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Past, present and future of nematophagous fungi as bio-agent to control plant parasitic nematodes

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A B S T R A C T

Nematophagous fungi (NF) are the major antagonists of nematodes. They include nematode trapping fungi as well as endoparasitic fungi. For more than a century scientists are studying different facets of biology of NF including their potential as a bioagents to control nematodes. Their inconsistent success in control of nematodes in field trials, however, is enigmatic. This paper takes a review of the researches done by various workers on the diversity, morphology ecology, physiology of nutrition, trap formation and mechanism of nematode capture as well as probable causes of death. The review traces the shift in the areas of research as well as ups and downs in the interest shown by the researchers. Guide lines for organized, coordinated research to i) screen different strains of NF that are tolerant to antagonism by other fungi, and ii) develop a bioagent based on nematophagous fungi which will show consistent success for the controlling of phytonematodes are also suggested.

Keywords: Nematophagous fungi (NF), mechanism of trapping nematodes, antagonism, opportunistic fungi

Introduction

Fungi that consume nematodes either by trapping or parasitizing them are termed NF. They are lesser known component of soil microflora. Fungi like *Arthrobotrys, Dactylella, Dactylaria* actively trap nematodes with the help of trapping devices on their mycelium. While NF is a broad term used with respect to these fungi, they are also called 'predacious fungi' or 'nematode destroying fungi" or 'nematode trapping fungi'. *Harposporium anguillulae, Haptoglossa mirabilis, Meria coniospora, Catenaria anguillulae* etc. are the endoparasites of nematodes whose spores are ingested by nematodes and develop inside the body. Basically NFs are saprophytes. Along with saprophytism they have evolved along lines of predation. Chances of occurrence of NF are more wherever their prey-nematodes occur. They are universal in distribution, being present in soil, leaf mould, humus, dung, decaying wood etc. Majority of NF belong to Deuteromycetes while few are members of Zygomycetes.

They actively trap nematodes with the help of various trapping devices as shown below:

Type of trapping device	Example
Sticky knobs	*Dactylella ellipsospora*
Sticky columns	*Dactylella cionopaga*
Three dimensional sticky network	*Arthrobotrys superba*
Constricting rings	*Dactylella bembicoides*
Non constricting rings	*Dactylella lysipaga*

Early History

History of NF can be divided into *three* periods. First period was the 'Period of Taxonomy and Ecology'. Second period was development of understanding trapping mechanism and physiology of nutrition while in third period attempts were made to establish its biocontrol aspects. In the first period many nematode trapping fungi as well as fungal endoparasites of nematodes were isolated from various substrates. Taxonomic and ecological studies of these fungi were done during this period. First report of endozoic fungal parasite of nematode - *Harposporium anguillulae* was made by Lodhe (1874). Zopf (1888) recorded trapping of active motile nematodes by *Arthrobotrys oligospora*. Over next 50 years there were only few reports of nematophagous fungi. Drechsler brought NF in limelight by publishing a series of research papers (Drechsler 1935-1962) on their morphology and taxonomy. His monumental work stands as one of the classic researches of NF in Mycology. Duddington (1940-1956) carried out extensive researches on taxonomy of these fungi in Britain. Das Gupta *et al.* (1964, 1966) reported four species of nematophagous fungi from North India. Singh (1967) reported *Catenaria vermicola* from India. Sacchidananda and Swarup (1966, 1967) reported eight species of NF from Delhi Soils. Sacchidananda (1965) and Sacchidananda & Ramkrishnan (1971) reported ten nematode trapping fungi from agriculture soils. Patil and Pendse (1981) reported thirteen species of nematophagous fungi from Maharashtra. Singh *et al.* (2005 a) studied distribution of predacious fungi in agriculture soils in Eastern Uttar Pradesh, Singh *et al.* (2007) studied occurrence of NF in rhizospheric soils in Uttar Pradesh. Kumar *et al*. (2010) studied colonization of these fungi in different substrates. Gupta *et al*. (2003) studied parasitism of nematodes by *Catenaria anguillulae* Sorokin in rhizosphere of different fruit plants.

Duddington (1951) reported presence of NF from humus at the bases of various mosses. Juniper (1953, 1954, 1957) recorded many of them from dung samples of different animals. Predacious fungi from aquatic habitat were studied by Peach (1950, 1952, 1954). Ecological studies of NF from Maharashtra were carried out by Patil and Pendse (1981). Ecological survey of NF in Britain was carried out by Duddington (1962) and Cooke (1962). Persmark *et al.* (1996) studied population dynamics of NF in agricultural soils. They observed that NF are more common in upper 30 cm soil. They also recorded highest density and diversity of NF in autumn. Srivastava (2002) studied distribution of NF in different types of soils. He enlisted nine species of NF belonging to seven genera. He observed that there is minimum correlation between frequency of NF and proportion of organic matter in soil.

In the second period which lasted for about thirty years, focus of interest shifted to physiology of nutrition and trap formation. Biochemical studies about nematode attracting substance as well as chemical responsible for death of nematode were carried out. Lot of work was done on the cultivation of different nematode trapping fungi. Trials were conducted to study their efficiency in controlling phytonematodes. Such shift in the paradigm can be linked with advances in agriculture such as intensive farming, drip irrigation and green-house cultivation. Nematodes which up till then were less important pests became a nuisance and then became a major problem. Chemical nematicides, though effective, were found to be ecotoxic. While searching for suitable alternative methods of nematode control, scientists focused attention on NF as bio-agents to control nematodes. Sincere and sustained researches were carried out to judge efficacy of nematode trapping fungi in laboratory as well as in field trials. Scientists in different countries observed that NF effectively control phytonematodes in laboratory experiments but they failed to show consistent success in controlling nematodes in field trials.

Aschner and Kohn (1958) studied biology of *Harposporium anguillulae.* Barron (1969) successfully isolated other endozoic parasitic fungi in pure cultures. Nutritional studies of two endozoic parasitic fungi in pure culture have been studied by Bricklebank and Cooke (1969). Gupta *et al*. (2004) studied effects of different factors on virulence of *Catenaria anguillulae.* Blackburn and Hayes (1966) studied nutritional requirements of different species of *Arthrobotrys, Dactylaria* and *Dactylella* in saprophytic phase. Hayes and Blackburn (1966) carried out similar studies on predacious phase. They observed that in saprophytic phase these fungi behaved like any other mycelial fungus while there was marked difference in their nutrition during predacious phase. Srivastava (1986) suggested some relationship between type of soil and higher frequency of NF with specific trapping device. Gupta *et al*. (2003) compared nutritional value of different oil cakes as media to culture *Catenaria anguillulae*. Morphological variations in *Arthrobotrys oligospora* using different media were studied by Singh *et al.* (2005).

It was observed that predacious fungi develop traps generally in presence of nematodes. Physical touch of the nematode with the mycelium was considered by Roubaud and Descazeaux (1939) as a stimulus for formation of traps. Lawton (1957) showed that sterilized nematode extract stimulated formation of constricting rings in *Arthrobotrys dactyloides*. Pramer and Stoll (1959) named the metabolic product of nematode which stimulated ring formation as 'Nemin'. Soprunov (1958) confirmed that chemical stimulus is responsible for formation of traps in NF. He showed that other than nematode extract substances like liver extract, blood-serum, glucose, ether, alcohol and even inorganic chemicals such as HCl, NaOH, Na2CO3, CaCl2, Na(OH)2 stimulate trap formation. Singh and Singh (2002) studied effect of various dungs on conidial trap formation in *Arthrobotrys oligospora*. Park *et al*. (2002) studied biological activity of different NF from Western Australia. They screened different NF for their biological activities including predacious, enzymatic, mycoparasitic activities and chemotaxis.

When the nematode is captured, the nematode struggles violently for a while to escape and in about an hour it becomes quiescent, dead. An outgrowth of the hypha from the trap where nematode is stuck, enters the nematode, a globular infection bulb develops at the tip. Many hyphae grow out from infection bulb, spread inside the nematode and absorb its contents. Cause of death of nematode after its capture is still an unsolved mystery. At first it was supposed to be due to either exhaustion or mechanical injury. Duddington (1946, 1950) suggested the possibility of some nematode poison as cause of death. Soprunov and Galiulina (1951) detected a nematicidal substance secreted by *Arthrobotrys parvicovi* in liquid medium. Olthof and Estey (1963) observed presence of nematotoxin in the nematode trapped in the three dimensional sticky network of *Arthrobotrys oligospora*. This nematotoxin had paralysing effect on the nematode. Chemical nature of the nematotoxin is not yet known.

Other interesting and important facet of NF is their potential to control phytonematodes. Linford and Olieveira (1938) recognized eleven species among more than fifty natural enemies of nematodes. Linford and Yap (1938, 1939) demonstrated capabilities of five species in controlling infection of root-knot nematode in potted pineapple plants. Different species showed variable success in controlling nematodes. Over the years, scientists from different countries carried out research on biological control of nematodes by using NF. The results of such experiments varied from total success to compete failure. Garlenko (1956) reported successful control of nematodes in plantation crops. Duddington and Duthoit (1960), Duddington *et al.* (1961) were successful in controlling cereal root-knot nematode *Heterodera major* infecting oats in small plots. Hams and Wilkins (1961) claimed successful control of pea root-knot nematode with lyophilised liquid-medium cultures of *Arthrobotrys robusta, Dactylaria candida* and *Genicularia,* with the help of *A. robusta* there was nine-fold increase in the yield. Equally promising results were obtained in controlling root-knot nematode of tomato. Authors successfully controlled infection of root-knot nematodes in potted plants of *Gerbera* in green-house using NF (personal observation). Singh *et al.* (2005) studied effects of mass-culture of *Arthrobotrys oligospora* for control of root-knot in rice. Control of root-knot nematode of rice by using *Catenaria anguillulae* (endoparasite of nematode) was attempted by Singh (2007).

Third period of research on NF began in last quarter of 20th century and continues till today. During this period failure of these fungi in controlling nematodes in field trials was confirmed to be mainly due to antagonism by other fungi. Mankau (1961a, 1961b, 1980), Tarjan (1961) was unable to establish them in soil due to presence of antagonistic microorganisms. He observed that species of *Gliocladium* and *Trichoderma* were antagonistic to *Arthrobotrys musiformis*. Cooke and Satchuthanandthavale (1968) observed that failure of NF to get established in soil was due to mycostasis. It caused inhibition of germination of conidia, formation of secondary conidia after germination and inhibition of hyphal development after germination of conidia. In mixed culture, mycelium of NF with three dimensional sticky network starts growing, within 2 days it traps and kills nematodes in large number. Authors believe that excess, unabsorbed body contents of nematodes get leached in the surrounding medium. Hyphae of some saprophytic fungi absorb that leached food material and grow faster than NF and suppress the growth of NF. In a short period, actively growing NF is exhausted and is overgrown by that saprophytic fungus [personal observation]. Due to variable natural conditions in vast area in field trials (in contrast to controlled conditions in limited area in laboratory trials), the negative impact of antagonism is very severe in field trials. As a result of these limitations, scientists lost interest in using NF in controlling phytonematodes.

At the same time, while searching for alternative bioagents to control nematodes, scientists came across some saprophytic fungi that infect eggs as well as sedentary stages of nematodes. These fungi have been appropriately, termed as opportunistic fungi (Trivedi 2012) Out of the different opportunistic fungi *Paecilomyces lilacinus, Pochonia chlamydosporia* and *Trichoderma* have been found to be very effective in controlling phytonematodes. Opportunistic fungi are common component of soil microflora; they grow faster by utilizing a variety of organic materials; they are least affected by antagonism and they can be easily grown in axenic cultures. At present, different commercial formulations like Paecilomite, Nemastin, Yorker, Nematox, Bionematon based on *Paecilomyces lilacinus*, Ecosom TH based on *Trichoderma*, Safeguard based on *Pseudomonas* are available to control phytonematodes. In contrast only two bioagents Royal 300 and Royal 350 composed of *Arthrobotrys* were commercially released in France to control infestation of *Meloidogyne* on vegetables. Most of the research work on NF has been done individually by scientists in different countries. This resulted in large amount of work in certain areas while very little development in an area like searching cause of antagonism

Coordinated researches on nematophagous fungi

In 1946, methodical, coordinated studies on predacious hyphomycetes were initiated in Russia in Turkmenistan and were continued even after twenty years (Soprunov 1966). After isolating and identifying different species of predacious fungi from various localities from different republics of Soviet Union, scientists focused their attention on the control of phytonematodes. Researches on use of these fungi for the control of nematodes pathogenic to animals were also carried out. Russian scientists recorded appreciable success in nematode control in agriculture as well as in animal husbandry.

Since more than last thirty years Indian scientists in Department of Mycology and Plant Pathology, Institute of Agriculture Sciences, Banaras Hindu University, Varanasi have been engaged in researches on NF. These researches earlier carried out on the isolation, taxonomic morphological and physiological studies of NF. (Singh *et al.* 2002, 2005a, 2005b) Among endoparasites major emphasis was given to *Catenaria anguillulae* to understand its biology (Singh 1967), culture technique (Gupta *et al*. 2004) and mass multiplication (Gupta *et al*. 2003) for its application as bioagent to control phytonematodes along with NF. Researches on NF were carried out in some of the other institution also in India but there is lack of coordinated work which hurdles the dissemination of research work and knowledge which has been confined at some places only. It is required to spread the utility and good potential bioagents throughout India by validating its performance in different agro-climatic zones through proper coordinated work.

Future of nematophagous fungi

Huffaker *et al.* (1971) have proposed certain desirable characteristics of a natural enemy to be effective as a biocontrol agent. NF does possess some of them. NF has proven ability to trap and kill nematodes only. As all of them are saprophytic fungi they do survive in absence of nematodes. Most of the species of NF are widely distributed. Still, isolates from different localities show variability in efficiency of trapping nematodes. These characteristics confirm the potential of NF as a bioagents to control nematodes. A very important drawback of them is that they are affected by antagonism of other soil fungi. This sensitivity to fungistasis results in their failure in controlling nematodes in field trials.

Future of these NF is in the hands of scientists in developing countries because at one hand farmers in such countries do not afford chemical nematicides and on the other hand they need certain remedy to control nematodes which are responsible for heavy loss in agriculture yields. At present they are not only overlooked but are totally neglected, only because no one has succeeded in solving the riddle of their sensitivity to fungistasis! If this riddle can be solved and a fungal bio-nematicide composed of Nematophagous fungi is developed it will give important boost to agriculture.

Future lines of researches that may improve biological management of phytonematodes with NF include:

- Isolation of different species of NF with three dimensional sticky network and constricting rings from various localities at national level.
- Isolation of predominant soil fungi from same localities.
- Study of levels of antagonism or co-association between NF and other fungi in mixed cultures.
- Selection of strains of NF with better trapping efficiency as well as tolerance (compatibility) to other fungi.
- Development of fungal bio-nematicide using selected strain(s) of NF in carrier based dry, powder form as well as in liquid form- for convenience of soil application and longer shelf life (Jackson 2013). Conidia of all NF are thin walled, in dry powder form they are not likely to remain viable for longer period.

- The fungal bio-nematicide developed by coordinated work can be simultaneously tried in various localities for different crops.

The outcome of proposed coordinated research will be development of a potential bio-agent to control phytonematodes in short span of time.

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