[1]Hamilton Boys High School, 34 Argyle Street, Hamilton, New Zealand.
[2]Landcare Research, Private Bag 3127, Hamilton, New Zealand.
Address for correspondence: 1422 Tauwhare Road, R.D.4, Hamilton, New Zealand.

GENERALIST ENTOMOPATHOGENS AS BIOLOGICAL INDICATORS OF DEFORESTATION AND AGRICULTURAL LAND USE IMPACTS ON WAIKATO SOILS

Summary: The relative abundance of entomopathogenic nematodes and fungi was estimated for 10 sites in each of indigenous forest, pasture, and cropland habitats by baiting soil samples with *Galleria* larvae. The steinernematid *Steinernema feltiae* (Filip) was the dominant nematode, occurring in soils from all three habitat types. The heterorhabditid *Heterorhabditis zelandica* Poinar was recovered only from soils of podocarp (*Dacrycarpus dacrydioides* (A. Rich.)) forests. *Galleria* infection by nematodes was higher in soils from forest habitat than in soils from pasture and cropland. Among the sampled forests, nematode infection was higher in soils from podocarp stands than those from broadleaf stands. The deuteromycete fungi *Beauveria bassiana* (Balsamo) Vuillemin, *Metarhizium anisopliae* (Metschnikoff) Sorokin, and *Paecilomyces* cf. *cicadae* (Miquel) Samson, and a Entomophthorales zygomycete, tentatively identified as a *Tarchium* species, were recovered from the *Galleria* baits. Infection of *Galleria* by *B. bassiana* and *M. anisopliae* occurred in soils from all habitat types, while that by *P. cicadae* occurred only in soils from forest habitats. *Tarchium* was recovered from a single pasture site. The frequency of *Galleria* infection by these entomopathogenic fungi collectively, and by *B. bassiana* alone, was higher in pasture soils than in soils from either forest or cropland. These results are discussed in relation to disturbance effects of land use changes and the potential role of generalist entomopathogens as biological indicators of soil health.

Keywords: agricultural disturbance, entomopathogenic nematodes, entomopathogenic fungi, soil, *Galleria mellonella*.

Introduction

At least 75% of New Zealand's land surface was forested until about 1200 years ago. Non-forested areas were largely restricted to alpine, coastal duneland or wetland areas. Since human colonisation of New Zealand, probably around A.D. 800 (Davidson, 1984), the transformation of its vegetation cover has been dramatic (Salmon, 1975; Cumberland, 1981; McGlone, 1983; O'Loughlin and Owens, 1987). Considerable modification and loss of forest cover occurred during the era of exclusive Polynesian occupation. After European contact and settlement, the rate of deforestation increased, reaching a peak in the decades around the beginning of the 20th century. Deforestation following European settlement occurred predominantly for establishment of pastoral agriculture, although large areas of forest were also heavily modified by timber extraction. Present land use is dominated by pastoralism: farmed land occupies over 60% of the total area of New Zealand and only 14% remains in indigenous forest.

Soil erosion as a direct consequence of deforestation has long been recognised as a limitation on the sustainability of pastoral land use in New Zealand and this issue has been heightened by recent resource management legislation (Blaschke *et al*., 1992). In contrast, there have been few investigations on the effects of forest removal on the New Zealand soil fauna (Yeates, 1991). Contraction in distributional range has been a presumptive consequence of deforestation for many soil invertebrates dependent on forest cover but data has been available for only a few taxa (eg., earthworms; Lee, 1959, 1961). Most conservation effort has focused on the flora and fauna of the remaining natural forest habitats, and as a consequence no information is available on loss of indigenous biodiversity associated with deforestation and establishment of agricultural practices.

Following the conversion of forest land to pasture, several indigenous insects have become widespread and abundant in pastures. These include *Costelytra zealandica* (White), *Pyronota festiva* (F.), *Odontria* spp. (Scarabaeidae), *Irenimus aequalis* (Broun) (Curculionidae), *Wiseana* spp. (Hepialidae), and *Persectania aversa* (Walker) (Noctuidae). Their feeding can severely reduce the productive life of pasture. Remnant forest areas have been shown to be

potential source areas for predators and parasitoids of these native insects (eg., Merton, 1980), but there have been no serious attempts to exploit these natural control agents in the pasture environment. Instead, the focus of biological control for pasture pests has been on entomopathogens already resident in the pasture soils, or introduced into those soils following importation from overseas (e.g., Wright & Jackson, 1992). As a consequence, entomopathogens are known from the native habitat of several indigenous pest insects but information on the diversity of disease agents and their significance in population ecology in these habitats is limited in comparison to that in pasture. Thus, there is no information on the extent of loss of potentially useful entomopathogen diversity with forest conversion to pasture, or on factors constraining survival of indigenous entomopathogens in the pasture environment. Further, the consequences for the entomopathogens of annual cropping systems imposed on former pasture land is unknown.

The present investigation sought to provide information on the changes in generalist entomopathogen loadings in soils along the disturbance gradient indigenous forest to pasture to annual cropping. The occurrence and relative abundance of entomopathogenic nematodes and fungi were used as indicators of disturbance effects.

Materials and Methods

Sites in the Waikato Province, North Island, New Zealand, were sampled in April 1992 to provide soils from 10 indigenous forests, 10 permanent pastures, and 10 croplands (Fig. 1). Two types of indigenous forests were sampled: five sites in *Beilschmiedia tawa* (A. Cunn.) Benth. - *Weinmannia racemosa*

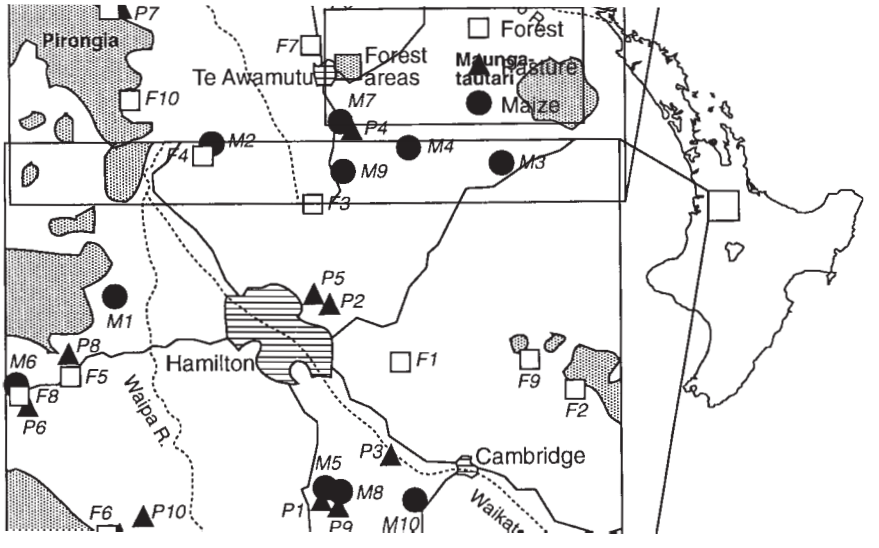

Figure 1. *The location of the sampling sites in the vicinity of Hamilton City, in the central Waikato Province. The natural cover of this region comprised a mosaic of lowland forests and wetlands, but the contemporary landscape is dominated by agricultural land use, predominantly pasture. The remaining indigenous forest is highly fragmented, with numerous small (mostly <1 ha) patches scattered in agricultural areas and the remaining larger tracts (shaded) confined to the steeplands of andesitic and basaltic volcanic cones.*

Linn. f. dominant broadleaf forest on slopes of andesitic and basaltic volcanic cones, and five sites in *Dacrycarpus dacrydioides* (A. Rich.) dominant podocarp forest on alluvial flats and hillside seepage basins. The sampled pastures had been established prior to 1900 on land formerly in forest, and comprised predominantly either of *Lolium perenne* L., *Poa annua* L. and *Trifolium repens* L., or *Anthoxanthum odoratum* L., *Agrostis tenuis* Sibth., *L. perenne*, *T. repens* and *Lotus corniculatus* L. The croplands sampled had been planted in *Zea mays* L. annually for 10 to 21 years on land previously in pasture. For each site, four soil samples of about 3 litre volume were gathered by digging with a spade to 75 mm depth. Each sample was hand crumbled and passed through a 4mm mesh sieve.

To determine the relative abundance of entomopathogenic nematodes and fungi, five third instar *Galleria mellonella* (L.) (Lepidoptera: Pyralidae, Galleriinae) larvae were added to each soil sample to act as a bait, as described by Bedding and Akhurst (1975). The larvae were placed at the bottom of a 1L plastic container (depth 75mm) to which the soil sample was gently added, and covered with a glass sheet to prevent insect escape. The soil samples prepared in this way were left for five days at a constant 20° C, after which the larvae were recovered by hand sorting and maintained on moist filter paper in Petri dishes at 20°C for a further 7 days. Infection by nematodes and fungi were initially based on characteristic signs and symptoms of entomopathogens (Poinar, 1979; Samson, 1981). Dead *Galleria* were then dissected or placed on modified White traps (White, 1927) to confirm nematode infection. Fresh *G. mellonella* larvae were exposed in Petri dishes to juvenile nematodes isolated from the samples to confirm pathogenicity and to provide material for specific identification based on morphological criteria (Poinar 1979; Wright, 1990). Fungal conidia were isolated from *G. mellonella* cadavers exhibiting mycosis and applied topically to fresh *G. mellonella* larvae to confirm their pathogenicity and specific identification (Samson, 1981).

Sites within habitat category were treated as replicates, within which the results for the four samples were pooled. Data on recovery frequency for seeded *G. mellonella* larvae (number of larvae recovered per total larvae added) and relative abundance of infective nematodes and fungi (number of positive *G. mellonella* infections per total *G. mellonella* exposed) were subjected to analysis of variance for the completely randomised experimental design following arcsine transformation. All analyses were performed using the MINITAB statistical package.

Results

The majority of *Galleria* placed in the soils were recovered at the end of the experiment, with 71%, 82%, and 79% recovery from soil samples from the habitat types forest, pasture and cropland, respectively: these recoveries were not significantly different between habitat types ($F = 2.99$, *d.f.* = 2, 117, $P = 0.054$) (Table 1).

A high proportion of the bait *G. mellonella* larvae recovered from the soil samples were infected by entomopathogenic nematodes or fungi (Tables 1 and 2). Species of Heterorhabditidae, Steinernematidae, Diplogasteridae and Rhabditidae were identified in *G. mellonella* larvae found to be infected by nematodes. The diplogasterids and rhabditids were considered as facultative or secondary parasites (T.A. Jackson, pers. comm.) and were excluded from the analyses. Infections attributed to primary parasites comprised 23% *Heterorhabditis zelandica* Poinar, a heterorhabditid, and 77% *Steinernema feltiae* (Filip), a steinernematid. Infections by entomopathogenic nematodes were found to be significantly more common in soils from the forest sites than the soils from pasture and cropland ($F = 20.31$, *d.f.* = 2, 117, $P < 0.001$) (Table 2). Furthermore, the proportion of *G. mellonella* larvae that became infected by nematodes varied between forest sites ($F = 4.00$, *d.f.* = 9, 30, $P = 0.002$), largely reflecting higher infection rates in soils from podocarp forest (mean 0.59) compared to those in broadleaf forest soil (mean 0.21) ($F = 7.59$, *d.f.* = 1, 35, $P = 0.009$) (Table 3). Rates of *G. mellonella* infection by entomophagous nematodes did not vary significantly among pasture ($F = 0.76$, *d.f.* = 9, 30, $P = 0.657$) and cropland ($F = 0.87$, *d.f.* = 9, 30, $P = 0.562$) sites. *Heterorhabditis zelandica* infections were confirmed only for *G. mellonella* larvae placed in soil from podocarp forests, while

Table 1: *Rate of recovery of Galleria mellonella larvae from soil samples and frequency at which infection by entomopathogenic nematodes and fungi occurred at sites within three habitat types.*

	Habitat type		
	Forest	Pasture	Cropland
Number of *Galleria* larvae recovered[1]	142	164	158
Proportion of sites where infection occurred:			
Nematodes	0.9	0.6	0.5
Fungi	0.6	0.9	0.7

[1]Out of 200 *Galleria* per habitat type

Table 2: *Frequency of infection by entomopathogenic nematodes and fungi in Galleria mellonella larvae placed in soil samples from three habitat types.*

	Habitat type			
G. mellonella larvae infected by	Forest	Pasture	Cropland	L.S.D.[1]
Nematodes				
Heterorhabditis zelandica	0.04	0.00	0.00	0.03
Steinernema feltiae	0.37	0.06	0.05	0.22
All nematodes (range)	0.41 (0-0.93)	0.06 (0-0.13)	0.05 (0-0.22)	0.26
Fungi				
Beauveria bassiana	0.03	0.08	0.02	0.05
Metarhizium anisopliae	0.07	0.22	0.13	0.16
Paecilomyces cf. *cicadae*	0.07	0.00	0.00	0.06
Tarchium species.	0.00	0.04	0.00	0.07
All fungi (range)	0.16 (0-0.50)	0.34 (0-0.56)	0.15 (0-0.37)	0.27

[1]Approximate values for least significant difference (at $P = 0.05$). Analysis for variance performed on arcsine transformed data. See text for F values.

Table 3: *Frequency of infection by entomopathogenic nematodes in Galleria mellonella larvae placed in soil samples from two forest types.*

	Habitat type		
	Podocarp forest	Broadleaf forest	L.S.D.[1]
Proportion of *Galleria* larvae infected by:			
Heterorhabditis zelandica	0.11	0.00	0.06
Steinernema feltiae	0.50	0.18	0.28
All nematodes (range)	0.61 (0.11-0.92)	0.21 (0-0.55)	0.36

[1] Approximate values for least significant difference (at $P = 0.05$). Analysis for variance performed on arcsine transformed data. See text for F values.

S. feltiae was recovered from larvae placed in soil from podocarp and broadleaf forests, pasture and cropland.

The deuteromycete fungi *Beauveria bassiana* (Balsamo) Vuillemin, *Metarhizium anisopliae* (Metschnikoff) Sorokin, and *Paecilomyces* cf. *cicadae* (Miquel) Samson, and a zygomycete species belonging to Entomophthorales, tentatively identified as *Tarchium* sp., were identified from *G. mellonella* cadavers. Isolates of each fungus were shown to be pathogenic to *G. mellonella* when topically applied to fresh hosts in Petri dishes. The frequency of *G. mellonella* infections by entomopathogenic fungi was higher in pasture soils than in soils from either forest or cropland ($F = 4.32$, $d.f. = 2, 114$, $P = 0.016$) (Table 2). Infection rates by all fungal species combined did not vary significantly among sites within habitat type ($F = 1.45$, $d.f. = 9, 108$, $P = 0.177$). *Beauveria bassiana* and *M. anisopliae* were recovered from *G. mellonella* placed in forest, pasture and cropland soils. *Beauveria* was recovered more frequently from *G. mellonella* larvae placed in soil from pasture (mean proportion infected = 0.08) than from soil from other habitats (mean proportion infected = 0.02) ($F = 3.54$, $d.f. = 2, 27$, $P = 0.043$). A similar trend was apparent for *Metarhizium* (mean proportions infected: forest = 0.07, pasture = 0.22, cropland = 0.13) but this failed to reach statistical significance ($F = 2.20$, $d.f. = 2, 27$, $P = 0.130$) due to high variability among sites. *P. cicadae* was recovered only from *G. mellonella* placed in forest soils (podocarp and broadleaf) ($F = 4.52$, $d.f. = 2, 27$, $P = 0.020$) and *Tarchium* sp. was recovered from *G. mellonella* placed in one pasture soil.

Discussion

The baiting technique using *G. mellonella* larvae was developed by Bedding and Akhurst (1975) to detect entomophagous nematodes in soils and has been widely used to survey the occurrence and relative prevalence of these parasites. The present study has confirmed the usefulness of the insect baiting technique for estimating the occurrence of

entomophagous fungi in soils, as earlier shown by Zimmermann (1986) and Mietkiewski *et al*. (1991). The technique itself, while being simple in concept and easy to implement, does have limitations. For example, low soil moisture conditions (eg., Molyneux and Bedding, 1984; Kaya, 1990; Koppenhopper *et al*., 1995) can restrict infectivity and thus detection of nematodes by the insect bait technique. In the current study sampling was delayed until autumn rains returned soil moisture to near field capacity. Furthermore, it is unclear whether infection by fungi is often masked or inhibited by nematode infection of the same host. The high prevalence of nematode infection in *G. mellonella* placed in forest soil in the present study may have lead to under-estimation of fungal occurrence in those soils. Conversely, the apparent higher prevalence of entomophagous fungi recorded for pasture soils may in part reflect a lower prevalence of nematodes in this habitat type. Barbercheck and Kaya (1990) found that entomopathogenic nematodes were able to exclude entomopathogenic fungi when applied to *G. mellonella* within one day of the fungus being applied. For the purposes of our analyses, infection of *G. mellonella* by fungi was assumed to be independent of infection by nematodes.

While *G. mellonella* is highly susceptible to insect pathogens, the bait insect method could be biased for the isolation of lepidopteran-active, or even *Galleria*-active, strains of fungi (Prior, 1992). However, Chandler *et al*. (1997) found that fungi isolated from soil by the *Galleria* method were also infective in several *Delia* sp. (Diptera). Entomopathogenic nematodes have a broad host range compared to fungi (Kaya and Gaugler, 1993), but competition between differentially pathogenic species or strains in a soil sample could still introduce bias into sampling with insect baits (Stuart and Gaugler, 1994).

The prevalence of entomophagous nematodes was markedly higher in soils from indigenous forest habitat than in soils under agriculture. This result seems to support the hypothesis that deforestation and agricultural land use adversely affects entomopathogen activity in the indigenous soil fauna. Our results closely match those of Mracek (1980) who found that, in Czechoslovakia, steinernematids were more common in forests than in cropland or meadows. However, other surveys (*e.g*., Akhurst and Brooks, 1984; Akhurst and Bedding, 1986; Hominick and Briscoe, 1990ab; Hara *et al*., 1991; Mracek and Webster, 1993; Amarasinghe *et al*., 1994; Liu and Berry, 1995) have shown heterorhabditid and steinernematid nematodes to be widely and non-uniformly distributed, but fail to indicate a pattern of occurrence and prevalence consistent with habitat type or degree of habitat disturbance. Many biotic and abiotic soil factors have been shown to influence persistence and virulence of entomophagous nematodes.

Mracek and Webster (1993) found that heterorhabditid and steinernematid nematodes occurred in western Canadian sites where human impact had been substantial, and no nematode-positive soil samples were recorded at sites where the impact of humans had been slight. They suggested that this may be the result of the outbreaks of insect pests associated with crop monoculture. The link between occurrence of insect hosts and that of the nematodes is obligate, but one not readily quantified given the temporal dynamics of insect populations and the ability of heterorhabditid and steinernematid to persist in the absence of hosts. Nematode survival is enhanced in soil where they are buffered from environmental extremes (Kaya and Gaugler, 1993) and the protection afforded by the vegetation may have been one of the central factors for nematodes being more prevalent in forest soils in the present study. Several studies (Burman *et al*., 1986; Blackshaw, 1988; Glazer *et al*., 1991; Hara *et al*., 1991; Liu and Berry 1995; Amarasinghe *et al*., 1994) indicate entomopathogenic nematode populations to be more abundant in sandy or sandy loam soils than those of clay. These differences have been attributed to porosity and moisture characteristics of soils (Poinar, 1983a,b; Molyneux and Bedding, 1984). We found nematodes to be generally more prevalent in soils from podocarp forests than in soils from broadleaf forest. While no measurements were taken of soil physical parameters, the prevalence of nematodes was apparently unrelated to soil texture which varied from sandy loam to heavy clay. A more likely explanation for the higher prevalence in soils of the podocarp forests is their generally higher moisture status due to site topography and seasonally high water table.

The lower frequency of entomopathogenic fungi in intensely cultivated soils than in forest soil has been reported for several northern hemisphere regions (Kleespies *et al*., 1989; Vänninen *et al*., 1989; Mietkiewski *et al*., 1991; Vänninen, 1995). However, individual fungal species often exhibit differing responses. Working with Finnish soils, Vänninen (1995) found *M. anisopliae* to be common in both natural and cultivated habitat, and *Paecilomyces fumosoroseus* (Wise) Brown & Smith to occur only in natural habitats or in relatively undisturbed cultivated habitats such as orchards. *Beauveria bassiana* and *P. farinosus* (Holmsk.) were

found to be very sensitive to the disturbance effects of cultivation and thus restricted to natural habitats. The ability of *M. anisopliae* to persist in cultivated soils is well established (Kleespies *et al*., 1989; Rath *et al*., 1992).

Arthropod hosts are needed for the persistence of *B. bassiana* in soil (Wojchiechowska *et al*., 1977; Daoust and Pereira, 1986). The long-term survival of *B. bassiana* seems to depend on its spread to secondary hosts by utilizing the energy obtained from its primary hosts, whereas *M. anisopliae* does not use this strategy (Gottwald and Tedders, 1984). In intensely tilled soils, *B. bassiana* may suffer from a lack of targets for secondary infection, whereas *M. anisopliae* is capable of long-term survival due to persistence of its conidia on the primary host. The almost ubiquitous occurrence of suitable insect hosts, such as *Listronotus bonarensis* (Kuschel) (Barker *et al*., 1989) may largely explain the prevalence of *B. bassiana* in Waikato pasture soils.

Glare *et al*. (1993) have provided a checklist of the entomopathogenic nematodes and fungi that naturally occur in New Zealand. Only two species of entomopathogenic nematodes and four species of entomopathogenic fungi were isolated in our study. Low species richness is a feature of entomopathogenic nematode communities in soil, reflecting the apparent low global generic and species diversity in both the Heterorhabditidae and Steinernematidae (Kaya and Gaugler, 1993; Nguyen and Smart, 1996). The richness of fungi in our samples is low compared to that recorded for tropical habitats (e.g., Evans, 1982) and the estimated global diversity that exceeds 700 species (Charnley, 1989), but is similar to that recorded for other temperate regions (Vänninen *et al*., 1989). It should be noted, however, that this study gave no indication as to the extent of intraspecific diversity, which can be considerable in both entomopathogenic fungi (Gillespie and Moorhouse, 1989; Glare and Inwood, 1998) and entomopathogenic nematodes (Bedding *et al*., 1983).

Conclusion

Soil food-webs are complex, involving a great diversity of organisms across a number of trophic groups. Disturbance and stress effects on one trophic level can potentially have marked bottom-up or top-down, cascade effects on the soil biota. This complexity has hindered the development of biological indicators of soil biodiversity and soil health because of perceived technical difficulties. However, organisms in the higher trophic levels within soil, such as the entomopathogenic nematodes and fungi, may be particularly sensitive to environmentally-induced, bottom-up cascade effects that alter availability of their prey or hosts. Our results indicate marked shifts in relative abundance of entomopathogenic nematodes and fungi occur in Waikato soils associated with land use changes. Further research is needed to ascertain if these organisms are sufficiently sensitive to be useful for monitoring changes in soil biological activity over narrower disturbance/stress gradients. The *Galleria* baiting technique provides a simple, cheap, and apparently effective method of such monitoring of these generalist entomopathogens.

Acknowledgements

The work reported in this paper formed the basis of an ECNZ Science Fair project completed by the senior author in 1993. Many thanks to the land owners for allowing collection of soil samples from their properties. Biosupplies (Auckland) provided the *Galleria* larvae. Drs Travis Glare and Trevor Jackson (AgResearch, Lincoln) for identifying fungi and nematodes, respectively, and for providing comment on an earlier draft of this paper.

References

Akhurst R.J.; Bedding R.A. 1986. Natural occurrence of insect pathogenic nematodes (Steinernematidae and Heterorhabditidae) in soil in Australia. *Journal of the Australian Entomological Society 25:* 241-244.

Akhurst R.J.; Brooks, W.M. 1984. The distribution of entomophilic nematodes (Heterorhabditidae and Steinernematidae) in North Carolina. *Journal of Invertebrate Pathology 44:* 140-145.

Amarasinghe, L.D.; Hominick, W.M.; Briscoe, B.R.; Reid, A.P. 1994. Occurrence and distribution of entomopathogenic nematodes in Sri Lanka. *Journal of Helminthology 68:* 277-286.

Barbercheck, M.E.; Kaya, H.K. 1990. Interactions between *Beauveria bassiana* and the entomopathogenic nematodes, *Steinernema feltiae* and *Heterorhabditis heliothidis*. *Journal of Invertebrate Pathology 55:* 225-234.

Barker, G.M.; Pottinger, R.P.; Addison, P.J. 1989. Population dynamics of the Argentine stem weevil (*Listronotus bonariensis*) in pastures of Waikato, New Zealand. *Agriculture, Ecosystems and Environment 26:* 79-115.

Bedding R.A.; Akhurst R.J. 1975. A simple technique for the detection of insect pathogenic nematodes in soil. *Nematologica 21:* 109-110.

Bedding, R.A.; Molyneux, A.S.; Akhurst, R.J. 1983. *Heterorhabditis* spp., *Neoaplectana* spp., and *Steinernema kraussei*: interspecific and intraspecific differences in infectivity for insects. *Experimental Parasitology 55:* 249-257.

Blackshaw, R.P. 1988. A survey of insect parasitic nematodes in Northern Ireland. *Annals of Applied Biology 113:* 561-565.

Blaschke, P.M.; Trustrum, N.A.; DeRose, R.C. 1992. Ecosystem processes and sustainable land use in New Zealand steeplands. *Agriculture, Ecosystems and Environment 41:* 153-178.

Burman, M.; Abrahamsson, K.K.; Ascard, J.; Sjoberg, A.; Erikson, B. 1986. Distribution of insect parasitic nematodes in Sweden. *In:* Samson, R.A.; Vlak, J.M.; Peters, D. (Editors), *Fundamentals and applied aspects of invertebrate pathology*, p. 312. Foundation of the Fourth International Colloquium on Invertebrate Pathology, 18-22 August, 1986. Wageningen, Netherlands.

Chandler, D.; Hay, D.; Reid, A.P. 1997. Sampling and occurrence of entomopathogenic fungi and nematodes in UK soils. *Applied Soil Ecology 5:* 133-141.

Charnley, A.K. 1989. Mycoinsecticides: present use and future prospects. In: *Progress and prospects for insect control*, pp. 165-181. British Crop Protection Council Monograph 43.

Cumberland, K.B. 1981. *Landmarks*. Readers Digest Services, Sydney. 304pp.

Daoust, R.A.; Pereira, R.M. 1986. Survival of *Beauveria bassiana* (Deuteromycetes: Moniliales) conidia on cadavers of cowpea pests stored outdoors and in laboratory in Brazil. *Environmental Entomology 15:* 642-647.

Davidson, J. 1984. *The Prehistory of New Zealand.* Longman Paul, Auckland. 207pp.

Evans, H.C. 1982. Entomogenous fungi in tropical forest ecosystems: an appraisal. *Ecological Entomology 7:* 47-60.

Gillespie, A.T.; Moorhouse, E.R. 1989. The use of fungi to control pests of agricultural and horticultural importance. *In:* Whipps, J.M.; Lumsden, R.D. (Editors), *Biotechnology of fungi for improving plant growth*, pp. 85-126. Cambridge University Press, Cambridge, U.K.

Glare, T.R.; Inwood, A.J. 1998. Morphological and genetic characterisation of *Beauveria* spp. from New Zealand. *Mycological Research 102:* 250-256.

Glare, T.R.; O'Callaghan, M.; Wigley, P.J. 1993. Checklist of naturally occurring entomopathogenic microbes and nematodes in New Zealand. *New Zealand Journal of Zoology 20:* 95-120.

Glazer, I.; Liran, N.; Steinberg, Y. 1991. A survey of entomopathogenic nematodes (Rhabditida) in the Negev desert. *Phytoparasitica 19:* 291-300.

Gottwald, T.R.; Tedders, W.L. 1984. Colonization, transmission, and longevity of *Beauveria bassiana* and *Metarhizium anisopliae* (Deuteromycotina: Hypomcetes) on pecan weevil larvae (Coleoptera: Curculuionidae) in the soil. *Environmental Entomology 13:* 557-560.

Hominick, W.M.; Briscoe, B.R. 1990b. Survey of 15 sites over 28 months for entomopathogenic nematodes (Rhabitida; Steinernematidae). *Parasitology 100:* 289-294.

Hominick, W.M.; Briscoe, B.R. 1990b. Occurrence of entomopathogenic nematodes (Rhabitida: Steinernematidae and Heterorhabditidae) in British soils. *Parasitology 100:* 295-302.

Kaya, H.K. 1990. Soil ecology. *In:* Gaugler, R.; Kaya, H.K. (Editors), *Entomopathogenic nematodes in biological control*, pp. 93-115. CRC, Boca Raton, Florida.

Kaya, H.K.; Gaugler, R. 1993. Entomopathogenic nematodes. *Annual Review of Entomology 38:* 181-206.

Kleespies, R.; Bathon, H.; Zimmermann, G. 1989. Untersuchungen zum natürlichen Vorkommen von entomopathogenen Pilzen und Nematoden in verschiedenen Böden in der Umgebung von Darmstadt. *Gesunde Pflanzen 41:* 350-355.

Kopppenhöfer, A.M.; Kaya, H.K.; Taormino, S.P. 1995. Infectivity of entomopathogenic nematodes (Rhabditida: Steinernematidae) at different soil depths and moistures. *Journal of Invertebrate Pathology 65:* 193-199.

Lee, K.E. 1959. The earthworm fauna of New Zealand. New Zealand *Department of Scientific and Industrial Research Bulletin 130:* 1-486.

Lee, K.E. 1961. Interactions between native and introduced earthworms. *Proceedings of the New Zealand Ecological Society 8:* 60-62.

Liu, J.; Berry, R.E. 1995. Natural distribution of entomopathogenic nematodes (Rhabditida: Heterorhabditidae and Steinernematidae) in Oregon soils. *Environmental Entomology 24:* 159-163.

Merton, J.M. 1980. *The interrelationships of* Costelytra zealandica *(White) (Coleoptera: Scarabaeidae), in New Zealand grass grub, and its parasite,* Proscisso cana *Hutton (Diptera: Tachinidae)*. M.Sc. Thesis, University of Canterbury, Christchurch, 111pp.

McGlone, M.S. 1983. Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania 18:* 11-25.

Mietkiewski, R.; Tkaczuk, C.; Badowska-Czubik, T. 1992a. Entomogenous fungi isolated from strawberry plantation soil infested by *Otiorhynchus ovatus* L. *Roczniki Nauk Rolniczych, Seria E, 22:* 39-46.

Mietkiewski, R.; Tkaczuk, C.; Zasada, L. 1992b. Wystepowanie grzybów entomopatogennych w glebie ornej i lakowej. *Acta Mycologica 27:* 197-203.

Mietkiewski, R.; Zurek, M.; Tkaczuk, C.; Balazy, S. 1991. Wyestepowanie entomopatogennych grzybów w glebie ornej, lesnej oraz sciólce. *Roczniki Nauk Rolniczych, Seria E, 21:* 61-68.

Molyneux, A.S.; Bedding, R.A. 1984. Influence of soil texture and moisture on the infectivity of *Heterorhabditis* sp. D1 and *Steinernema glaseri* for larvae of the blowfly, *Lucilia cuprina*. *Nematologica 30:* 358-365.

Mracek, K. 1980. The use of *Galleria* traps for obtaining nematode parasites of insects in Czechoslovakia (Lepidoptera: Nematoda, Steinernematidae). *Acta Entomologica Bohemoslovaca 77:* 378-382.

Mracek, Z.; Webster, J.M. 1993. Survey of Heterorhabditidae and Steinernematidae (Rhabditida, Nematoda) in Western Canada. *Journal of Nematology 25:* 710-717.

Nguyen, K.B.; Smart, G.C. 1996. Identification of entomopathogenic nematodes in the Steinernematidae and Herorhabditidae (Nematoda: Rhabditida). *Journal of Nematology 28:* 286-300.

O'Loughlin, C.L.; Owens, I.F. 1987. Our dynamic environment. *In:* Holland, P.G. (Editor), *Southern approaches*, pp. 59-90. New Zealand Geographical Society, Christchurch.

Poinar, G.O. 1979. *Nematodes for biological control of insects*. CRC, Boca Raton, Florida.

Prior, C. 1992. Discovery and characterisation of fungal pathogens for locust and grasshopper control. *In:* Lomer, C.J.; Prior, C. (Editors), *Biological control of locusts and grasshoppers*, pp. 159-180. CAB International, Wallingford, U.K.

Rath, A.C.; Koen, T.B.; Yip, H.Y. 1992. The influence of abiotic factors on the distribution and abundance of *Metarhizium anisopliae* in Tasmanian pasture soils. *Mycological Research 96:* 378-384.

Salmon, J.T. 1975. The influence of man on biota. *In:* Kuschel, G. (Editor), *Biogeography and ecology in New Zealand*, pp. 643-661. Dr W. Junk, The Hague.

Samson, R.A. 1981. Identification: entomopathogenic Deuteromycetes. *In:* Burges, H.D. (Editor), *Microbial control of pest and plant disease 1970-1980*, pp. 93-106. Academic Press, New York.

Vänninen, I. 1995. Distribution and occurrence of four entomopathogenic fungi in Finland: effect of geographical location, habitat type and soil type. *Mycological Research 100:* 93-101.

Vänninen, I.; Husberg, G.-B.; Hokkanen, H.M.T. 1989. Occurrence of entomopathogenic fungi and entomoparasitic nematodes in cultivated soils in Finland. *Acta Entomologica Fennica 53:* 65-71.

White, G.F. 1927. A method for obtaining infective nematode larvae from cultures. *Science 66:* 302-303.

Wojchiechowska, M.; Kmitowa, K.; Fedorko, A.; Bajan, C. 1977. Duration of activity of entomopathogenic microorganisms introduced into the soil. *Polish Ecological Studies 3:* 141-148.

Wright, P.J. 1990. Morphological characterisation of the entomogenous nematodes *Steinernema* spp. and *Heterorhabditis* spp. (Nematoda: Rhabditida). *New Zealand Journal of Zoology 17:* 577-585.

Wright, P.J.; Jackson, T.A. 1992. Efficacy of entomogenous nematodes for control of porina (*Wiseana cervinata*) in Canterbury pastures during winter. *New Zealand Journal of Agricultural Research 35:* 435-439.

Yeates, G.W. 1991. Impact of historical changes in land use on the soil fauna. *New Zealand Journal of Ecology 15:* 99-106.

Zimmermann, G. 1986. "*Galleria* bait method" for detection of entomopathogenic fungi in soil. *Zeitschrift fuer Angewandte Entomologie 2:* 213-215.