REVIEW

Exploitation of the Mycoparasitic Fungus *Pythium oligandrum* in Plant Protection

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Abstract

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Pythium oligandrum Drechs. belongs to the order *Oomycetes*. It is parasitic on many fungi from the same or other orders. The antagonism of *P. oligandrum* is a multifaceted process dependent on the target species involved. *P. oligandrum* is nonpathogenic on 12 species of crops from six families. It does not attack their tissue but occurs on the root surface, predominantly in the regions of hypocotyl – taproot, together with plant pathogenic fungi. It utilises the root exudates and fungus hyphae on the root surface, including those of the plant pathogens, for its own support. A growth stimulation of plants was observed. *P. oligandrum* can be utilised for biological control on a wide spectrum of crop plants. Different methods of application have been developed. The effect of a mycoparasite preparation is more preventive.

Keywords: biological control; soil fungi; antagonism; rhizosphere; growth stimulation; *Botrytis cinerea*

The importance of plant protection in modern agriculture increases as crop yields and concerns about production quality rise. Plant protection should be sufficiently effective, affordable and considerate of the environment.

Integrated pest management takes advantage of a complex of methods with minimal effect on harmless organisms. The integration of biological with chemical control has a potential for success because of a possible synergism of effects.

It is necessary to look for organisms suitable for use in biological control, and to study the mechanisms of their action and the optimal conditions for applying them in plant protection and integrated management systems. One of such organisms is *Pythium oligandrum*.

Hosts of the mycoparasite *Pythium oligandrum*

Pythium oligandrum Drechs. is a soilborne fungus belonging to the order *Oomycetes*. It is able to live as a saprophyte, but is antagonistic to and parasitic on many fungi from the same or other orders (Table 1). It can penetrate their hyphae and live on the contents.

Some genera, species and isolates of fungi are more susceptible to attack by *P. oligandrum* than others. Some of the attacked ones (e.g. *P. aphanidermatum* [Edson] Fitzpatrick) are able to wind around and penetrate the mycoparasitic hyphae (CHANG *et al.* 1993).

For producers of mushrooms could be important that *P. oligandrum* inhibited the growth of *Agaricus bisporus* (Lange) Singer, especially in mushroom compost with a high nitogen level (FLETCHER *et al.* 1990).

Mycoparasitism of *Sclerotinia sclerotiorum* (Lib.) de Bary sclerotia by the three mycoparasitic species of the genus *Pythium,* including *P. oligandrum,* was not detected (RIBEIRO & BUTLER 1992).

The type of host fungus markedly influences the efficiency of detection of different mycoparasites. *Fusarium culmorum* (W. G. Sm.) Sacc. is most efficient for *P. oligandrum.* No single host is suitable for consistent detection of any single mycoparasite (MULLIGAN & DEACON 1992).

Table 1. Host of *Phytium oligandrum* Drechs.

Hosts of *Pythium oligandrum*	Reference
Agaricus bisporus (Lange) Singer	FLETCHER *et al.* 1990
Aphanomyces cochlioides Drechs.	MCQUILKEN *et al.* (1990)
Botryotrichum piluliferum Sacc. et March	LAING & DEACON (1991
Botrytis cinerea Pers. ex Fr.	LAING & DEACON (1991
Fusarium culmorum (W. G. Sm.) Sacc.	LAING & DEACON (1991); MULLIGAN & DEACON (1992)
Fusarium oxysporum Schlecht.: Fr.	LAING & DEACON (1991)
Fusarium oxysporum f.sp. *radicis-lycopersici* Ja. et S.	BENHAMOU *et al.* (1999)
Fusarium solani f.sp. *pisi* (Hall/Linf.) Sny. Ha	BRADSHAW-SMITH *et al.* (1991)
Gaeumannomyces graminis (Sacc.) v. Arx et Olivier	VESELÝ & KOUBOVÁ (1993)
Mycosphaerella pinodes (Berk. et Blox.) Stone	BRADSHAW-SMITH *et al.* (1991)
Ophiostoma sp. Syd. et P. Syd.	ČÍŽOVÁ & ŠVECOVÁ (1997)
Phialophora sp. Medlar	FOLEY & DEACON (1986); LAING & DEACON (1991)
Phoma medicaginis var. *pinodella* (Jones) Boer.	BRADSHAW-SMITH *et al.* (1991)
Phytophthora megasperma Drechs.	BENHAMOU *et al.* (1999)
Pythium aphanidermatum (Edson) Filtzpatrick	CHANG *et al.* (1993)
Pythium graminicola Subramanian	CHANG *et al.* (1993); LAING & DEACON (1991)
Pythium irregule Buisman	HE *et al*. (1992)
Pythium nunn Lifshitz et al.	LAING & DEACON (1991)
Pythium spinosum Sawada	HE *et al*. (1992)
Pythium ultimum Trow	HE *et al*. (1992); CHANG *et al.* (1993); MCQUILKEN *et al.* (1990)
Pythium vexans de Bary	CHANG *et al.* (1993); LAING & DEACON (1991)
Rhizoctonia solani Kühn	HE *et al*. (1992); LAING & DEACON (1991)
Trichoderma aureoviride Rifai	LAING & DEACON (1991)
Verticillium albo-atrum Reinke et Berthold	BENHAMOU *et al.* (1999)

Antagonism by *Pythium oligandrum*

The different interactions between *Pythium oligandrum* and the various plant pathogens show that the antagonism of *P. oligandrum* is not a simple process mediated by one simple antimicrobial metabolite. Instead, the studies suggest that each interaction is mediated by highly specific events that ultimately determine the outcome of the interaction. From the scope of ultrastructural and cytochemical changes it is evident that the antagonism is a multifaceted process and dependent on the target species involved (BENHAMOU *et al.* 1999).

Various antagonistic behaviours are found under different support conditions (BRADSHAW-SMITH *et al.* 1991). Growth inhibition of the host mycelium was most pronounced, particularly at high nitrogen levels, when the partners were inoculated simultaneously or if *P. oligandrum* was inoculated 3 or 5 d earlier. Inoculation with the mycoparasite 5 d later had no apparent effect on growth of the host fungus (FLETCHER *et al.* 1990).

The structural changes in hyphae of the pathogens *Pythium ultimum, P. aphanidermatum, Fusarium oxysporum* f.sp. *radicis-lycopersici, Verticillium albo-atrum* and *Rhizoctonia solani* occurred soon after contact with the antagonist *P. oligandrum.* The intimate contact between both partners precedes a sequence of degradation events including aggregation of host cytoplasm and penetration of the altered host hyphae. *P. oligandrum* grew abundantly on hyphae of a plant pathogen and colonised the agar medium. When transferred to fresh medium, *P. oligandrum* mycelium continued to grow abundantly, while hyphae of the plant pathogen were unable to grow (BENHAMOU *et al.* 1999).

In the case of *Phytophthora megasperma*, hyphal interactions did not occur. Its hyphae stopped growing on the first day after inoculation. The morphologic changes of the hyphae were visible at the edge of the colony of the host. Its cells were severely damaged even though there was no contact between hyphae of antagonist and plant pathogen. In most cases the cytoplasm was reduced to some aggregated or vesicular remnants. By contrast, the wall structure appeared preserved (BENHAMOU *et al.* 1999).

HE *et al.* (1992) observed that *P. oligandrum* was hyperparasitic on *Rhizoctonia solani,* but was antagonistic toward *P. ultimum* by the production of antibiotics. FO-

LEY & DEACON (1986) did not detect a production of toxins.

BENHAMOU *et al.* (1999) found by light and electron microscopy that hyphae of *P. oligandrum* established close contact with the plant pathogen host *Rhizoctonia solani* by frequent coiling around the hyphae early on during parasitism. At this stage of the colonisation process, no external damage was visible on the intertwined hyphae of the host, although some wrinkles could be seen on their surface. There was an abnormal deposition of amorphous wall-like material at sites of potential penetration, but the antagonist was able to circumvent this barrier. The interaction of *P. oligandrum* and *R. solani* resulted in disorganisation of most of the cytoplasm of the latter (80%) whereas the thick host wall looked well preserved. At a later stage of the interaction, both plant pathogen and antagonist appeared to suffer from some damage, mainly characterised by a marked loss of turgor and by obvious morphological alterations. In *P. oligandrum* the changes in hyphae consisted of disorganisation of the cytoplasm.

By video microscopy it was found that hyphae of *P. oligandrum* typically coiled around the hyphae of its hosts and penetrated them after 50 min. Tips of host hypha were disrupted up to 1.2 mm ahead of the contact points (BERRY *et al.* 1993).

Although protoplasm of the host mycelium gradually degenerated as it was affected by the parasite, mycelium was newly developed from the protoplasm remaining in the hypha and this also produced oospores, oogonia, and hyphal swellings inside and outside the plant roots (KINOSHITA & ICHITANI 1996).

Hyphae of *P. oligandrum* grew along the hyphae walls of host *P. ultimum* and established tight binding. At this early state of parasitism, the surface of hyphae of *P. ultimum* was turgescent and the integrity of their surface was similar to that observed in single cultures. Also in a 2-day-old culture the structural integrity of *P. ultimum* protoplasm appeared intact, although close examination found a slight retraction of plasmalemma from the wall. Alteration and disortion of the hyphal cell wall were visible at sites of potential penetration by the antagonist. Three days after inoculation, active growth of the antagonist was associated with pronounced host hyphae collapse and loss of turgor. At a more advanced stage of the parasitic process, *P. oligandrum* growth in host hyphae was very active and associated with marked host necrosis. Hyphae of the antagonist ramified extensively in host hyphae. Similar changes in host cells were observed in *P. aphanidermatum* (BENHAMOU *et al.* 1999).

P. oligandrum produced oospores abundantly on the mycelium of *Ophiostoma* spp. while part of the *P. oligandrum* colony obtained the nutrients from a pure agar medium. Inhibition zones were formed by all isolates tested, but the width of the zone was different because the inhibitory ability of isolates varied (ČÍŽKOVÁ & ŠVECOVÁ 1997).

P. oligandrum can affect the sporulation of attacked plant pathogens. It caused a marked reduction in the sporulation of *Fusarium culmorum*. A significant correlation was found between the formation of zoospores of *P. oligandrum* and the degradation of *Fusarium* conidia. Random contact between hyphae of the mycoparasite and those of the host was followed by cessation of growth of the latter, lysis or vacuolation and coagulation of the cytoplasm, and penetration and growth of the mycoparasite within the afflicted hyphae. Parasitism of conidia was seen as rapid loss of cytoplasm followed by degradation of the cell walls (HOCKENHULL *et al.* 1995).

LAING & DEACON (1991) did not observe a pre-contact inhibition or tropism between *P. oligandrum* or *P. nunn* and their plant pathogen hosts, but susceptible host hyphae stopped growing soon after contact. This reaction was faster in contacts between host tips and sub-apical regions of parasitic hyphae. Cessation of growth was often followed by lysis of host cells at the contact point or by vacuolation of their contents. Penetration of host hyphae occured in 69 of 148 interactions that were observed.

Pythium oligandrum in soil and the plant rhizosphere

P. oligandrum occurs on plant roots together with plant pathogens. It was isolated above all from mineral soils with neutral or slightly acidic pH used for agricultural and horticultural purposes. On a farm where the main crops were wheat, rye, beet and carrot, colonyforming units (CFU) counts were generally high (65.3 CFU/g of soil). A single application of metalaxyl-mancozeb to a crop of carrots reduced these counts to a mean of 23.5 CFU/g of soil. Where rotations included carrots, potatoes and parsnips, all of which routinely received sprays of metalaxyl and mancozeb, the fungus either had low CFU counts or was not detected. Populations of *P. oligandrum* were generally low when barley was a major component of the rotations (WHITE 1992).

The addition of oospores of *P. oligandrum* to soil did not raise the number of the mycoparasite in it, even after the 6th introduction when the CFU was 1.2×10^8 in non-sterile soil in Drigall dishes. On the contrary, its numbers gradually went down while simultaneously the number of the antagonist *Mucor piriformis* Fisher increased. The spectrum of the other mycoflora was not changed during the experiment (VESELÝ 1997).

P. oligandrum actively colonised the endosperms and emerging radicles of sugar beet when seed had been treated with oospores. The fungus was isolated from seedling roots predominantly at the junction between the primary root and the hypocotyl and rarely from secondary roots. Seed treatment did not affect seedling growth, and tissue necrosis or reduction in shoot growth was not observed (MARTIN & HANCOCK 1987).

Abundant mycelia of *P. oligandrum* were found on the root surface of cucumber, but a few hyphae penetrated into the roots. There it can easily attack plant pathogens.

One day after sugar beet seeds had been planted in field soil, *Pythium ultimum* had colonised the seed coats of 77% of the untreated seeds but only 10% of the seeds treated with *P. oligandrum*. Fungal growth on the surface of untreated seeds was minimal, whereas treated seeds were covered with dense mycelium. Colonisation of endosperm and radicle by *P. ultimum* was also higher for untreated seeds (63–71%) than for treated seeds (3–7%). Endosperms colonised by *P. ultimum* were often necrotic, and the radicles were infected non soon after emergence (MARTIN & HANCOCK 1987).

Zoospores of the two mycoparasitic species *P. oligandrum* and *P. periplocum* were not attracted to cucumber roots and were accumulated on the roots in very low numbers compared to pathogenic species (WULFF *et al.* 1998).

P. oligandrum was not a component of the rhizosphere of cress or sugar beet (MCQUILKEN *et al.* 1990).

The exploitation of *Pythium oligandrum* in plant protection

Pythium oligandrum can be used for biological control in a wide spectrum of crops because of its ability to attack fungal plant pathogens. Different methods of application, such as inoculation of the seed surface with spores before sowing, soil drench or spraying of plants, have been developed. It was found that an application of the mycoparasite had a more preventive effect on the occurrence of plant diseases, therefore it is important to add it to an environment as early as possible.

Coating sugar beet seeds with oospores of *P. oligandrum* controlled preemergence damping-off caused by *P. ultimum* as effectively as treating seeds with fenaminosulf. The treatment significantly improved seedling emergence. When field soil naturally infested with *P. ultimum* was amended with oospores of *P. oligandrum,* the emergence of sugar beet seedlings was significantly higher than that of untreated controls (MARTIN & HANCOCK 1987).

Seeds of cress and sugar beet were coated with oospores of *P. oligandrum* using two commercial procedures. Both types of treatment reduced damping-off of cress caused by *P. ultimum* in artificially infested sand and potting compost and by *Rhizoctonia solani* in artificially infested sand. The level of control was equivalent to fungicide drenches. Damping-off of sugar beet in soil naturally infested with *Aphanomyces cochlioides* and *P. ultimum* was also reduced by *P. oligandrum.* The control was equivalent to that achieved with hymexazol fungicide seed coating treatments and was related to inoculum potential of *A. cochlioides* in the soil. But *Pythium oligandrum* can faile to prevent damping-off in soil naturally infested with *A. cochlioides* and a low concentration of *P. ultimum* too (WHIPS *et al.* 1993).

Positive effects against *Pythium* root rot on tulips were obtained when the antagonist was applied with a sandy soil treatment, but bulb dips were less effective (GREFF *et al.* 1992).

Treating tomato seeds with zoospores of *P. oligandrum* reduced seed rot and damping-off caused by *P. ultimum* and *Rhizoctonia solani* by 79% and 64%, respectively (HE *et al.* 1992).

Seed treatment of chickpea by *P. oligandrum* was also effective against *Pythium* seed rot and preemergence damping-off in the field (TRAPERO-CASAS *et al.* 1990).

Interaction between *Pythium oligandrum* and plants and growth stimulation of plants

Pythium oligandrum was nonpathogenic on 12 species of economic crop plants of six families. It does not attack their tissues but utilises root exudates and fungus mycelia, including plant pathogens, on the root surface for its own nutrition.

When hydroponically grown cucumber seedlings were inoculated with zoospores of *P. oligandrum,* it caused a reduction in root length during the first 2 days. Later, the treated roots quickly reached the length of the control and on the 8th day and remaining experimental period, stimulation of root elongation was noted. *Pythium oligandrum* was not pathogenic on cucumber and no differences in fresh weight between treatment and control were observed (WULFF *et al.* 1998).

The responses of cucumber to the mycoparasite *P. oligandrum* and plant pathogen *P. ultimum* were similar at first, but differences became apparent later. *Pythium oligandrum* stimulated phosphate uptake, whereas *P. ultimum* inhibited it. These effects were reflected in changes in phosphorus metabolism, although neither organism affected phosphate efflux. *Pythium oligandrum* caused an increase in the auxin – indole-3-acetic acid (IAA) – content and enhanced plant growth, whereas *P. ultimum* caused a decrease in IAA content and inhibited growth. The results indicated that the negative effects of *P. oligandrum* on growth and P-metabolism of cucumber were only temporary, and that presence of the mycoparasite was beneficial to cucumber (KRÁTKÁ *et al.* 1994).

In another study, cucumber responded to the mycoparasite that had been applied as bioagens against some plant pathogens by increased weight of aboveground plant parts and plant roots enlarge magnify leaf blude and extend magnify IAA contents. Not only did *P. oligandrum* have a direct effect, such as protection against attack by different plant pathogens in the rhizosphere, but it also had a stimulating influence on plants (KRÁTKÁ 1991).

More hyphae of the pathogen *P. ultimum* than of *P. oligandrum* penetrated into cucumber roots. Mycelia of both species and lateral root tissues were stained pale to dark red, depending on the degree of damage (KINOSHITA & ICHITANI 1996).

A treatment of plants with a biopreparation should not only reduce the occurrence of pathogens in the soil, but also prevent infection, for example by stimulation of plant growth. It is evident that a biopreparation including oospores of *P. oligandrum* has indeed a positive influence on plants even in absence of a pathogen.

Polygandron-treated seeds of sugar beet produced healthier plants with both higher germination rate and weight than untreated plants. After treatment an initial retardation in emergence and growth rate was observed until the cotyledons were formed. Afterwards, plant growth was stimulated, with the change from suppression to stimulation occurring at the stage of one to two pairs of true leaves. Stimulation was expressed by taller plants and deep green leaves. The stimulating effects were mostly prominent at harvest. Sometimes a small reduction in the number of plants at harvest was observed, but without any significant effect on yields (VESELÝ *et al.* 1989).

After treatment of plants with Polyversum a stimulation of plant and root growth was observed often (DUŠKOVÁ 1995b).

Biological preparations based on *Pythium oligandrum*

The biological preparation Polygandron containing oospores of *P. oligandrum* conferred protection against damping-off of sugar beet in field trials. The effectiveness of this biological control preparation was similar to that achieved with thiram (VESELÝ *et al*. 1989).

The biofungicide Polyversum was registered in 1994 and is prepared in the Czech Republic. It contains oospores of *P. oligandrum* at a number of 10^6–10^7/g of preparation. It is licenced for seed and seedling treatment of trees, against fungal diseases of cucumbers and damping-off of wheat.

The efficacy of the treatment of peas by the biofungicide Polyversum against *Pythium ultimum* and *Rhizoctonia solani* was conclusively influenced by properties of the cultivar and soil quality. The force against *Fusarium oxysporum* f.sp. *pisi* was higher by resistant peas then the susceptible. There was a distict interaction between pathogens, host and mycoparasite.

The preparation was effective against *P. ultimum*, with the level of resistance of the cultivar having a significant influence on effect. The biofungicide Polyversum can be used on suitable cultivars and in proper soils (DUŠKOVÁ 1995a).

Roots of plants grown from seeds treated with *P. oligandrum* were attacked less than those from untreated or chemically treated seeds (VESELÝ 1991).

In a field trial, seed treatment using a powder preparation of *P. oligandrum* gave good disease control compared with plants treated with Agronal (phenylmercury chloride) or the untreated control (VESELÝ 1993).

The efficacy of biopreparation Polyversum is strongly dependent on natural conditions, as temperature, humidity, pH of soil, and plant species or cultivar.

Polyversum can successfully be used to establish plants from *in vitro* cultures, for example of gerberas, nephrolepis and philodendrons (DUŠKOVÁ 1995b).

Table 2 presents a summary of positive effects of a biopreparation.

Use of treatments containing *Pythium oligandrum* oospores on aboveground parts of plants

Annual control of grey mould on grapevine is necessary because this disease could cause high losses in yield. Therefore, the antagonistic properties of the mycoparasite *P. oligandrum* against *Botrytis cinerea* on grapevine

Table 2. Effect of the *Pythium oligandrum* biopreparation Polyversum

Pathogen or disease	Crop	Reference
Damping-off	sugar beet	VESELÝ (1989)
Pythium ultimum	peas	DUŠKOVÁ (1995a)
Rhizoctonia solani	peas	DUŠKOVÁ (1995a)
Fusarium oxysporum	peas	DUŠKOVÁ(1995a)
Damping-off	gerberas	DUŠKOVÁ (1995b)
Damping-off	nephrolepis	DUŠKOVÁ (1995b)
Damping-off	philodendrons	DUŠKOVÁ (1995b)
Botrytis cinerea	grapevine	MÍŠA (1997)
Fungal diseases	tree seedling	registration
Damping-off	wheat	registration
Fungal diseases	cucumber	registration

was tested in a three-year study, and a good effect of the biopreparation Polyversum by foliar application was found. In 1995, when infection pressure was high, the treatment efficacy was 13.2%, while during the lower infection pressure of 1996 the efficacy was 56.8%. In contrast to the biopreparation Polyversum, chemical fungicides have a good effect also by early applications in August. The differences in effect between biological or chemical treatment and untreated check were statistically significant. The treatment of grapevine with the biopreparation had a positive influence on the sensorial properties of wine (MÍŠA 1997).

The inhibition of fermentation by residues from spraying the grapevines was investigated. Biopreparations gave better results than chemical spraying. The inhibition was lowest if the preparation Polyversum had been used (KYSELÁKOVÁ & NĚMCOVÁ 1997).

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Souhrn

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Pythium oligandrum je zástupcem řádu *Oomycetes*. Je schopno parazitovat na řadě hub a houbových organismů z téhož i jiných řádů. Jeho antagonismus je složitý biochemický proces závislý na interakci s příslušným hostitelem (BENHAMOU *et al.* 1999). Jak uvádějí MARTIN & HANCOCK (1987), je nepatogenní pro 12 druhů hospodářských rostlin z šesti čeledí. Nenapadá jejich pletiva, ale využívá pro svou výživu kořenové exsudáty a vlákna jiných hub vyskytujících se na povrchu kořenů včetně těch, která mohou být pro rostlinu patogenní. Byla pozorována stimulace růstu rostlin. Přednostně se *Pythium oligandrum* na povrchu kořene vyskytuje v oblasti mezi hypokotylem a kořenovou špičkou ve společenství s rostlinnými patogeny (MARTIN & HANCOCK 1987). *Pythium oligandrum* může být využito pro biologickou ochranu u širokého spektra hospodářských plodin. Jsou zkoušeny různé způsoby aplikace. Použití mykoparazita má spíše preventivní účinek.

Klíčová slova: biologická ochrana rostlin; půdní houby; antagonismus; rhizosféra; stimulace růstu; *Botrytis cinerea*

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