



## Review

# Filamentous fungi as biocontrol agents in olive (*Olea europaea* L.) diseases: Mycorrhizal and endophytic fungi

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## ABSTRACT

Olive (*Olea europaea*) is a crop of great agronomic, economic and cultural interest for the Mediterranean Basin, although the increase in world demand for olive oil is expanding its cultivation by other countries in the southern hemisphere. The main olive pathogens include bacteria (*Pseudomonas savastanoi* pv. *savastanoi*, *Xylella fastidiosa*), fungi (*Colletotrichum* spp., *Verticillium dahliae*, *Fusarium* spp. *Rhizoctonia solani*), oomycetes (*Phytophthora* spp.) and nematodes (*Meloidogyne* spp.). To combat these pathogens, different biocontrol strategies have been developed with bacteria and yeasts, although its capacity for establishment in the field entails several difficulties. In this sense, filamentous fungi represent an efficient and effective alternative in the control of the different pathogens of the olive tree. The present review compiles all the studies existing so far in the biocontrol of these pathogens through the use of mycorrhizal and endophytic filamentous fungi, making a separate section for the genus *Trichoderma* due to the special interest that their use has generated. The mechanisms used by these fungi include competition for space and nutrients, parasitism, antibiosis or activation of the plant's defensive responses, among others.

## 1. Introduction

Olive (*Olea europaea*) is cultivated in hundreds different varieties to produce fruit for table consumption and for oil in various geographical areas around the world. This species has its origins linked to the emergence of some of the oldest civilizations (about six millennia ago), being considered the most emblematic tree in the Mediterranean basin (Besnard et al., 2018). In the last two decades, the increasing international demand for olive oil and table olives, has led to expansion of olive cultivation in other countries such as Australia, Chile, Argentina or Peru (Torres et al., 2017). The world's total harvested olive area is 10.7 million hectares, being Spain the largest grower (2.6 million hectares), above Tunisia (1.6 million hectares) and Italy (1.2 million hectares) (Willer and Lernoud, 2019).

Olive oil has been accepted internationally as a healthy natural product, culturally-shaped since the earliest times in the history of Western civilization and the main component of the Mediterranean diet, whereas its health benefits such as anticancer, anticholesterol, and antioxidant activities are well-known (Rodríguez-Cohard et al., 2019;

Souilem et al., 2017). Nowadays, worldwide olive oil production is about 2.5 million tons, being more than 80% in Mediterranean countries (Seçmeler and Galanakis, 2019).

Currently, olive sustainability is threatened by different factors including those linked to climate variability, pathogens and pests. Strategies for olive disease control relies mostly on the application of chemical pesticides, in particular of copper-based products. It is typically applied twice a year, but sometimes can be higher (up to 5 times per year) (Roca et al., 2007). Frequent application of copper may led to the development of resistance in pathogens (Nguyen et al., 2018) and may have a negative impact on beneficial organisms (Martins et al., 2012). In this sense, it becomes necessary to promote new control strategies against olive diseases that are respectful of the environment and health, such as biocontrol strategies (Sardaro et al., 2016; Mairech et al., 2020).

Thanks to biocontrol, plant pathogens can be managed by different antagonistic microorganisms, which compete for space and nutrients, and produce cell wall degrading enzymes and antimicrobial compounds (Köhl et al., 2019). Furthermore, as plant disease management is a

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significant cost component in crop production, the current market for this type of biocontrol formulations is booming, continuously developing new biocontrol agents (BCAs) (O'Brien, 2017; Simionato et al., 2017). In this sense, different groups of filamentous fungi have been reported in the laboratory and in the field as effective biocontrol agents against a diverse array of plant pathogens, not only through their direct action but also thanks to the interaction with the plant and the activation of its defensive responses (Poveda et al., 2020a).

## 2. Principal olive pathogens

The current agricultural development in olive cultivation, based on the implantation of intensive monocultures with few varieties selected for their productive characteristics, makes the agro-system very fragile against the entry of pathogens (Arenas-Castro et al., 2020). Among the main pathogens of the olive tree we find bacteria, fungi, oomycetes and nematodes.

The most widely known and studied bacterium in olive cultivation is *Pseudomonas savastanoi* pv. *savastanoi*, which is the causal agent of olive knot disease (Rodríguez-Moreno et al., 2009). The main observed symptoms in infected olive trees is the formation of tumorous galls or knots on the stems and branches, although they can also appear on leaves and fruits. The so-called olive knot disease can cause serious problems for olive crops, by reducing growth, productivity and oil quality (Penyalver et al., 2006).

Currently, as a consequence of its introduction into the European Union through Italy, in 2013, the *Xylella fastidiosa* bacterium has focused a large part of the European research programs on olive disease control. This was the first time that the bacterium was detected in the Mediterranean Basin, causing serious damage to the olive groves of this region, by causing the olive quick decline syndrome (OQDS), which begins with a severe branch desiccation that continues with the rapid death of the affected olive tree (Bucci, 2018; Sicard et al., 2018; Saponari et al., 2019).

Regarding fungi, the main disease that affects the aerial part is olive anthracnose, caused by the fungal complex species *Colletotrichum gloeosporioides sensu lato*, *C. acutatum sensu lato* and *C. boninense sensu lato* (Scheda et al., 2014). Olive anthracnose affects mostly the fruits and is considered one of the most destructive and widespread olive disease around the world (Moral et al., 2017a). Even with a low effect on the fruits (5%), the olive oil obtained cannot be marketed as extra virgin olive oil, due to the chemical and organoleptic changes caused (Moral et al., 2017a). Other important diseases affecting the aerial part of olive tree include peacock spot, caused by *Venturia oleaginea*, and cercosporiosis, caused by *Pseudocercospora cladosporioides*. Trees affected by these two diseases begin with the defoliation of their leaves until the death of the branches, considerably reducing their productivity (Varanda et al., 2019). In the last decade, other fungal pathogens have also been identified to affect the aerial part of the olive tree, such as *Fomitiporia mediterranea* (causal agent of wood decay) (Markakis et al., 2019), *Alternaria alternata* (causal agent of blossom blight and *Alternaria* bud of olives) (Lagogianni et al., 2017), or *Botryosphaeria dothidea* (causal agent of "escudete" or small shield of olive fruit) (Moral et al., 2017b), among others.

Soil-borne pathogens can persist in the soil and cause deep and severe symptoms, making the disease control difficult. As far as fungi-roots are concerned, currently, *Verticillium* wilt of olive (VWO) is considered the most limiting disease of olive production and one of the most devastating (Montes-Osuna and Mercado-Blanco, 2020). It is caused by *Verticillium dahliae*, an hemibiotrophic soil-borne fungus which invades the xylem vessels through the roots, causing symptoms derived from the absence of acute transport, such as chlorosis, early senescence, stunting, necrosis, defoliation and the death of the olive tree (Montes-Osuna and Mercado-Blanco, 2020). Other species of soilborne fungi that infect olive roots are *Fusarium* spp. (causal agents of death of nursery and young olive plants), *Cylindrocarpum destructans* and *Rhizoctonia solani* (causal

agents of root rot) (Trabelsi et al., 2017).

Within the group of oomycetes there are several species of the genus *Phytophthora* that affect the olive tree, rotting its roots, such as *P. oleae*, *P. megasperma*, *P. inundata* or *P. palmivora* (Ruano-Rosa et al., 2018). Its presence in the field is often unknown because they cause similar symptoms to VWO and, as *V. dahliae*, which is so widespread, the presence of the fungus is always thought (Msairi et al., 2016).

On the other hand, olive trees are also affected by different genera of plant-parasitic nematodes. Due to their wide distribution and their sanitary importance in olive cultivation, the genera *Meloidogyne* (root-knot nematodes) and *Xiphinema* (transmitters of *Nepovirus*) stand out (Archidona-Yuste et al. 2016, 2018; Hamza et al., 2018).

In response to the attack of pathogens, plants activate local and systemic defensive responses controlled, mainly, by the phytohormones salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) (Poveda, 2020a). These defenses in olive trees include the synthesis and tissue accumulation of different secondary metabolites, such as terpenes (oleanolic acid), phenolics (coumarins, lignin, astringin, kaempferol, hydroxytyrosol glucoside, tannins, caftaric acid, quercetin, genistein and hesperidin), quinic acid or kynurenic acid (Vergine et al., 2020).

## 3. Biocontrol of olive pathogens by filamentous fungi

Due to the great diversity of pathogens that affect olive cultivation, many farmers are increasingly using chemical pesticides dangerous for the environment and human health. In contrast, many research groups have focused their efforts on developing new eco-friendly strategies based on the use of beneficial microorganisms (Bizos et al., 2020). These microorganisms, which include some bacterial and fungal groups, have been shown to play a crucial role in plant health and growth (del Carmen Orozco-Mosqueda et al., 2018). We will specifically focus on the role of filamentous fungi (mycorrhizal and endophytic fungi) on olive crop protection against diseases and on mechanisms involved. In Table 1 is shown schematically all the studies carried out with the different groups of filamentous fungi in the control of olive pathogens, together with the mechanisms of action involved.

### 3.1. Mycorrhizal fungi

Mycorrhizal fungi are obligate symbionts that can be found in 97% of the upper plants. According to their way of colonizing the roots, they are classified into ectomycorrhizal fungi (ECMF) and arbuscular mycorrhizal fungi (AMF), colonizing the intercellular space or intracellularly forming arbuscles, respectively (Berruti et al., 2016; Ferlian et al., 2018).

Once the symbiosis is established, the fungal mycelium increases the volume of soil accessible to the plant, absorbing nutrients (phosphorus, ammonium, potassium, iron, sulfur, copper, zinc or molybdenum) and water for the plant (Chen et al., 2018), while the plant yields photo-assimilates to the fungus (Berruti et al., 2016). Furthermore, mycorrhizal fungi increase plant tolerance to abiotic stresses such as drought, salinity, heavy metals and extreme of temperatures (Begum et al., 2019).

As BCAs, mycorrhizal fungi develop mechanisms that include competition for photosynthates or colonization/infection sites, improvement of plant nutrition, production of morphological changes in the root system, changes in mycorrhizosphere microbial populations, and activation of plant defense mechanisms (Pozo et al., 2013; Singh et al., 2019). The effectiveness of mycorrhizal fungi as BCAs against fungal pathogens (Hilbig and Allen, 2019), oomycetes (Hou et al., 2019), nematodes (Poveda et al., 2020a) and/or bacteria (Poveda et al., 2021), are mainly due to these different mechanisms that frequently operate simultaneously.

The activation of systemic resistance in the plant against pathogens and/or pests by mycorrhizal fungi is a mechanism denominated as mycorrhizal induced resistance (MIR) and widely reviewed by different authors (Pozo and Azcón-Aguilar, 2007; Hohmann and Messmer, 2017;

**Table 1**  
Mechanisms of action of filamentous fungi as biocontrol agents for olive pathogens.

FILAMENTOUS FUNGI		PATHOGENS	EXPERIMENTAL CONDITIONS	MECHANISMS	REFERENCES
GROUPS	SPECIES				
Mycorrhizal fungi	<i>Glomus mosseae</i>	<i>Verticillium dahliae</i>	Greenhouse	Not indicated	Karajeh and Al-Raddad, 1999
	<i>G. mosseae</i>		Field	Not indicated	Porrás-Soriano et al. (2006)
	<i>G. intraradices</i>				
	<i>G. claroideum</i>				
	<i>Rhizofagus irregularis</i>		Field	Restrict the fungal sporulation and growth	Arici and Demirtas, 2019 <sup>a</sup>
	<i>G. mosseae</i>				
	<i>G. aggregatum</i>				
	<i>G. clarum</i>				
	<i>G. monosporus</i>				
	<i>G. deserticola</i>				
Endophytic fungi	<i>G. brasilianum</i>				
	<i>G. etunicatum</i> , <i>G. margarita</i>				
	<i>Glomus irregulare</i>		Greenhouse	Not indicated	Boutaj et al. (2019)
	Rhizolive: mycorrhizal consortium inoculum with 25 species of <i>Glomus</i> , <i>Acaulospora</i> , <i>Gigaspora</i> , <i>Entrophospora</i> and <i>Scutellospora</i>				
	<i>Paraglomus occultum</i>		Greenhouse	Not indicated	Khriebe et al. (2019)
	<i>Glomus etunicatum</i>				
	<i>G. fasciculatum</i>				
	<i>G. clarum</i>				
	Rhizolive: mycorrhizal consortium inoculum with 25 species of <i>Glomus</i> , <i>Acaulospora</i> , <i>Gigaspora</i> , <i>Entrophospora</i> and <i>Scutellospora</i>		Greenhouse	Competition in the rhizosphere for root penetration sites Increase lignin deposition, PAL activity and accumulation of phenolic compounds	Boutaj et al. (2020b) Boutaj et al. (2020c)
	<i>G. intraradices</i>		Field	Not indicated	Mulero-Aparicio et al. (2020a)
					Berardo et al. (2018)
Endophytic fungi	<i>Epicoccum nigrum</i>	<i>Pseudomonas savastanoi</i> pv. <i>savastanoi</i>	<i>In silico</i>	Antibiosis	
	<i>Drechslera gigantea</i>	<i>Xylella fastidiosa</i>	<i>In vitro</i>	Antibiosis	Bleve et al. (2018)
	<i>Alternaria</i> sp.	<i>Colletotrichum acutatum</i>	<i>In vitro</i>	Antibiosis	Landum et al. (2016)
	<i>Diaporthe</i> sp.				
	<i>Nigrospora oryzae</i>				
	<i>Chondrostereum purpureum</i>		<i>In vitro</i>	Antibiosis	Preto et al. (2017)
	<i>Chaetomium globosum</i>				
	<i>Aspergillus</i> sp.				
	<i>Epicoccum nigrum</i>				
	<i>Aspergillus brasiliensis</i>				
Endophytic fungi	<i>Fusarium oxysporum</i>	<i>V. dahliae</i>	Greenhouse	No indicated	Varo et al. (2016a)
	<i>Phoma</i> sp.				
	<i>F. oxysporum</i>		<i>In vitro</i>	Antibiosis	Varo et al. (2016b)
	<i>Phoma</i> sp.		Greenhouse	Activation of plant defenses	
	<i>F. oxysporum</i>		<i>In vitro</i>	No indicated	Varo et al. (2018)
			Growth chamber		
	<i>F. oxysporum</i>		<i>In vitro</i>	Rhizosphere competition for space and nutrients	Mulero-Aparicio et al. (2019)
	<i>F. oxysporum</i>		Field	No indicated	Mulero-Aparicio et al. (2020a)
	<i>F. oxysporum</i>		Field	Antibiosis	Mulero-Aparicio et al. (2020b)
	<i>Metarhizium brunneum</i>		<i>In vitro</i>	Rhizosphere competition for space	Mulero-Aparicio et al. (2020b)
Endophytic fungi	<i>Beauveria bassiana</i>			Antibiosis	Lozano-Tovar et al. (2013)
	<i>M. brunneum</i>		<i>In vitro</i>	Antibiosis	Lozano-Tovar et al. (2017)
	<i>M. brunneum</i>	<i>Phytophthora megasperma</i>	<i>In vitro</i>	Antibiosis	Lozano-Tovar et al. (2013)
	<i>B. bassiana</i>				
	<i>M. brunneum</i>		<i>In vitro</i>	Antibiosis	Lozano-Tovar et al. (2017)
	<i>Talaromyces assiutensis</i>	<i>Meloidogyne javanica</i>	In field	Parasitism	Hamza et al. (2017)
	<i>Arthrobotrys brochopaga</i>				
	<i>A. conoides</i>				
	<i>Drechslerella brochopaga</i>				
	<i>Monacrosporium thaumasium</i>				
Trichoderma	<i>Purpureocillium lilacinum</i>				
	<i>T. harzianum</i>	<i>X. fastidiosa</i>	<i>In vitro</i>	Antibiosis	Bleve et al. (2018)
	<i>T. citrinoviride</i>				
	<i>T. harzianum</i>	<i>F. oxysporum</i>	Greenhouse	Not indicated	Mousa et al. (2006)
		<i>F. solani</i>			
		<i>R. solani</i>			
		<i>Sclerotium rolfsii</i>			

(continued on next page)

Table 1 (continued)

FILAMENTOUS FUNGI		PATHOGENS	EXPERIMENTAL CONDITIONS	MECHANISMS	REFERENCES
GROUPS	SPECIES				
	<i>T. harzianum</i>	<i>Alternaria alternata</i> <i>F. solani</i>	<i>In vitro</i> Greenhouse	Mycoparasitism Activation of plant defenses	Amira et al., (2017), 2018
	<i>T. atroviride</i>	<i>V. dahliae</i>	<i>In vitro</i>	Antibiosis	Lozano-Tovar et al. (2013)
	<i>T. asperellum</i>		<i>In vitro</i> Greenhouse	Antibiosis	Carrero-Carrón et al. (2016)
	<i>T. harzianum</i>		<i>In vitro</i>	Mycoparasitism	Ruano-Rosa et al. (2016)
	<i>T. harzianum</i>		Greenhouse	Rhizosphere competition for space	Carrero-Carrón et al., 2018
	<i>T. harzianum</i>		Field	Restrict the fungal sporulation and growth	Arici and Demirtas, 2019 <sup>a</sup>
	<i>T. asperellum</i>		<i>In vitro</i>	Antibiosis	Morán-Díez et al. (2019)
	<i>T. asperellum</i>		Field	Not indicated	Mulero-Aparicio et al. (2020a)
	<i>T. atroviride</i>	<i>Phytophthora inundata</i> <i>P. megasperma</i>	<i>In vitro</i>	Antibiosis	Lozano-Tovar et al. (2013)
	<i>T. asperellum</i> <i>T. harzianum</i>	<i>M. javanica</i>	In field	Parasitism	Hamza et al. (2017)

<sup>a</sup> The inoculum used presented together the arbuscular mycorrhizal fungi and *T. harzianum*.

Jacott et al., 2017). Once plant and mycorrhizal fungi come into contact, the plant activates its defensive responses mediated by salicylic acid (SA), similar to against biotrophic pathogen. Subsequently, a down-regulation of this defensive response is required to enable the establishment of the symbiosis. Once the symbiosis is established, a systemic defensive response controlled by jasmonic acid (JA) and ethylene (ET) pathways is induced. (Hohmann and Messmer, 2017). Examples of MIR have been reported against the bacteria *Xanthomonas translucens* in wheat leaves (Fiorilli et al., 2018) or the fungi *A. alternata* in leaves (Nair et al., 2015; Song et al., 2015) and *Fusarium oxysporum* f. sp. *lycopersici* in roots (Math et al., 2018) of tomato.

In olive, there are numerous studies that report the benefits of symbiosis with mycorrhizal fungi, with a great diversity of species capable of forming this association (Palla et al., 2020). It has been verified how the plantlet establishment improves significantly after its micropropagation (Binet et al., 2007) since the symbiosis increases the acquisition of nutrients by the plant (Tekaya et al., 2017; Jiménez-Moreno et al., 2018; Boutaj et al., 2020a), its growth and development (Chenouchi et al., 2020), and improves the biochemical profile of olives and oil (Kara et al., 2015). Faced with abiotic stresses, the olive-mycorrhizal fungal symbiosis has been reported as increasing plant tolerance under situations of salinity (Kavroulakis et al., 2020) or drought (Bompadre et al., 2013; Ouledali et al., 2018). In what concerns the biocontrol role of AMF against olive tree diseases, numerous examples have been reported in the literature (Table 1). In this sense, one of the mechanisms of action of mycorrhizal fungi against olive-pathogens are concerned is the ability to completely modify the plant-related microbiota, as a consequence of establishing the symbiosis and modifying the nutritional profile of the rhizosphere (Mechri et al., 2014). Numerous greenhouse and field studies have been carried out with the aim of reducing olive damage by *V. dahliae* through the use of AMF. In greenhouse conditions, the root inoculation with the species *Paraglomus occultum*, *Glomus etunicatum*, *G. fasciculatum* and *G. clarum* decreases the harmful effect caused by *V. dahliae*, increasing fresh and dry weight of shoots and roots and the rate of leaf number (Khriebe et al., 2019). Also, the application of the Rhizolive formula, which includes a mycorrhizal consortium inoculum with 26 species of *Glomus*, *Acaulospora*, *Gigaspora*, *Entrophospora* and *Scutellospora* genus, and of the species *Glomus irregulare* (formerly known as *Rhizophagus irregularis*) significantly reduced the disease severity and percentage of dead plants, along with a lower dwarfing index and leaf alteration index (Boutaj

et al., 2019). Subsequently, it has been verified with the Rhizolive consortium how the AMF compete in the rhizosphere for root penetration sites with the pathogen and increase lignin deposition, phenylalanine ammonia-lyase (PAL) activity and accumulation of phenolic compounds, which significantly reduced the presence of *V. dahliae* in the roots and stems of olive plants (Boutaj et al. 2020b, 2020c). In greenhouse conditions has been determined how *Glomus mosseae* (formerly known as *Funneliformis mosseae*), *G. intraradices* (formerly known as *Rhizophagus irregularis*) and *G. claroideum* (formerly known as *Claroideoglomus claroideum*) species are able to reduce the damaging effect of *V. dahliae* on olive plantlets, and provide more and longer shoots and higher plant N, P and K concentrations (Porrás-Soriano et al., 2006), being *G. intraradices* able to inhibit the inoculum density of *V. dahliae* in soils 2 and 12 months before the infection (Mulero-Aparicio et al., 2020a). These results could be the consequence of a restriction of sporulation and growth of the pathogen, as it has been verified with the species *Rhizophagus irregularis*, *G. mosseae*, *G. aggregatum*, *G. monosporus*, *G. clarum*, *G. deserticola*, *G. etunicatum*, *G. brasilianum* and *G. margarita*, capable of suppressing the Verticillium wilt disease in combination with *Trichoderma harzianum* (Arici and Demirtas, 2019). Despite the results obtained, under desert conditions both *G. intraradices* and *G. mosseae* did not appear to improve resistance of Picual and Barnea varieties to *V. dahliae* (Kapulnik et al., 2010). However, under this condition AMF colonization enhanced vegetative growth, quantified as tree height and trunk circumference, and increased fruit and oil yields.

### 3.2. Endophytic fungi

Plant endophytic microorganisms include archaea, bacteria, fungi and protists that can be isolated from plant tissues after having been superficially disinfected and that do not cause damage to their host (Lugtenberg et al., 2016; Yan et al., 2019). Endophytic fungi can favor plant growth and protect their host plants against abiotic and biotic stresses, in addition to having great biotechnological potential (enzyme production, bioremediation, biotransformation, etc.) (Zheng et al., 2016). Indeed, once the plant dies, the endophytic fungi begin to behave like saprophytes, recycling nutrients from plant tissues (Saikkonen et al., 2015).

Today there are numerous reviews on the use of endophytic fungi as BCAs, for example, by Chadha et al. (2015), Card et al. (2016), De Silva et al. (2019), or Rabiey et al. (2019). Their biocontrol abilities rely on



the direct inhibition of the pathogen through parasitism, production of secondary metabolites and/or lytic enzymes, and competition for space and/or nutrients (Deshmukh et al., 2015; Larran et al., 2016; De Vries et al., 2018). Furthermore, endophytes can act as BCAs inducing host resistance, by triggering a systemic resistance through JA/ET-dependent and/or salicylic-acid (SA)-dependent signaling pathways (Bastías et al., 2018; Li et al., 2018; Vahabi et al., 2018). In olive, the diversity of endophytic fungi present in its different organs (aerial and root) has been extensively studied through various approaches (Nicoletti et al., 2020). Up to date, the results showed that olive-associated endophytic fungal community is diverse and shaped by host cultivar (Fernández-González et al., 2019), season and geographic location (Martins et al., 2016), and plant organ (Abdelfattah et al., 2015). Important biotechnological tools have been obtained from the wide diversity of endophytic fungi present in olive plants, such as different antimicrobial compounds (Malhadas et al., 2017) and anticancer (Mady et al., 2016). Also used for the decomposition of the pruning remains of olive-trees (Martín-Sampedro et al., 2017) or to improve the acclimatization process in soil after micropropagation processes (Oražem et al., 2016). However, the potential use of olive-associated fungal endophytes as BCAs to improve crop production has become a major priority recently (Table 1). Regarding pathogenic bacteria of olive, several endophytic fungi associated with the presence and absence of *P. savastanoi* disease have been identified, therefore, being components of the olive microbiota with a possible role in the promotion or suppression of olive knot disease (Gomes et al., 2019). One of these fungal species showed the ability to reduce the growth/biomass of the pathogenic bacteria around 96% after 48h of *in vitro* confrontation (Berardo et al., 2018). Similarly, the importance play by the endophytic microbiota in olive tree resistance to *X. fastidiosa* was demonstrated based on a study comparing the endophytic microbiota of olive trees susceptible (Cellina di Nardò) and resistant (Leccino) to *X. fastidiosa* after bacterial infection (Vergine et al., 2020). The exploitation of non-native olive-associated endophytic microorganisms in the control of *X. fastidiosa* has been similarly studied. For instances, the compound ophiobolin A (a sesterterpene) produced by the fungus *Drechslera gigantea* isolated from crabgrass plants (*Digitaria sanguinalis*) showed to be effective in inhibiting the growth of *X. fastidiosa* under *in vitro* assays (Bleve et al., 2018).

Against pathogenic fungi of olive, the use of endophytic fungi to control the anthracnose of the olive tree has been recently reviewed (Martins et al., 2019). Several endophytic fungi isolated from olive tree revealed to be effective in reducing the growth, sporulation, germination or cause hyphae abnormalities in the pathogen *Colletotrichum acutatum* under *in vitro* conditions (Landum et al., 2016; Preto et al., 2017). Some of these fungal endophytes include, for instances, *Alternaria* sp., *Diaporthe* sp., *Nigrospora oryzae*, *Chondrostereum purpureum*, *Chaetomium globosum*, *Quambalaria cyanescens*, *Epicoccum nigrum*, and several *Aspergillus* species. The inhibitory effect displayed by some of these endophytes was ascribed to the production and release of various volatile organic compounds (VOCs), such as phenylethyl alcohol, benzothiazole, 4-methylquinazoline, linal, galaxolide and benzyl alcohol (Landum et al., 2016).

With regard to Verticillium wilt, there are several reports of the effectiveness of the non-pathogenic *F. oxysporum* and *Phoma* sp. isolates in inhibiting *V. dahliae* mycelial growth and spore germination in *in vitro* assays, and in reducing the symptoms of the disease in greenhouse or field conditions as well as in suppressing microsclerotia viability in soil (Varo et al. 2016a, 2016b, 2018). The biocontrol effect of these endophytes has been associated to the production of different secondary metabolites with antifungal activity, such as VOCs, the competition in the rhizosphere for the nutrients and space with the pathogen, and the activation of plant defenses (Mulero-Aparicio et al. 2019, 2020a, 2020b). The ability of endophytic fungi typically used as entomopathogens, such as *Metarhizium brunneum* and *Beauveria bassiana*, to inhibit *V. dahliae* mycelial growth, conidia germination and microsclerotia formation has been similarly reported (Lozano-Tovar et al. 2013, 2017);

same results obtained using these endophytic fungi against the pathogenic oomycete *Phytophthora megasperma*, inhibiting the germination of propagules.

In the case of phytopathogenic nematodes, the active parasitism of several endophytic fungi species isolated from the olive rhizosphere, such as *Talaromyces assiutensis*, *Arthrobotrys brochopaga*, *A. conoides*, *Drechslerella brochopaga*, *Monacrosporium thaumasium* and *Purpureocillium lilacinum*, proved to be effective against the root-knot nematode *Meloidogyne javanica* (Hamza et al., 2017).

The different mechanisms indicated through which some species of endophytic fungi are capable of controlling different pathogens of the olive tree can be studied to isolate the genes involved and use them in the transformation of olive plants, conferring resistance to diseases. In this sense, olive plants capable of expressing the gene that codes for an antifungal protein produced by *Aspergillus giganteus* have been obtained, which showed greater resistance against the pathogen *Rosellinia necatrix*, but not against *V. dahliae* (Narvaez et al., 2018).

### 3.2.1. The *Trichoderma* genus

*Trichoderma* is a genus of endophytic filamentous fungi, although they colonize only the outermost layers of the root without ever reaching the vascular bundle (Alonso-Ramírez et al., 2014; Poveda et al., 2020b). Due to the existing studies with this specific fungal genus, it will be treated in a different section than that of endophytic fungi.

In its interaction with the plant, *Trichoderma* acts as a root colonizing symbiont, for which it establishes a complex molecular signal exchange with the plant. By interacting with olive roots, it has been proven how the species *T. harzianum* and *T. atroviride* are able to stimulate different biosynthetic routes in a systemic way, improving the profile of phenolic compounds in the leaves, of great interest for food, pharmaceutical and cosmetic industries (Dini et al., 2020).

The mechanisms of action used by *Trichoderma* as BCAs and beneficial fungus in agriculture are the competition with the pathogen, the antibiosis, the mycoparasitism, the promotion of plant growth, the increase of its tolerance against abiotic stresses and the stimulation of host defenses against pathogens (Poveda et al. 2019a, 2019b, 2020b; Poveda, 2020b).

Antibiosis occurs during interactions with other microorganisms and involves a wide variety of secondary metabolites produced by *Trichoderma* capable of inhibiting microbial growth and, therefore, plant colonization by pathogens (Bailey et al., 2008). An example of this mechanism of action as BCA is found in a study conducted by Marques et al. (2018), in which they observed the ability of different strains of this genus to produce non-volatile secondary metabolites capable of inhibiting the growth of *Sclerotinia sclerotiorum*, as well as the ability of two strains of *T. brevicompactum* to act against a wide variety of olive pathogens, including *C. gloesporioides*, *V. dahliae* and *F. oxysporum* (Marques et al., 2018). The bactericidal and bacteriostatic capacity of different secondary metabolites from *T. harzianum* and *T. citrinoviride* against *X. fastidiosa* has been similarly demonstrated (Bleve et al., 2018).

Together with the competition for space or specific sites of infection, *Trichoderma* uses competition for nitrogen, carbon, and other growth factors, in order to control plant pathogens (Vinale et al., 2008). *Trichoderma* has a superior ability to mobilize and absorb nutrients from the soil compared to other organisms (Harman, 2006). For example, *T. asperellum* was reported to be effective in protecting tomato plants against the pathogen *F. oxysporum* f.sp. *lycopersici* through competition for iron, in addition to exerting a protective effect against the toxicity of this metal (Segarra et al., 2010).

In mycoparasitism, *Trichoderma* secretes cell wall degrading enzymes ( $\beta$ -glucosidase, endochitinases, proteases and mannosidases) (de Lima et al., 2016). *T. harzianum* demonstrated effectiveness against the olive root rot disease, caused by *F. solani*, being the main biocontrol mechanisms ascribed to direct mycoparasitism and the activation of plant defensive responses (Amira et al. 2017, 2018). As far as activation of systemic plant defenses is concerned, probably, the first clear

demonstration of resistance induced by *Trichoderma* was published in 1997 by Bigirimana et al. showing that *T. harzianum*-root application reduced the diseases caused by fungal pathogens *Botrytis cinerea* and *Colletotrichum lindemuthianu* in bean plants. Subsequently, numerous studies have shown that, by colonizing the roots of plants, *Trichoderma* stimulates their defense mechanisms against numerous phytopathogenic microorganisms (Poveda et al., 2019b).

Several *Trichoderma* species were very effective against *Verticillium* wilt and root rot. *T. harzianum* in the field has provided very good results in the control of *V. dahliae* when applied in combination with AMF, thanks to restrict the fungal sporulation and growth (Arici and Demirtas, 2019). The effectiveness of *T. harzianum* also relies on mycoparasitism towards *V. dahliae* (Ruano-Rosa et al., 2016) and on the competition for space and nutrients, both on the surface and inside the roots (Carrero-Carrón et al., 2018). On the other hand, *T. asperellum* and *T. atroviride* significantly inhibit the growth of *V. dahliae* *in vitro*, and *in planta* reduce the severity of symptoms and increase plant growth (Lozano-Tovar et al., 2013; Carrero-Carrón et al., 2016). Their biocontrol abilities rely on the production of secondary metabolites in the form of diffusible molecules and VOCs (Morán-Díez et al., 2019), including in the field (Mulero-Aparicio et al., 2020a).

The bactericidal and bacteriostatic capacity of different secondary metabolites from *T. harzianum* and *T. citrinoviride* against *X. fastidiosa* has been demonstrated against olive bacteria (Bleve et al., 2018). But the largest number of studies in olive trees have been carried out against soil-borne pathogens, as *F. oxysporum*, *F. solani*, *R. solani*, *Sclerotium rolfsii* and *Alternaria alternata*, against whom it has been determined how a commercial formulation with *T. harzianum*, called *Trichoderma* 2000, significantly reduced incidence of root rot on olive transplants (Mousa et al., 2006).

#### 4. Conclusions

For many countries, especially in the Mediterranean Basin, olive cultivation represents an important part of their economic and even cultural system. Currently, various pathogens threaten the correct development of the crop in its traditional areas in a very marked way, with examples such as the *V. dahliae* fungus or the *X. fastidiosa* bacteria. In this sense, BCAs represent an efficient, effective and environmentally friendly alternative whose development is in full expansion, with the group of filamentous fungi having good results as a consequence of their greater capacity for survival in the field compared to bacteria or yeast.

Different species of filamentous endophytic fungi, including *Trichoderma*, are able to control the pathogens *P. savastanoi* and *X. fastidiosa* through the production and release of secondary metabolites, as well as oomycetes and *Colletotrichum*. On the other hand, against *V. dahliae* all the groups of filamentous fungi indicated are effective through several mechanisms, including competition for space and nutrients in the rhizosphere, antibiosis, mycoparasitism and/or the activation of plant defensive responses. Finally, for the control of nematodes, the different filamentous endophytic fungi showed to act by active parasitism.

All the commented studies show the efficacy in the laboratory, greenhouse and even in the field of the use of the different groups of filamentous fungi in the control of olive pathogens. Its massive use in agricultural production systems could develop successfully in a short time, since there are many different formulations on the market with some of the reported species. The correct development of sustainable agriculture that respects the environment and human health in olive cultivation must be linked to the implementation of successful biological strategies, such as those mentioned here.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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