxidant defense system against <i>Fusarium</i> in tomato	Zehra et al. (2017)

Abbreviations: Reactive oxygen species (ROS), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), Abscisic acid (ABA),

TABLE 2. List of plant pathogens controlled by *Trichoderma* spp. in some vegetable crops

References	Plant pathogens	<i>Trichoderma</i> strain
I. Tomato (<i>Solanum lycopersicum</i> L.)		
Bader et al. (2020)	Wilt disease (<i>Fusarium oxysporum</i>)	<i>Trichoderma harzianum</i>
Cucu et al. (2020)	Fusarium wilt, caused by <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	<i>Trichoderma</i> sp.TW2
Singh et al. (2020)	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	<i>Trichoderma asperellum</i>
Yu et al. (2020)	Leafspot disease (<i>Alternaria alternata</i>)	<i>Trichoderma asperellum</i>
Sallam et al. (2019)	Wilt disease (<i>F. oxysporum</i> f.sp. <i>lycopersici</i>)	<i>Trichoderma atroviride</i> and <i>T. longibrachiatum</i>
Elshahawy and El-Mohamedy (2019)	Rootrot (<i>Pythium aphanidermatum</i>)	<i>Trichoderma harzianum</i> , <i>T. asperellum</i> , and <i>T. virens</i>
Konappa et al. (2018)	Bacterial wilt caused by <i>Ralstonia solanacearum</i>	<i>T. asperellum</i>
Li et al. (2018)	Fusarium wilt, caused by <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	<i>Trichoderma asperellum</i>
II. Onion (<i>Allium cepa</i> L.)		
Rivera-Méndez et al. (2020)	White rot (<i>Sclerotium cepivorum</i>)	<i>Trichoderma asperellum</i>
Zapata-Sarmiento et al. (2020)	Leaf blight disease caused by <i>Stemphylium vesicarium</i>	<i>Trichoderma asperellum</i>
da Silva et al. (2020)	White mold or sclerotinia rot or wilt <i>Sclerotinia sclerotiorum</i> (Lib.)	<i>T. lentiforme</i>
Bunbury-Blanchette and Walker (2019)	Fusarium basal rot (<i>F. oxysporum</i> f. sp. <i>cepae</i>)	<i>Trichoderma hamatum</i> and <i>T. harzianum</i>
Bayoumi et al. (2019)	Purple blotch disease (<i>Alternaria porri</i>)	<i>T. harzianum</i> and <i>T. viride</i>
Abdelrahman et al. (2016)	<i>Fusarium oxysporum</i> f. sp. <i>cepa</i>	<i>T. longibrachiatum</i>
III. Cucumber (<i>Cucumis sativus</i> L.)		
Zhang and Zhuang (2020)	Pathogenic fungus <i>Rhizoctonia solani</i>	<i>Trichoderma brevicrassum</i>
Yuan et al. (2019)	Graymold disease (<i>Botrytis cinerea</i>)	<i>T. longibrachiatum</i>
Cong et al. (2019)	Fusarium wilt (<i>F.oxysporum</i> f.sp. <i>cucumerinum</i>)	<i>T. pseudokoningii</i>
Li et al. (2019)	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i> Owen	<i>T. asperellum</i> , <i>T. harzianum</i> , and <i>T. pseudokoningii</i>
Nawrocka et al. (2019)	Pathogenicfungus <i>Rhizoctonia solani</i>	<i>Trichoderma atroviride</i> TRS25
Nawrocka et al. (2018)	<i>Rhizoctonia solani</i>	<i>Trichoderma atroviride</i>
IV. Potato (<i>Solanum tuberosum</i> L.)		
Mohamed et al. (2020)	<i>Ralstonia solanacearum</i>	<i>Trichoderma asperellum</i>
Elazouni et al. (2019)	<i>Ralstonia solanacearum</i>	<i>T. harzianum</i> and <i>T. viride</i>
Wang et al. (2019)	Potato scab (<i>Streptomyces</i> spp.)	<i>Trichoderma harzianum</i>

***Trichoderma* as Biofertilizer**

Cultivated plants depend mainly on the nutrient available forms from organic and inorganic sources to satisfy their needs. The mineral sources of nutrients may lead to several environmental problems e.g., groundwater pollution and its negative implications on human health (Kumari and Singh, 2019). Thus, these mineral fertilizers alone do not guarantee sustainable and safe production of food. The organic farming is considered a proper way in replacing several agrochemicals by potential microbes and their products towards a sustainable and high crop production. Moreover, the combined application of both organic fertilizers and biofertilizers like *Trichoderma* are needed to achieve these aims. The efficiency of this approach was comparable with the traditional mineral fertilization one (Zhang et al. 2018). Biofertilizers have the magical ability to support plant growth and its development (Yin et al. 2020). On the other hand, biosafety criteria, based on the European Regulation 2019/1009, are needed for microorganism selection as biofertilizers or bio-stimulants (Barros-Rodríguez et al. 2020). Biofertilizer as a technique has been improved and many new techniques in its processing had been developed as well to enhance its effects on plant system. This bio-approach can be used safely as biocontrol against plant pathogens and also as plant growth promoters (Sahu et al. 2018). The term biofertilizer is defined as a product containing beneficial micro-organisms, which has the potential to improve the fertility of soils and crop productivity as well as an eco-friendly environmental tool (El-Ghamry et al. 2018; Atieno et al. 2020).

Several exudates (e.g., IAA and GA3) could be secreted from the active roots in the rhizosphere attracting many microorganisms, then associate and enhance nutrients availability in the active feeding area of plant roots (Rebolledo-Prudencioa et al. 2020). These all beneficial microbes could be divided into two classes plant health promoters and plant growth promoters (Sahu et al. 2018). *Trichoderma* spp. are well-known as plant growth-promoting fungi, which could enhance the plant uptake of nutrients, producing plant growth hormones and protecting

cultivated plants from pathogen infection (Zhang et al. 2018). Several studies emphasized the role of *Trichoderma* as a biofertilizer in vegetable crop production such as tomato (Khan et al. 2017; De Palma et al. 2019; Sani et al. 2020), cucumber (Zhang et al. 2019) and cabbage (Liu et al. 2016; Ji et al. 2020).

It could be classified biofertilizers into different types based on the group of microorganisms in biofertilizers and these types may include: (1) nitrogen fixing biofertilizers, (2) phosphorus biofertilizers, (3) plant growth promoting biofertilizers, (4) potassium biofertilizers, (5) zinc solubilizing biofertilizers, (6) sulfur oxidizing biofertilizers, and (7) silicate solubilizing biofertilizers (Maçik et al. 2020). On the other hand, several species of *Trichoderma* have been used successfully as biofertilizers for many cultivated crops such as :

1. Rice (*Oryza sativa* L.): *T. asperellum* SL2 (Doni et al. 2018), *T. erinaceum* (Swain et al. 2018), *T. reesei* (Singh et al. 2019),
2. Brassica rapa: *T. harzianum* (Caporale et al. 2019),
3. Brassica chinensis: *T. brevicompactum* (Yin et al. 2020),
4. Chinese cabbage: a mixture of *T. harzianum*, *T. asperellum*, *T. hamatum*, and *T. atrovirideon* (Ji et al. 2020),
5. Alfalfa (*Medicago sativa* L.): *Trichoderma harzianum* (Zhang et al. 2020),
6. Sorghum (*Sorghum bicolor* L.): *Trichoderma viride* (Wang et al. 2018),
7. Bean (*Phaseolus vulgaris* L.): *Trichoderma harzianum* strains (Eslahi et al. 2020a),
8. Lettuce (*Lactuca sativa* L.): *Trichoderma asperellum* (Wonglom et al. 2020),
9. Black pepper (*Piper nigrum* L.): *Trichoderma harzianum* (Umadevi et al. 2018), and
10. Maize (*Zea mays* L.): *Trichoderma harzianum* T-soybean (Zhang et al. 2020).

***Trichoderma* under stress**

The genus of *Trichoderma* as a fungal species is considered the most promising microorganisms that improve the growth of cultivated plants by enhancing the uptake of nutrients and supporting them against environmental abiotic and biotic stresses (Khoshmanzar et al. 2020). *Trichoderma*

can colonize the roots of cultivated plants and then produce some secondary metabolites stimulating the growth of plants, improving water use efficiency, and alleviating ROS damage under abiotic and biotic stress conditions by secretion of some phytohormones (Khoshmanzar et al. 2020). Several studies have been confirmed that the treated plants with *Trichoderma* have the ability to increase the tolerance of cultivated plants to abiotic and biotic stresses (Table 3).

In this context, *Trichoderma* could activate the plant systemic resistance against phytopathogens through the induction of the signaling pathways of jasmonic acid and ethylene as well as salicylic acid. Moreover, *Trichoderma* has the ability to prime plants against subsequent attacks by pathogens. Concerning biotic stress, several plant species showed the increased resistance to pathogen attack when pretreated with *Trichoderma* like cotton, common bean, tomato, cucumber, pepper, lettuce, maize, and rice (Rebolledo-Prudencioa et al. 2020). Different *Trichoderma* strains can also induce protective effects against different pathogens as presented in Table 3. For instance, the colonization of maize roots can effectively reduce the damage caused by many phytopathogens when treated with some *Trichoderma* spp. (Fig. 6). like *T. asperellum* GDFS1009 for *Fusarium graminearum* (Karuppiyah et al. 2019), and *T. harzianum* INAT11 for *Fusarium verticillioides* and *Fusarium graminearum* (Ferrigo et al. 2020). The ameliorative role of *Trichoderma* under abiotic stress has been also confirmed by many investigations like treating wheat with *Trichoderma longibrachiatum* under salinity (10 and 20 g l⁻¹ NaCl) as published by Zhang et al. (2019). It is reported also that, chlorophyll and water contents in both leaves and roots increased significantly in wheat plants inoculated with *T. longibrachiatum* under salinity stress conditions. Its defence mechanism may take place through stimulating antioxidant activities of the plant defense enzymes *i.e.*, catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD), enzymes compared to wheat-untreated plants (Rebolledo-Prudencioa et al. 2020). Under drought stress, it is common the reduction in

plant content of chlorophyll and carotenoids as well as the severe damage in maize membrane; however, this damage can be avoided when maize inoculated with *T. atroviride* ID20G. Also, inoculating rice with *Trichoderma* spp. Was found effective in improving the growth parameters of plants grown under drought conditions and sheath blight (*Rhizoctonia solani*) disease (Mishra et al. 2020).

***Trichoderma* for Sustainable Agriculture**

Sustainability in agriculture may include building and maintaining the soil health, managing water and its quality, minimizing the pollution in soil, water, and air environments, and promoting soil biodiversity (Thakur 2020). No doubt that sustainable agricultural practices are needed to be the key for food security of the world's burgeoning population and *Trichoderma* might offer a lot of solutions for sustainable agriculture (Sachdev and Singh, 2020). *Trichoderma* could also alleviate the abiotic and/or biotic stress as plant symbionts through the colonization of plant roots and establishing a communication with the host plant *via* chemical signals. These signals may induce the plant resistance against stresses by secreting phytohormones (*e.g.*, salicylic acid and jasmonate) and other secondary metabolites (Malinich et al. 2019). Then, *Trichoderma* may support the bio-protection against the phytopathogens by release antibiotic compounds, competing for nutrition and space, improve the plant uptake of water and nutrients, and acidify ambient environment. This acidification could be achieved through secretions of many organic acids, which increase the solubility of micronutrients and minerals for biofertilization (Sachdev and Singh 2020). It is reported that *Trichoderma* is considered the most widespread genus of fungi marketed as bio-pesticides, which may contribute more than 60% of registered global bio-fungicides (Abbas et al. 2017). More than 250 bio-fungicides are already registered globally as *Trichoderma*-formulated products and are considered acceptable worldwide (Kashyap et al. 2017). The sustainable management of plant disease can be achieved using *Trichoderma* as reported by Al-Ani (2018).

TABLE 3. List of plant stress controlled by *Trichoderma* spp. in some cultivated crops

References	Abiotic and/or biotic stress	Host plant	Trichoderma strain
			Vegetable crops
Khoshmanzar et al. (2020)	Water-deficit (available water depletion 70-90%)	Tomato	<i>T. longibrachiatum</i> , <i>T. harzianum</i>
Kashyap et al. (2020)	Tomatoroot rot (<i>Rhizoctonia solani</i>) and 250 mM NaCl	Tomato	<i>Trichoderma asperellum</i> F01763
Sani et al. (2020)	Reduced NPK doses (by 50%)	Tomato	<i>T. harzianum</i> T22
Ghorbanpour et al. (2018)	Low temperature (8 °C) for 6 days	Tomato	<i>Trichoderma harzianum</i> (AK20G)
Eslahi et al. (2020b)	Pathogen (<i>Rhizoctonia solani</i>)	Common bean	<i>T. harzianum</i> (T13, T15 and wild-type; Tw)
Vieira et al. (2018)	Pathogen (<i>Fusarium oxysporum</i>)	Common bean	<i>Trichoderma harzianum</i>
Juniors et al. (2020)	Cu stress as fungicide and CuSO ₄ at 100 mg L ⁻¹ Cu	Onion	<i>Trichoderma asperellum</i>
Zhang and Zhuang (2020)	The fungus plant-pathogenic <i>Rhizoctonia solani</i>	Cucumber	<i>T. brevicrassum</i> TC967
Zhang et al. (2019)	<i>Fusarium oxysporum</i> and irrigated with 200 mM NaCl	Cucumber	<i>Trichoderma harzianum</i> KC753767
Yuan et al. (2019)	Graymold in cucumber caused by <i>Botrytis cinerea</i>	Cucumber	<i>T. longibrachiatum</i> H9
			Field crops
Mishra et al. (2020)	Drought and sheath blight (<i>Rhizoctonia solani</i>)	Rice	<i>Trichoderma</i> spp.
Mishra et al. (2019)	Elevated CO ₂ (550 ppm)	Rice	<i>T. reesei</i> , MTCC5659
Karuppiah et al. (2020)	Wheat rot disease caused by <i>Fusarium graminearum</i>	Wheat	<i>Trichoderma atroviride</i> T23
Zhang et al. (2019)	Salinity (10 and 20 g L ⁻¹ NaCl)	Wheat	<i>Trichoderma longibrachiatum</i>
Jaroszuk-Łcis et al. (2019)	Phytopathogen of <i>Fusarium</i> spp. (<i>F. culmorum</i> , <i>F. oxysporum</i> , <i>F. graminearum</i>)	Wheat	<i>Trichoderma</i> DEMTKZ3A0
Pehlivan et al. (2021)	Potentially toxic elements (e.g., As, Cd, Cu, Pb, and Zn) in soil (200, 500 and 1000 mg L ⁻¹)	Maize	<i>Trichoderma harzianum</i> TS 143
Estévez-Gefriaud et al. (2020)	Drought (under two different water regimes)	Maize	<i>Trichoderma asperellum</i> T34
Ferrigo et al. (2020)	<i>Fusarium verticillioides</i> and <i>Fusarium graminearum</i>	Maize	<i>Trichoderma harzianum</i> (INAT11)
Karuppiah et al. (2019)	<i>Fusarium graminearum</i>	Maize	<i>T. asperellum</i> GDFS1009
Fu et al. (2018)	Saline-alkaline soil (pH 9.30)	Maize	<i>Trichoderma asperellum</i>
Pehlivan et al. (2017)	Salinity (50 and 100 mM NaCl)	Maize	<i>Trichoderma lixii</i> ID11D
Prasad et al. (2020)	<i>Macrophomina phaseolina</i> , <i>Fusarium oxysporum</i> f. sp. <i>ricini</i> and <i>Aspergillus niger</i> Nematode	Groundnut and safflower	<i>Trichoderma harzianum</i> (Th4d)
de Oliveira et al. (2021)	disease (<i>Pratylenchus brachyurus</i>)	Soybean	<i>T. asperellum</i> T00 and <i>T. harzianum</i> ALL 42
Mishra and Nautiyal (2018)	Collar rot disease caused by <i>Sclerotium rolfsii</i>	Chickpea	<i>T. viride</i> (MTCC 5661)
Tripathi et al. (2017)	Arsenic stress (100 mg l ⁻¹ arsenate as Na ₂ HAsO ₄ ·7H ₂ O)	Chickpea	<i>Trichoderma</i> sp.
			Viticulture crops
Carro-Huerta et al. (2020)	<i>Phaeoacremonium minimum</i> CBS 100398 pathogen	Common grape vine	<i>Trichoderma</i> sp. strain T154
Marraschi et al. (2019)	<i>Lasiodiplodia theobromae</i> pathogen	Common grape vine	<i>Trichoderma</i> spp.
			Forage crops
Zhang et al. (2020)	Alkaline-saline soils (pH, 8.7; EC = 5.4 dS m ⁻¹)	Alfalfa	<i>T. harzianum</i> NAU14
Anam et al. (2019)	Sodic-saline-alkali red mud flooded soil (pH 12, NaCl 4%)	Sorghum-sudangrass	<i>Trichoderma asperellum</i> RM-28

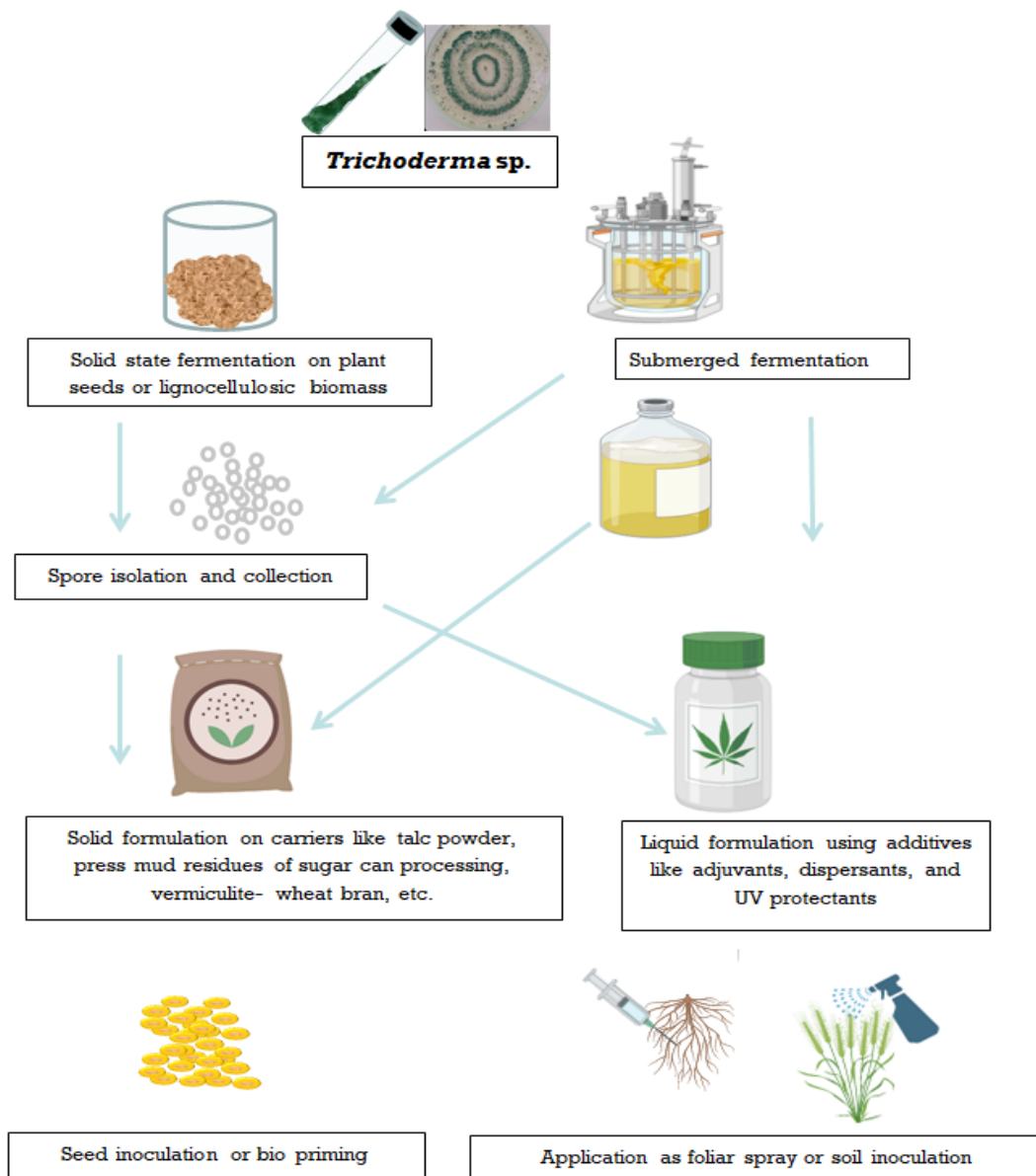


Fig. 6. Schematic diagram for main commercial production methods of *Trichoderma* sp.

Biofortification of several crops as a sustainable approach could be performed by the application of many beneficial microorganisms (i.e., *Trichoderma* spp., mycorrhiza fungi and plant growth-promoting rhizobacteria) through enhancing the uptake of nutrients. Therefore, using *Trichoderma* spp. in crop production could be considered a sustainable and environmentally friendly approach to secure yield stability under low-input conditions (Fiorentino et al. 2018). The biofortification using *Trichoderma* spp. may increase the plant growth and its development as well the natural antioxidants like total polyphenol

and flavonoid and mineral content in cultivated plants (Gorai et al. 2020).

Using the efficiency of rhizospheric bacteria and fungi (*Trichoderma* sp.) has been utilized for bio-or phyto-remediation purpose. Theremediation of contaminated soils from the toxic heavy metals (e.g., Cu, Cd, Ni, Pb and Zn) or/ and organic pollutants (like pentachlorophenol) could be achieved using many species of *Trichoderma* due to their effective colonization, capacity of quick asexual reproduction within the rhizospheric and their symbiosis impacts (Gorai

et al. 2020). It is reported that genus *Trichoderma* is tolerant to a range of recalcitrant pollutants including pesticides, polyaromatic hydrocarbons and heavy metals. Therefore, *Trichoderma* sp. can be successfully applied and established as an agent of bio- or phyto-remediation of different environmental pollutants. Some ecological, biochemical, molecular and genetic approaches should also be integrated for developing of novel technologies (Gorai et al. 2020). Based on the recent studies, many researchers confirmed the role of *Trichoderma* in the bioremediation of many organic contaminants such as TNT by *Trichoderma viride* (Alothman et al. 2020), chromium by *Trichoderma viride* (Zapana-Huarache et al. 2020), and copper or chromium by *Trichoderma lixii* CR700 (Kumar and Dwivedi 2019, 2021), diesel by *Trichoderma harzianum* strain T22 (Elshafie et al. 2020), and polycyclic aromatic hydrocarbons by *T. longibrachiatum* (Li et al. 2021).

Conclusion

Trichoderma is an important fungus that live symbiotically with plants. This symbiotic relation has many sustainable benefits in the agriculture sector. These benefits may include their applications as biofertilizers, biopesticides, biostimulants and soil amendments as well as their roles in biofortification, bioremediation, and phytoremediation. *Trichoderma* as a biocontrol agent has been widely used against several phytopathogens including bacteria, viruses, nematodes, fungi and higher parasitic plants. Based on their useful mechanisms, *Trichoderma* might be the best microbe to the plants. These mechanisms may include enhancing the plant growth, producing the secondary metabolites and enzymes, parasitism and antibiosis. The sustainable approaches in using *Trichoderma* is mainly depend on its useful protection and inhibition a lot of phytopathogens, using as biopesticides, biofertilizers and biostimulants, which save the ecosystem by reducing the residue of chemical synthetic fertilizer and pesticides. The high efficiency of *Trichoderma* as biostimulants has been approved by modulating the microbial populations in the rhizosphere and by improving N-uptake efficiency, yield and its nutritional quality of some cultivated leafy vegetables.

Ethics approval and consent to participate

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication

All authors declare their consent for publication.

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Conflicts of Interest

The author declares no conflict of interest.

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- Env. Biodiv. Soil Security* Vol. 4 (2020)

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