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Penicillium restrictum as an Antagonist of Plant Pathogenic Fungi

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ABSTRACT

The genus *Penicillium* includes many ubiquitous species which are able to colonize very diverse natural and anthropic contexts as a result of their capacity to adapt to extreme environmental conditions and utilize almost any kind of organic substrate. A number of species are reported to assume agricultural relevance at some extent based on their interactions with cultivated plants and/or other organisms which may sort an effect on the crop outcome. The monoverticillate species *Penicillium restrictum* is cosmopolitan and mostly regarded as a soil saprotroph. Such a widespread occurrence is reflected in an extensive literature introducing its ecological role and biological properties which are considered and exploited in several biotechnological fields. This review particularly focuses on the antagonistic activity which has been documented against soil-borne plant pathogenic fungi, with special consideration for its recently discovered aptitude to exert mycoparasitism, in view of possible implications for use as an effective biocontrol agent in crop protection.

Keywords: biocontrol, crop protection, mycoparasitism, rhizosphere, soil fungi

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INTRODUCTION

The cosmopolitan genus *Penicillium* includes many ubiquitous species which are considered for various aspects related to human activities. A particular field is represented by the agricultural application in plant protection, especially against soil-borne fungal pathogens, based on an adaptation to the soil environment which has stimulated consistent competitive abilities toward other microorganisms. Even not considering the former subgenus *Biverticillium* including well known mycoparasites such as *P. dangeardii* (syn. *P. vermiculatum*) and *P. pinophilum*, whose more pertinent classification in the teleomorphic genus *Talaromyces* has been recently agreed after the results of a phylogenetic study (Samson *et al.* 2011), a number of *Penicillium* species have been reported as antagonists of plant pathogens with a mechanism of action based on the induction of resistance (Madi and Katan 1998; Hossain *et al.* 2007), the production of antibiotic compounds (Nicoletti *et al.* 2004; Yang *et al.* 2008), and the establishment of mycoparasitic interactions (Sempere and Santamarina 2008). Recent data gathered by several research groups indicate that *Penicillium restrictum* is another species to be considered with reference to its properties as a fungal antagonist, which are reviewed in the present paper.

TAXONOMY AND OCCURRENCE

Occasionally referred to as an interfaces between the genera *Penicillium* and *Aspergillus* (Raper and Thom 1949; Pitt and Hocking 1985), the species *Penicillium restrictum* Gilman *et* Abbott is classified in the section *Exilicaulis* of the subgenus *Aspergilloides* (Pitt 2000; Houbraken and Samson 2011) based on its monoverticillate conidiophores which are non-vesciculate, smooth, quite short (10-30 µm), and bear few ampulliform phialides producing conspicuously roughened conidia with a globose to ellipsoid shape. These conidial structures are the smallest in the genus *Penicillium*, recalling the species name which also reflects a quite restricted colony development on agar media. Mycelial growth can be appreciated at 37°C, while no conidial germination is generally observed at 5°C. However, intraspecies variation is far from being occasional, and many strains have been found to show some deviation (Pitt 2000). No teleomorph has been observed so far. To this regard, it must be considered that a number of studies have pointed out phylogenetic relationships between monoverticillate *Penicillium* species and the genus *Eupenicillium* (*Eurotiales*), which have now been combined and included in the new family *Aspergillaceae* (Houbraken and Samson 2011); however, the case is reported of a *Talaromyces* species, *T. purpureus*, presenting a conidial stage to be ascribed to the *P. restrictum* series (Stolk and Samson 1972). Recognized synonyms of *P. restrictum* are *Penicillium gilmanii* Thom and *Penicillium kazachstanicum* Novobr. (CBS database on

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Review

Table 1 Checklist of isolations of *Penicillium restrictum* from substrates other than soil.

Source	Location	Reference
Butter	Manitoba (Canada)	Bisby *et al*. 1933
Living moss	Pullman, Washington (USA)	Bridge Cooke 1955
Flowers of *Cucumis sativus*	Ayden, North Carolina (USA)	Etchells *et al*. 1958
Airborne	Manhattan, Kansas (USA)	Kramer *et al*. 1960
Cucumber salt-stock brines	Ontario (Canada)	Hamilton and Johnston 1961
Frozen fruit-filled pastry	New Jersey (USA)	Kuehn and Gunderson 1962
Fresh, brackish and sea water	Hercegovina (Bosnia)	Ristanović and Miller 1969
Mattress dust	France	Mallea 1974
Human toeweb	San Francisco, California (USA)	McGinnis *et al*. 1975
Rhizoplane of *Oryza sativa*	Dacca (Bangladesh)	Jalaluddin 1975
Human lung	Tokyo (Japan)	Okudaira *et al*. 1977
Horse dung	Viña del Mar (Chile)	Piontelli *et al*. 1981
Starch	Spain	Suarez *et al*. 1981
Coral (*Goniastrea australensis*)	Lizard Island (Australia)	Kendrick *et al*. 1982
Coral (*Porites australensis*)	Heron Island (Australia)	Kendrick *et al*. 1982
Phylloplane of *Capsicum annuum*	India	Tyagi and Chauhan 1982
Seeds of *Cedrus deodara*	Nainital (India)	Mittal 1983
Cinnamon	Mayagüez (Puerto Rico)	Ramirez *et al*. 1988
Gut of larva of *Vespula pensylvanica*	Tilden Park, California (USA)	Gambino and Thomas 1988
Roots of *Triticum aestivum* and *Lolium rigidum*	Western Australia	Dewan and Sivasithamparam 1988
Soybean and wheat crop residues	Columbia, Missouri (USA)	Broder and Wagner 1988
Wheat grains	Iran	Lacey 1988
Floor dust in school	Palestine	Ali-Shtayeh and Arda 1989
Leaves of *Citrus sinensis*	Riverside, California (USA)	Fenn *et al*. 1989
Wall of mycological laboratory	Singapore	Lim *et al*. 1989
Cured Burley tobacco	England	Mutasa *et al*. 1990
Airborne and leaf surface in greenhouse	Sardinia (Italy)	Cosentino and Palmas 1991
Hive, pollen	Las Marías and Mayagüez (Puerto Rico)	Seguí-Crespo *et al*. 1991
Corn grains	Bulgaria	Mantle and McHugh 1993
Seeds of *Glycine max*	Thailand	Pitt *et al*. 1994
Corn grains	Argentina	Gonzalez *et al*. 1995
Paper of historic documents	Paris (France)	Dartois 1995
Wall paintings	Florence (Italy) and Ikaruga (Japan)	Garg *et al*. 1995
Dry-cured ham	Spain	Núñez *et al*. 1996
Leaves of *Guarea guidonia* and *Manilkara bidentata*	El Verde (Puerto Rico)	Polishook *et al*. 1996
Leaves of *Solanum tuberosum*	Hermiston, Oregon (USA)	Donegan *et al*. 1996
Babassu (*Orbignya oleifera*) cake	Brazil	Freire *et al*. 1997
Sorghum grains	Pergamino (Argentina)	Gonzalez *et al*. 1997
Cheese	Southern Spain	Barrios *et al*. 1998
Poultry feed	Rio Cuarto, Cordoba (Argentine)	Dalcero *et al*. 1998
Airborne in food warehouses	Bursa (Turkey)	Simsekli *et al*. 1999
Hay	Lanco and Rio Bueno la Union (Chile)	Zaror *et al*. 1999
Airborne in rural areas	Banyapara, west Bengal (India)	Adhikari *et al*. 2000
Airborne in Sistine Chapel	Rome (Italy)	Montacutelli *et al*. 2000
Cherries of *Coffea arabica*	Sul de Minas (Brazil)	Silva *et al*. 2000
Library shelf	Rome (Italy)	Maggi *et al*. 2000
Wall of church	Okoličné (Slovakia)	Šimonovičová *et al*. 2000
Airborne in cheese factory	Franche-Comté (France)	Chaumont *et al*. 2001
	Arzúa, Galicia (Spain)	Vazquez *et al*. 2001
Airborne in houses	Upper Silesia (Poland)	Zyska 2001; Górny and Dutkiewicz 2002
Airborne in rural areas	Edirne (Turkey)	Sen 2001
Airborne in wine cellars	Arbois (France)	Simeray *et al*. 2001
House dust	Wallaceburg, Ontario (Canada)	Scott 2001
Library	Paris (France)	Roquebert *et al*. 2001
Salt lake water	Dead Sea (Israel)	Kis-Papo *et al*. 2001
Leaf pack of *Phragmites australis*	Lake Vico (Italy)	Mancinelli *et al*. 2002
Needles of *Chamaecyparis obtusa*	Lake Biwa (Japan)	Osono *et al*. 2002
Airborne	Istanbul (Turkey)	Çolakoğlu 2004
House dust	Ohio (USA)	Meklin *et al*. 2004
Roots of *Betula pendula*	East of Vilnius (Lithuania)	Lygis *et al*. 2004
Roots of *Hypericum perforatum*	Fajsławice (Poland)	Zimowska 2004
Seeds of *Phaseolus vulgaris*	Salta province (Argentina)	Castillo *et al*. 2004
Compost and vermicompost	Piedmont (Italy)	Anastasi *et al*. 2005
House dust	England	Vesper *et al*. 2005
Naked pumpkin seeds	Serbia	Dimić *et al*. 2005
Rhizoplane of *Dactylis glomerata*, *Lolium perenne* and *Trifolium repens*	San José de la Mariquina (Chile)	Quitral Villanueva 2005
Airborne in peat moss processing plant	Quebéc (Canada)	Mériaux *et al*. 2006
Cherries (*Prunus cerasus*), onions (*Allium cepa*)	Lithuania	Lugauskas *et al*. 2006
Cork	Ponte de Sôr (Portugal)	Basilio *et al*. 2006
Tap water	Norway	Hageskal *et al*. 2006
Wheat grains	Lithuania	Lugauskas *et al*. 2006

Table 1 (Cont.)

Source	Location	Reference
Grains of *Pennisetum typhoides*	Andhra Pradesh (India)	Raghavender *et al*. 2007
Plants micropropagated *in vitro*	Poland	Kowalik 2007
Rice grains	Central Vietnam	Minh Tri 2007
Airborne in child day care centres	Edirne (Turkey)	Aydogdu *et al*. 2008
Cattle feed	Rio de Janeiro state (Brazil)	Rosa *et al*. 2008
Fresh water	Žitava river (Slovakia)	Javorekova and Felšociova 2008
Marine sponge (*Suberites zetekii*)	Hawaii	Gao *et al*. 2008
Paper of historic documents	Genoa (Italy)	Zotti *et al*. 2008
Sand and marine water	Olinda, Pernambuco (Brazil)	Gomes *et al*. 2008
Airborne in cave	Domica Cave (Slovakia)	Novakova 2009
Endophyte in *Dactylis glomerata*	Spain	Sánchez Márquez 2009
Iron mine	Orissa (India)	Sabat and Gupta 2009
Oilseed cake	Calvados (France)	Lanier *et al*. 2009
Rhizoplane of *Vitis vinifera*	Kiedrich (Germany)	Neuhauser *et al*. 2009
Surface water	Portugal	Pereira *et al*. 2009
Airborne	Thrace (Turkey)	Asan *et al*. 2010
Airborne in rabbit farm	Qingdao (China)	Miao *et al*. 2010
Dry-fermented sausage	Tandil (Argentina)	Castellari *et al*. 2010
Endophyte in root of *Myriophyllum spicatum*	Lewisville, Texas (USA)	Shearer 2010
Grapes (*Vitis vinifera*)	Loire Valley (France)	Guérin *et al*. 2010
Sea floor	Amur river plume (Russia)	Slinkina *et al*. 2010
Gardens of *Tachymyrmex septentrionalis*	Smithville, Texas (USA)	Rodrigues *et al*. 2011
Paper of historic documents	Tanta City (Egypt)	Abdel-Maksoud 2011
Rhizoplane of *Myristica fatua* var. *magnifica*, *Myristica malabarica* and *Gymnacranthera farquhariana*	Kathalkan, Karnataka (India)	Rama Bhat and Kaveriappa 2011
Wood core of *Pseudotsuga menziesii*	McDonald-Dunn Forest, Oregon (USA)	Kiser *et al*. 2011
Apple of *Malus sylvestris*	Alma Ata region (Kazakhstan)	CBS Database 2012

filamentous fungi, 2012), while other taxa formerly reported in synonymy, such as *Penicillium striatisporum* Stolk, *Penicillium kurssanovii* Chalab., *Penicillium griseolum* G.Sm. and *Penicillium malacaense* C.Ramírez *et* A.T.Martínez, are now regarded as separated species (Peterson and Horn 2009; Houbraken and Samson 2011). Finally, validity of synonymy with *Penicillium griseum* Sopp (Asan 2004) is questionable, since this species was never satisfactorily identified (Raper and Thom 1949), and a possible mismatch with the valid name *P. griseolum* cannot be excluded.

P. restrictum presents a worldwide geographical distribution, and is commonly regarded as a typical soil species. Nevertheless, it has been recovered from very diverse natural contexts (**Table 1**), including any kind of plant organs and products, farms, and even a few sea organisms. It also displays an aptitude to colonize the ‘anthropic’ environment, as attested by its finding in air, water, food processing plants, buildings, libraries, etc. Particularly, the occurrence in houses may have some implications on human health considering that this species proved to be capable to produce hemolysins when growing at 37°C, and that these substances have been reported to play a role in the sick building syndrome (Vesper and Vesper 2004).

IMPLICATIONS IN BIOTECHNOLOGY AND SOIL ECOLOGY

Such a widespread occurrence has stimulated the study and the employment of *P. restrictum* strains for several biotechnological purposes, starting from the exploitation of enzyme activities. To this regard, the use of a strain recovered from babassu (*Orbignya oleifera*) cakes in Brazil (Freire *et al.* 1997) as a source of lipases (Jesus *et al.* 1999; Palma *et al.* 2000; de Azeredo *et al.* 2007) has been particularly considered for the treatment of wastewaters with a high oily content, such as dairy (Cammarota *et al.* 2001; Rodrigues Rosa *et al.* 2006) and poultry slaughterhouse effluents (Valladão *et al.* 2007, 2011). Other investigated enzyme complexes include amylases (Xie and Zhang 1994; Palma *et al.* 2000), proteases (Rodríguez *et al.* 1998; Palma *et al.* 2000; Nathiya *et al.* 2011), inulinases (de Souza-Motta *et al.* 2003), and tannases (Batra and Saxena 2005), while cellulolytic and hemicellulolytic functions find an application in the pre-treatment of biomasses to be used for the production of biofuels (Muthukkaruppan 2002; Palaniswamy *et al.* 2008).

P. restrictum strains have been also considered for soil bioremediation in consequence of contamination by metals (Kendrick 1962; Schoenlein *et al.* 2008), hydrocarbons (Cabello and Arambarri 1993; Châıneau *et al.* 1999; Garon *et al.* 2000; Belviso *et al.* 2005) and nonylphenol (Girlanda *et al.* 2009). Other strains have showed to be able to degrade bioplastic (polyhydroxyalkanoate) films (Lopez-Llorca *et al.* 1993; Mergaert *et al.* 1993). Finally, an effectiveness has been also demonstrated for the removal of dyes from aqueous solutions (Iscen *et al.* 2007; Ilhan *et al.* 2008).

Bioremediation properties may be also exploited in cropped soils based on the capacity of *P. restrictum* to degrade pesticides. In fact, the species proved to be able to defluorinate sodium monofluoroacetate (1080), even by using this molecule as the sole carbon source *in vitro* (Wong *et al.* 1992). Moreover, it has showed to resist or promptly recover after fumigations with D-D (dichloropropene-dichloropropane) and vapam (Martin *et al.* 1956), or herbicide treatments (Wacha and Tiffany 1979; Mekwatanakarn and Sivasithamparam 1987), and exhibited tolerance to the bioherbicide phosphinothricin (Ahmad and Malloch 1995) and the fungicide dithane (Mittal 1983).

A beneficial outcome on crops may also derive from an increased availability of phosphorous and microelements for root uptake. In fact, the ability to solubilize phosphates with ensuing benefits on plant growth has been experimentally demonstrated on wheat in India, where the use of rock phosphate coupled with the inoculation of *P. restrictum* resulted in a notable increase in the grain yield (Gupta and Baig 2001). The same effects on phosphorous mobilization resulted for strains recovered in southern Chile (Quitral Villanueva 2005; Morales *et al.* 2011). Besides degradation of rock phosphate, other isolates from India have proved to be able to leach iron from low grade ores (Sabat and Gupta 2009; Sharma 2011), a property which again may establish more favourable nutritional conditions for crop plants in certain soils.

Besides influencing plant nutrition, *P. restrictum* may be directly involved in the food pyramide of soil. In fact, the species has been found to sustain typical fungal feeders such as collembolans (Tiunov and Scheu 2005), while an *in vitro* investigation showed it to support growth of the fungivorous nematodes *Aphelenchus avenae* and *Aphelenchoides bicaudatus* (Ikonen 2001). More recently, a natural trophic association resulted in a survey on microfungal communities developing in gardens of fungus-growing ants, where *P. restrictum* was found to be the dominant fungal species in anthills of *Tachymyrmex septentrionalis* during winter (Rodrigues *et al.* 2011).

ANTAGONISTIC PROPERTIES

The occurrence of *P. restrictum* in rhizosphere and rhizoplane in both natural and agricultural contexts (Jalaluddin 1975; Arora and Dwivedi 1976; Požárová *et al.* 2001; de Souza-Motta *et al.* 2003; Lygis *et al.* 2004; Jamiołkowska and Wagner 2005; Quitral Villanueva 2005; Neuhauser *et al.* 2009; Das and Dkhar 2010; Hindumathi and Reddy 2011; Rama Bhat and Kaveriappa 2011) represents a clue for a possible involvement in antagonism against fungal pathogens. Circumstantial evidence in this sense has resulted on St. John's wort (*Hypericum perforatum*) affected by a complex of soil-borne pathogens including *Rhizoctonia solani*, *Botrytis cinerea*, *Phoma exigua* var. *exigua* and a number of *Fusarium* species (*F. avenaceum*, *F. culmorum*, *F. equiseti*, *F. oxysporum* and *F. solani*), where *P. restrictum* was isolated from roots and basal stem with rot symptoms (Zimowska *et al.* 2004). In a lupin (*Lupinus albus*) field heavily infested with a similar pathogen complex, including *Pythium ultimum*, *R. solani* AG-2-1 and AG-4, *F. culmorum*, *F. oxysporum* and *F. solani*, the occurrence of *P. restrictum* was particularly notable in the rhizosphere of plants growing in patches which had escaped the disease (Nicoletti *et al.* 2008a). *P. restrictum* was also found amidst saprotrophs occurring in the rhizosphere of potato plants, but it was reported not to be able to exert a protective effect against *R. solani* and *Helminthosporium solani* (Kurzawińska 2006). Nevertheless, this conclusion is somehow questionable since it is not clear how the author numerically quantifies the 'individual biotic effect' and the 'general biotic effect' on which her judgement on the outcome of the interaction with the above pathogens is based.

It is quite reasonable to assume that the occurrence of *P. restrictum* in soil is largely influenced by its competitiveness toward the other microbial components, as at least in part regulated by the bioactivity of the extrolites it may produce. To this regard, indications of an ability to possibly overcome fungistasis and antibiosis promoted by other microorganisms was inferred based on the tolerance toward the staling products released by fungi inhabiting lentil rhizosphere (Arora and Dwivedi 1976, 1979), while assays in dual cultures against *Sporotrichum schenckii* and *Scopulariopsis brevicaulis* (Blunt and Baker 1968) first documented its ability to exert antibiosis toward soil fungi. Consistent inhibitory capacities were later showed against *Gaeumannomyces graminis* var. *tritici* (Mekwatanakarn and Sivasithamparam 1987), although in a following assay carried out at the same laboratory isolates from ryegrass (*Lolium rigidum*) and wheat roots were reported not to be able to inhibit the same pathogen in dual cultures *in vitro* (Dewan and Sivasithamparam 1988), introducing a possible diversity in the range of fungitoxic extrolites produced by isolates within the species. Again and independently, *in vitro* effectiveness against the agent of the take-all disease was pointed out in Poland (Tashein 1988). Finally, antifungal properties resulting in dual cultures have been reported against other soil saprotrophs, namely *Paecilomyces lilacinus* and *Humicola fuscoatra* (Stahl and Christensen 1992), and more recently against widespread polyphagous pathogens, such as *Pythium aphanidermatum* and *P. ultimum* (Gravel *et al.* 2005), *P. ultimum* and *R. solani* AG-2-1 and AG-4 (Nicoletti *et al.* 2008a) (**Fig. 1**), and *Verticillium dahliae* (Arriagada *et al.* 2012).

Fig. 1 Inhibition of mycelial growth of *R. solani* AG-2-1 by isolate XLT3S of *P. restrictum* in dual culture.

Besides these indirect evidences, antifungal products have been actually extracted and characterized by soil strains of *P. restrictum* which may account for its antagonistic properties at some extent. The first secondary metabolites reported from this species were dehydrocarolic acid and gliotoxin (Sankhala 1968). Both compounds had been previously found in culture filtrates of another species belonging in the section *Exilicaulis*, *Penicillium cinerascens* (Bracken and Raistrick 1947). While the former has never been reported to possess significant antibiotic properties, the latter is a potent mycotoxin (Gardiner *et al.* 2005) which has been shown to play an effective role in fungal antagonism (Lumsden *et al.* 1996). Afterwards, two more extrolites, namely 2,3-dihydro-3,6-dihydroxy-2-methyl-4-pyrone and curvularin, were evidenced in cultures of a strain mentioned as *P. gilmanii* (Raistrick and Rice 1971), and the production of a derivative of the latter compound, dihydrocurvularin, was documented at the same laboratory (Rice and Chen 1984). Compounds of this macrolide series are produced by a number of *Penicillium* species (Houbraken *et al.* 2011), and are known for some extent of antifun-

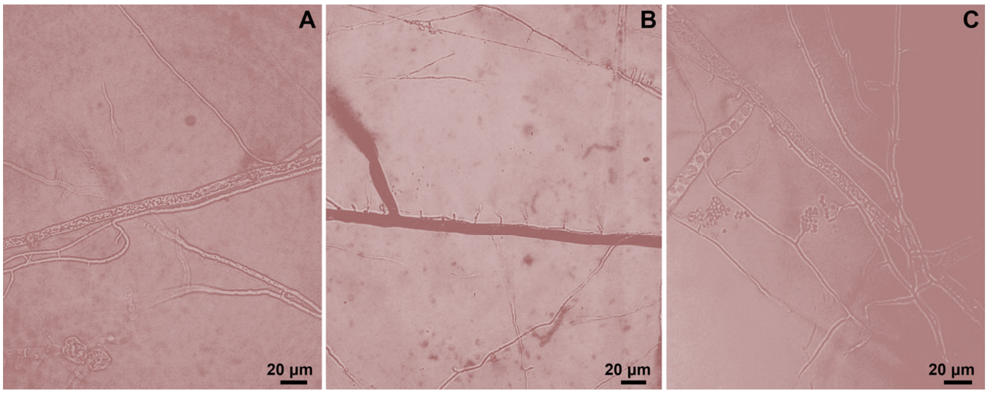

Fig. 2 Parasitic interactions of *P. restrictum* with *P. ultimum* (**A**), and *R. solani* AG-2-1 (**B**) and AG-4 (**C**).

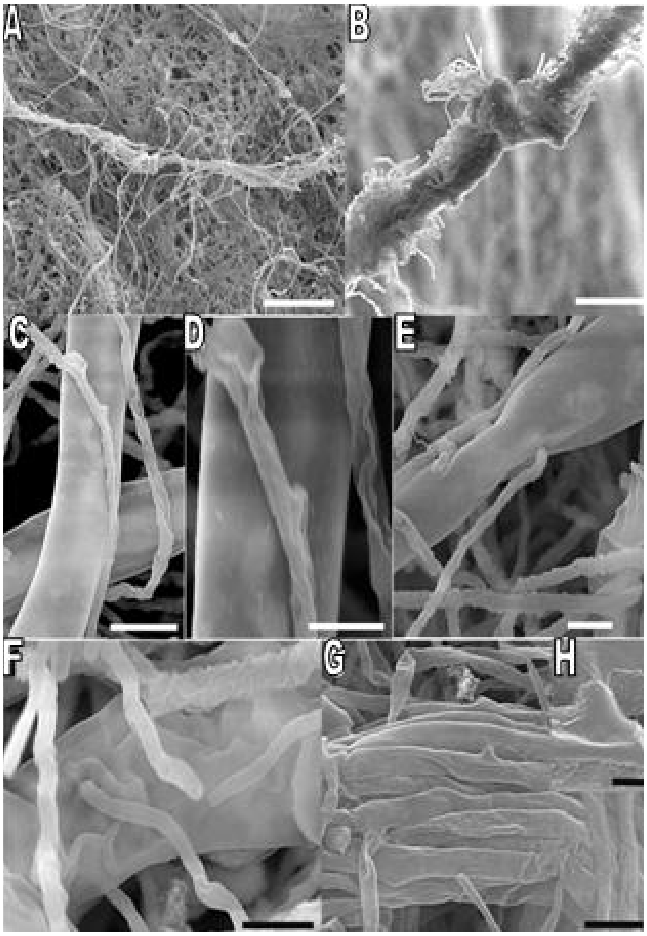

Fig. 3 Images at SEM of mycoparasitism by *P. restrictum.* Hyphae wrapping those of *P. ultimum* (**A**; bar = 20 µm) and *R. solani* AG-2-1 (**B**; bar = 10 µm). Magnification of hyphal interactions with *R. solani* AG-4 (**C**-**F**; bars: C and E = 5 µm, D and F = 2 µm) and *C. gloeosporioides* (**G**-**H**, bars: G = 10 µm, H = 1 µm).

gal activity (Dai *et al.* 2010). Later on, a new class of antifungal compounds including restricticin and its dimethyl derivative was characterized from culture extracts of an Indian isolate; these extrolites, whose molecule presents triene, pyran and glycine ester functionalities, are active against a broad range of yeasts and filamentous fungi (Hensens *et al.* 1991; Schwartz *et al.* 1991). Furthermore, the calbistrin complex, whose denomination is derived by the inhibitory properties against *Candida albicans*, was extracted by liquid cultures of a Brazilian isolate (Jackson *et al.* 1993). The structure of such compounds is based on a carboxylic acid conjugated tetraene which is attached to a hexahydronaphthalene system (Brill *et al.* 1993). More recently, the production of patulin and penicillic acid has been reported in a strain isolated from dry-cured ham (Martín *et al.* 2004). Both compounds are well-known mycotoxins of a number of *Penicillium* species, which have been also found to be implicated in the expression of antagonism against other fungi (Steiman *et al.* 1989; Frisvad *et al.* 2004; Kang and Kim 2004; Nicoletti *et al.* 2004).

Although the described inhibitory effects may prevent hyphal contacts in dual cultures with fungal pathogens, our investigations concerning *P. restrictum* isolates from lupin rhizosphere showed them to be able to slowly overgrow the inhibition zone in pairings with *R. solani* and *P. ultimum*, creating an opportunity for a direct hyphal interaction (Nicoletti *et al.* 2008b). In the above conditions, hyphae of *P. restrictum* grew adpressed to those of the challenged strains with occasional sketches of coiling, establishing hyphal penetration through haustorium-like structures produced at quite regular intervals, as shown in **Fig. 2**. Such an aptitude has been confirmed by observations carried out through scanning electron microscopy (SEM), which unequivocally demonstrate the capacity of *P. restrictum* to develop mycoparasitically (**Fig. 3**). Considering that the above plant pathogens are not taxonomically related, a more comprehensive study was carried out to evaluate if mycoparasitism could actually be exerted against other plant pathogens. Within a group of strains belonging to the species *Fusarium culmorum*, *F. solani*, *Cladosporium oxysporum*, *Macrophomina phaseolina*, *Sclerotinia sclerotiorum*, *Sclerotium rolfsii*, *Thielaviopsis basicola* and *Colletotrichum gloeosporioides*, the latter was the only one to disclose susceptibility (Sinapi 2009). These results indicated that the range of mycoparasitism by the tested strains of *P. restrictum* may not be broad, and that *P. restrictum* itself may be affected by competitive capacities of soil fungal pathogens, as particularly evident in the case of *S. sclerotiorum* which consistently inhibited its hyphal growth in dual cultures.

CONCLUSIONS

The widespread occurrence of *P. restrictum* has incited a notable amount of studies considering its ecology and biological properties which are occasionally exploited in biotechnology. Particularly, the available literature underlines its competitive ability in the rhizosphere of plants in both natural and agricultural contexts, introducing it as a plausible and effective antagonist of plant pathogenic fungi.

The establishment of a favourable balance among microbial species in the rhizosphere is more and more considered as a fundamental factor in crop development and protection against biological adversities, and fungal antagonists are recognized to play a key role to this regard, even by inducing soil suppressiveness (Whipps 2001; Weller *et al.* 2002; Mazzola 2004). Therefore the finding of new species able to ultimately improve soil fertility by interacting in a multiple mode with cultivated plants and their pathogens deserves to be highlighted and exploited. The available data are oriented to qualify *P. restrictum* as a species exerting such a biocenotic role, not only based on the production and possible effects of antifungal extrolites, but also on the capacity to more directly affect the subsistence of a number of fungal pathogens which may be susceptible to its mycoparasitic aptitude. Indeed these properties stimulate further investigations concerning the possible application of *P. restrictum* strains as biocontrol agents in crop protection.

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