



Trichoderma: Potential bio-resource for the management of tomato root rot diseases in Africa

Olumayowa Mary Olowe^{a,b}, Lidia Nicola^b, Michael Dare Asemoloye^c,
Akinlolu Olalekan Akanmu^a, Olubukola Oluranti Babalola^{a,*}

^a Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Private Bag X2046, Mmabatho 2735, South Africa

^b Laboratory of Mycology, Department of Earth & Environmental Sciences, University of Pavia, 27100 Pavia, Italy

^c School of Pharmaceutical Science and Technology, Tianjin University, 92 Weijin Road, Nankai District, Tianjin 300072, China

ARTICLE INFO

Keywords:

Plant disease management
Tomato diseases
Biocontrol
Abiotic and biotic stresses
Soil-borne pathogens

ABSTRACT

Trichoderma spp. are among the front-line microorganisms commonly employed in novel biotechnology applications. They have been well-proven as biopesticides, biofertilizers, and biostimulants for managing plants against biotic and abiotic stresses. They are instrumental in managing plant diseases of economic importance, such as tomato root rot. However, this group of fungi has not been well-exploited en-mass in developing countries, while the use of bioagents in-lieu of chemical pesticides is still not a common practice in many African countries. Africa contributes 11.8% to global tomato production. Unfortunately, more than half of the actual product is lost due to diseases. The root rot of tomatoes predominantly caused by soil-borne fungal pathogens are among significant problems of tomato cultivation in Africa. Here, we review the constraints of tomato root rot in Africa and the roles of *Trichoderma* in repositioning the crop for optimum productivity. We gave a comprehensive overview of the economic importance, root rot epidemiology, and how to circumvent it through gene pool to resistant tomato and employ *Trichoderma*'s biological control potentials. Furthermore, this review gives an overview of the mechanisms of action of *Trichoderma*, gaps in the advocacy, adoption, commercialization, and regulation of *Trichoderma* as biocontrol agents of tomato rot diseases in Africa.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is the world's most widely eaten vegetable belonging to Solanaceae. It is a crop extensively grown worldwide, rich in potassium, antioxidants, ascorbic acid, vitamin A, lycopene, and tocopherols for nourishing human health (Capobianco-Uriarte et al., 2021). Africans are part of significant tomato producers. Africa accounts for 11.8% of global production, while Asia, Europe, and America produce 61.1%, 13.5%, and 13.4% of the total tomato yield, respectively (Quinet et al., 2019). Based on tomato productivity, Egypt (6.8 million tonnes) is the leading tomato producer in Africa, followed by Nigeria (3.8 million tonnes), while South Africa (630 thousand tonnes) is the least producer of tomatoes (Dube et al., 2020). However, its output in Africa is mainly reduced by various factors, including biotic constraints. Attacks by different viral, bacterial, arthropod pests, and fungal diseases are poorly controlled, contagious, and may swiftly spread from plant to plant in a tomato field when appropriate conditions (Ochilo et al., 2019).

The root rot of tomato, in particular, is commonly caused by soil-borne fungal pathogens such as *Rhizoctonia solani*, *Fusarium solani*, *Phytophthora* species, and *Sclerotium rolfsii* that delays growth, reduce harvest yield and quality, and subsequent death of severely infected plants (Ajilogba et al., 2013a; Hamza et al., 2016; Kashyap et al., 2020). This disease is favored by environmental factors such as temperature for pathogen growth, moderate to high soil moisture content, soil compaction, poor drainage, and other factors that contribute to plant stress (Sharath Chandran et al., 2021). Root rot was revealed to reduce the yield of tomatoes by up to 25% in developed countries and more than 50% in developing countries (Nicastro and Carillo, 2021). This is a big challenge considering the multi-pathogenic cause of this disease and poor technologies for its management.

Enormous success has been recorded on plant disease control via a variety of methodologies like the use of independent disease management, plant breeding for resistant varieties/genetically modified plants, use of agrochemicals/excellent agronomic and horticultural practices, as well as biological control agents (Ajilogba and Babalola, 2013b; Ons,

* Corresponding author.

E-mail address: olubukola.babalola@nwu.ac.za (O.O. Babalola).

<https://doi.org/10.1016/j.micres.2022.126978>

Received 15 December 2021; Received in revised form 24 January 2022; Accepted 28 January 2022

Available online 2 February 2022

0944-5013/© 2022 Elsevier GmbH. This article is made available under the Elsevier license (<http://www.elsevier.com/open-access/userlicense/1.0/>).

2020). Using fungi as biological control agents is an essential, economically viable, environmentally safe, and long-term strategy for plant disease management that many developed countries are already implementing (Figlan et al., 2020; Olowe et al., 2020). *Trichoderma* species have been reported as excellent mycofungicides (Babu and Pallavi, 2013; Woo et al., 2014; Kuzmanovska et al., 2018; Manandhar et al., 2019). They are good bioagents with excellent competitive attributes in the rhizosphere, intense aggressiveness against phytopathogenic fungi, and aided suppression mechanisms (Filizola et al., 2019). They have a high tolerance to soil-applied agrochemicals, modify the rhizosphere for plants benefits, can utilize any available soil nutrients efficiently, survive under unfavorable conditions, and promote plant growth (Vinale et al., 2008; Köhl et al., 2019).

Biological control has not yet been widely used in Africa due to concerns about its efficacy, a lack of expertise, high costs, technological compatibility, and a lack of technical assistance (Ons et al., 2020). Despite many results on in-vivo antagonistic effects of native African *Trichoderma* species on different plant pathogens, especially on common soil-borne pathogens such as *Rhizoctonia* and *Fusarium*, they have not been fully explored as tools for the management of crop diseases and their use as biological products in Africa (del Carmen et al., 2021). In most developing countries, most farmers cannot utilize disease management practices because of financial constraints, limited knowledge, and research on different alternatives (Kuehne et al., 2017). Most African farmers lack the physical access and financial means to technical solutions (Perez et al., 2017) but revert to alternatives such as pesticides and local irrigation. This could contribute to tackling disease resistance and other pertinent issues currently faced by African farmers (Rush et al., 2021).

This review again affirms *Trichoderma* species as bioresources with potential application for adequate control/management of root rot disease of tomatoes in Africa; their mechanism of action, efficacy, application style, and packaging were discussed. Their roles, if well implemented in the management of tomato root rot with good commercial strategies, policy, and advocacy in Africa, indeed hold a potential breakthrough for the management of root rot disease of tomatoes.

2. Tomato production in Africa and root rot disease

2.1. Economic importance of tomatoes in Africa

Tomato is the most widely consumed vegetable in Africa (Rwomushana et al., 2019). In 2019, more than 21 million tons of tomatoes were produced in Africa, with a production increase of more than 60% in the last 20 years (FAOSTAT, 2021). The area with the highest tomato production is Saharan Africa, Egypt, Algeria, Morocco, and Tunisia, while Nigeria is the biggest producer among sub-Saharan countries (FAOSTAT, 2021). The cultivation of tomatoes is also essential from a socio-economical point of view since it represents a significant source of income for rural producers in several developing African countries (Arah, 2015; Mulugeta et al., 2020). It also offers employment to women, who represent more than 60% of the labor force in this cultivation (Rwomushana et al., 2019).

However, tomato yields in Africa are still far below their estimated potential due to some abiotic stresses (climate change, low soil fertility, drought, high temperatures) and biotic stresses (microbial plant pathogens, insect pests, weeds). It has been estimated that in most sub-Saharan countries, the actual tomato yield is only 10–30% of the estimated potential production (Nordey et al., 2020).

2.2. Root rot of tomatoes: epidemiology and susceptibility in Africa

Many varieties of tomatoes have been developed and distributed widely in Africa. In Kenya, tomato varieties such as Assila F1, Eden F1, Milele F1, Rambo F1, Kilele F1, Shanty improved, Star 9065, Eva F1, Tylka F1, Steve F1, and different companies have developed many more

for greenhouse and open ground cultivation. These varieties have been developed for high yielding, high shelf-life and resistance to diseases like *Alternaria solani* (As) Fusarium wilt (Fol), Fusarium Crown and Root Rot (Fol), Nematodes (N), Tomato Yellow Leaf Curl Virus (TYLCV), and Verticillium wilt (Vd). Root rot of tomato plants is a serious and common problem worldwide. Its symptoms include not only browning and softening of root tips and root lesions but also wilted leaves, stunted plant growth, and reduced yield (Williamson-Benavides and Dhingra, 2021). The causal agents for tomato root rot can be numerous fungi, and they can also vary according to the geographical region. Unfortunately, there is no general compendium of tomato root rot epidemiology for the whole African continent, and this phenomenon remains unstudied, mainly in most African countries. More studies managed to isolate the causal fungal pathogens of tomato root rot is Egypt (El-Mougy et al., 2011), followed by Nigeria (Ewekeye and Odebode, 2021) and Algeria (Yezli et al., 2019), and South Africa (Thabet and Khalifa, 2018). Based on the available literature, the most common root rot fungal pathogen for tomatoes in Africa is *Fusarium oxysporum* Schldt., it has been reported from Egypt, Algeria, and Nigeria. *F. oxysporum* is a ubiquitous soil-borne pathogen with approximately 150 *formae speciales* that can infect a wide range of plants (Pareek and Rajam, 2017).

The *F. oxysporum* f. sp. *radicis-lycopersici* Jarvis and Shomaker (FORL) is most commonly associated with tomato root rot in Africa. This strain of *Fusarium* is highly virulent and affects tomato-growing areas worldwide (Debbi et al., 2018). Strains of FORL have been isolated from Egypt on tomato plants with root rot in the Giza Governorate (Mosa and Youssef, 2021), in El-Ismaïlia, El-Tahrir, and El-Fayoum, while no exact sampling site was specified by El-Abeid et al. (2020) and Shenashen et al. (2017). These strains have also been found associated with diseased tomato plants in the Algerian Sahara (Goudjal et al., 2016) and in the Algerian regions of Biskra, Boumerdes, Algiers, Mostagenem, and Jijel (Debbi et al., 2018). Another strain of the *F. oxysporum* group which is often associated with tomato root rot is f. sp. *lycopersici* (Sacc.) Snyder and Hansen (FOL) was isolated from the Algerian regions of Boumerdes, Algiers, Biskra, Jijel, and Tipaza (Debbi et al., 2018), and in Nigeria, in the Obio-Akpor Local Government of Rivers State (Wokoma, 2008). In other cases, it was not possible to discern the *formae speciales*. There is only the indication of *Fusarium oxysporum* at the species level, such as in Ibadan, Nigeria (Etaware and Oyetuji, 2019), in Jijel, Algeria (Debbi et al., 2018), and in Egypt (Muhanna et al., 2016). The other two species of *Fusarium* associated with tomato root rot were found in Africa; the first one is *Fusarium solani* (Mart.) Sacc., isolated at Beni Suef and Fayoum governorates in Egypt (Elshahawy et al., 2018), while the second one, *Fusarium equiseti* (Corda) Sacc. was isolated for the first time from tomato plants affected by the crown and root rot in Algeria and completed Koch's postulates (Yezli et al., 2019).

A species that is often found associated with tomato root rot in African literature is *Rhizoctonia solani* J.G. Kühn (Williamson-Benavides and Dhingra, 2021). This basidiomycete is a soil-borne pathogen that can severely damage tomato plants and reduce their yield (Nikraftar et al., 2013). This pathogen was isolated in Egypt from diseased plants, for example, in the El-Behira governorate (Heflish et al., 2021) and other unspecified tomato fields (Muhanna et al., 2016; Hamza et al., 2016). It was also discovered in Nigeria, in the Obio-Akpor Local Government of Rivers State (Wokoma, 2008). Another possible cause of tomato root rot is the oomycetes *Pythium* and *Phytophthora*. *Pythium* generally causes damage to the hypocotyl of the seedling, followed by stunted growth and often plant death. Specifically, *Pythium aphanidermatum* (Edson) Fitzpatrick is one of the most common causal agents of tomato root rot all over the world (Christy Jeyaseelan et al., 2012), and it was isolated for the first time in Egypt in 2018, at Beni Suef and Fayoum governorates (Elshahawy et al., 2018). This pathogen was also isolated near Barberton and Pretoria in South Africa and Selebi Phikwe in Botswana (Labuschagne et al., 1994). Moreover, another member of the genus *Pythium*, *P. perplexum* H. Kouyeas & Theoh., was isolated from hydroponic tomato cultivations in South Africa (Gull et al., 2004). On the other hand,

regarding *Phytophthora*, there is the first record of *Phytophthora capsici* Leonian as the causal agent of tomato root rot in South Africa (near Barberton and Pretoria) and Botswana (Srelebi Phikwe) in 1994 (Labuschagne et al., 1994). Moreover, *Macrophomina phaseolina* (Tassi) Goid., another soil-borne fungus that invades tomato plants through roots, was isolated from naturally infected roots from tomato plants showing root rot symptoms in Egypt (Muhanna et al., 2016).

3. *Trichoderma*, an untapped resource for the management of tomato root rot in Africa

Excessive application of synthetic chemical pesticides and inorganic fertilizers to control plant pathogens has been rebuked due to their ecological impact. In contrast, biopesticides and biological control methods have been well advocated (Wang and Zhuang, 2019). Many researchers have justified using biological control methods in place of chemical control due to its environmental friendliness and cost-effectiveness (Contreras-Cornejo et al., 2020; Moosavi and Zare, 2012). *Trichoderma* is a group of ascomycete fungal Genus of Order-Hypocreales, Family-Hypocreaceae. They are ubiquitous and widely distributed in diverse environments. *Trichoderma* fungi have for long been reported as decomposers (Druzhinina et al., 2006), many authors have reported them as saprobic organisms, while many reports are emerging on many species of *Trichoderma* as mycoparasitic and endophytic organisms (Harman et al., 2004; Samuels et al., 2006; Mukherjee et al., 2013). *Trichoderma* species are well known as biological control agents (BCA) against various plant pathogens ranging from viral, bacteria, fungi, nematodes, protozoans, insect, plant, or animal pathogens (Samuels, 1996; Woo et al., 2006). Many mycoparasitic *Trichoderma* species have been well characterized for biocontrol of different fungal pathogens of plants.

Persoon (1794) first described this group of fungi and was later linked to a sexual state in the Hypocrea species. The first detailed work on identifying these fungi was made by Rifai (1969) and later expanded by Samuels (2006). They are well known for their role in either enhancing the plant growth and development, inducing resistance in plants against pathogens, enhancing the rhizosphere, or directly attacking the plant pathogens (Harman et al., 2004; Schuster and

Schmoll, 2010; Pandya et al., 2011; Keswani et al., 2014). Since *Trichoderma* can grow in different habitats, these abilities have made them very popular among the science community. As a result, several works have been published on the importance of *Trichoderma* in agriculture and plant disease control. Their mode of action against plant pathogens is shown in Fig. 1.

- (i) **Competition**, they compete to inhibit the growth of pathogens by starving or depriving plants of accessing basic life needs (Alabouvette et al., 2009). Many *Trichoderma* strains have been reported to be capable of secreting substances like siderophores to starve pathogens of essential elements (Latorre et al., 2001). Also, cellulose, glucan, and chitin to reduce carbon availability (Chet et al., 1997), and proteins to enhance root colonization as protection against pathogens (Saloheimo et al., 2002; Viterbo et al., 2004; Brotman et al., 2008; Samolski et al., 2012).
- (ii) **Antibiosis**, by the production of toxic substances like gliovirin, harzianic acid, alamethicins, tricholin, peptaibols, antibiotics, 6-pentyl- α -pyrone, massoialactone, viridin, glisoprenins, and heptelidic acid, polyketide, peptaibol, flocculosin, and terpenoid/steroid (Rey et al., 2001; Vey et al., 2001; Raaijmakers et al., 2009).
- (iii) **Mycoparasitism**, a condition where *Trichoderma* fungi can parasitize or grow on the fungal pathogens of plants to inhibit their growth. These groups have been well explored for the biological control of many plant pathogens (Zeilinger et al., 1999). This involves direct attacks by penetrating the cells of the pathogen and obtaining nutrients from them (Harman et al., 2004).
- (iv) **Induced resistance**, *Trichoderma* can interact with plants to trigger resistance against pathogens or disease. This, unlike others, is an indirect action of *Trichoderma* against plant pathogens. The first demonstration of induced resistance by *T. harzianum* strain T-39 was confirmed on bean plants against *B. cinerea* and *Colletotrichum lindemuthianum* (Bigirimana et al., 1997). This fungus has been reported to enhance the resistance of 10 different dicots and monocots against bacterial infections caused by *Xanthomonas* spp., and *Pseudomonas syringae*. Including the fungal infections caused by *B. cinerea*, *R. solani*, *Colletotrichum*

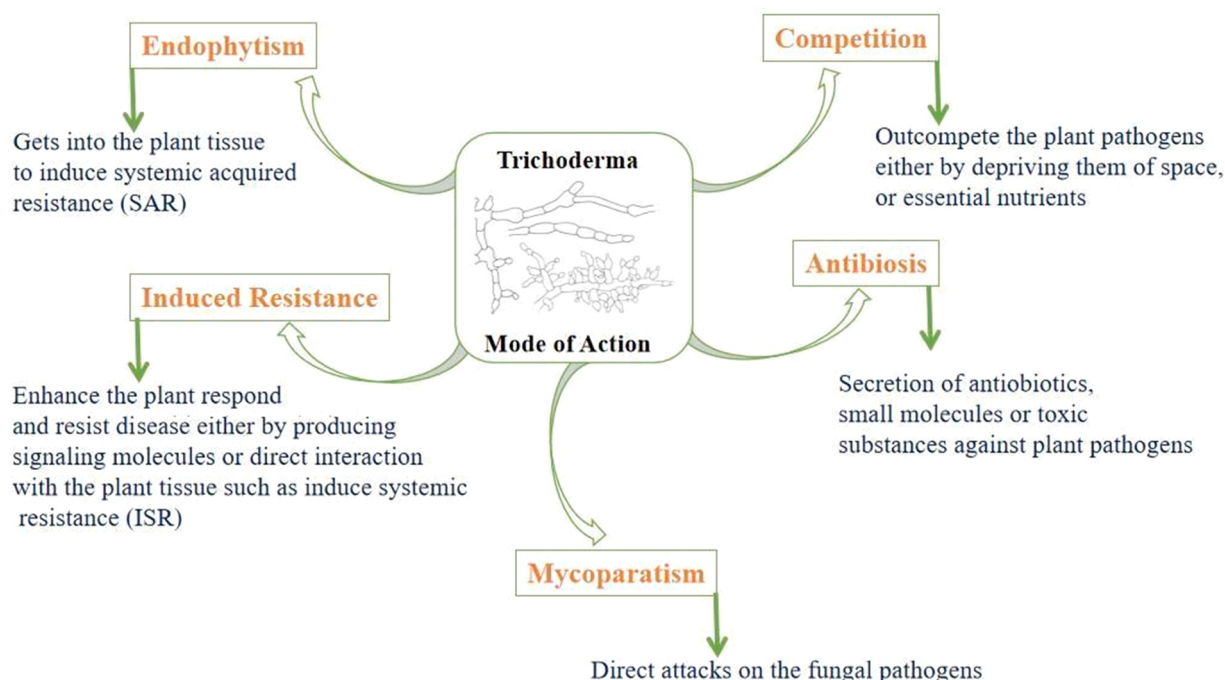


Fig. 1. *Trichoderma* modes of action as bioagent.

spp., *Phytophthora* spp., *Alternaria* spp., and *Magnaporthe grisea*; as well as CMV virus (De Meyer et al., 1998). This capability was established in *T. harzianum* T-22 in model plants (Conteras-Cornejo et al., 2011; Salas-Marina et al., 2011; Yoshioka et al., 2012; Harman et al., 2012). Other *Trichoderma* strains such as *T. virens*, *T. asperellum*, *T. harzianum*, and *T. atroviride* have been proven to stimulate the metabolism of their plant hosts against pathogens (Fig. 2).

- (v) **Endophytes** grow inside the tissue of their plant hosts without harming them. This phenomenon is similar to induced resistance, but in this case, the plants are induced with resistance against disease caused by abiotic stress causes like drought, toxins, or radiation (Piotrowski and Volmer, 2006; Gazis and Chaverri, 2010; Chaverri and Gazis, 2011). The endophytic association between *Trichoderma* and their host plant is in most times, reported as mutually beneficial, although it may require complex interactions from direct contact to internal tissue colonization (Qin and Zhuang, 2016). The endophytic *Trichoderma* may act as commensals or as true symbionts that stimulate defense mechanisms in their host plants. The mechanism of how these fungi induce disease defense in their host plants has been well studied. They can either induce plant defense against pests, external abiotic stress, promoting their growth and photosynthesis rate, or contribute to their solubilization and uptake of nutrients from the soil (Vinale et al., 2008; Shoresh et al., 2010; Hermosa et al.,

2012; Harman et al., 2019; Hyde et al., 2019; Ikram et al., 2019; Kiarie et al., 2020).

Trichoderma spp. are particularly popular for different biological activities and have been well studied over the last two decades (Jiang et al., 2016; Chaverri et al., 2015). As such, many reputable fungal species have emerged under this group, but many studies on reporting new valuable species are often conducted mostly in Asia, Europe, and the United States (Kubicek et al., 2003; Qin and Zhuang, 2016; Chen and Zhuang, 2017; a&b; Inglis et al., 2020). *Trichoderma* strains have a good reputation in the management of tomato plants. Several species of *Trichoderma* have been reported either for the management of Tomato diseases and/or improving plant growth (Table 1). However, Africa has not yet been well covered in terms of quality studies on assessing or characterizing indigenous *Trichoderma* fungi. Some studies have detailed the diversity of *Trichoderma* in the soil at some specific regions of South Africa (du Plessis et al., 2018). In the case of the endophytic and plant-growth-promoting *Trichoderma* strains, studies are much limited in Africa at large. A study was carried out by del Carmen et al. (2021), which characterized the *Trichoderma* endophytes from Coffee plants, while some other authors isolated the *Trichoderma* strains from the rhizosphere from *Coffea arabica* in Ethiopia (Mulaw et al., 2010; Carmen et al., 2021). Studies that analyzed the effect of these fungi on perennial crops, particularly on the wild types, have revealed that they contain novel taxa that can be of great importance in carefully explored, important wild-type indigenous strains of *Trichoderma* have been

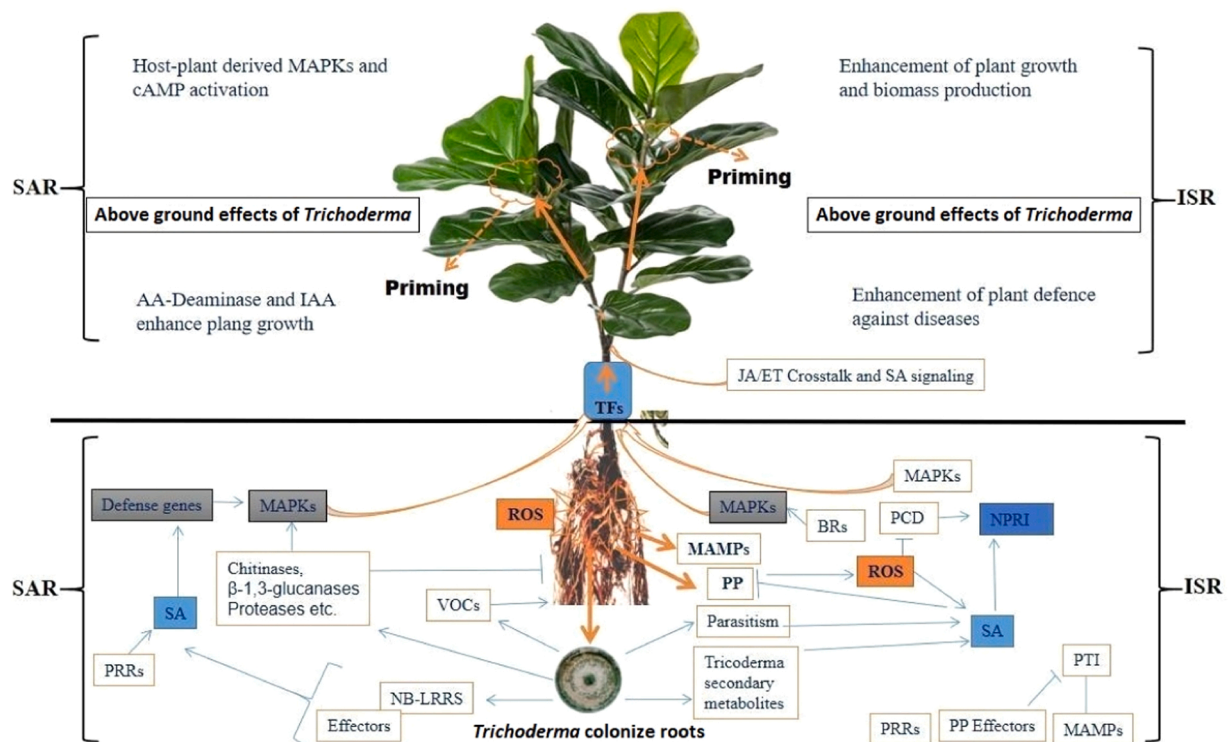


Fig. 2. Mechanisms of *Trichoderma* induced resistance and signaling pathways in plants against plant diseases. The Plant pathogens (PP) like bacteria, nematodes, viruses or fungi can secrete various enzymes to degrade the plant's cell wall, and insight infection or develop feeding sites for their growth and multiplication. Some PP can also produce some effector proteins to suppress the plant triggered immunity (PTI). *Trichoderma* can inhibit PP by producing different kinds of toxic metabolites or directly parasitize on tissue, egg, hyphae, or cell of PP, they can as well produce some elicitor proteins or chemical signals like the salicylic acid (SA) or jasmonic acid (JA) to either enhance the plant's defense mechanism against the PP a process called The induce systemic resistance (ISR). Some PP-like nematodes can produce a high level of reactive oxygen species (ROS) to avoid cell death inside living cells or tissue, *Trichoderma* can help plants by triggering cell death around parts already colonized by the PP. In addition, another biocontrol mechanism of *Trichoderma* on PP is by induction of systemic acquired resistance (SAR) in plants. This they do by their interference with or triggering in plants, the production of the microbial-associated molecular pattern (MAMP), and volatile organic compounds (VOCs) which can also induce indole acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate-deaminase (ACC-deaminase) secretion by plants. Others include the cell wall degrading enzymes (CWDEs) such as Chitinases, β -1,3 glucanases, and proteases, and induce mitogen-activated protein kinases (MAPKs). The cross-talk among the elements of SAR triggered pathogens and ISR signaling by *Trichoderma* can activate the plant defense response pathways of cyclo adenosine monophosphate (cAMP) and MAPKs from uninfected plant's part to the infected parts.

Table 1
Some examples of *Trichoderma* interactions with tomato host plants.

Importance	<i>Trichoderma</i> strain	Mode of action	References
Growth promoting action	<i>Trichoderma asperellum</i>	improved crop health and productivity	(Calin et al., 2019)
	<i>T. asperellum</i>	Induce nitric oxide (NO) accumulation and phytoalbumin PHYTOGB1 transcriptional regulation	(Martinez Medina et al., 2017)
	<i>Trichoderma</i> sp.	Induce early plant growth	(Eltbany et al., 2019)
	<i>T. harzianum</i> strain M10	– Increase germination of tomato seeds and improve the growth of the seedlings – Produce harzianic acid	(Vinale et al., 2013)
	<i>T. harzianum</i> strain SQR-T037	– Give better root development for the enhancement of root length and tips. promoted tomato seedling growth	(Cai et al., 2015).
Biocontrol (Antagonism)	<i>T. asperellum</i>	Attack <i>Fusarium oxysporum</i> f. sp. lycopersici (FOL) a wilt pathogen of tomato	(El Komy et al., 2015)
	<i>T. viride</i> , <i>T. virens</i>	Attack collar rot pathogen of Tomato, <i>Sclerotium rolfsii</i>	(Amin and Razdan (2010)
	<i>T. viride</i> , <i>T. virens</i>	Attack fruit rot pathogen of Tomato, <i>Rhizoctonia solani</i>	(Amin and Razdan (2010)
	<i>Trichoderma</i> sp.	Antagonistic against <i>Meloidogyne incognita</i> causing disease of tomato	(Khan et al., 2020)
	<i>Trichoderma</i> sp.	Antagonistic against <i>Meloidogyne incognita</i> causing disease of tomato	(Pocurull et al., 2020)
	<i>Trichoderma</i> sp.	Antagonistic against <i>Meloidogyne hapla</i> causing disease of tomato	(Braithwaite et al., 2016)
	<i>T. harzianum</i> T-39	Antagonist against tomato disease caused by <i>Botrytis cinerea</i>	(Meller et al., 2013)
Induced systemic acquired resistance	<i>T. virens</i> and <i>T. atroviride</i>	Secreted proteins- Sm1 and Epl1 both induced systemic acquired resistance <i>Alternaria solani</i> , <i>B. cinerea</i> , and <i>Pseudomonas syringae</i> pv. <i>tomato</i> (Pst DC3000)	(Salas-Marina et al. (2015)
	<i>T. harzianum</i> with other two botanicals	Induce resistance of tomato against <i>Meloidogyne incognita</i> pathogen	(Belay et al., 2016)

reported from the cacao tree, *Theobroma cacao* (Evans et al., 2003; Samuels et al., 2000; Gazis et al., 2010), and *Hevea brasiliensis*, rubber (Chaverri et al., 2011; Vaz et al., 2018) while many reports have presented novel species of *Trichoderma* from native Amazonian habitats, these species are capable of producing varieties of metabolites ranging from plant defense elicitors, mycotoxins to antibiotics (Chaverri et al., 2011; Schuster et al., 2010).

Mycoparasitic attributes of many *Trichoderma* strains have been established and have been well explored for the biological control of

various plant pathogens (Howell et al., 2003). Many of such strains are now packaged under different trade names for the usage of farmers. *T. stromaticum* is a notable example patented as ‘Tricovab’ for the control of fungus *Moniliophthora perniciosa* causing the witches’ broom disease of cacao which is the major problem of cacao in Neotropics (Souza et al., 2006; Samuels et al., 2012). This product has been well distributed to farmers in southern Bahia in Brazil for many years (Bettiol et al., 2012; Samuels and Hebbbar, 2015) and has now been employed as part of the integrated pest management strategy for controlling cacao pests (Medeiros et al., 2010). Another prominent example is *T. harzianum* which can colonize and degrade sclerotia of many fungal pathogens (Elad et al., 1984; Druzhinina et al., 2011), this fungus has been widely distributed as bio-fungicide (Samuels and Hebbbar, 2015; Whipps and Lumsden, 2001).

4. *Trichoderma* advocacy, commercialization, and regulations

Biocontrol activity involves a variety of biological control agents such as bacteria and fungi, among which the fungal genus, *Trichoderma*, is significant in the management of plant diseases. This fungus produces a variety of enzymes that aid in the biocontrol activities such as biotic and abiotic stress tolerance, cell wall disintegration, hyphal development, and antagonistic action against plant diseases. *Trichoderma* species are pervasive and frequently dominating components of the mycoflora in natural and agricultural soils across all temperate zones. They are resident in both the terrestrial and marine environment and have adapted to almost every ecology, and contribute significantly to the health status of the ecosystem. Species of *Trichoderma* colonize the plant endosphere and rhizosphere and have also been recovered from soil organic matter, plant litter, and human tissues (Mukherjee et al., 2013).

The capacity of *Trichoderma* fungi to function as biocontrol agents against plant diseases has been recognized as early as the 1920 s (Hartman, 2006). The ability to detect, invade, and destroy other fungi are the reason for its economic success and commercial application, as *Trichoderma*-based biopesticides constitute over 60% of all registered biopesticides (Mukherjee et al., 2013). Apart from providing resistance against plant diseases, these fungi also increase plant growth and vigor, solubilize plant nutrients, enhance nutrient absorption in plants, and bioremediate heavy metals and environmental contaminants while producing clinically important secondary metabolites and enzymes to both human and plant safety (Singh et al., 2018; Sood et al., 2020). *Trichoderma* species are often employed as biological control agents against phytopathogenic microbes, including those which cause the tomato root rotting disease that is of interest in this study. They act through mechanisms such as antibiosis, mycoparasitism, and competition for space and resources, while their impacts on plants such as induced systemic or localized resistance are also of importance in the biological management processes (Howell, 2003). *Trichoderma* spp. are not only successful plant symbiotic organisms, but they also act as a low-cost, effective, and environmentally benign biocontrol agent. They may establish themselves in a variety of pathosystems, have a low influence on soil balance, and do not harm beneficial species that aid in pathogen management (Sood et al., 2020).

Trichoderma products are promoted as biofungicides, biopesticides, bioprotectants, bio-stimulants, bio-inoculants, bio-fertilizers, bio-composers, plant growth promoters, and so on (Woo et al., 2014). Some *Trichoderma* isolates such as *T. polysporum*, *T. harzianum*, *T. asperellum*, *T. atroviride*, *T. viride* *T. polysporum* are particularly known for their broad-spectrum biofungicidal potentials against a range of foliar, vascular, and soilborne diseases caused by *Rhizoctonia solani*, *Botrytis cinerea*, *Sclerotium* spp., *Sclerotinia sclerotiorum*, *Pythium ultimum*, *Armillaria* spp., *Phytophthora* spp., *Verticillium* spp., *Fusarium oxysporum* and *Gauemannomyces graminis* (Ghazanfar et al., 2018; Woo et al., 2014). These properties broaden the range of potential applications for *Trichoderma*-based products in the agricultural market, not only as a phytopathogen biofungicide, but also as a general bio-inoculant that

boosts plant resistance to biotic and abiotic stresses, improves plant growth and yield, and enhances the agro-ecosystem (Hill et al., 2010).

Despite its efficacy, *Trichoderma* as a biocontrol agent has its limitations. Although *Trichoderma* successfully colonizes the spermosphere, it does not thrive in the rhizosphere (Harman, 2000). Also, *Trichoderma* spp. are active only in certain types of soil and seasons, therefore achieving only transitory localized dominance of the rhizosphere. Moreover, the inactive and dormant nature of *Trichoderma* spores in soil suggests that *Trichoderma* cannot be supplied as spores (Aamir et al., 2020). In addition, various mechanisms have been uncovered in vitro, but the validity of such has not been successfully validated in the field of biocontrol systems (Woo et al., 2014). More so, biological control agents are fragile and could be denatured in hostile environmental conditions. Some of the measures to curtail these limitations are through adequate formulation. Hence the development of cost-effective, stable, and easy to apply biological control formulations is essential for the enhanced efficiency of the deployed biocontrol formulations (Lewis and Papavizas, 1987). The *Trichoderma*-based formulation in pelletized form is viable for over three months (Cuevas et al., 2001). It has been shown as effective against seedling diseases of vegetables caused by *S. rolfii* when applied in pelletized form (Ram et al., 2020). In addition, *Trichoderma* formulations had also been commercialized as a wettable powder (WP), granular, powder preparation, liquid, and solids products. In contrast, others are emulsions, dry flowable, concentrated liquid suspensions, and talc, among others (Table 2) (Woo et al., 2014).

In general, the European Commission and other agencies around the world have indicated that about 38 *Trichoderma* commercial products (single species and combination mixtures) are registered or in the process of being registered in various countries, while four products have received special registration or temporary approval only for use in field experiments (Topolovec-Pintaric, 2019). Furthermore, the species of *Trichoderma* mostly present on the label of the commercial products are *T. atroviride*, *T. asperellum*, *T. hamatum*, *T. gamsii*, *T. koningii*, *T. harzianum*, *T. lignorum*, *T. polysporum*, *T. parceanamosum*, *T. viride*, *T. virens*, and *Trichoderma* spp. However, following the trend in the usage of several *Trichoderma* spp., nearly half of these new products contain *T. harzianum* (Bal and Altintas, 2006).

More than 250 *Trichoderma*-based products have recently been registered and identified on the international market (Ram et al., 2020). Yet, there occurs a huge disparity in the actual number of biological control agents in use compared to those registered. However, out of the *Trichoderma*-based registered products, Asia made the most significant contributions of 39%, and Africa, with nine registered products, had the least contributions of 3.5% among the regions of the world (Fig. 3). On the other hand, South Africa, Kenya, Zambia, Morocco, and Tunisia had registered and produced at least a *Trichoderma*-based product among the African nations (Table 2). While *Trichoderma* poses enormous promise in Africa, as evidenced in many scientific investigations into the genus conducted in the region, most African scientists and entrepreneurs seem not to be aware of the full potential of this product, especially in solving the peculiar cropping problem in Africa, as in the case of tomato farming. Hence, the smallholder farmers that constitute the bulk of agricultural productions in most African countries are stocked with chemical fertilizer in the face of non-viable and available organic alternatives.

Governing authorities across the globe, notably in Europe, are currently enacting legislation to reduce agriculture's reliance on pesticides to improve consumer and environmental safety. Directives will promote low pesticide input by implementing integrated pest management (IPM) and will provide the means to establish the necessary conditions and measures to employ these practices, as well as to ensure the security of commercial products, to reduce the risks associated with pesticide applications and reduce dependency on their use. As an alternative to synthetic agrochemicals, one strategy is to employ biological control agents and their products (Masip et al., 2013). Hence, *Trichoderma* species are qualified candidates, having been extensively

Table 2
Different substrates that have been used for *Trichoderma* production.

Type	Species	Substrates	References
Grains	<i>T. harzianum</i> and <i>T. viride</i>	Sorghum	Rini and Sulochana (2007)
	<i>T. viride</i>	Sorghum, wheat	Bhagat et al. (2010)
	<i>T. harzianum</i> and <i>T. viride</i>	Rice, sorghum, pearl millet	Parab et al. (2008)
	<i>T. harzianum</i> and <i>T. viride</i>	Maize	Pramod and Palakshappa (2009)
	<i>T. harzianum</i>	Sorghum	Upadhyay and Mukhopadhyay (2009)
Organic matters	<i>T. harzianum</i> P26	Neem cake, coircompost, FYM, Gliricida leaves	Saju et al. (2002)
	<i>T. harzianum</i> (T5), <i>T. viride</i> , <i>T. hamatum</i> (T16)	Cotton cake	Sharma and Trivedi (2005)
	<i>T. harzianum</i>	FYM, Local cow dung, Jersey cow dung	Pramod and Palakshappa (2009)
	<i>T. harzianum</i> and <i>T. viride</i>	Cow dung with neem cake, coir pith, coir pith in combination with neem cake	Rini and Sulochana (2007)
	<i>T. harzianum</i>	Tapioca waste	Jayraj and Ramabadrana, 1996
	Rifai	Pigeonpea husk and press mud	Palanna et al. (2007)
	<i>T. viride</i>	FYM, vermicompost, poultry manure, goat manure, decomposed coconut, coir pith	Tewari and Bhanu (2004)
	<i>T. harzianum</i>	FYM, spent compost	Parab et al. (2008)
	<i>T. harzianum</i> <i>T. viride</i>	FYM, compost FYM, Peat	Bhagat et al. (2010)
	<i>T. harzianum</i>	Jatropha cake and neem cake	Tomer et al. (2015)
Agricultural wastes	<i>T. harzianum</i>	Rice bran, paddy straw, groundnut shells	Parab et al. (2008)
	<i>T. harzianum</i> , <i>T. viride</i> and <i>T. virens</i>	Spent Malt	Gopalkrishnan et al., 2003
	<i>T. harzianum</i>	Wheat straw, paddy straw, shelled maize cob, paper waste, saw dust, sugarcane bagasse, spent straw, wheat bran, rice bran	Tewari and Bhanu (2004)
	<i>T. viride</i> and <i>T. harzianum</i>	Tapioca rind, tapioca refuse, mushroom spent straw, paddy chaff, wheat bran, groundnut shell, rice bran, sugarcane bagasse, wheat straw, shelled maize cob, paddy straw, chickpea husk	Gangadharan and Jeyarajan (1990)
	<i>T. harzianum</i> and <i>T. viride</i>	Saw dust, rice bran	Rini and Sulochana (2007)
	<i>T. harzianum</i>	Shelled maize cobs, paddy straw, paddy husk, wheat bran, baggase, sawdust, groundnut shell	Pramod and Palakshappa (2009)
	<i>Trichoderma harzianum</i> , <i>T. virens</i> and <i>T. atroviride</i>	Onion rind (dry onion skin), apple and strawberry pomace, rapeseed meal	Smolinska et al. (2014)
	<i>T. harzianum</i> (T5), <i>T. viride</i> , <i>T. hamatum</i> (T16)	Tea waste, sorghum straw, wheat straw, wheat bran	Sharma and Trivedi (2005)

(continued on next page)

Table 2 (continued)

Type	Species	Substrates	References
Liquid based	<i>T. hamatum</i> , <i>T. harzianum</i> , <i>T. viride</i>	Molasses and Brewer's yeast	Papavizas et al. (1984)
	<i>T. harzianum</i> strain P1,	Defined basal culture medium with mineral solution	Agosin, 1997
	<i>T. harzianum</i>	RM8	Jin et al. (1991)
	<i>T. harzianum</i> strain 1295–22	Modified RM8	Jin et al. (1991)
	<i>T. harzianum</i>	Czapeck's Dox Broth and V8 Broth	Harman, 2012
	<i>T. harzianum</i> Rifai	Potato Dextrose Broth, V8 juice and molasses yeast medium	Prasad et al. (2002)
	<i>T. harzianum</i> Rifai	Potato Dextrose Broth, Czapeck's Dox Broth and Modified Richards' Broth	Das et al. (2006)
	<i>T. harzianum</i>	Local cow urine, Jersey cow urine, Buttermilk, Vermiwash	Parab et al. (2008)

researched and one of the most widely employed microbial biological control agents (MCBAs) in Agriculture, and is presently marketed as biofertilizers, growth promoters, biopesticides, and natural resistance stimulants.

5. Gene pool to resistant varieties versus biological control agents: the constraints of African populace

5.1. Gene pool to resistant tomato varieties

The economic importance of tomatoes motivates genetically varied parents to achieve desired plant attributes such as increased yield, drought, disease resistance, and coping with other stressful situations such as harsh temperatures. The wild crop relatives have been domesticated over thousands of years. Some of the resulting cultivars have continued to hybridize naturally with their wild cousins to maintain stable agricultural production. This type of spontaneous gene flow aids in crop vigor and can lead to the genesis of new crops. Analysis of the genetic diversity of wild relatives and cultivated crops provides insight

into domestication's geographic and temporal details.

In contrast, its estimation may provide the basis for developing suitable strategies for crop conservation, improvement, and sustainable use (Tamburino et al., 2020), towards tomato cultivation less prone to disease in Africa. Plant breeders use genetically varied parents to achieve these qualities, as genetic variety is vital in tomato breeding (Plucknett and Smith, 2014). Meanwhile, the availability of enhanced cultivars that can tolerate biotic and abiotic pressures caused by the environment is critical for successful tomato (*Solanum lycopersicum*) production (Dube et al., 2020).

As in line with the standard practice in Africa, crop domestication either by natural or artificial selection reduces genetic diversity and eliminates many adaptive features present in wild counterparts (Meyer et al., 2012). While the selection of genotypes with desired character combinations that may exist in nature or through hybridization increases the productivity and quality of farmed tomatoes, the genetic diversity present in a crop collection needs to be estimated to improve the crop's genetics. The genetic examination of germplasm aids in interpreting a crop's genetic basis since there are interrelationships between characteristics that aids in the selection of essential yield contributing qualities. The breeder that is interested in specific features for the tomato improvement program such as the tomato resistance to root rotting disease in Africa will employ a gene pool that is considerably less varied than the overall available, with local germplasm known to contribute significantly to genetic variation (Kouam et al., 2018). Molecular approaches for assessing genetic variations have been employed for decades. High throughput DNA sequencing technology has lately given a tremendous boost to assessing genetic and adaptive variation in crops and model organisms (Meyer et al., 2012). Since the genome has already been linked to morphological and metabolic variation, the availability of tomato genomes, together with its phenotypic and molecular characterization, permits genome-wide association analyses to be developed (GWAS). The genome has already been linked to morphological and metabolic variation, according to GWAS studies (Mata-Nicolás et al., 2020) (Table 3).

Genes code for proteins and execute specific roles in all living creatures. Biocontrol genes regulate certain signals and cause the production of enzymes or proteins that aid in pathogen degradation. *Trichoderma* species have genes that can be exploited to offer resistance to biotic and abiotic stressors, including salt, heat, and drought, which are the most prominent problem of tomato in Africa. Some of the major types of

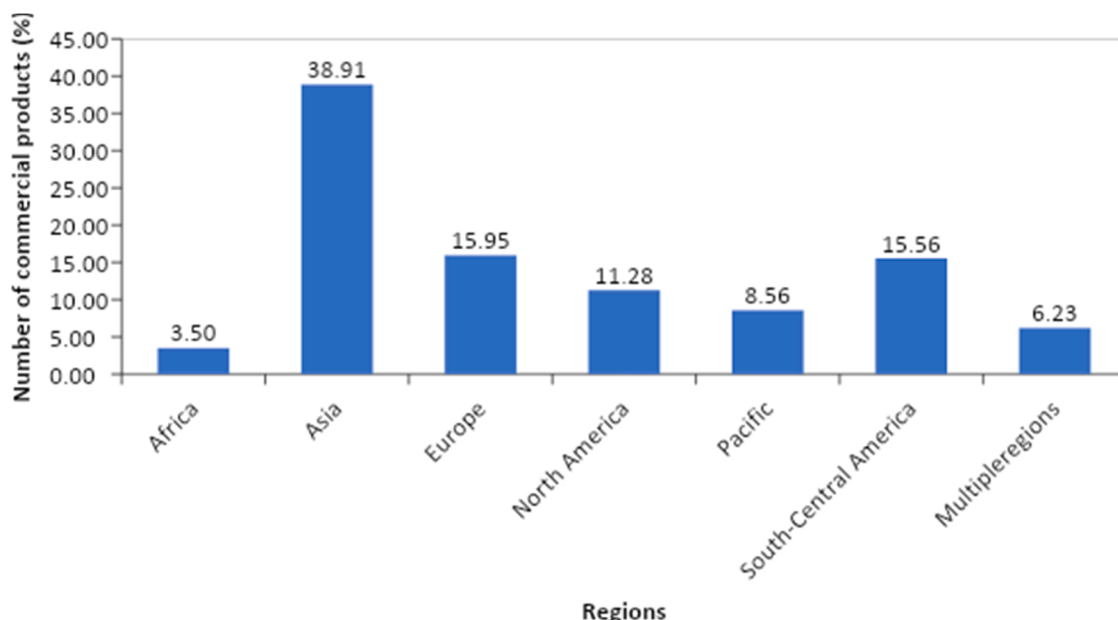


Fig. 3. Regional contribution to the registered *Trichoderma*-based biological control formulations.

Table 3
African registered biological products found on the international market that contain *Trichoderma*.

Product	Company / Distributor	Country	Active substances	Claims & Recommended Crops	Target Pests	Formulations	Product claims
Bio-Tricho	Agro-Organics (http://www.agroorganics.co.za/biotricho.php)	South Africa	<i>T. harzianum</i> strain SF	Can be applied to all crops	Control Botrytis and root diseases such as <i>Rhizoctonia</i> , <i>Phytophthora</i> , <i>Pythium</i> , <i>Fusarium</i> , etc.	WP	F
Eco-77	Plant Health Products (http://www.planthealth.co.za/)	R South Africa, R in process. Kenya, Zambia	<i>T. harzianum</i> strain B77			WP	F
Eco-T	Plant Health Products (Pty)Ltd (http://www.planthealth.co.za)	R South Africa, Kenya, Zambia, FR, UK, Morocco, Tunisia, India	<i>T. harzianum</i> strain kd	control of crop root diseases and for enhanced plant growth	<i>Rhizoctonia</i> , <i>Pythium</i> , <i>Fusarium</i> and <i>Phytophthora</i>	WP, seed trt, irrigation	F, ST
Promot WP	Biofa AG (Biofarming systems) - http://www.biofarming.de/	Kenya (temp. 2010), R in Germany	<i>T. harzianum</i> , <i>T. koningii</i>	Horticultural and ornamental crops	Control of damping- off and root rot caused by <i>Pythium</i>	WP	F

WP = Wettable Powder, ST= Stimulant, growth promoter/ enhancer of roots, plant or yield, F = Fungicide, fungal pathogen control, preventive, curative
Adapted from: Woo et al. (2014).

biocontrol genes that can be easily isolated, cloned and characterized includes chitinase, protease, tubulins, glucanase, proteinase, mono-oxygenase, galacturonase, xylanase, cell adhesion proteins, and stress-tolerant genes, they play specific functions in the biocontrol mechanism such as hyphal growth, cell wall degradation, parasitic activity and cell wall degradation (Sharma et al., 2011). The biocontrol genes can be cloned and manufactured in huge quantities for commercial use (Sharma, Kumar et al., 2011; Srivastava et al., 2014).

Pozo et al. (2004) cloned *tvsp1*, a gene from *T. virens* encoding serine protease into *E. coli* using a pET-30 vector, this strain was used to induce resistance of tomato plant against *Rhizoctonia solani* (tomato blight pathogen), the gene according to them also enhance degradation of the pathogen cell wall. In another study, *tri5*, a trichodiene synthase gene was isolated from *T. harzianum* and cloned into a pGEMT vector for controlling the *Fusarium* pathogen of tomatoes (Gallo et al., 2004). Likewise, the expression of *tag83* gene encoding cell wall degrading enzyme α -1,3-glucanase and from *T. asperellum* (Marcello et al., 2010).

Genetic engineering has also been used to enhance the biocontrol abilities of *Trichoderma* fungi. In a study, *T. virens* strains that were transformed with *TvBgn2* and *TvBgn3*, which are genes that encode β -1,3 and β -1,6 glucanase, efficiently inhibited the growth of *R. solani*, *Rhizopus oryzae*, and *Pythium ultimum*, according to Djonovic et al. (2007a), (2007b). Likewise, Donzelli et al. (2001) using pGEM-T vector, successfully cloned an antifungal glucan1,3- β -glucosidase gene called *gluc78* into *T. atroviridae* cells for effective biocontrol of several plant pathogens. This gene was in another study carried out by Saadia et al. (2008) was also cloned a glucose repressor gene from *T. harzianum* and cloned it into *E. coli* for expression of cellulase and xylanase from pathogens using pTZ57R/T plasmid vector. Several other works that have reported various genes in *Trichoderma* for the control of plant pathogens are presented in Table 4.

However, there is a need for adequate knowledge of the biocontrol mechanism of a specific species before its employment as a commercial product (Zaidi et al., 2014). Although, reports from some earlier studies had recognized *Trichoderma harzianum* as the most effective biocontrol agent among the *Trichoderma* species (Sharma, Kumar et al., 2011).

6. Future perspectives

New contributions of new valuable *Trichoderma* species are being

made yearly thanks to molecular or genome analysis. Valuable genes, related to biological control potentials, their defense induction in plants, or stress tolerance, have been identified using these methods. These genes can hence be enhanced using the advancing biotechnological/genetic tools. Their example of the gene that controls complex mechanisms used by *Trichoderma* against pathogens, for example, *T. atroviridum* (Fanelli et al., 2018). In other studies, it was revealed that the bioactivity of secondary metabolites produced by some *Trichoderma* strains helps attack plant pathogens, and the genes that control the secretion of these metabolites were cloned in bacterial cells. Likewise, the metabolites of *T. viridae* and *T. pseudoharzianum* (T113) were toxic against the eggs of *M. incognita* (Khan et al., 2020). More than twenty species of *Trichoderma* were reported to be able to secrete about 390 important non-volatile nematocidal metabolites (Li et al., 2019). In tomato plants, *T. harzianum* T22 and *T. asperellum* T-34 strains were employed for systemic resistance induction against *M. incognita*. This was reflected in the over-expression of *Mi-1.2* gene in the inoculated tomato plants (Pocurull et al., 2020).

Trichoderma genus is already a well-known group of fungi with known importance and applications for sustainable agriculture. It is one of the most studied groups of fungi for use as plant disease control. They can evolve quickly with diversified metabolic pathways leading to the production of several bioactive compounds, enzymes, and secondary metabolites that can, in addition, be explored for human benefits. They have vast importance with potential value commercially and industrially apart from their importance in agriculture. Their ability to produce commercially important enzymes like amylases, cellulases, glucanases, and chitinases are reported every year with interesting results (Harman et al., 2004). Recently, they have been associated with the production of siderophores and silver nanoparticles (Maliszewska et al., 2009; Vahabi et al., 2011). More than 200 species have been reported as biopesticides (Bissett et al., 2015), while many have been well packaged commercially for use as biofungicides (Samuels and Hebbard, 2015).

The mass production of *Trichoderma* is of interest due to its valuable application in the biological control of plant disease pathogens. Commercial production of these bioagents has now come into reality, and several formulations have been reported (Table 1). The potential of *Trichoderma* as a tool for managing the plant's pest is now widely recognized globally. However, this approach has virtually not been well implemented in the management of many tropical crops, especially in

Table 4
Biocontrol genes that have been isolated or expressed in Trichoderma strains and their functions.

S/N	Biocontrol gene	Trichoderma strain	Function	Reference
1	<i>tga1</i> gene	<i>T. atroviride</i> strain P1ATCC 74058	Chitinase formation and production of antifungal metabolites	Reithner et al. (2005)
2	tvsp1 serine protease encoding gene	<i>T. virens</i> wildtype strain Gv29–8 and an arginine auxotrophic strain, Tv10.4	Involved in pathogenesis or biocontrol process of <i>R. solani</i> .	Pozo et al. (2004)
3	1,3- β -glucosidase gene, <i>gluc78</i>	<i>T. atroviride</i> strain P1(ATCC 74058)	Cell wall degradation of pathogens Pythium and Phytophthora	Donzelli et al. (2001)
4	beta tubulin gene	<i>T. harzianum</i> T88	Exhibits biocontrol activities like mycoparasitism, and antifungal activity.	Li and Yang (2007)
5	Chitinase chit42 and proteinase prb1 gene	<i>T. hamatum</i> strain LU593	Mycoparasitic activity against Sclerotinia sclerotiorum	Steyaert et al. (2004)
6	CRE1 gene	<i>T. harzianum</i> E58	Production of cellulase and hemicellulase enzymes.	Saadia et al. (2008)
7	Di/tri peptide transporter gene, <i>ThPTR2</i>	<i>T. harzianum</i> CECT 2413	Involves in mycoparasitic activity against <i>B. cinerea</i>	Vizcaino et al. (2006)
8	Endochitinase encoding gene, <i>ech42</i>	<i>T. harzianum</i> strain P1 74058	Trichoderma expressing this gene show efficient inhibition of <i>Botrytis cinerea</i> and <i>R. solani</i>	Woo et al. (1999)
9	Endopolygalacturonase ThPG1 gene	<i>T. harzianum</i> T34 CECT 2413	Secretion of plant cell wall degrading enzymes against <i>R. solani</i> and <i>P. ultimum</i>	Moran Diez et al. (2009)
10	Endo- β -1–6-glactanase gene	<i>T. viride</i> IFO31137	A type of arabinogalactan proteins that involves in cell-cell adhesion, expansion and cell death.	Kotake et al. (2004)
11	Enzymology Group collection,UFG-ICB, tag 3 gene	<i>T. asperellum</i>	Production of cell wall degrading enzyme glucanase	Marcello et al. (2010)
12	<i>erg1</i> gene	<i>T. harzianum</i> CECT 2413	Silencing of the <i>erg1</i> gene enhances resistance to terbinafine that shows antifungal activity	Cardoza et al. (2006)
13	Genes encoding for NAGases (exc1 and exc2), chitinases (chit42 and chit33), proteases (prb1) and b-glucanases (bgn13.1)	<i>T. harzianum</i> CECT 2413	Mycoparasitic activity against <i>F. oxysporum</i>	Modezar et al. 2011
14	Mitogen Activated Protein kinase gene, <i>TmkA</i>	<i>T. virens</i> strain IMI 304061	Biocontrol activity against pathogens like <i>S. rolfisii</i> and <i>R. solani</i>	Mukherjee et al. (2003)
15	monoxygenase gene	<i>T. hamatum</i> LU593	Antagonist activity against <i>S. sclerotiorum</i> , <i>S. minor</i> and <i>S. cepivorum</i>	Carpenter et al. (2008)
16	proteinase gene <i>prb1</i> and endochitinase gene <i>ech42</i>	<i>T. harzianum</i> strain IMI206040	Regulation of hydrolytic enzymes to enhance parasitism of Trichoderma against Sclerotium rolfisii and Rhizoctonia solani	Cortes et al. (1998)
17	<i>qid74</i> gene	<i>T. harzianum</i> Rifai CECT 2413	Involved in cell protection and adherence to hydrophobic surfaces that helps in antagonism against <i>R. solani</i>	Rosado et al. (2007)
18	serine protease gene SL41	<i>T. harzianum</i>	Biocontrol activity against pathogens	Liu et al. (2009)
19	Sm1 gene, cysteine-rich protein	<i>T. virens</i> strain TvSMOE38	A small cysteine-rich protein that induces defense responses in dicot and monocot plants and in protecting crop diseases	Buensanteai et al. (2010)
20	T34 hsp70 gene	<i>T. harzianum</i> CECT 2413	Increases fungal resistance to heat and abiotic stresses	Hermosa et al. (2011)
21	Taabc2 gene	<i>T. atroviride</i> P1 (ATCC 74058)	Plays key role in antagonism against <i>R. solani</i> , <i>P. ultimum</i> , and <i>B. cinerea</i>	Ruocco et al. (2009)
22	<i>tac1</i> , adenylate cyclase gene	<i>T. virens</i> IMI 304061	Mycoparasitism against <i>R. solani</i> , <i>S. rolfisii</i> , Pythium Spp. and production of secondary metabolism	Mukherjee et al. (2007)
23	TgaA, TgaB genes	<i>T. virens</i> strain IMI 304061	Antagonism against <i>S. rolfisii</i> and <i>R. solani</i>	Mukherjee et al. (2004)
24	Th-Chit gene	<i>T. harzianum</i>	Antifungal activity in transgenic tobacco	Saiprasad et al. (2009)
25	Thctf1 transcription factor gene	<i>T. harzianum</i> CECT 2413	Antifungal activity against <i>R. solani</i> , <i>Fusarium oxysporum</i> and <i>B. cinerea</i> and production of 6-pentyl-2 H-pyran-2	Rubio et al. (2009)
26	Thke11 gene	<i>T. harzianum</i> CECT 2413	Expression of this gene in <i>A. thaliana</i> modulates glucosidase activity, and enhances tolerance to salt and osmotic stresses	Hermosa et al. (2011)
27	<i>tmkA</i> gene	<i>T. virens</i> IMI 304061	Induction of plant systemic resistance and biocontrol activity against <i>R. solani</i> . (Tested in green house condition)	Viterbo et al. (2004)
28	TrCCD1 gene	<i>T. reesei</i> QM9414 (ATCC 26921)	Helps in hyphal growth, conidiospore development and carotenoid pigment production.	HuaZhong et al. 2009
29	<i>tri5</i> gene	<i>T. brevicompactum</i> IBT40841	Production of trichodermin and antifungal activity against <i>C. albicans</i> , <i>C. glabrata</i> and <i>A. fumigatus</i>	Tijerino et al. (2011)
30	Trichodiene synthase gene, <i>tri5</i>	<i>T. harzianum</i> strain ATCC 90237	Production of toxin for inhibiting DNA or protein synthesis, and enhances virulence against <i>Fusarium</i> spp.	Gallo et al. (2004)
31	TvBgn2 and TvBgn3 genes	<i>T. virens</i> Gv29–8	These genes help in encoding cell wall degrading enzymes	Djonovic et al. (2007a), (2007b)
32	TvGST glutathione transferase gene	<i>T. virens</i> (strain IMI 304061)	Enhances cadmium tolerance in plants	Dixit et al. (2011)
33	Xylanase gene, <i>Xyl</i>	Trichoderma strain SY	Helps in breakdown of hemicellulose	Min et al. (2002)
34	β -1,4-endoglucanase gene, <i>egl1</i>	<i>T. longibrachiatum</i> strain CECT2606	Cell wall degrading enzyme for inhibition against <i>Pythium ultimum</i> on cucumber.	Migheli et al. (1998)

Africa. Most of the studies that investigated and reported the diversity of endophytic *Trichoderma* strains on different plant hosts were based on surveys restricted to the United States, Hawaii, and other countries other than the Africas. However, Africa is rich in biodiversity of different plants, which could also be rich in novel species of *Trichoderma*. For example, del Carmen et al. (2021) and Schulz and Boyle (2005) investigated the endophytic fungi associated with coffee plants observing that the fungi from America and Hawaii were dominated by *Colletotrichum*, *Fusarium*, *Penicillium*, *Pestalotia*, and *Xylaria* species which are in most cases existing as opportunistic endophytes of their host plants. The study from Africa in contrast, yielded more of *Trichoderma* as endophytic fungi; in detail, they reported endophytic *Trichoderma* from the aerial tissues of coffee plants, including four new species (Leylaie and Zafari, 2018). The new taxa described by these authors may be geographically restricted to Africa or even to coffee plants.

The Africans are rich in diversity of *Trichoderma*, especially in the Neotropics. Some studies have reported a close association between *Trichoderma* species and *C. arabia* from Ethiopia (Mulaw et al., 2010, 2013). These studies focused majorly on the rhizosphere and root tissue species. They reported several species of *Trichoderma* such as *T. asperelloides*, *T. atroviride*, *T. gamsii*, *T. hamatum*, *T. koningiopsis*, *T. longibrachiatum*, *T. spirale*, and *T. sensulato*. *T. hamatum*, *T. spirale*, and *T. koningiopsis* are cosmopolitan species commonly associated with stems, leaves, berries from tropical habitats and the soil (Kubicek et al., 2003; Hoyos-Carvajal et al., 2009; Samuels et al., 2006; Druzhinina et al., 2005). Some species, such as *T. koningiopsis* and *T. spirale* have been isolated from more than one plant tissue from the leaf and stem of *C. canephora*, *C. arabica*, and tomatoes. Other reports have also identified *T. koningiopsis*, *T. hamatum*, and *T. spirale* as endophytes of tropical woody plants, notably cacao and rubber (Samuels and Hebbbar, 2015). *T. atroviride*, *T. guizhouense*, *T. breve*, and *T. theobromicola* are very common in the tropical soils, mushroom compost, in leaf-cutting ant colonies decaying wood and bark, they have also been reported as endophytes of *Theobroma* sp. (Malvaceae) (Samuels and Hebbbar, 2015; Chaverri et al., 2015; Montoya et al., 2016).

T. theobromicola is an endophyte of cacao sapwood native to South America (2006; Almeida et al., 2018), while *T. breve*, native to China was recently isolated from soil (Chen and Zhuang, 2017). They both have been reported as new geographical pantropical endophytes from Africa (del Carmen et al., 2021). Many *Trichoderma* such as *T. atroviride*, *T. hamatum*, *T. longibrachiatum*, *T. reesei*, and *T. virens* have been characterized as mycoparasitic fungi (Mukherjee et al., 2013; Kubicek et al., 2019). They have a wide host range against several plant pathogenic fungi like *Alternaria alternata*, *Botrytis cinerea*, *Fusarium* sp., *Rhizoctonia solani*, as well as the Oomycetes like *Pythium ultimum* (Karlsson et al., 2017). Those from Africa as revealed by del Carmen et al. (2021) included *T. aggressivum*, *T. andinense*, *T. parareesei*, *T. petersenii*, and *T. pseudopyramidal* are mycoparasites of *H. vastatrix* and can also attack *Hemileia* rusts of coffee plants. Other mycoparasitic *Trichoderma* species isolated by these authors from Africa were *T. atroviride*, *T. hamatum*, and *T. virens*. *Trichoderma pseudopyramidale*. Authors advocated that these fungi from Africa deserved attention with vast potential for use in the biological control of plant diseases.

While many reports are identifying native *Trichoderma* strains from Africa, there is limited information on their new capabilities or details on their potential application or mechanism of action. Most studies from Africa are data monitoring experiments without an in-depth characterization of the fungi actions. Information on the ecology of *Trichoderma* species from Africa at large is relatively circumscribed del Carmen et al. (2021), in their work, observed that about 60% of their isolated plant endophytic fungi of wild coffee from both Cameroon and Ethiopia were *T. botryosum* and *T. pseudopyramidale*. These strains were reported as good mycoparasites of *Hemileia* rusts and suggested for use as the biological control in Central America, where this disease is endemic on coffee plants (Avelino, 2015; Ward et al., 2017; Oxfam International, 2014). There are claims that native *Trichoderma* bioagents can be more

virulent on foreign plant pathogens or vice versa (Jackson et al., 2012). However, the diversity of *Trichoderma* in Africa is still not well studied, as compared to other parts of the world (Sadfi-Zouaoui et al., 2009). To date, only a few species are reported from Africa, while there are fewer in-depth works on a wide range of characterization of *Trichoderma* from natural habitats in Africa (Askew and Laing, 1994; Chaverri and Samuels, 2004; De Respins et al., 2010; Mutawila et al., 2011). Most of the few reports of native African *Trichoderma* species were not on its biodiversity on large geographical areas but majorly on either in-vitro biological control or application on a few study areas. Only a few studies in Africa isolated *Trichoderma* from natural habitats or outside soil environments.

The genetic pool of major bioagents in this group are those from the above-ground habitat (López-Quintero et al., 2013). There is limited information about the ecology of new strains. *Trichoderma* species from Africa in general coupled with their potential application. The shelf-life of these bioagents under different formulations is a significant factor affecting their commercial distribution. *T. harzianum* and *T. viride* are well-known bioagents in different formulations. They have been grown on solid substrates like wheat straw, wheat bran, coffee husk, sorghum grains, and much other biomass to enhance their life span. Fermented molasses and brewer's yeast were suggested to prepare *Trichoderma* formulations (Agosin et al., 1997; Carmen et al., 2021) while some organic matter farmyard manure, as well as seasoned press, have also been suggested.

Most African nations had instituted integrative programmes tailored towards enhancing agricultural practices but most of the programmes failed. It should be noted that the result of an unending cycle of restructuring and recapitalization in agricultural production inputs as commonly practice, would be short lived when dynamic approach in disease management practices are not embraced. Hence, Africa's agricultural prosperity is hinged on her embracing indigenous bioresources in pest and disease management such as *Trichoderma*-based formulations investigated against tomato root rot in this review. More so, it is essential to reinforce the existing interlinked network system among the researchers, extension workers and farmers, to aid the timely acceptance and utilization of indigenously developed biological control agents to attain optimum production.

7. Conclusion

Africa contributes immensely to the global supply of tomatoes, yet many of its productions are inhibited either by abiotic or biotic stressors. While the adoption of bioagents as eco-friendly management of crop diseases is gaining global acceptance, most African countries still rely on chemical-based treatments. Whereas, *Trichoderma* has been recognized for its effectiveness in plant disease management, instilling of disease resistance, and enhancement of plant growths, among other researched qualities. To date, Africa has the least number of registered and commercialized *Trichoderma*-based formulations that have been engineered as broad-spectrum or specific targets such as the root rot of tomato. The peculiar constraints limiting agricultural productions in the African nations need to be addressed. More so, there calls for urgent collaborative efforts among the African governments, researchers, and the stakeholders in agriculture, to research into indigenous *Trichoderma*-based formulations, register and commercialize it while ensuring an enabling environment for its use and the smooth sailing of agricultural activities for both small- and large-scale farmers.

Author Contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Funding

OOB recognizes National Research Fund (NRF South Africa) for grants (UID123634 and UID132595) that support work in her research group.

Declaration of Competing Interest

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgment

OMO appreciates the Centro Internazionale Cooperazione per lo Sviluppo (CICOPS) of the University of Pavia for financing her research in the Department of Earth and Environmental Sciences, University of Pavia, Italy. She also thanks Prof Solveig Tosi of Mycology Laboratory, Department of Earth & Environmental Sciences, University of Pavia, Italy, for her supervisory role in the research and manuscript writing.

References

- Aamir, M., Rai, K.K., Zehra, A., Dubey, M.K., Kumar, S., Shukla, V., Upadhyay, R.S., 2020. Microbial Bioformulation-based Plant Biot stimulants: A Plausible Approach Toward Next Generation of Sustainable Agriculture. *Microbial Endophytes*. Elsevier, pp. 195–225.
- Agosin, E., Volpe, D., Munoz, G., San Martin, R., Crawford, A., 1997. Effect of culture conditions on spore shelf life of the biocontrol agent *Trichoderma harzianum*. *World J. Microbiol. Biotechnol.* 7 (13), 225–232.
- Ajillogba, C.F., Babalola, O.O., 2013b. Integrated management strategies for tomato *Fusarium* wilt. *Biocontrol Sci. (Jpn.)* 18 (3), 117–127. ISSN 13424815) J-Stage. http://www.jstage.jst.go.jp/article/bio/18/3/18_117/pdf.
- Ajillogba, C.F., Babalola, O.O., Ahmad, F., 2013a. Antagonistic effects of *Bacillus* species in biocontrol of tomato *Fusarium* wilt. *Stud. Ethno-Med.* 7 (3), 205–216. ISSN 0973-5070. <http://www.krepublishers.com/02-Journals/S-EM/EM-07-0-000-13-Web/S-EM-07-3-000-13-Abst-PDF/S-EM-07-3-205-13-296-Ajillogba-C-F/S-EM-07-3-205-13-043-Ajillogba-C-F-Ab.pdf>.
- Alabouvette, C., Olivain, C., Migheli, Q., Steinberg, C., 2009. Microbiological control of soil-borne phytopathogenic fungi with special emphasis on wilt-inducing *Fusarium oxysporum*. *New. Phytol.* 184, 529–544.
- Almeida, K.A., Armesto, C., Monteiro, F.P., de Souza, J.T., 2018. Diversity of *Trichoderma* species isolated from dead branches and sawdust of *Theobroma cacao* trees. *Trop. Plant Pathol.* 43, 90–94. <https://doi.org/10.1007/s40858-017-0191-z>.
- Amin, F., Razdan, V.K., 2010. Potential of *Trichoderma* species as biocontrol agents of soil-borne fungal propagules. *J. Phytol.* 2, 38–41.
- Arah, I.K. (2015). An overview of post-harvest challenges facing tomato production in Africa. In: African Studies Association of Australasia and the Pacific (AFSAAP) 37th Annual Conference Africa: Diversity and Development. Dunedin, New Zealand. pp. 1–21.
- Askew, D.J., Laing, M.D., 1994. The in vitro screening of 118 *Trichoderma* isolates for antagonism to *Rhizoctonia solani* and an evaluation of different environmental sites of *Trichoderma* as sources of aggressive strains. *Plant Soil* 159, 277–281.
- Avelino, J., et al., 2015. Te coffee rust crises in Colombia and Central America (2008–2013): impacts, plausible causes, and proposed solutions. *Food Sect.* 7, 303–321. <https://doi.org/10.1007/s12571-015-0446-9>.
- Babu, K., Pallavi, P., 2013. Isolation, identification and mass multiplication of *Trichoderma* an important bio-control agent. *Int. J. Pharm. Life Sci.* 4 (1), 2320–2323.
- Bal, U., Altintas, S., 2006. Effects of *Trichoderma harzianum* on the yield and fruit quality of tomato plants (*Lycopersicon esculentum*) grown in an unheated greenhouse. *Aust. J. Exp. Agric.* 46 (1), 131–136.
- Belay, F., et al., 2016. Evaluation of some botanicals and *Trichoderma harzianum* against root-knot nematode (*Meloidogyne incognita* (Kofoid and White) Chit wood) in tomato. *J. Entomol. Nematol.* 8, 11–18.
- Bettiol, W., et al., 2012. Prod. Comer. à base De. Agentes De. biocontrol De. Doença De. Plantas Vol. 88, 1–156. Embrapa Meio Ambiente (Document), Jaguariuna, 2012.
- Bhagat, D., Koche, M., Ingle, R.W., Mohod, Y.N., 2010. Evaluate the suitability of locally available substrates for mass multiplication of cellulolytic fungi and bacteria. *J. Plant Dis. Sci.* 5, 27–29.
- Bigirimana, J., Meyer, G., de Poppe, J., Elad, Y., Hofte, M., 1997. Induction of systemic resistance on bean (*Phaseolus vulgaris*) by *Trichoderma harzianum*. *Med. Fac. Landbouw Univ. Gent* 62, 1001–1007.
- Bissett, J., Gams, W., Jaklitsch, W., Samuels, G.J., 2015. *Trichoderma* names in the year 2015. *IMA Fungus* 6, 263–295. <https://doi.org/10.5598/imafungus.2015.06.02.02>.
- Braithwaite, M., et al., 2016. The density-dependent effect of initial nematode population levels on the efficacy of *Trichoderma* as a bio-nematicide against *Meloidogyne* hapla on tomato. *Australas. Plant Pathol.* 45, 473–479.
- Brotman, Y., Briff, E., Viterbo, A., Chet, I., 2008. Role of swollenin, an expansin-like protein from *Trichoderma*, in plant root colonization. *Plant Physiol.* 147, 779–789.
- Buensanteai, N., Mukherjee, P.M., Horwitz, B.A., Cheng, C., 2010. Expression and purification of biologically active *Trichoderma virens* proteinaceous elicitor Sm1 in *Pichia pastoris*. *Protein Express Purif.* 72, 131–138.
- 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.
- Calin, M., et al., 2019. Applications of Fungal Strains with Keratin-Degrading and Plant Growth Promoting Characteristics. *Agronomy* 9, 543.
- Capobianco-Uriarte, MdM., Aparicio, J., De Pablo-Valenciano, J., Casado-Belmonte, Md. P., 2021. The European tomato market. An approach by export competitiveness maps. *PLoS ONE* 16 (5), e0250867. <https://doi.org/10.1371/journal.pone.0250867>.
- Cardoza, R.E., Vizcaino, J.A., Hermosa, M.R., Gonzalez, F.J., Llobell, A., Monte, M., Gutierrez, S., 2006. Cloning and characterization of the *erg1* gene of *Trichoderma harzianum*: Effect of the *erg1* silencing on ergosterol biosynthesis and resistance to terbinafine. *Fungal Genet. Biol.* 43, 164–178.
- del Carmen, M., Rodríguez, H., Evans, H.C., de Abreu, L.M., de Macedo, D.M., Ndacnou, M.K., Bekele, K.B., Barreto, R.W., 2021. New species and records of *Trichoderma* isolated as mycoparasites and endophytes from cultivated and wild coffee in Africa. *Sci. Rep.*, 5671 <https://doi.org/10.1038/s41598-021-84111-1>.
- Carpenter, M.A., Ridgway, H.J., Stringer, A.M., Hay, A.J., Stewart, A., 2008. Characterization of a *Trichoderma hamatum* monooxygenase gene involved in antagonistic activity against fungal plant pathogens. *Curr. Genet.* 53, 193–205.
- Chaverri, P., et al., 2015. Systematics of the *Trichoderma harzianum* species complex and the re-identification of commercial biocontrol strains. *Mycologia* 107, 558–590. [https://doi.org/10.3852/14-147\(2015\)](https://doi.org/10.3852/14-147(2015)).
- Chaverri, P., Samuels, G.J., 2004. *Hypocrea/Trichoderma* (Ascomycota, Hypocreales, Hypocreaceae): species with green ascospores. *Stud. Mycol.* 48, 1–116.
- Chaverri, P., Gazis, R., Samuels, G.J., 2011. *Trichoderma amazonicum*, a new endophytic species on *Hevea brasiliensis* and *H. guianensis* from the Amazon basin. *Mycologia* 103, 139–151.
- Chen, K., Zhuang, W., 2017. Discovery from a large-scaled survey of *Trichoderma* in soil of China. *Sci. Rep.* 7, 1–37. <https://doi.org/10.1038/s41598-017-07807-3>.
- Chet, I., Inbar, J., Hadar, I., 1997. Fungal antagonists and mycoparasites. In: Wicklow, D. T., Söderström, B. (Eds.), *The Mycota IV: Environmental and microbial relationships*. Springer-Verlag, Berlin, pp. 165–184.
- Christy Jeyaseelan, E., Tharmila, S., Niranjana, K., 2012. Antagonistic activity of *Trichoderma* spp. and *Bacillus* spp. against *Pythium aphanidermatum* isolated from tomato damping off. *Arch. Appl. Sci. Res.* 4 (4), 1623–1627.
- Contreras-Cornejo, H.A., et al., 2020. Interactions of *Trichoderma* with Plants, Insects, and Plant Pathogen Microorganisms: Chemical and Molecular Bases. In: Merillon, J.–M., Ramawat, K.G. (Eds.), *Co-Evolution of Secondary Metabolites*. Springer International Publishing, Cham, pp. 263–290.
- Contreras-Cornejo, H.A., Macías-Rodríguez, L., Beltran-Pena, E., Herrera Estrella, A., Lopez-Bucio, J., 2011. *Trichoderma*-induced plant immunity likely involves both hormonal and camalexin dependent mechanisms in *Arabidopsis thaliana* and confers resistance against necrotrophic fungi *Botrytis cinerea*. *Plant Signal Behav.* 6, 1554–1563.
- Cortes, C., Gutierrez, A., Olmedo, V., Inbar, J., Chet, I., Herrera Estrella, A., 1998. The expression of genes involved in parasitism by *Trichoderma harzianum* is triggered by a diffusible factor. *Mol. Genet. Evol.* 260, 218–225.
- Das, B.C., Das, B.K., Dutt, A. P., Sarmah, D.K., 2006. Bioformulation of *Trichoderma harzianum* Rifai for management of soybean stem-rot caused by *Rhizoctonia solani* Kuhn. *J. Biol. Cont.* 20, 57–64.
- De Meyer, G., Bigirimana, J., Elad, Y., Hofte, M., 1998. Induced systemic resistance in *Trichoderma harzianum* T39 biocontrol of *Botrytis cinerea*. *Eur. J. Plant Pathol.* 104, 279–286.
- De Respins, S., Vogel, G., Benagli, C., Tonolla, M., Petrini, O., Samuels, G.J., 2010. MALDI-TOF MS of *Trichoderma*: a model system for the identification of microfungi. *Mycol. Prog.* 9, 79–100.
- Debbi, A., Bouregghda, H., Monte, E., Hermosa, R., 2018. Distribution and genetic variability of *Fusarium oxysporum* associated with tomato diseases in Algeria and a biocontrol strategy with indigenous *Trichoderma* spp. *Front. Microbiol.* 9, 282.
- del Carmen, H., Rodríguez, M., Evans, H.C., de Abreu, L.M., et al., 2021. New species and records of *Trichoderma* isolated as mycoparasites and endophytes from cultivated and wild coffee in Africa. *Sci. Rep.* 11, 5671. <https://doi.org/10.1038/s41598-021-84111-1>.
- Dixit, P., Mukherjee, P.K., Ramachandran, V., Eapen, S., 2011. Glutathione transferase from *Trichoderma virens* enhances cadmium tolerance without enhancing its accumulation in transgenic *Nicotiana tabacum*. *PLoS ONE* 6 (1), 1–15.
- Djonovic, S., Vittone, G., MendozaHerrera, A., Kenerley, C.M., 2007a. Enhanced biocontrol activity of *Trichoderma virens* transformants constitutively coexpressing β -1,3- and β -1,6-glucanase genes. *Mol. Plant Pathol.* 8 (4), 469–480.
- Djonovic, S., Vittone, G., MendozaHerrera, A., Kenerley, C.M., 2007b. Enhanced biocontrol activity of *Trichoderma virens* transformants constitutively coexpressing β -1,3- and β -1,6-glucanase genes. *Mol. Plant Pathol.* 8 (4), 469–480.
- Donzelli, B.G.G., Lorito, M., Scala, F., Harman, G.E., 2001. Cloning, sequence and structure of a gene encoding an antifungal glucan 1,3- β -glucosidase from *Trichoderma atroviride* (*T. harzianum*). *Gene* 277, 199–208.
- Druzhinina, I.S., et al., 2005. An oligonucleotide barcode for species identification in *Trichoderma* and *Hypocrea*. *Fungal Gen. Biol.* 42, 813–828. <https://doi.org/10.1016/j.fgb.2005.06.007>.
- Druzhinina, I.S., et al., 2011. *Trichoderma*: Te genomics of opportunistic success. *Nat. Rev.* 9, 749–759. <https://doi.org/10.1038/nrmicro2637>.

- Druzhinina, I.S., Kopchinskiy, A.L.G., Kubicek, C.P., 2006. The first 100 *Trichoderma* species characterized by molecular data. *Mycoscience* 47, 55–64. <https://doi.org/10.1007/S10267-006-0279-7>.
- Dube, J., Ddamulira, G., Maphosa, M., 2020. Tomato breeding in sub-Saharan Africa—Challenges and opportunities: a review. *Afr. Crop Sci. J.* 28 (1), 131–140.
- 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.
- El-Abeid, S.E., Ahmed, Y., Daròs, J.A., Mohamed, M.A., 2020. Reduced graphene oxide nanosheet-decorated copper oxide nanoparticles: a potent antifungal nanocomposite against *Fusarium* root rot and wilt disease of tomato and pepper plants. *Nanomaterials* 10, 1001.
- Elad, Y., Barak, R., Chet, I., 1984. Parasitism of sclerotia of *Sclerotium rolfsii* by *Trichoderma harzianum*. *Soil Biol. Biochem.* 16, 381–386. [https://doi.org/10.1016/0038-0717\(84\)90037-3](https://doi.org/10.1016/0038-0717(84)90037-3).
- El-Mougy, N.S., Abdel-Kader, M.M., Abdel-Kareem, F., Embaby, E.I., El-Mohamady, R., Abd El-Khair, H., 2011. Survey of fungal diseases affecting some vegetable crops and their rhizospheric soilborne microorganisms grown under protected cultivation system in Egypt. *Res. J. Agric. Biol. Sci.* 7 (2), 203–211.
- Elsahawy, I., Abouelnasr, H.M., Lashin, S.M., Darwesh, O.M., 2018. First report of *Pythium aphanidermatum* infecting tomato in Egypt and its control using biogenic silver nanoparticles. *J. Plant Prot. Res.* 58 (2), 137–151.
- Eltbany, N., et al., 2019. Enhanced tomato plant growth in soil under reduced P supply through microbial inoculants and microbiome shifts. *FEMS Microbiol. Ecol.* 95.
- Etaaware, P.M., Oyetuji, O.J., 2019. Endemic disease of cultivated tomato and microbial screening for infectious agents in Ibadan, Niger. *Res. Rev.: J. Agric. Allied Sci.* 8, 44–54.
- Evans, H.C., Holmes, K.A., Tomas, S.E., 2003. Endophytes and mycoparasites associated with an indigenous forest tree, *Teobroma gileri*, in Ecuador and a preliminary assessment of their potential as biocontrol agents of cocoa diseases. *Mycol. Prog.* 2, 149–160. <https://doi.org/10.1007/s11557-006-0053-4>.
- Ewekeye, T.S., Odebo, A.C., 2021. Isolation and identification of fungi associated with solanum lycopersicum L.(Tomato) leaves in alapoti, ogun state nigeria. *Int. J. Pathog. Res.* 1–11.
- Faneli, F., et al., 2018. Genomic characterization of *Trichoderma atrobrunneum* (T. harzianum species complex) ITEM 908: insight into the genetic endowment of a multi-target biocontrol strain. *BMC Genom.* 19, 662.
- FAOSTAT (2021, November 3) <https://www.fao.org/faostat/en/#data/QCL>.
- Figlan, S., Ntushelo, K., Mwadzingeni, L., Terefe, T., Tsilo, T.J., Shimelis, H., 2020. Breeding Wheat for Durable Leaf Rust Resistance in Southern Africa: Variability, Distribution, Current Control Strategies, Challenges, and Future Prospects. *Front. Plant Sci.* 11, 549. <https://doi.org/10.3389/fpls.2020.00549>.
- Filizola, P.R.B., Luna, M.A.C., de Souza, A.F., Coelho, I.L., Laranjeira, D., Campos-Takaki, G.M., 2019. Biodiversity and phylogeny of novel *Trichoderma* isolates from mangrove sediments and potential of biocontrol against *Fusarium* strains. *Micro Cell Fact.* 18 (1), 89.
- Gallo, A., Mule, G., Favilla, M., Altomare, C., 2004. Isolation and characterization of a trichodiene synthase homologous gene in *Trichoderma harzianum*. *Physiol. Mol. Plant Pathol.* 65, 11–20.
- Gangadharan, K., Jeyarajan, R., 1990. Mass multiplication of *Trichoderma* spp. *J. Biol. Cont.* 4, 70–71.
- Gaziz, R., Chaverri, P., 2010. Diversity of fungal endophytes in leaves and stems of wild rubber trees (*Hevea brasiliensis*) in Peru. *Fungal Ecol.* 3, 240–254. <https://doi.org/10.1016/j.funeco.2009.12.001>.
- Ghazanfar, M.U., Raza, M., Raza, W., Qamar, M.I., 2018. *Trichoderma* as potential biocontrol agent, its exploitation in agriculture: a review. *Plant Prot.* 2 (3).
- Goudjal, Y., Zamoum, M., Sabou, N., et al., 2016. Potential of endophytic *Streptomyces* spp. for biocontrol of *Fusarium* root rot disease and growth promotion of tomato seedlings. *Biocontrol. Sci. Technol.* 26 (12), 1691–1705.
- Gull, C., Labuschagne, N., Botha, W.J., 2004. *Pythium* species associated with wilt and root rot of hydroponically grown crops in South Africa. *Afr. Plant Prot.* 10 (2), 109–116.
- Hamza, A., Mohamed, A., Derbalah, A., 2016. Unconventional alternatives for control of tomato root rot caused by *Rhizoctonia solani* under greenhouse conditions. *J. Plant Prot. Res.* 56 (3), 298–305.
- Harman, G.E., 2000. Myths and dogmas of biocontrol changes in perceptions derived from research on *Trichoderma harzianum* T-22. *Plant Dis.* 84 (4), 377–393.
- Harman, G.E., 2006. Overview of mechanisms and uses of *Trichoderma* spp. *Phytopathology* 96 (2), 190–194.
- Harman, G.E., Howell, C.R., Viterbo, A., Chet, I., Lorito, M., 2004. *Trichoderma* species—opportunistic, avirulent plant symbionts. *Nat. Rev.* 2, 43–56. <https://doi.org/10.1038/nrmicro797>.
- Harman, G.E., Herrera-Estrella, A.H., Benjamin, A., Matteo, L., 2012. Special issue: *Trichoderma* – from Basic Biology to Biotechnology. *Microbiology* 58, 1–2.
- Harman, G.E., Doni, F., Khadka, R.B., Uphof, N., 2019. Endophytic strains of *Trichoderma* increase the plants' photosynthetic capability. *J. Appl. Microbiol.* 31, 12. <https://doi.org/10.1111/jam.14368>.
- Heflish, A.A., Abdelkhalek, A., Al-Askar, A.A., Behiry, S.I., 2021. Protective and Curative Effects of *Trichoderma asperelloides* Ta41 on Tomato Root Rot Caused by *Rhizoctonia solani* Rs33. *Agronomy* 11, 1162.
- Hermosa, R., Botella, L., Keck, M., Jimenez, J.A., MonteroBarrientos, M., Arbona, V., GomezCadenas, A., Monte, E., Nicolas, C., 2011. The overexpression in *Arabidopsis thaliana* of a *Trichoderma harzianum* gene that modulates glucosidase activity, and enhances tolerance to salt and osmotic stresses. *J. Plant Physiol.* 168, 1295–1302.
- Hermosa, R., Viterbo, A., Chet, I., Monte, E., 2012. Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* 158, 17–25. <https://doi.org/10.1099/mic.0.052274-0>.
- Hill, R.A., Stewart, A., Hohmann, P., & Braithwaite, M. (2010). Enhancing Growth and Health of *Pinus radiata* in New Zealand and *Acacia mangium* in Malaysia with selected *Trichoderma* isolates. *Proceedings of Trichoderma-Molecular mechanisms and applications of biocontrol in agriculture, Oct 12–15, 2010, Haifa, Israel*, 28.
- Howell, C., 2003. Mechanisms employed by *Trichoderma* species in the biological control of plant diseases: the history and evolution of current concepts. *Plant Dis.* 87 (1), 4–10.
- Hoyos-Carvajal, L., Orduz, S., Bissett, J., 2009. Genetic and metabolic biodiversity of *Trichoderma* from Colombia and adjacent neotropical regions. *Fungal Genet. Biol.* 46, 615–631. <https://doi.org/10.1016/j.fgb.2009.04.006>.
- Hyde, K.D., et al., 2019. The amazing potential of fungi: 50 ways we can exploit fungi industrially. *Fungal Divers* 97, 1–136. <https://doi.org/10.1007/s13225-019-00430-9>.
- Ikrum, M., et al., 2019. *Trichoderma reesei* improved the nutrition status of wheat crop under salt stress. *J. Plant Interact.* 14, 590–602. <https://doi.org/10.1080/17429145.2019.1684582>.
- Inglis, P.W., et al., 2020. *Trichoderma* from Brazilian garlic and onion crop soils and description of two new species: *Trichoderma azevedoi* and *Trichoderma pberdyi*. *PLoS ONE* 15, e0228485. <https://doi.org/10.1371/journal.pone.0228485>.
- Jackson, D., Skillman, J., Vandermeer, J., 2012. Indirect biological control of the coffee leaf rust, *Hemileia vastatrix*, by the entomogenous fungus *Lecanicillium lecanii* in a complex coffee agroecosystem. *Biol. Control* 61, 89–97. <https://doi.org/10.1016/j.biocontrol.2012.01.004>.
- Jiang, Y., et al., 2016. *Trichoderma* biodiversity of agricultural fields in east China reveals a gradient distribution of species. *PLoS ONE* 11, e0160613. <https://doi.org/10.1371/journal.pone.0160613>.
- Jin, X., Harman, G.E., Taylor, A.G., 1991. Conidial biomass and desiccation tolerance of *Trichoderma harzianum* produced at different medium water potentials. *Biol. Cont.* 7, 243–267.
- Karlsson, M., Atanasova, L., Jensen, D.F., Zeilinger, S., 2017. Necrotrophic mycoparasites and their genomes. *Microbiol. Spectr.* 5, 1–21. <https://doi.org/10.1128/microbiolspec.FUNK-0016-2016>.
- Kashyap, P.L., Solanki, M.K., Kushwaha, P., et al., 2020. Biocontrol potential of salt-tolerant *Trichoderma* and *Hypocrea* isolates for the management of tomato root rot under saline environment. *J. Soil Sci. Plant Nutr.* 20, 160–176. <https://doi.org/10.1007/s42729-019-00114-y>.
- Keswani, C., Mishra, S., Sarma, B., Singh, S., Singh, H., 2014. Unraveling the efficient applications of secondary metabolites of various *Trichoderma* spp. *Appl. Microbiol. Biotechnol.* 98, 533–544.
- Khan, R.A.A., et al., 2020. Bioactive Secondary Metabolites from *Trichoderma* spp. against Phytopathogenic Bacteria and Root-Knot Nematode. *Microorganisms* 8, 23.
- Kiarie, S., Nyasani, J.O., Gohole, L.S., Maniania, N.K., Subramanian, S., 2020. Impact of fungal endophytes on induced resistance to thrips- and aphid-transmitted viruses. *Plants* 6, 416. <https://doi.org/10.3390/plants9040416>.
- Köhl, J., Kolnaar, R., Ravensberg, W.J., 2019. Mode of Action of Microbial Biological Control Agents Against Plant Diseases: Relevance Beyond Efficacy. *Front. Plant Sci.* 10, 845. <https://doi.org/10.3389/fpls.2019.00845>.
- Kotake, T., Kaneko, S., Kubomoto, A., Haque, M.A., Kobayashi, H., Tsumuraya, Y., 2004. Molecular cloning and expression in *Escherichia coli* of a *Trichoderma viride* endo-β-(1–6)-galactanase gene. *Biochem. J.* 377, 749–755.
- Kouam, E.B., Dongmo, J., Djeugap, J., 2018. Exploring morphological variation in tomato (*Solanum lycopersicum*): a combined study of disease resistance, genetic divergence and association of characters. *Agric. Trop. Subtrop.* 51, 71–82.
- Kubicek, C.P., et al., 2019. Evolution and comparative genomics of the most common *Trichoderma* species. *BMC Genom.* 20, 485. <https://doi.org/10.1186/s12864-019-5680-7>.
- Kubicek, C.P., Bissett, J., Druzhinina, I.S., Kullnig-Gradinger, C., Szakacs, G., 2003. Genetic and metabolic diversity of *Trichoderma*: A case study on South-East Asian isolates. *Fungal Genet. Biol.* 38, 310–319. [https://doi.org/10.1016/S1087-1845\(02\)00583-2](https://doi.org/10.1016/S1087-1845(02)00583-2).
- Kuehne, G., Llewellyn, R., Pannell, D., et al., 2017. Predicting farmer uptake of new agricultural practices: A tool for research, extension and policy. *Agric. Syst.* 156, 115–125. <https://doi.org/10.1016/j.agsy.2017.06.007>.
- Kuzmanovska, B., Rusevski, R., Jankulovska, M., Oreshkovikj, K., 2018. Antagonistic activity of *Trichoderma asperellum* and *Trichoderma harzianum* against genetically diverse *Botrytis cinerea* isolates. *Chil. J. Agric. Res.* 78 (3), 391–399. <https://doi.org/10.4067/s0718-58392018000300391>.
- Labuschagne, N., Thompson, A.H., Botha, W.J., 1994. Stem and root rot of tomato caused by *Phytophthora capsici* – a first report from South Africa. *Plant Dis.* 87 (12), 1540.
- Latorre, B.A., Lillo, C., Rioja, M.E., 2001. Eficacia de los tratamientos fungicidas para el control de *Botrytis cinerea* de la vid en función de la época de aplicación. *Cienc. Inv. Agric.* 28, 61–66.
- Lewis, J., Papavizas, G., 1987. Application of *Trichoderma* and *Gliocladium* in alginate pellets for control of *Rhizoctonia* damping-off. *Plant Pathol.* 36 (4), 438–446.
- Leylaie, S., Zafari, D., 2018. Antiproliferative and antimicrobial activities of secondary metabolites and phylogenetic study of endo-phytic *Trichoderma* species from *Vinca*. *Plants. Front. Microbiol.* 9, 1484. <https://doi.org/10.3389/fmicb.2018.01484>.
- Li, M., Yang, Q., 2007. Isolation and characterization of a β-tubulin gene from *Trichoderma harzianum*. *Biochem. Genet.* 45, 529–534.
- Li, M.-F., et al., 2019. Non-Volatile Metabolites from *Trichoderma* spp. *Metabolites* 9, 58.
- Liu, Y., Yang, Q., Song, J., 2009. A new serine protease gene from *Trichoderma harzianum* is expressed in *Saccharomyces cerevisiae*. *Appl. Biochem. Microbiol.* 45 (1), 22–26.

- López-Quintero, C.A., Atanasova, L., Franco-Molano, A.E., Gams, W., Komon-Zelazowska, M., Theelen, B., Müller, W.H., Boekhout, T., Druzhinina, I., 2013. DNA barcoding survey of *Trichoderma* diversity in soil and litter of the Colombian lowland Amazonian rainforest reveals *Trichoderma strigosellum* sp. nov. and other species. *Antonie Van Leeuwenhoek* 104, 657–674.
- Maliszewska, I., Aniszewicz, L., Sadowski, Z., 2009. Biological synthesis of gold nanostructures using the extract of *Trichoderma koningii*. *Acta Phys. Pol. A* 116, 163–165.
- Manandhar, S., Pant, B., Manandhar, C., Baidya, S., 2019. In-vitro evaluation of bio-control agents against soil borne plant pathogens. *J. Nep. Agric. Res. Counc.* 5, 68–72.
- Marcello, C.M., Steindorff, A.S., Silva, S.P., Silva, R.N., Bataus, L.A.M., 2010. Expression analysis of the exo- β -1,3-glucanase from the mycoparasitic fungus *Trichoderma asperellum*. *Microbiol. Res.* 165, 75–81.
- Masip, G., Sabalza, M., Pérez-Massot, E., Banakar, R., Cebrian, D., Twyman, R.M., Christou, P., 2013. Paradoxical EU agricultural policies on genetically engineered crops. *Trends Plant Sci.* 18 (6), 312–324.
- Mata-Nicolás, E., Montero-Pau, J., Gimeno-Paez, E., Garcia-Carpintero, V., Ziarsolo, P., Menda, N., Van, der Knaap, E., 2020. Exploiting the diversity of tomato: the development of a phenotypically and genetically detailed germplasm collection. *Hortic. Res.* 7 (1), 1–14.
- Medeiros, F.H.V., et al., 2010. A novel, integrated method for management of witches' broom disease of cacao in Bahia, Brazil. *Crop Prot.* 29, 704–711. <https://doi.org/10.1016/j.cropro.2010.02.006>.
- Meller, H.Y., Haile, M.Z., David, D., Borenstein, M., Shulchani, R., Elad, Y., 2013. Induced systemic resistance against grey mould in tomato (*Solanum lycopersicum*) by benzoethiadiazole and *Trichoderma harzianum* T39. *Phytopathology* 104, 150–157.
- Meyer, R.S., DuVal, A.E., Jensen, H.R., 2012. Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *N. Phytol.* 196 (1), 29–48.
- Migheli, Q., Gonzalez-Candelas, L., Deallesi, L., Camponogara, A., Ramon Vidal, D., 1998. Transformants of *Trichoderma longibrachiatum* overexpressing the β -1,4-endoglucanase gene *egl1* show enhanced biocontrol of *Pythium ultimum* on cucumber. *Biol. Control* 88 (7), 673–677.
- Min, Y.S., Kim, B.G., Lee, C., Ho Gil, H., Joong, Hoon, A.H.N., 2002. Purification, Characterization, and cDNA cloning of Xylanase from fungus *Trichoderma* strain SY. *J. Microbiol. Biotechnol.* 12 (6), 1–5.
- Moosavi, M.R., Zare, R., 2012. Fungi as Biological Control Agents of Plant-Parasitic Nematodes. In: Mérillon J., Ramawat K. (eds) *Plant Defence: Biological Control*. Biol. Control 12. https://doi.org/10.1007/978-94-007-1933-0_4.
- Moran Diez, E., Hermosa, R., Ambrosino, P., Cadoza, R.E., Gutierrez, S., 2009. The ThPG1 endopolygalacturonase is required for the *Trichoderma harzianum*-Plant beneficial interaction. *Am. Phytopathol. Soc.* 22 (8), 1021–1031.
- Mosa, M.M., Youssef, K., 2021. Topical delivery of host induced RNAi silencing by layered double hydroxide nanosheets: an efficient tool to decipher pathogenicity gene function of *Fusarium crown* and root rot in tomato. *Physiol. Mol. Plant Pathol.* 115, 101684.
- Muhanna, N.A.S., Essa, T.A., El-Gamal, M.A.H., Kamel, S.M., 2016. Efficacy of free and formulated arbuscular mycorrhiza, *Trichoderma viride* and *Pseudomonas fluorescens* on controlling tomato root rot diseases. *Egypt. J. Biol. Pest Control* 26 (3), 477–486.
- Mukherjee, M., Latha, J., Hadar, R., Horwitz, B.A., 2004. Role of two Gprotein alpha subunits, *TgaA* and *TgaB*, in the antagonism of plant pathogens by *Trichoderma virens*. *Appl. Environ. Microbiol.* 70 (1), 542–549.
- Mukherjee, M., Mukherjee, P.K., Kale, P.S., 2007. cAMP signalling is involved in growth, germination, mycoparasitism and secondary metabolism in *Trichoderma virens*. *Microbiology* 153, 1734–1742.
- Mukherjee, P.K., Horwitz, B.A., Herrera-Estrella, A., Schmolli, M., Kenerley, C.M., 2013. *Trichoderma* research in the genome era. *Annu. Rev. Phytopathol.* 51, 105–129.
- Mukherjee, P.M., Latha, J., Hardar, R., Horwitz, B.A., 2003. *TmkA*, Mitogen activated Protein Kinase of *Trichoderma virens* is involved in biocontrol properties and repression of conidiation in the dark. *Eukaryot. Cell* 2, 446–455.
- Mulaw, T.B., Kubicek, C.P., Druzhinina, I.S., 2010. The rhizosphere of *Cofea arabica* in its native highland forests of Ethiopia provides a niche for a distinguished. *Divers. Trichoderma*. *Divers.* 2, 527–549. <https://doi.org/10.3390/d2040527>.
- Mulaw, T.B., Druzhinina, I.S., Kubicek, C.P., Atanasova, L., 2013. Novel endophytic *Trichoderma* spp. isolated from healthy *Cofea arabica* roots are capable of controlling coffee tracheomyces. *Diversity* 5, 750–766. <https://doi.org/10.3390/d5040750>.
- Mulugeta, T., Muhinyuza, J.B., Gous-Meyer, R., Matsaunyane, L., Andreasson, E., Alexandersson, E., 2020. Botanicals and plant strengtheners for potato and tomato cultivation in Africa. *J. Integr. Agric.* 19 (2), 406–427.
- Mutawila, C., Fourie, P.H., Rancois, F., Mostert, L., 2011. Grapevine cultivar variation to pruning wound protection by *Trichoderma* species against trunk pathogens. *Phytopathology* 50, 264–276.
- Nicasoto, R., Carillo, P., 2021. Food loss and waste prevention strategies from farm to fork. *Sustainability* 13, 5443. <https://doi.org/10.3390/su13105443>.
- Nikraftar, F., Taheri, P., Rastegar, M.F., Tarighi, S., 2013. Tomato partial resistance to *Rhizoctonia solani* involves antioxidative defense mechanisms. *Physiol. Mol. Plant Pathol.* 81, 74–83.
- Nordey, T., Schwarz, D., Kenyon, L., Manickam, R., Huat, J., 2020. Tapping potential of grafting to improve the performance of vegetable cropping systems in sub-Saharan Africa. *Rev. Agron. Sustain. Dev.* 40, 23.
- Ochilo, N.W., Nyamasyo, G.N., Kilalo, D., Otieno, W., Otipa, M., Chege, F., Karanja, T., Lingeera, E.K., 2019. Characteristics and production constraints of smallholder tomato production in Kenya. *Sci. Afr.* Volume 2, 2019. <https://doi.org/10.1016/j.sciaf.2018.e00014>.
- Olowe, O.M., Akanmu, A.O., Asemoloye, M.D., 2020. Exploration of microbial stimulants for induction of systemic resistance in plant disease management. *Ann. Appl. Biol.* 177 (3), 282–293.
- Ons, L., Bylemans, D., Thevissen, K., Cammue, B., 2020. Combining biocontrol agents with chemical fungicides for integrated plant fungal disease control. *Microorganisms* 8 (12), 1930. <https://doi.org/10.3390/microorganisms8121930>.
- Oxfam International. (2014). Coffee rust fungus threatens employment collapse in Central America. (www.oxfam.org).
- Palanna, K.B., Palaiah, B., Muthumilan, M., 2007. Effect of manures on growth, sporulation and antifungal activity of *Trichoderma viride*. *Karnataka J. Agric. Sci.* 20, 861–863.
- Pandya, J.R., Sabalpara, A.N., Chawda, S.K., 2011. *Trichoderma*: a particular weapon for biological control of phytopathogens. *J. Agric. Technol.* 7, 1187–1191.
- Papavizas, G.C., Dunn, M.T., Lewis, J.A., Beagle-Ristaino, J.E., 1984. Liquid fermentation technology for experimental production of biocontrol fungi. *Phytopathology* 74, 1171.
- Parab, P.B., Diwakar, M.P., Sawant, U.K., Kadam, J.J., 2008. Studies on mass multiplication, different methods of application of bioagent *T. harzianum* and their survival in rhizosphere and soil. *J. Plant Dis. Sci.* 3, 215–218.
- Pareek, M., Rajam, M.V., 2017. RNAi-mediated silencing of MAP kinase signaling genes (*Fmk1*, *Hog1*, and *Pbs2*) in *Fusarium oxysporum* reduces pathogenesis on tomato plants. *Fungal Biol.* 121, 775–784.
- Perez, K., Froikin-Gordon, J.S., Abdourhamane, I.K., et al., 2017. Connecting smallholder tomato producers to improved seed in West Africa. *Agric. Food Secur.* 6, 42. <https://doi.org/10.1186/s40066-017-0118-4>.
- Person, C.H., 1794. Neuer Versuch einer systematischen Einteilung der Schwämme. *Racodium Römer's Neues Mag. der Bot.* 1, 123.
- Piotrowski, M., Volmer, J.J., 2006. Cyanide metabolism in higher plants: cyanoolanine hydratase is a NIT4 homolog. *Plant. Mol. Biol.* 61, 111–122.
- du Plessis, I., Druzhinina, I.S., Atanasova, L., Yarden, O., Jacobs, K., 2018. The diversity of *Trichoderma* species from soil in South Africa with five new additions. *Mycologia* 110, 559–583. <https://doi.org/10.1080/00275514.2018>.
- Plucknett, D.L., Smith, N.J., 2014. 8. Wild Species: The Wider Gene Pool. *Gene Banks and the World's Food*. Princeton University Press., pp. 155–170.
- Pocurull, M., et al., 2020. Commercial formulations of trichoderma induce systemic plant resistance to meloidogyne incognita in tomato and the effect is additive to that of the Mi-1.2 resistance gene. *Front. Microbiol.* 10.
- Pozo, M.J., JongMin, B., Garcia, J.M., Kenerley, C.M., 2004. Functional analysis of *tvsp1*, a serine protease-encoding gene in the biocontrol agent *Trichoderma virens*. *Fungal Genet. Biol.* 41, 336–348.
- Pramod, K.T., Palakshappa, M.G., 2009. Evaluation of suitable substrates for on farm production of antagonist *Trichoderma harzianum*. *Karnataka J. Agric. Sci.* 22, 115–117.
- Prasad, R.D., Rangeshwaran, R., Anuroop, C.P., Phanikumar, P.R., 2002. Bioefficacy and shelf life of conidial and chlamydo-spore formulations of *Trichoderma harzianum* Rifai. *J. Biol. Control.* 16, 145–148.
- Qin, W., Zhuang, W., 2016. Seven wood-inhabiting new species of the genus *Trichoderma* (Fungi, Ascomycota) in Viride clade. *Sci. Rep.* 6, 1–14. <https://doi.org/10.1038/srep27074>.
- Quinet, M., Angosto, T., Yuste-Lisbona, F.J., Blanchard-Gros, R., Bigot, S., Martinez, J.P., Lutts, S., 2019. Tomato fruit development and metabolism. *Front. Plant Sci.* 10, 1554. <https://doi.org/10.3389/fpls.2019.01554>.
- Raaijmakers, J.M., Paulitz, T.C., Steinberg, C., Alabouvette, C., Moëgne, Loccoz, Y., 2009. The rhizosphere: a playground and battle-field for soil-borne pathogens and beneficial microorganisms. *Plant Soil* 2009 (321), 341–361.
- Ram, R.M., Rajput, R.S., Vaishnav, A., 2020. Management of Sclerotium rolfsii Induced Diseases in Crops by *Trichoderma* Species. *Rhizosphere Microbes*. Springer., pp. 593–617.
- Reithner, B., Brunner, K., Schuhmacher, R., Peissl, I., Seidl, V., Krška, R., Zeilinger, S., 2005. The G protein α subunit Tga1 of *Trichoderma atroviride* is involved in chitinase formation and differential production of antifungal metabolites. *Fungal Genet. Biol.* 42, 749–760.
- Rey, M., Delgado-Jarana, J., Benítez, T., 2001. Improved antifungal activity of a mutant of *Trichoderma harzianum* CECT 2413 which produces more extracellular proteins. *Appl. Microbiol. Biotechnol.* 55, 604–608.
- Rifai, M.A., 1969. A revision of the genus *Trichoderma*. *Mycol. Pap.* 116, 1–56.
- Rini, C.R., Sulochana, K.K., 2007. Substrate evaluation for multiplication of *Trichoderma* spp. *J. Trop. Agric.* 45, 58–60.
- Rosado, I.V., Rey, M., Codon, A.C., Govantes, J., MorenoMateos, M.A., Benítez, T., 2007. QID74 Cell wall protein of *Trichoderma harzianum* is involved in cell protection and adherence to hydrophobic surfaces. *Fungal Genet. Biol.* 44, 950–964.
- Rubio, M.B., Hermosa, R., Reino, J.L., Collado, I.G., Monte, E., 2009. *Thc1f* transcription factor of *Trichoderma harzianum* is involved in 6-pentyl-2H-pyran-2-one production and antifungal activity. *Fungal Genet. Biol.* 46, 17–27.
- Ruocco, M., Lanzuise, S., Vinala, F., Marra, R., Turra, D., LoisWoo, S., Lorito, M., 2009. Identification of a New Biocontrol Gene in *Trichoderma atroviride*: the role of an ABC transporter membrane pump in the interaction with different plant-pathogenic fungi. *Am. Phytopathol. Soc.* 22 (3), 291–301.
- Rush, T.A., Shrestha, H.K., Gopalakrishnan Meena, M., Spangler, M.K., Ellis, J.C., Labbé, J.L., Abraham, P.E., 2021. Bioprospecting trichoderma: a systematic roadmap to screen genomes and natural products for biocontrol applications. *Front. Fungal Biol.* 2, 716511 <https://doi.org/10.3389/ffunb.2021.716511>.
- Rwomushana, I., Beale, T., Chipabika, G., Day, R., Gonzalez-Moreno, P., Lamontagne-Godwin, J., Makale, F., Pratt, C., Tambo, J., 2019. Evidence note: tomato leafminer (*Tuta absoluta*): impacts and coping strategies for Africa. *CABI Work. Paper*, 12, 1–56.

- Saadia, M., Ahmed, S., Jamil, A., 2008. Isolation and cloning of *cre1* gene from a filamentous fungus *Trichoderma harzianum*. Pak. J. Bot. 40 (1), 421–426.
- Sadfi-Zouaoui, N., Hannachi, I., Rouaissi, M., Hajlaoui, M.R., Rubio, M.B., Monte, E., Boudabous, A., Hermosa, M.R., 2009. Biodiversity of *Trichoderma* strains in Tunisia. Can. J. Microbiol. 162, 154–162.
- Saiprasad, G.V.S., Mythili, J.B., Anand, L., Suneetha, C., Rashmi, H.J., Naveena, C., Ganeshan, G., 2009. Development of *Trichoderma harzianum* gene construct conferring antifungal activity in transgenic tobacco. Indian J. Biotechnol. 8, 199–206.
- Saju, K.A., Anandaraj, M., Sarma, Y.R., 2002. On farm production of *Trichoderma harzianum* using organic matter. Indian Phytopathol. 55, 277–281.
- Salas-Marina, M.A., Silva-Flores, M.A., Uresti-Rivera, E.E., Castro-Longoria, E., Herrera-Estrella, A., Casas-Flores, S., 2011. Colonization of *Arabidopsis* roots by *Trichoderma atroviride* promotes growth and enhances systemic disease resistance through jasmonic acid/ethylene and salicylic acid pathways. Eur. J. Plant. Pathol. 131, 15–26.
- Salas-Marina, M.A., Isordia-Jasso, M., Islas-Osuna, M.A., Delgado-Sánchez, et al., 2015. The Epl1 and Sm1 proteins from *Trichoderma atroviride* and *Trichoderma virens* differentially modulate systemic disease resistance against different life style pathogens in *Solanum lycopersicum*. Front. Plant Sci. 23, 77.
- Saloheimo, M., Paloheimo, M., Hakola, S., Pere, J., Swanson, B., Nyssönen, E., Bhatia, A., Ward, M., Swollenin, M.P., 2002. A *Trichoderma reesei* protein with sequence similarity to the plant expansins, exhibits disruption activity on cellulosic materials. Eur. J. Biochem 269, 4202–4211.
- Samolski, I., Rincón, A.M., Pinzón, L.M., Viterbo, A., Monte, E., 2012. The *qid74* gene from *Trichoderma harzianum* has a role in root architecture and plant biofertilization. Microbiology 158, 129–138.
- Samuels, G.J., 1996. *Trichoderma*: a review of biology and systematics of the genus. Mycol. Res. 100, 923–935.
- Samuels, G.J., et al., 2000. *Trichoderma stromaticum* sp. nov., a parasite of the cacao witches' broom pathogen. Mycol. Res. 104, 760–764. <https://doi.org/10.1017/S0953756299001938>.
- Samuels, G.J., et al., 2006. *Trichoderma theobromicola* and *T. paucisporum*: two new species isolated from cacao in South America. Mycol. Res. 110, 381–392. <https://doi.org/10.1016/j.mycres.2006.01.009>.
- Samuels, G.J., 2006. *Trichoderma*: systematics, the sexual state, and ecology. Phytopathology 96, 195–206.
- Samuels, G.J., Hebbbar, P.K., 2015. *Trichoderma*: Identification and Agricultural Applications. APS Press, St. Paul, 2015.
- Samuels, G.J., Ismaiel, A., de Souza, J., Chaverri, P., 2012. *Trichoderma stromaticum* and its overseas relatives. Mycol. Prog. 11, 215–254. <https://doi.org/10.1007/s11557-011-0743-4>.
- Schulz, B., Boyle, C., 2005. The endophytic continuum. Mycol. Res. 109, 661–686. <https://doi.org/10.1017/S095375620500273X>.
- Schuster, A., Schmol, M., 2010. Biology and technology of *Trichoderma*. Appl. Microbiol. Biotechnol. 87, 787–799. <https://doi.org/10.1016/C2012-0-00434-6>.
- Seaman, A., 2003. Efficacy of PMRI-approved products for tomato foliar disease control. New York State. Integr. Pest Manag. Program Publ. 129, 164–167.
- Sharath Chandran, U.S., Tarafdar, A., Mahesha, H.S., Sharma, M., 2021. Temperature and soil moisture stress modulate the host defense response in chickpea during dry root rot incidence. Front. Plant Sci. 12, 653265 <https://doi.org/10.3389/fpls.2021.653265>.
- Sharma, P., Prakash, V.G., Singh, D., Chowdappa, P., 2011. Biocontrol strategies 2030: Research and industry applications. Plant Pathology in India: Vision 2030 278–287.
- Sharma, N., Trivedi, P.C., 2005. Microbial bioagents: economic multiplication and management of fungal nematode complex on cumin. Indian J. Biotechnol. 4, 419–421.
- Sharma, P., Kumar, V., Ramesh, R., Saravanan, K., Deep, S., Sharma, M., Dinesh, S., 2011. Biocontrol genes from *Trichoderma* species: a review. Afr. J. Biotechnol. 10 (86), 19898–19907.
- Shenashen, M., Derbalah, A., Hamza, A., Mohamed, A., El Safty, S., 2017. Antifungal activity of fabricated mesoporous alumina nanoparticles against root rot disease of tomato caused by *Fusarium oxysporum*. Pest Manag. Sci. 73, 1121–1126.
- Shoresh, M., Harman, G.E., Mastouri, F., 2010. Induced systemic resistance and plant responses to fungal biocontrol agents. Annu. Rev. Phytopathol. 48, 21–43. <https://doi.org/10.1146/annurev-phyto-073009-114450>.
- Singh, A., Shukla, N., Kabadwal, B., Tewari, A., Kumar, J., 2018. Review on plant-*Trichoderma*-pathogen interaction. Int. J. Curr. Microbiol. Appl. Sci. 7, 2382–2397.
- Smolinska, U., Kowalska, B., Kowalczyk, W., Magdalena, S., 2014. The use of agro-industrial wastes as carriers of *Trichoderma* fungi in the parsley cultivation. Sci. Hortic. 179, 1–8.
- Sood, M., Kapoor, D., Kumar, V., Sheteiwy, M.S., Ramakrishnan, M., Landi, M., Sharma, A., 2020. *Trichoderma*: the “secrets” of a multitasking biocontrol agent. Plants 9 (6), 762.
- Souza, J.T., et al., 2006. Genetic and biological diversity of *Trichoderma stromaticum*, a mycoparasite of the cacao witches' broom pathogen. Popul. Biol. 96, 61–67. <https://doi.org/10.1094/PHYTO-96-0061>.
- Srivastava, M., Shahid, M., Pandey, S., Singh, A., Kumar, V., Gupta, S., Maurya, M., 2014. *Trichoderma* genome to genomics: a review. J. Data Min. Genom. Proteom. 5 (162), 2153-0602.
- Steyaert, J.M., Stewart, A., Jaspers, M.V., Carpenter, M., Ridgway, H.J., 2004. Co-expression of two genes, a chitinase (*chi42*) and proteinase (*prb1*), implicated in mycoparasitism by *Trichoderma hamatum*. Mycologia 96 (6), 1245–1252.
- Tamburino, R., Sannino, L., Cafasso, D., Cantarella, C., Orrù, L., Cardì, T., Scotti, N., 2020. Cultivated Tomato (*Solanum lycopersicum* L.) Suffered a Severe Cytoplasmic Bottleneck during Domestication: Implications from Chloroplast Genomes. Plants 9 (11), 1443.
- Tewari, L., Bhanu, C., 2004. Evaluation of agro-industrial wastes for conidia based inoculum production of bio-control agent: *Trichoderma harzianum*. J. Sci. Ind. Res. 63, 807–812.
- Thabet, M., Khalifa, W., 2018. Antifungal activities of clove oil against root rot and wilt pathogens of tomato plants. Am. Eurasia J. Agric. Environ. Sci. 18, 105–114.
- 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.
- Tomer, A., Singh, R., Maurya, M., 2015. Determination of compatibility of *Pseudomonas fluorescens* and *Trichoderma harzianum* grown on deoiled cakes of neem and jatropha for mass multiplication of *P. Fluoresc.* T. harzianum Vitro. 10, 67–75.
- Topolovec-Pintaric, S., 2019. *Trichoderma*: Invisible partner for visible impact on agriculture. <https://doi.org/10.5772/intechopen.83363>.
- Upadhyay, J.P., Mukhopadhyay, A.N., 2009. Biological control of *Sclerotium rolfsii* by *Trichoderma harzianum* in sugarbeet. Trop. Pest Manag. 32, 216–220.
- Vahabi, K., Mansoori, G.A., Karimi, S., 2011. Biosynthesis of silver nanoparticles by fungus *Trichoderma reesei*: a route for large scale production of AgNPs. Insidencies J. 1, 65–79.
- Vaz, A.B.M., et al., 2018. A multiscale study of fungal endophyte communities of the foliar endosphere of native rubber trees in eastern Amazonia. Sci. Rep. 8, 16151. <https://doi.org/10.1038/s41598-018-34619-w>.
- Vey, A., Hoagland, R.E., Butt, T.M., 2001. Toxic metabolites of fungal biocontrol agents. In: Butt, T.M., Jackson, C., Magan, N. (Eds.), *Fungi as biocontrol agents: Progress, problems and potential*. CABI, Bristol, UK, pp. 311–346.
- Vinale, F., et al., 2008. A novel role for *Trichoderma* secondary metabolites in the interactions with plants. Physiol. Mol. Plant Pathol. 72, 80–86. <https://doi.org/10.1016/j.pmp.2008.05.005>.
- Vinale, F., Nigro, M., Sivasithamparan, 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. Lett. 347, 123–129.
- Viterbo, A., Harel, M., Chet, I., 2004. Isolation of two aspartyl proteases from *Trichoderma asperellum* expressed during colonization of cucumber roots. FEMS Microbiol. Lett. 238, 151–158.
- Vizcaino, J.A., Cardoza, R.A., Hauser, M., Hermosa, R., Rey, M., Lobell, A., Becker, J.M., Gutierrez, S., Monte, E., 2006. *ThPTR2*, a di/tri-peptide transporter gene from *Trichoderma harzianum*. Fungal Genet. Biol. 43, 234–246.
- Wang, C., Zhuang, W.-Y., 2019. Evaluating effective *Trichoderma* isolates for biocontrol of *Rhizoctonia solani* causing root rot of *Vigna unguiculata*. J. Integr. Agric. 18, 2072–2079. <https://doi.org/10.1016/S2095-62593-1>.
- Ward, R., Gonthier, D., Nicholls, C., 2017. Ecological resilience to coffee rust: varietal adaptations of coffee farmers in Copán, Honduras. Agroecol. Sustain. Food Syst. 41, 1081–1098. <https://doi.org/10.1080/21683565.2017.1345033>.
- Whipps, J.M., Lumsden, R.D., 2001. Commercial use of fungi as plant disease biological control agents: Status and prospects. In: Butt, T.M., et al. (Eds.), *Fungi as Biocontrol Agents: Progress, Problems and Potential*, Vol. 9–22. CAB International, Wallingford.
- Williamson-Benavides, B.A., Dhingra, A., 2021. Understanding root rot disease in agricultural crops. Horticulturae 7, 33.
- Wokoma, E.C.W., 2008. Preliminary report on diseases of tomato in choba, rivers state. J. Appl. Sci. Environ. Manag. 12, 117–121.
- Woo, S.L., Donzelli, B., Scala, F., Mach, R., Harman, G.E., Kubicek, C.P., Sorbo, G.D., Lorito, M., 1999. Disruption of the *ech42* (endochitinase encoding) gene affects biocontrol activity in *Trichoderma harzianum* P1. Am. Phytopathol. Soc. 12 (5), 219–229.
- Woo, S.L., Scala, F., Ruocco, M., Lorito, M., 2006. The molecular biology of the interactions between *trichoderma* spp., phytopathogenic fungi, and plants. Phytopathology 96 (2), 181–185. <https://doi.org/10.1094/PHYTO-96-0181>.
- 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 (1).
- Yezli, W., Hamini-Kadar, N., Zebboudj, N., Blondin, L., Tharreau, D., Kihal, M., 2019. First report of crown and root rot of tomato caused by *Fusarium equiseti* in Algeria. J. Plant Pathol. 101 (4), 1249–1249.
- Yoshioka, Y., Ichikawa, H., Naznin, H.A., Kogure, A., Hyakumachi, M., 2012. Systemic resistance induced in *Arabidopsis thaliana* by *Trichoderma asperellum* SKT-1, a microbial pesticide of seed-borne diseases of rice. Pest Manag. Sci. 68, 60–66.
- Zaidi, N.W., Dar, M.H., Singh, S., Singh, U., 2014. *Trichoderma* species as abiotic stress relievers in plants. Biotechnology and biology of *Trichoderma*. Elsevier, pp. 515–525.
- Zeilinger, S., Galhaup, C., Payer, K., Woo, S.L., Mach, R.L., Fekete, C., Lorito, M., Kubicek, C.P., 1999. Chitinase gene expression during mycoparasitic interaction of *Trichoderma harzianum* with its host. Fungal Genet. Biol. 26, 131–140.