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POTENTIAL FOR BIOLOGICAL CONTROL OF SOIL INSECTS IN THE CARIBBEAN BASIN USING ENTOMOPATHOGENIC NEMATODES

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ABSTRACT

The numerous species and geographic isolates of entomopathogenic nematodes have a diversity of biological attributes which make them adaptable to many uses, especially management of soil pests. Entomopathogenic nematodes are viable substitutes for soil insecticides due to wide host range, persistence, mobility, safety, ease of application, and absence of registration restrictions. Efficacy is often comparable to chemical insecticides, which tend not to perform well in soil. Although soil is generally a very suitable habitat for nematodes, abiotic and biotic constraints are serious impediments in some locales. Surveys should be conducted in Caribbean countries to identify pre-adapted strains.

Recent advances have made nematodes more economic to produce, and storage life has been extended. Entomopathogenic nematodes are appropriate for the Caribbean Basin environment due to favorable soil, humidity and temperatures, occurrence of hosts throughout most of the year, and a high incidence of damage caused by coleopterans and lepidopterans—pests which are usually quite susceptible to infection. In vitro production methods, which require medium-level technology and low cost labor, may be particularly suitable for the Caribbean.

Resumen

Las numerosas especies y cepas geograficas de nematodos entomopatogenos tienen diversos atributos biologicos los cuales los hacen adaptables para muchos usos, especialmente para el manejo de plagas del suelo. Los nematodos entomopatogenos pueden sustituir los insecticidas del suelo, dado el amplio numero de hospederos, su persistencia, movimiento, seguridad y facilidad de aplicacion, y la ausencia de restricciones de registro. Su eficacia los hace comparables con insecticidas quimicos, los cuales no actuan bien en el suelo. Aunque el suelo es un ambiente propicio para los nematodos, ciertos factores bioticos y abioticos pueden restringir su accion en ciertos suelos. Se deben efectuar muestreos en los paises del Caribe, para identificar las cepas que estan pre-adaptadas. Los resultados recientes, hacen que los nematodos sean mas economicos de ser producidos, y su sobrevivencia en almacenamiento es mayor que anteriormente. Los entomopatogenos son apropiados para el Caribe, dadas las condiciones de tipo de suelo favorable, humedad y temperatura, presencia de hospederos durante el año, la alta incidencia de daño causado por coleopteros y lepidopteros, siendo estas plagas muy susceptibles a infeccion. Los metodos de produccion *in vitro*, los cuales requiren un nivel tecnologico medio y un bajo costo de mano de obra, pueden ser muy apropiados para la region de Caribe.

Only within the last decade have entomogenous nematodes been given serious consideration by the academic community and industry for possible use as biological control agents. Since this is a relatively new field, fundamental information is lacking, and there is a particular dearth of information on practical utilization of nematodes under field conditions. However, a recent publication (Gaugler & Kaya 1990) provides a thorough overview of the state-of-the-art. Rather than attempt to repeat an already comprehensive treatment of the general subject, we will provide only a brief synopsis, and emphasize how entomopathogenic nematodes may be particularly well suited for management of soil pests in the Caribbean Basin.

Why Nematodes?

The two factors principally responsible for increased interest in entomopathogenic nematodes are (1) recognition of their industrial potential, both in the United States and elsewhere, and (2) exemption of steinernematid and heterorhabditid nematodes from registration and regulation by the U.S. Environmental Protection Agency. Certainly the growing concern by people everywhere over the potential effects of pesticide residues in food, water, and in the general environment underlies the support for use of entomopathogenic nematodes. However, this is not specific support for nematodes, but rather a negative reaction to pesticides and a positive response to non-chemical pest management techniques, which could include, for example, fungi, viruses, or parasitoids.

Entomopathogenic nematodes have many attributes which make them attractive for commercialization; foremost is the insecticidal-like qualities of nematodes. Many nematode species, unlike most biological control agents, have extremely broad host ranges. In many cases insecticides are not highly efficacious against pests in soil; thus, nematode use is especially attractive. Mass production is achieved rather easily, so economical use is possible. Nematode application can be made with conventional pesticide application equipment (Georgis 1990), and nematodes are not adversely affected by many agricultural pesticides (Forschler et al. 1990).

Entomopathogenic nematodes, while providing insecticide-like qualities, also offer advantages over insecticides. Entomopathogenic nematodes, and the bacteria they vector, are not toxic to mammals. Honeybees, while nominally susceptible, are functionally immune because the high temperature of the hive prevents nematode reproduction (Kaya et al. 1982). Other non-target organisms, including arthropods, also commonly escape infection (Georgis et al. 1991). Nematodes can be quite persistent in some environments, and have the advantage of mobility. Unlike insecticides and other entomopathogenic microorganisms, nematodes can relocate, seek out, and penetrate susceptible hosts. The entomopathogenic nematodes of greatest potential are steinernematids and heterorhabditids.

STEINERNEMATIDAE AND HETERORHABDITIDAE

Like many nematodes of the order Rhabditida, steinernematid and heterorhabditid nematodes are bacterial feeders. They differ, however, in that they have an infective stage juvenile which harbors and transports mutualistic bacteria in the genus *Xenorhabdus*. These bacteria are not sporeformers, and hence are susceptible to environmental degradation; they have no means of penetrating insects, where they normally propagate, without being transported by the nematodes (Poinar and Thomas 1966). Host infection occurs when the juvenile nematode enters a host, usually through the spiracle, mouth, or anus, and penetrates into the hemocoel. Generally they are unable to penetrate directly the host cuticle unless the insects possess a very thin intersegmental membrane (Mracek et al. 1988, Kondo & Ishibashi 1989); heterorhabditids reportedly are more successful in this regard. Release of the bacteria from the nematode into the hemolymph results in rapid host septicemia, and death normally occurs within 48 h. Commonly two nematode generations occur within a host cadaver, with infective stage juveniles from the second generation escaping in search of new hosts.

There has been considerable debate concerning the taxonomy of these nematodes. Presently there are about 10 species of Steinernematidae and 3 species of Heterorhabditae recognized (Table 1; Poinar 1990). Certainly many additional species await discovery. Strains or races of both nematode and bacterium species are recognized; these usually have a geographic basis. In some cases the species and strains differ significantly in biological properties. Because of these differences and the ease of finding locally-adapted nematode species, local isolations are encouraged. Most isolations have occurred in temperate climates, but this appears to be more a result of effort than availability; most attempts at locating native nematodes are successful. Very few attempts have been made in Caribbean Basin countries.

ENVIRONMENTAL CONSTRAINTS ON NEMATODE USE

Constraints on the use of entomopathogenic nematodes for biological control include abiotic (physical), biotic, and host-related factors. Of these three categories, physical factors have received the most thorough research, and are best understood.

TABLE 1. RECOGNIZED SPECIES OF *STEINERNEMA* AND *HETERORHABDITIS*, THEIR ASSOCIATED BACTERIUM, GEOGRAPHIC AND HOST RANGES (FROM POINAR 1990).

Nematode species	Bacterium species	Geographic range	Insect host
S. kraussei	*X. bovienii*	Czechoslovakia	sawfly
S. feltiae	*X. bovienii*	Europe, Australia and New Zealand	various
S. affinis	*X. bovienii*	No. Europe	march fly
S. carpocapsae	*X. nematophilis*	Europe, No. & So. America, Australia, New Zealand	various
S. anomali	*X.* sp.	U.S.S.R.	chafer
S. intermedia	*X. bovienii*	South Carolina	unknown
S. rara	*X.* sp.	Argentina	*Heliothis*
S. kushidai	*X.* sp.	Japan	chafer
S. scapterisci	*X.* sp.	Uruguay, Florida	mole cricket
S. glaseri	*X. poinarii*	No. & So. America	scarabs
H. bacteriophora	*X. luminescens*	Worldwide	various
H. zealandica	*X. luminescens*	Europe, Australia New Zealand	scarabs, others
H. megidis	*X. luminescens*	Ohio	*Popillia*

Abiotic Factors. Isolates of entomopathogenic nematodes generally are well adapted to exist in their site of origin. Thus, heterorhabditids, which are thought to be of tropical origin, are infective at higher temperatures than are steinernematids; various strains exhibit similar tendencies. Infectivity occurs over a wider range of temperature than does reproduction and development. Depending on the nematode involved, infection may occur from about 2 to 35°C, whereas reproduction and development may be largely limited to 20 to 30°C (Woodring & Kaya 1988, Kaya 1990). Unfortunately, there has been a tendency to apply certain species and strains which are easily cultured, principally *S. carpocapsae*, without strict regard to how well it is adapted to the temperature regime it will encounter. Laboratory selection for temperature tolerance has not been very successful (Dunphy & Webster 1986).

Solar radiation and ultraviolet light can be detrimental to nematode survival (Gaugler & Boush 1979). Applications of nematodes often are made in the evening or in conjunction with UV-screens to avoid this problem (Georgis 1990). This complicates application considerably. Soil surface application of nematodes is often made at rates much higher than necessary because so many nematodes are destined to perish on the hostile soil-surface environment. Injection into irrigation systems (Reed et al. 1986) assists in avoidance of UV, and also the related problem of desiccation.

Like nearly all nematodes, entomopathogenic nematodes can survive some degree of desiccation if it occurs slowly (Womersley 1990). The rapid drying which may occur on plant foliage is usually fatal, even if the nematode is protected from direct sunlight. The soil environment is generally favorable because it provides shielding from sunlight, and buffers against extremes in temperature and humidity. Only the soil surface region is particularly hazardous. Nematodes also can suffer from excess moisture, both because they are obligate aerobes and because their mobility is impeded. Species vary in their tolerance of soil moisture. *S. scapterisci*, for example, is effective at lower soil moisture levels than *S. carpocapsae* (Ames 1990). The high humidities and soil moistures which characterize many Caribbean locations are conducive to survival of entomopathogenic nematodes. This may explain the unusually long persistence reported by Jansson et al. (1991) in southern Florida.

Soil texture has repeatedly been shown to affect movement and infectivity of entomopathogenic nematodes. They are subject to the same physical constraints as plant-parasitic nematodes, which tend to be most injurious in sandy soils. Thus, it is not surprising that entomopathogenic species are more dispersive (Georgis & Poinar 1983a, 1983b), infective (Molyneux & Bedding 1984), and persistent (Kung et al. 1990) in sandy soils. There is little difference between sandy loam and pure sand, but when clay attains a level of about 20% nematode activity is significantly inhibited. The small soil pore spaces in clay-rich soil probably exacerbate oxygen deprivation of nematodes due to high moisture retention capabilities. Nematode species differ in their response to soil texture; *S. glaseri*, for example, better tolerates coarse sand, relative to other *Steinernema* spp., possibly due to the large size of the infective juveniles (Kaya 1990). The soils in Caribbean basin countries are extremely varied, suggesting that there will be major differences in effective utilization of entomopathogenic nematodes.

Biotic Factors. Laboratory studies demonstrate that there is potential for long-term persistence of nematodes, especially in soil. However, nearly all studies utilize pasteurized soil, resulting in the complete destruction of nematode antagonists. When comparisons are made, survival is much greater in sterile soil, suggesting an important role for antagonists. Quantitative assessment of antagonists is particularly lacking, but entomopathogenic nematodes are known to be affected by such organisms as fungi, microsporidia, mites, collembolans, tardigades, and other nematodes (Kaya 1990).

In many field studies nematode populations decline within a few days, weeks, or months of application to levels where adequate pest suppression is no longer attained. However, long-term survival is possible; *S. glaseri* has persisted for 24 years in some plots. The availability of hosts may be a limiting factor in many instances. When supplemental hosts are provided, nematode persistence is enhanced and/or abundance increases (Kaya 1990). Tropical and subtropical environments may be especially supportive of endemic nematode populations because of the continuous supply of insect hosts. An area of research which warrants investigation is the use of artificial hosts or sterile insects, which could be "seeded" into a field to help maintain high parasite densities.

Host-related Factors. Although some entomopathogenic nematodes have an extremely broad host range, others apparently are more restricted. For example, *S. scapterisci*is reported to infect crickets but not lepidopterans (Nguyen and Smart 1991). While it is true that the host range of *S. scapterisci* is more restricted than some species, as this little-known species is studied it will become evident that many orthopteroids are good hosts. Many of the other little-known species listed in Table 1 will also be shown to have broad host ranges once they are evaluated thoroughly.

The biological basis for host selection and suitability is poorly known. There is reportedly a directed response toward host-produced carbon dioxide (Choo et al. 1989, Gaugler et al. 1980). While this certainly would assist in host location, there are numerous sources of carbon dioxide in the soil, most of which are not host-produced. Kairomonal stimuli probably exist, as they do for nearly all systems which have been studied adequately. However, thus far it appears that nematodes do not orient from appreciable distances, and locate hosts principally by random encounter. *H. bacteriophora* has greater host-finding ability than *S. carpocapsae* (Choo et al. 1989). Some chemical activators are known, principally weak nematicides, which enhance parasitism (Ishibashi & Kondo 1990). Additional activators are needed. Searching behavior appears to differ among species. *S. carpocapsae* seems to search at the soil surface while *H. bacteriophora* moves downward from the surface (Gaugler 1988). Most species demonstrate little tendency to move more than 30 cm downwards or laterally within 30 days. Upwards dispersal occurs more freely, and *S. glaseri* seems to be exceptionally dispersive (Schroeder & Beavers 1987).

Suitability for successful infection is known to be a function of host size, age and stage. Generally, small hosts are more susceptible than large hosts, younger hosts are more susceptible than older hosts, and larvae and adults are more susceptible than pupae. Exceptions occur when the small size of the host physically impedes penetration (Gaugler & Molloy 1981, Kaya 1985). Holometabolous insects are more susceptible than hemimetabolous species, with Lepidoptera and Coleoptera being the most successful targets. Many of the most serious pests in the Caribbean basin are members of these orders, and spend at least a portion of their life cycle in the soil or in a similar crytic habitat which is suitable for nematode survival and infectivity.

ECONOMICS OF NEMATODE USE

A common concern when contemplating use of entomopathogenic nematodes is cost. Nematodes can be produced *in vivo*, as a cottage-type industry, where technology is limited and labor is relatively inexpensive. Poinar (1972) estimated production costs in wax moth larvae, *Galleria mellonella* (L.), at U.S. $1 per million; similar estimates were made for semi-refined diets such as dog food. Improved diets and yield resulted in cost reductions to U.S. $0.02 per million 10 years later (Bedding 1981, 1984). Other improvements in *in vitro* culture have since been made (Friedman 1990), reducing costs further, in some cases with relatively small increases in production technology.

Of particular interest is the high cost of labor in the medium-level technology, solid phase production methods of Bedding, relative to capital and material costs (Friedman 1990). In low labor cost areas, such as some Caribbean Basin countries, production unit costs would be significantly less than the aforementioned estimate. Also, production scale increases do not produce large decreases in total production costs using this system, which would foster numerous, local production facilities. Thus, storage and transport problems are lessened. The more advanced-technology, liquid culture techniques have relatively high capital costs, and realize greater benefit from increases in production scale. This is more suitable for high labor cost, industrialized countries.

Much of the purportedly high cost of nematode use is due to the need to overproduce nematodes. Overproduction occurs because historically storage has been difficult, yet adequate stocks must be maintained to deal with unforeseen emergencies. Recent developments in storage technology are changing this situation, with shelf life of 6 months under refrigerated conditions and 1 month at 25°C virtually assured. Recent advances in desiccation technology promise long-term storage at room temperature (Friedman 1990).

When considering the economics of nematode-based insect control there are really two issues of concern: comparative cost and comparative advantage. We have argued that for Caribbean Basin countries, low-technology production techniques might prove surprisingly feasible compared with high-technology production in industrialized countries. This is especially true when the social benefits of increased employment associated with local production are included. Comparative advantage accrues when the production/protection system using entomopathogenic nematodes offers additional benefits, such as minimized applicator hazard, reduction of expensive imported insecticide and insecticide residues, and/or improved levels of control with nematode use. Increasingly, insecticide registrations do not exist for specialty crops, which may prove to be a serious problem if crops are produced for export to the United States. While dollar figures cannot be assigned to many of the comparative advantages of entomopathogenic nematode use, they are nonetheless important considerations.

ACKNOWLEDGMENT

Approved for publication as Florida Agricultural Experiment Station Journal Series No. R-02135.

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