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Review

Paecilomyces and Its Importance in the Biological Control of Agricultural Pests and Diseases

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Abstract: Incorporating beneficial microorganisms in crop production is the most promising strategy for maintaining agricultural productivity and reducing the use of inorganic fertilizers, herbicides, and pesticides. Numerous microorganisms have been described in the literature as biological control agents for pests and diseases, although some have not yet been commercialised due to their lack of viability or efficacy in different crops. *Paecilomyces* is a cosmopolitan fungus that is mainly known for its nematophagous capacity, but it has also been reported as an insect parasite and biological control agent of several fungi and phytopathogenic bacteria through different mechanisms of action. In addition, species of this genus have recently been described as biostimulants of plant growth and crop yield. This review includes all the information on the genus *Paecilomyces* as a biological control agent for pests and diseases. Its growth rate and high spore production rate in numerous substrates ensures the production of viable, affordable, and efficient commercial formulations for agricultural use.

Keywords: biological control; diseases; pests; *Paecilomyces*

1. Introduction

The genus *Paecilomyces* was first described in 1907 [1] as a genus closely related to *Penicillium* and comprising only one species, *P. variotii* Bainier. The description of this genus was revised by Brown and Smith [2], and Samson [3] defined 31 species divided into two sections: *Paecilomyces* characterized by thermophilic, thermotolerant, and mesophilic species, with yellow-brown colonies showing teleomorphic states corresponding to the genera *Byssochlamys*, *Talaromyces*, and *Thermoascus*; and *Isarioidea* characterized by mesophilic species with purple, pink, yellow, or green colonies. The former section includes the nematophagous or entomopathogenic species, also known as *Paecilomyces lilacinus* or *P. fumosoroseus* [4,5]. The different species in *Paecilomyces* are related to two genera of fungi: *Cordyceps* and *Torrubiella* [3].

Studies carried out by Luangsa-ard et al. [6] and Inglis and Tigano [4] confirm the polyphyletic origin of this genus that belongs to the Sordariomycetidae and Eurotiomycetidae subclasses. The Fungorum database [7] currently includes a list of 145 *Paecilomyces* species. Of all the species, some retain their original name, while others have been reclassified into other genera. One clear example is *Paecilomyces lilacinus* (Thom) Samson, which has been assigned to the genus *Purpureocillium* [8]. Despite its re-assignment to a different genus, *Paecilomyces lilacinus* will be included in this literature review, because of its importance in disease and pest control. Given the polyphyletic nature of the genus *Paecilomyces*, the evolution of these taxonomic studies is of great importance for developing microbial formulations that can be used in agriculture [9].

The genus *Paecilomyces* has hyaline to yellowish septate hyphae, often with smooth walls and verticillated or irregularly branched conidiophores, and phialides with a wide base and an elongated neck. The conidia are unicellular; hyaline, in chains; and the youngest conidium is at the basal end [10]. The conidial thermotolerance is correlated with their size and shape. Thus, the smaller and more spherical asexual conidia or ascospores are more vulnerable to high temperature [11–14]. *Paecilomyces* has high growth sporulation rates and grows over a wide range of temperatures and substrates. As a result, its rapid multiplication ensures viable and affordable development of commercial formulations [15].

The genus *Paecilomyces* has many species, both pathogenic and saprophytic, and can be found in a wide range of habitats, including soil [16,17], decomposing plant material or food [18,19], pasteurized food products [2,20,21], marine sediments [22,23], compost [24,25], insects [26–29], nematodes [30,31], or the rhizosphere of various plants [32,33], among others.

Paecilomyces also plays a significant role as an endophyte in numerous plants by providing several advantages for plant development. It can be used directly or indirectly as a potential biostimulant. When used directly, *Paecilomyces* or its metabolites increases the plant morphological parameters and crop yield [15,34–37]. The plant–*Paecilomyces* interaction improves plant health through different mechanisms and provides protection from phytopathogens [38]. This interaction showed a production of phytohormones, such as gibberellins and indole-acetic acid, that promoted growth and mitigated the effects of abiotic stress, such as salinity [39,40]. When used indirectly in combination with pathogenic agents such as nematodes or fungi, *Paecilomyces* has positive effects on crop growth by acting as a biological control agent [41–44].

Numerous species of the genus *Paecilomyces* produce a wide variety of secondary metabolites with different chemical structures and diverse biological activities, such as herbicidal [45], insecticidal [46,47], bactericidal [48], fungicidal [49], nematicidal [50–52] or cytotoxic [53]. There are also descriptions of metabolites with antitumour activity [54,55] or enzyme inhibitors, such as Paecilomide, which acts as an acetylcholinesterase inhibitor and can be used to control human diseases such as Alzheimer's [56]. In addition, they have a role in aromatic compound degradation [57,58], ethanol production from agro-industrial wastes [59], or removal of ammonium from synthetic media or ammonia emission reduction in poultry manure [60,61]. Nevertheless, we cannot ignore the fact that *Paecilomyces* has been associated with several human infectious diseases in immunosuppressed patients [62,63] and has also been described as a phytopathogen. *P. variotii* was described by Aminaee et al. [64], as the causal agent of pistachio dieback, although subsequent molecular and phylogenetic studies reported that it was caused by *P. formosus* (Sakag., May., Inoue and Tada) Houbraken and Samsoninstead [65]. According to the map shown in Figure 1, there are few species of *Paecilomyces* responsible for the biological control of pests and diseases.

In this review, we will analyse the significant role of *Paecilomyces* in plant pest and disease control. In this sense, *Paecilomyces* is described as a biological control agent against bacteria, phytopathogenic fungi, nematodes, and numerous pests, using its extracts, secondary metabolites, or mycelium. To our knowledge, this is the first review of the genus *Paecilomyces* as a biological control agent against plant pests and diseases.

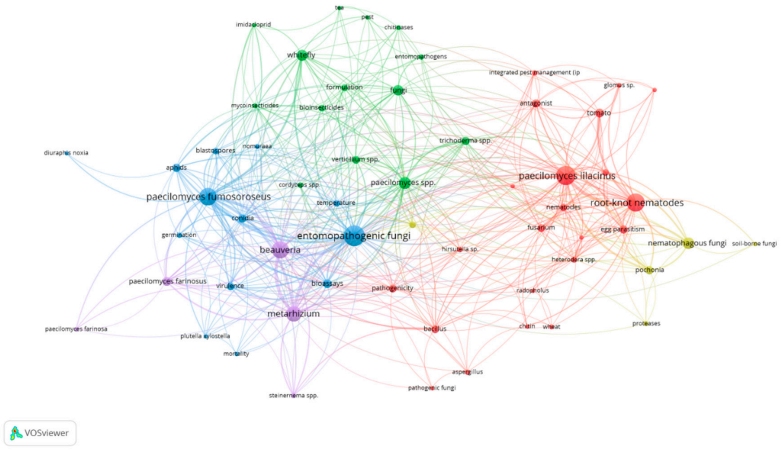

Figure 1. Network map of co-occurrence matrix for the 486 documents published in *Paecilomyces* research. VOSviewer software (version 1.6.15, Leiden University, The Netherlands) was used to map the frequency of keyword co-occurrence networks. Differences in font size imply differences in relevance. The different colors refer to the groups or clusters formed.

2. Biological Control Mechanisms of the Genus *Paecilomyces*

Although many biological control mechanisms are unknown, advances in metagenomics provide some information on the plant–pathogen–antagonist interaction [66,67]. In the genus *Paecilomyces*, microbial mechanisms involved in pest and disease suppression have been direct, such as parasitism, competition or antibiosis, and indirect, which involve plant protection through induced systemic resistance (ISR) mechanisms [68–70].

2.1. Parasitism

Paecilomyces is capable of parasitizing fungi [71], nematodes and arthropods [72,73]. After recognition and pathogen-antagonist interaction take place, penetration and/or secretion of enzyme complexes occurs, leading to antagonist growth at the expense of its host [74,75]. Penetration can be mechanical, through appressoria development [76,77], or enzymatic, through cellulase, glucanase, laccase, leucinoxin, lipase, pectinase, protease, chitinase or xylanase release, which are involved in the infection process [78–82]. Thus, in vitro production of cellulases, lipases, and xylases by *P. tenuis* [83], chitinases and proteases by *P. fumosoroseus* (Wize) A.H.S. Br. and G. Sm. [84,85], or chitinolytic enzymes secreted by *P. lilacinus* [17] has been described. Chitinase production by *P. javanicus* leads to mycelia inhibition of *Aspergillus nidulans*, *Colletotrichum gloeosporioides*, *Rhizoctonia solani* and *Sclerotium rolfsii* [86].

On the other hand, Khan et al. [87] reported that lipases, proteases and chitinases have the strongest entomopathogenic effect. Thus, the production of these enzymes by *P. fumosoroseus* has been effective in the control of *Tenebrio molitor* [88], *Trialeurodes vaporariorum* [89] and *Plutella xylostella* [90]. *P. farinosus* (Holmsk.) A.H.S. Br. and G. Sm. proteases intervene in the control of *Galleria mellonella* [91].

Various studies refer to the nematicidal activity of *Paecilomyces*. Species of this genus, namely *P. lilacinus*, can penetrate both the eggshells and structural components of juvenile and adult stages of different species of nematodes through spore germination and subsequent hyphal branching and appresoria formation [92,93]. Regarding the production of lytic enzymes causing a nematicidal effect, the synthesis of amylases, lipases, proteases, and chitinases associated with this species has been described [77,78,85,87,94,95]. Overexpression of genes regulating the synthesis of these enzymes increases *P. lilacinus* virulence and parasitic ability against *Meloidogyne incognita*, *Panagrellus redivivus*, and *Caenorhabditis elegans* [96,97].

2.2. Competition

Competition for nutrients and space regulates the growth of pathogens coexisting in the same niche [67,82,98]. Siderophore production limits the availability of iron for pathogens [75,99]. In vitro synthesis of hydroxamate and carboxylate siderophores, such as ferrirubin trihydroxamate, has been described mainly in *P. lilacinus* and *P. variotii* [15,100–104].

While this mechanism has a direct impact on control, competition is often accompanied by other mechanisms [70]. The rapid growth of *Paecilomyces* species prevents the development of certain pathogens [105,106]. For instance, spraying sunflower seeds with *P. variotii* spores prevents penetration and infection by pathogen *Macrophomina phaseolina* [107]. However, this competition can sometimes have a negative impact on the rest of the beneficial microbiota [108].

2.3. Antibiosis

The production of secondary metabolites with antimicrobial effect by *Paecilomyces* species has been widely described. Among them, we can highlight the synthesis of alkaloids, phenolic compounds, volatile organic compounds, steroids, flavonoids, peptides, polyketides, quinones and terpenoids [109,110]. Li et al. [111] recently described a total of 148 active metabolites produced by different *Paecilomyces* species that can be used for drug or agrochemical development. In the following sections, we will show the importance of these metabolites in the biological control of pests and diseases.

2.4. Induced Resistance in Plants

The literature does not provide many examples on the effect of induced resistance after *Paecilomyces* colonizes the root system of a plant. Suárez-Estrella et al. [112] observed that inoculation of tomato plant roots with *P. variotii* significantly inhibited the signs caused by the bacterium *Xanthomonas campestris* on leaves. Similarly, López et al. [113] observed a reduction in the *Aphis gossypii* population in cotton plants whose seeds had been previously inoculated by being immersed in a *P. lilacinus* spore suspension. The combined use of *P. lilacinus* and salicylic acid improved the cellulose, hemicellulose, lignin, and pectin contents in cotton plants compared to inoculation treatments using *Pythium debaryanum* and *Fusarium oxysporum*, which showed that wall lignification provides a high level of protection against pathogen invasion. Likewise, concentration of soluble proteins and phenolic compounds increased in the root, which reduced the incidence of both diseases [114]. This also occurs when okra plants are inoculated with *P. lilacinus* [115].

Similarly, the effect of induced resistance can also be produced by *Paecilomyces* extracts. A commercial extract of *P. variotii* known as ZhiNengCong (ZNC) could also induce resistance against *Xanthomonas oryzae* or *Pseudomonas syringae* in rice plants or Arabidopsis, respectively. A dose of 500 ng/mL of ZNC could not inhibit the development of pathogens *in vitro*, while the use of a smaller dose of 100 ng/mL did generate immunity against said bacteria. On the other hand, reactive oxygen substances such as superoxide and hydrogen peroxide or callose also increase, compared to untreated Arabidopsis plants, in addition to activating salicylic acid synthesis, which is necessary for the defence response [36].

3. Biological Control of Diseases Caused by Phytopathogenic Bacteria

Few studies show the effectiveness of *Paecilomyces* against different species of phytopathogenic bacteria. *Paecilomyces variotii* isolated from municipal solid waste compost showed a reduction in 27% of diseases caused by *X. campestris* in melon, and a decrease in the pathogen population [112]. Nesha and Siddiqui [44] observed a reduction in soft rot and leaf blight caused by *P. carotovorum* pv. *carotovorum* and *X. campestris* pv. *carotae* after using *P. lilacinus*, alone or in combination with *A. niger* and an increase in the dry weight and chlorophyll content of a carrot crop.

Metabolites produced by this genus play a significant role in disease control due to its antagonistic effect, although there is little information on the matter compared to phytopathogenic bacteria. There are descriptions on the importance of antibacterial metabolites such as viriditoxin or betulin against non-phytopathogenic bacteria such as *S. aureus, Enterococcus* sp. *Micrococcus* sp., *Aeromonas Hydrophila, Flavobacterium* sp., *Pseudomonas aeruginosa*, and *Vibrio cholera* [116,117]. Sornakili et al. [83] recently reported the inhibition of *Erwinia carotovora, Xanthomonas oryzae* pv. *oryzae*, and *Ralstonia solanacearum* with in vitro inhibition between 13–45% using *P. tenuis*, an endophyte isolated from rice leaves. Various metabolites, such as octadecanoic acid, acetic acid, and 2-ethylhexyl ester, as well as enzymatic activities, xylanases, cellulases, and lipases, were involved in this control.

4. Biological Control of Diseases Caused by Phytopathogenic Fungi

Various *Paecilomyces* species have shown their antagonistic effect against phytopathogenic fungi causing root and aerial plant diseases through various mechanisms (Table 1). *P. variotii* and *P. lilacinus* species have proven to be quite effective, although most studies are in vitro. The antagonistic effect observed in most cases is explained by a competition for space and nutrients (Figure 2). However, other mechanisms associated with secondary metabolite production have been observed, which cause plasmolysis in spore germ tubes or hyphal melanisation in *Pyrenophora tritici-repentis* [118], hyphal lysis in *Moniliophthora roreri* caused by *Paecilomyces* sp. [71], mycoparasitism of *F. oxysporum* caused by *P. variotii* and *P. lilacinus* [119], or antibiosis against *R. solani* [120], among others. Viriditoxin, sphingofungins E and F [121], or eicosenoic acids are reported to have an antifungal effect against various phytopathogenic fungi such as *Biscogniauxia mediterranea, Phytophthora cinnamomi* or *Fusarium moniliforme* [61]. Varioxepin A or 6-Pentyl-α-pyrone inhibits perithecia formation and mycelial growth of *Fusarium graminearum* [122,123] or Paecylaminol, which inhibits soft rot development in tomatoes caused by *Mucor racemosus* [124].

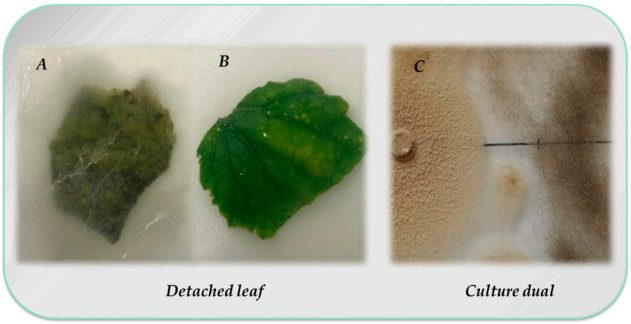

Figure 2. Detached leaf method to evaluate *P. variotii* as biological control agent against *B. cinerea*. (**A**) control leaves four days post infection with *B. cinerea*; (**B**) Leaf inoculated with spores *B. cinerea* and *P. variotii*. Photographs were taken four days after incubation in a moist petri dish at 20 °C under continuous white light. (**C**) Dual culture assay for in vitro inhibition of mycelial growth of *B. cinerea* by *P. variotii*.

Some in vivo studies show a direct effect on plant growth promotion after using *Paecilomyces* [15], but also an indirect effect due to fungal disease control [72]. Yang et al. [125] observed inhibited *S. sclerotiorum* mycelial growth and sclerotia germination and a reduced disease severity after using *P. lilacinus* on a rapeseed crop. Results did not show differences after using spores or filtering without fungi cells, which highlighted the importance of *Paecilomyces* metabolites in pathogen control. In tomatoes, spraying *P. variotii* spores on the leaves significantly reduces damage caused by *Alternaria solani* [126]. On the other hand, the increase in polyphenols and antioxidant activity due to the use of *P. lilacinus* on okra roots improves plant development and control of various phytopathogenic fungi causing root rot [115]. Likewise, prior use of *P. fumosoroseus* delays the development of powdery mildew caused by *Podosphaera xanthii* [127], leading to mycelium and spore destruction due to the close contact of fungi and with some degree of mycoparasitism depending on the environmental conditions.

Table 1. Control of phytopathogenic fungi by *Paecilomyces* species.

Species	Phytopathogen	Assay/Plant	Reference
Byssochlamys nivea	*Rhizoctonia solani, Sclerotinia sclerotiorum, Aspergillus flavus*	In vitro	[128]
P. farinosus	*Blumeria graminis*	Dual culture, barley	[129]
	Oidium neolycopersici	Dual culture, tomato	
	Golovinomyces orontii	Dual culture, tobacco	
	Podosphaera xanthii	Dual culture, cucumber	
P. fumosoroseus	*Fusarium solani, R. solani, Sclerotium rolfsii*		[130]
	Macrophomina phaseolina	Dual culture	
	Pythium aphanidermatum		[43]
	P. xanthii	Cucumber	[127]
P. lilacinus	*R. solani*	Dual culture, poinsettia Sorghum, okra	[115,131]
		In vitro	[119]
	Pyrenophora tritici-repentis	Wheat	[118]
	S. Sclerotiorum	Dual culture, canola	[124]
	A. flavus, A. parasiticus	In vitro, soil	[132,133]
	Magnaporthe oryzae	Dual culture, rice	[134]
	Fusarium oxysporum	Chickpea	[135]
		Sorghum, okra	[115]
	S. sclerotiorum	Wheat	[136]
	F. oxysporum, P. debaryanum	Cotton	[114]
	R. bataticola	Dual culture	[137]
	F. chlamydosporum	In vitro, tomato seeds	[42]
	M. phaseolina, F. solani, F. oxysporum	Dual culture, mung bean Okra	[115,138,139]
	F. oxysporum f. sp. *lycopersici*	Tomato	[72]
	P. aphanidermatum, S. rolfsii	In vitro	[43]
P. marquandii	*Verticilium dahliae*	Dual culture	[140]
	R. solani	Dual culture	[120]

Table 1. *Cont.*

Species	Phytopathogen	Assay/Plant	Reference
P. variotii	*Pythium spinosum*	Dual culture, soybean	[141]
	F. oxysporum	Tomato	[142]
	Biscogniauxia mediterránea, F. moniliforme, Phytophthora cinnamomi	Rigid ryegrass	[61]
	S. rolfsii, A. flavus	Dual culture, in vitro	[43,131,143]
	M. oryzae	Dual culture	[133]
	F. oxysporum	Dual culture, chickpea	[134]
	F. oxysporum	Dual culture, melon	[112]
	Alternaria solani, F. oxysporum	Tomato	[126]
	V. dahliae	Dual culture	[106]
	M. phaseolina	Dual culture, sunflower	[107,138,144–146]
	P. aphanidermatum	Dual culture	[43]
	F. oxysporum. f. sp. *ciceris*	Chickpea	[134]
Paecilomyces sp.	*R. solani, S. sclerotiorum, A. flavus*	Dual culture	[126]
	Moniliophthora roreri	In vitro	[71]
	Colletotrichum gloeosporoides	Chili pepper	[146]
	Phytophthora palmivora	In vitro	[105]
	F. graminearum	In vitro	[122]
	Ceratobasidiumtheobromae	Cocoa	[147]
	Mucor racemosus	In vitro	[124]
Paecilomyces spp.	*Pyricularia oryzae*	In vitro	[28]
P. sulphurellus	*R. solani*	In vitro	[120]
P. tenuis	*M. phaseolina, M. grisea, Pythium* sp., *R. solani, F. oxysporum, Colletotrichum falcatum*	In vitro	[83]

5. Biological Control of Diseases Caused by Nematodes

As a nematophagus fungus, *Paecilomyces* has been widely studied and can be found in a variety of biological formulations for agricultural use [93]. There are many examples where *Paecilomyces* spp. act as nematicidal agents, especially against *Meloidogyne* spp., but also against other genera such as *Globodera* [52], *Rotylenchulus*, *Heterodera*, *Xiphinema* or *Pratylenchus* [51] (Table 2). One example is the use of *P. lilacinus* and *P. fumosoroseus* against *M. incognita* or *M. javanica*, which drastically reduces their populations [44,51,148,149], in both in vitro [43,87] and field tests [50,150]. The spores of these species must germinate on the host to penetrate and colonize its surface, in order to modify its physiology [51]. *Paecilomyces* acts according to the fungal and nematode species it parasitizes.

Paecilomyces spp. can act at different nematode developmental stages by infecting eggs, young or adult nematodes. Nematode eggshell is the main barrier against parasite agents and provides resistance to both chemical nematicides and biological compounds. *Paecilomyces* species are capable of secreting enzymes to degrade this barrier and deploying mechanisms involved in nematode parasitism [151,152]. Thus, observations have shown that *Meloidogyne incognita* eggs at early stages of development are more vulnerable than eggs containing fully developed juveniles, although the latter are also affected [153–155]. Hollan et al. [76] confirm that eggs are parasitized by *P. lilacinus* at all stages, including unhatched juveniles. Egg infection occurs when hyphae lie flat on the egg surface and appresoria are formed. Then, the fungus spreads and conidiophores are formed. Studies carried out by Khan et al. [92] concluded that said juveniles show various degrees of deformities and developmental abnormalities, such as reduced mobility inside the eggs. Different studies show the significant role of proteases and chitinases in the penetration of the fungus through eggshells. Thus, *M. arenaria* eggshells showed vitelline membrane disaggregation, and chitin and lipid layer destruction after using *P. lilacinus* [156].

Juvenile *M. hapla* eggs were highly vulnerable to serine proteases produced by *P. lilacinus* than eggs containing more developed juveniles. On the contrary, larvae showed no signs of damage. Jatala et al. [157] reported that *P. lilacinus* is capable of infecting female *Meloidogyne* spp. and *Heterodera* spp. and *Globodera* spp. cysts. In these cases, hyphae entered through natural openings of the body [158]. Evidence shows that various hydrolytic proteins, such as proteases (mainly serine proteases), collagenases and chitinases are involved in nematode cuticle penetration and subsequent cell degradation [77,97,159–161]. Likewise, different secondary metabolites produced by *Paecilomyces* also play a significant role in nematode control [162].

Nematode control effectiveness using *Paecilomyces* depends on the crop itself, as it affects fungal activity in many cases [163]. Thus, the use of an antagonist in combination with organic substances increases parasitism by *Paecilomyces* in both eggs and larvae of nematodes [164]. On the other hand, it has been reported that the use of *P. lilacinus* on recently solarised soil does not increase control effectiveness compared to non-solarised soil. However, a certain reduction in fungal activity is observed when both techniques are applied [165]. When comparing effectiveness using chemical compounds, *P. lilacinus* provides adequate control during crop growth, although the combination of both techniques shows better results compared to nematode control. [119,166–169].

As shown in Table 2, *P. lilacinus* is the most important nematophagous fungus, as it is capable of controlling various nematode species in different crops, though other species such as *P. marquandii* (Massee) *S. Hughes* [170–172] or *P. variotii* [173] can be equally effective. Reports by Chen et al. [171] on the use of *P. marquandii* against *M. hapla* showed an increase in lettuce weight, a decrease in gall formation by 25.7% and a reduction in egg production by 46.3%. According to Al-Assas, et al. [174], *P. variotii* reduces the number of galls by more than 90%, showing more effectiveness compared to chemical compounds.

Table 2. Nematode control by *Paecilomyces* species.

Species	Nematode	Assay/Plant	Reference
P. fumosoreseus	*Meloidogyne javanica*	In vitro	[51,175]
P. lilacinus	*M. enterolobii*	In vitro	[176]
	M. arenaria	Tomato	[177]
	M. incognita	Melon	[178]
		Tomato	[51,95,149,166,177,179–188]
		Eggplant	[181]
		Green beans	[163]
		Cotton, peanut, corn	[189,190]
		Cucumber	[44,191]
		In vitro	[95,154,155,162,192]
		Soybean	[193]
		Indian ginseng	[194]
		Carrot	[195]
		Potato	[153]
		Legumes	[196]
		In vitro	[197]
	M. javanica	Tomato	[168,169,198,199]
		Carrot	[44]
		In vitro	[87,175,200]
		Cherry	[201]
	M. hapla	In vitro, tomato	[192,202–204]
	M. exigua	Rubber tree	[205]
	M. graminicola	Wheat	[206]
	M. marylandi	Grass	[207]
	M. paranaensis	Coffee	[208]
		Tomato	[209]
	Meloidogyne spp.	In vitro	[173,210,211]
		Tomato	[165]
	Heterodera avenae	In vitro, soil	[92,212,213]
	H. glycines	In vitro, Cotton	[190,214]
		Soybean, Wheat	[215]
	H. schachtii	In vitro	[92,213]
	H. trifolii	Tomato	[216]
	Heterodera spp.	Potato	[157]
	Globodera pallida	In vitro	[119]
	Globodera spp.	Potato	[157]
	Pratylenchus thornei	In vitro, wheat	[157,217]
	Pratylenchus spp.	Sugar cane	[218]
		Cotton	[219]
	Rotylenchulus reniformis	Tomato	[152]
		In vitro, cotton	[210,220]
	Tylenchulus semipenetrans	In vitro	[221,222]
	Radopholus similis	Banana	[167]
	R. reniformis	In vitro	[210]
P. marquandii	*M. hapla*	Lettuce	[171]
	M. hapla	Lettuce	[172]
	R. similis, H. multicinctus	Banana	[223]
	M. incognita	Tomato	[170]
P. variotii	*Meloidogyne* spp.	In vitro	[173]
Paecilomyces spp.	*Meloidogyne* spp.	In vitro	[197]
	G. rostochiensis	Bean, chickpea	[224]
	M. incognita	Cucumber	[162]

6. Biological Control of Diseases Caused by Arthropods

The genus *Paecilomyces* includes multiple species described as pest control agents capable of providing natural control without the need for exogenous applications [225], many of which have been tested under controlled conditions for elaborating bioinsecticides to fight pests of great economic importance worldwide [226,227]. Among entomopathogenic fungi, *Paecilomyces* species are viable sources to elaborate mycoinsecticides, as affordable stable propagule substrates such as blastospores

or conidia can be easily produced on a large scale [228]. According to Ruiu [229], bioformulations containing mainly *P. lilacinus* and *P. fumosoroseus* have been commercialised for pest control.

However, initial results obtained under in vitro culture conditions were not always consistent when assessing their effectiveness under field conditions. For this reason, parameters such as the application method should be assessed. In this case, most tests under controlled laboratory conditions are assessed by immersing samples in *Paecilomyces* spp. conidia suspensions, which provide clear results on the infectivity of the tested species [230]. Then, in planta tests are conducted under semi-natural conditions to assess effectiveness by spraying infected seedlings with conidial suspensions inside closed structures to prevent insects from going in or out [231]. Finally, mortality is assessed under field conditions by sprinkling crops showing a specific pest density with pre-commercial *Paecilomyces* spp. formulations [232]. In this sense, new application methods are currently being assessed, such as the one described by López et al. [113], where *P. lilacinus* used as an endophyte on cotton seeds provides induced resistance to plants by causing negative effects on *Aphis gossypii* feeding and reproduction.

Environmental conditions at the time of application are crucial and high temperatures and relative humidity are the most favourable for infection. In this sense, *P. fumosoroseus* caused a mortality of 60%, 80% and 85% in *Myzus persicae*, and of 90%, 95% and 100% in *Aphis fabae*, at 10 °C, 18 and 23 °C, respectively [233]. Regarding humidity, Demirci et al. [121] reported that *I. farinosa* showed increased pathogenicity against *Planococcus citri* under high relative humidity conditions at the time of application. Another aspect to bear in mind is the insects' physiological state or size. Nymphal and larval stages tend to be more vulnerable than eggs as they have defence structures in their chorion. *P. fumosoroseus* is capable of affecting whitefly *Aleurodicus cocois* at various developmental stages [234]. Similarly, the physical barriers of *Leptinotarsa decemlineata* pupae make them more resistant than their larvae to *Isaria fumosorosea* infection [235]. In terms of size, Hunter et al. [236] showed a negative correlation between insect mortality and size mainly because larger sizes are associated with thicker cuticles, as in the use of *I. fumosorosea* on *Diaphorina citri* (psyllid) and *D. citri* (curculionidae), in which case the latter is bigger. Insect integument sclerotisation is also important, as it has an impact on *Paecilomyces* spp. ease of penetration and infection [237]. In order to avoid these obstacles, the use of formulations containing *Paecilomyces* spp. with high conidia densities is advised, as well as a focalised and prolonged exposure, to obtain an improved control effect against insects [238].

Paecilomyces has been described to control pests by limiting insect growth as a result of reduced feeding [236,239] reproduction [240] or simply causing their death due to mycosis [241]. In addition, it has been shown that *P. fumosoroseus* is capable of causing more deaths than some commercial insecticides such as fipronil when used against *Frankliniella occidentalis* [242]. Similar to when they act as nematophagous fungi, the potential of *Paecilomyces* spp. as a biological control agent that parasitises insects by penetrating their cuticle and subsequently spreading through haemolymph has been described [243]. This is possible owing to the excretion of enzymes, such as protease or chitinase synthesis [17,90], or different types of toxins, such as beauvericin [244], dipicolinic acid [46] or dibutyl succinate [245], which are described as bioactive metabolites with insecticidal or insect repellent effects, which turns them into significant virulence factors. Numerous orders of arthropods that are vulnerable to the use of *Paecilomyces* spp. (Table 3), including hemiptera, have been described, such as aleurodids [246], aphids [238], thysanoptera [242], diptera [247], lepidoptera [73], hymenoptera [248] and coleoptera [235].

Table 3. Biological control of pests using *Paecilomyces*.

Species	Pest	Assay/Plant	Reference
P. carneus	*Pteroma pendula*	In vitro	[249]
P. cinnaomeus	*Aleurocanthus camelliae*	In vitro	[250]
P. javanicus, P. lilacinus	*Spodoptera litura, Plutella xylostella*	In vitro	[73]
P. farinosus	*Sitophilus oryzae, Myzus persicae*	In vitro	[251,252]
	Lygus rugulipennis	In vitro	[253]
	Planococcus citri	In vitro	[254]
	Tribolium confusum	In vitro	[255]
	Pristiphora abietina	In vitro	[256]
	Delia antiqua	In vitro	[257]
	Eurygaster integriceps	Wheat	[258]
	Hypothenemus hampei	In vitro	[259]
	Vespula, Dolichovespula	Review	[260]
P. formosa	*Prays oleae*	In vitro	[261]
P. fumosoroseus	*Mamestra brassicae, S. littoralis*	In vitro	[262]
	Hoplia philantus	In vitro and grass	[263]
	Monellia caryella, M. caryaefoliae *M. pecanis*	In vitro	[264]
	Diuraphis noxia	In vitro	[265]
	P. xylostella	In vitro	[266]
	Agriotes lineatus	In vitro	[267]
	Ceratitis capitata	In vitro	[230,268]
	Aphis fabae	In vitro	[269]
	Bemisia argentifolii	Tomato, cabbage, cucumber	[270]
	Diaphorina citri	Orange, In vitro	[232,271]
	Eutetranychus orientalis	In vitro	[240]
	Thrips palmi	Bean	[272]
	S. frugiperda	Corn	[273]
	Thrialurodes vaporariorum	Tomato	[274]
		In vitro	[275]
	Bemisia tabaci	In vitro	[276]
	Tetranychus urticae	Tomato	[277]
	Toxoptera citricida	In vitro	[278]
	Hyalopterus pruni	In vitro	[279]
	Coccinelidos	Review	[280]
	Schizaphis graminum	In vitro	[281]
	B. tabaci	Cotton	[282]
	Anoplophora glabripennis	In vitro	[283]
	D. noxia	Wheat	[284]
	Delia radicum, D. floralis	In vitro	[285]
	Bactrocera zonata, B. cucurbitae	In vitro	[286]
	Haematobia irritans	In vitro	[287,288]
	Coptotermes curvignathus, C. gestroi	In vitro	[241]
	Leptinotarsa decemlineata	In vitro	[235]
	S. littoralis	In vitro	[289]
	Epilachna varivestis	In vitro	[290]
	Polyphagotarsonemus latus	In vitro	[291]
	B. argentifolii	In vitro, hibiscus	[292–296]
	P. xylostella	In vitro	[297]
	B. tabaci	In vitro	[298]
	B. tabaci, T. vaporariorum	In vitro	[299]
	Serangium parcesetosum	In vitro	[300]
	Drosophila suzukii	In vitro	[301]
	T. vaporariorum	Tomato	[302]

Table 3. *Cont.*

Species	Pest	Assay/Plant	Reference
P. fumosoroseus *P. lilacinus*	*Leptinotarsa decemlineata*	In vitro	[303]
P. fumosoroseus *P. farinosus*	*Rhagoletis cerasi*	In vitro	[304]
P. fumosoroseus *P. carneus* *P. lilacinus* *P. marquandii* *P. farinosus*	*Aedes aegypti*	In vitro	[305]
P. lilacinus	*Leptinotarsa decemlineata* *Phthorimaea operculella*	In vitro	[306]
	Acromyrmex lundii	In vitro	[248]
	Aleurocanthus woglumi	In vitro	[307]
	Duponchelia fovealis	In vitro	[308]
	Rhipacephalus microplus	In vitro	[309]
	Tribolium confusum, Rhyzopertha dominica, *Sitophilus zeamai*	In vitro	[29]
	A. schlechtendali	In vitro	[310]
	T. vaporariorum, A. gossypii *Frankliniella occidentalis* *Tetranychus urticae*	In vitro	[243]
	Oligonychus coffeae	In vitro	[311]
	C. capitata	In vitro	[312]
	Galleria mellonella	In vitro	[81,313]
	A. gossypii	Cotton	[113]
	Solenopsis invicta	In vitro	[314]
	Tessaratoma papillosa	In vitro	[315]
	S. zeamais	In vitro	[316]
	Cyclocephala signaticollis	In vitro	[317]
P. lilacinus *P. fumosoroseus*	*A. fabae*	In vitro	[318]
P. niveus	*Nasonovia ribisnigri*	In vitro	[319]
P. tenuipes	*S. frugiperda, S. exigua* *Helicoverpa zea, H. virescens*	In vitro	[320]
	Otiorhynchus sulcatus	In vitro	[321]
	P. xylostela	In vitro	[322]
P. variotii	*S. litura*	In vitro	[323]
	S. avenae	In vitro	[324]
	Earias insulana	In vitro	[325]
Paecilomyces sp.	*Lygus lineolaris*	In vitro	[326]
	Carmenta foraseminis	In vitro	[327]
	Cyrtomenus bergi	In vitro	[328]
	Rhynchophorus ferrugineus	In vitro	[329]
	B. tabaci	In vitro	[330]
	S. litura	In vitro	[331]
Paecilomyces spp.	*Hedypathes betulinus*	In vitro	[332]

7. Conclusions

The loss of pesticide effectiveness against certain pathogens, waste limitation in harvested products, the problems that these products cause to the environment and human health, and the ineffectiveness of genetic resistance due to quick alterations in pathogen virulence require the development of new control methods. While it is currently difficult to reduce the total amount of chemical active substances without causing losses in production, their gradual decrease and the use of bioestimulants can help optimize the use of chemical products and reduce environmental pollution. This review is the first to gather information on the potential of various *Paecilomyces* species as biological control agents against multiple diseases and pests, using different mechanisms of action and/or specificity that can be used in combination with cultural and chemical control in agriculture.

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