

Nematode ecology

Gregor W. Yeates¹

Landcare Research, Private Bag 11052, Palmerston North, New Zealand, e-mail: yeatesg@landcare.cri.nz

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Summary. Plant and soil nematodes belong to the animal kingdom and thus the continued existence of each species requires that individuals obtain sufficient food to meet the requirements of the basic energy budget (consumption = respiration + wastes + body growth + reproduction). To fulfil these requirements nematodes must interact with other organisms in, and other components of, their environment. These interactions can be included under the following headings: food; temperature and moisture regimes; physical substrate; biological competition; developmental stage; assemblage (reflecting the total environment); soil or substrate processes. Although novel techniques enable new information to be obtained, it requires a problem to be defined to focus scientific enquiry. Currently, it appears that the dominant, unifying problem to be addressed in nematode ecology is that of the duration of nematode activity as temperature and moisture regimes fluctuate in real substrates. Integrating such knowledge into conceptual or mathematical models would help to provide an understanding of the migration of plant-pathogenic nematode species to roots, the dispersal and survival of entomophilic nematodes, the relation between activity and biodiversity, the importance of micro-sites, and the proportion of time microbial-feeding nematodes actively contribute to soil processes.

Key words: nematode, development, ecology, soil, temperature, moisture, activity.

A broad background is provided here to enable a wide range of nematodes to be considered in relation to ecological factors. A series of examples is used to provide a better understanding of the relationships between nematodes and their physical, chemical and biological environment.

Plant and soil nematodes belong to the animal kingdom thus the continued existence of each species requires and that individuals obtain sufficient food to meet the requirements of the basic energy budget which can be interpreted in various ways:

Consumption (ingestion) = digestible energy + faecal waste

= metabolizable energy + urinary waste + faecal waste

= respiration + production

= respiration + body growth + reproduction

To achieve these requirements there must be adequate *food* to ingest, there must be a suitable *temperature and moisture regime*, the *physical substrate* must be appropriate, *biological competition* and *predation* must not be too great, and each of these requirements must be met for each *developmental*

stage.

In most soils and sediments there is an *assemblage* of nematode species. Each of these species, by definition, interacts differently with the environment. There is a paucity of information of these interdependencies, however, the number of species present and their relative abundance reflects the *total environment*. The total environment is the product of not only changes during the year but also the long term history of the site; it is not simply that pertaining to the time of sampling.

Soil inhabiting nematodes affect the environment in which they live and their activities are an integral part of *soil processes*. Plant and soil nematodes have historically been associated is that of crop loss but they also have positive effects on soil processes.

Food

Feeding by plant-nematodes is traditionally considered as causing loss of plant yield (Fig. 1A), the loss being the sum of actual consumption by nematodes, plant reaction and secondary infection. Given the correct combination of nematode race and plant variety, the larger and more productive a plant root system the larger the population of nematodes it can support. There are many problems associated with

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understanding conceptually, or modelling mathematically, such interactions. One of the most important is the variation in soil physical, chemical and biological conditions between the rhizospheres of plants growing across a single field. Plot or field data invariably integrate micro-site variability and it is this variability that probably accounts for many of the apparently anomalous results reported by breeders and agronomists.

Studies on bacterial and fungal-feeding nematodes show marked differences in the rate of nematode reproduction on differing microbial foods. However, little is known of the factors determining these differences under culture conditions and even less is known of what occurs in the field. Examination of fungal-feeding nematode populations from various ecosystems has revealed that in some it is tylenchids and in others it is dorylaimids which are predominant although the reasons for such differences are not known. A possible explanation is that fungal-feeding dorylaimids predominate in situations where there is a more stable source of fungal hyphae.

Temperature and moisture regimes

Wallace (1963) carried out several fundamental experiments on the effect of soil moisture content on the migration of plant-feeding nematodes through soil. Soil at field capacity appears optimum for nematodes which migrate through the interstitial water. If the soil is drier migration is impeded.

'Accumulated degree days', above some threshold, have been used by entomologists to measure insect development and during the past 20 years it has been applied to plant and soil nematodes (Jones, 1975). Being an accumulation of temperature with time this measure accommodates fluctuation.

'Accumulated degree days' intrinsically appear to provide a satisfactory measure of development once a sedentary plant-feeding nematode has penetrated its host root and begun feeding. However, not all nematodes live in such a 'simple' situation. Bacterial-feeding nematodes may have to move between sites of microbial activity in order to maintain their feeding rate. Under field conditions there will be fluctuations not only in temperature but also in soil moisture. The bacterial-feeding nematode may be 'stranded' in a discontinuous water film without sufficient bacteria to maintain its development at the particular temperature. At best the nematode's development will cease or there may be a consumption of reserves which results in a loss of developmental time.

Such a situation could apply to any migratory nematode. Interpreting changes in *Pratylenchus* populations presents a problem when the nematodes

move in and out of roots depending on somewhat ill-defined conditions. The situation for bacterial-feeding nematodes can thus be generalised to include most, or all, migratory soil nematodes.

Physical substrate

Jones *et al.* (1969) provided a valuable overview of the inter-relationship between plant-feeding nematodes and soil structure. Pore neck diameter can directly limit nematode movement. However, soil moisture is a further contributory factor. Studies on microbial-feeding nematodes have shown that soil texture may protect bacteria from bacterial-feeding nematodes; however, these bacteria may be fed on by protozoa which, in turn, are fed upon by nematodes such as *Diplogaster* (Ingham *et al.*, 1985). Thus, the protection offered by pore necks is only relative.

In a recent study of nematodes in Welsh grassland soils it was found that the nematode fauna of the coarser textured soils had a higher value on Bongers' (1990) Maturity Index due to, on average, larger nematodes being present in the coarser soil.

The appearance and structure of soils in the field varies with cultivation and moisture. Soil structure is a complex of many factors and not simply an arithmetic combination of sand, silt and clay. The binding together of the primary particles by oxide or organic glues is critical in determining the pattern and size of voids available for nematodes and other biota in any soil.

Biological competition

The diverse array of nematodes in a particular soil has to co-exist and, while there may be some differentiation in food source and in optimum depth, many species have to partition the available ecological and environmental resources between them. Some of this partitioning may serve to disguise future problems in economic nematology. For example, a study of the time sequence of population development of *Heterodera*, *Meloidogyne* and *Pratylenchus* spp. in white clover roots in New Zealand pastures revealed a simple, temporal sequence (Yeates *et al.*, 1985). When breeding nematode-resistant plants the resultant consequences on nematode assemblages when using these plants needs to be identified e.g. what happens when a plant is specifically resistant to the particular *Heterodera* sp.? Also, three co-existing species of predatory mononchid show marked differences in stoma size in adults (Yeates, 1987) which probably directly affected the size of prey they could utilize or, at least, the size of pore necks through which they could recover prey organisms.

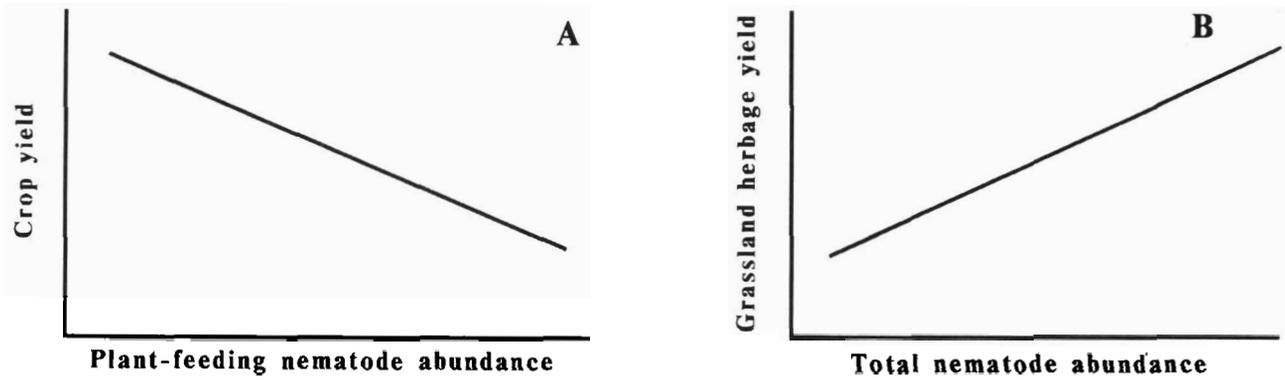


Fig. 1. A: The relationship between populations of plant-feeding nematodes and plant yield (emphasises crop loss). B: The relationship between total nematode populations and plant yield (emphasises overall contribution of nematodes to soil processes as a whole).

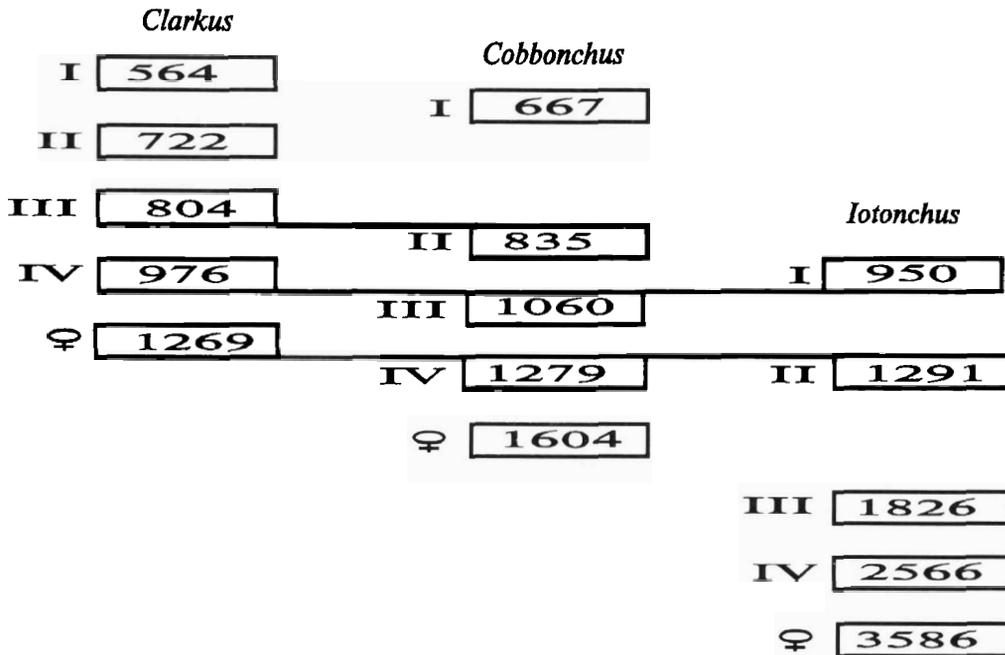


Fig. 2. The relationship between mean body length (μm) of four juvenile stages and females of three coexisting species of Mononchoidea; stages not linked differ significantly ($p < 0.05$) in length.

Developmental stage

In the Heteroderidae the requirements for each developmental stage appear well-known; stage 1 occurs within the egg, stage 2 must migrate into a root, and subsequent sedentary stages develop within roots; the cyst provides for dispersal. For parasites of invertebrates and vertebrates similar differentiation of roles and requirements for the stages can be found.

However, in many cases we are not aware of differing roles. It has long been known that tylenchids have only three juvenile stages outside the egg. In the past five years species of *Xiphinema* and *Longidorus*

with only three juvenile stages have been reported. The reason(s) why several populations within the Longidoridae apparently have 'lost' a stage are not known. Despite its direct economic importance, the literature contains virtually no information on the developmental stages of *Pratylenchus* and similar information is relatively scarce for many economically important plant parasitic nematode species.

Figure 2 gives an example of the value of determining the developmental stages of co-existing species. In the three co-existing species of mononchids mentioned above there is a differentiation in the size of the juvenile stages similar to that of the

adults (at least 5 'forms' [developmental stages] for each species). Despite there being overlap, based on simple morphometrics, between some of the forms present the various 'forms' would probably turn out to show very little competition if it were possible to add moisture or temperature parameters to discriminate the biologies of these 5 'forms'.

Assemblage reflects the total environment

Plant and soil nematode assemblages are diverse - Saly's (1975) estimate of 92 species for a Slovakian oak-hornbeam forest is small in comparison with the 154 species recently reported from an English chalk grassland (Hodda & Wanless, 1994). Conversely, *Heterodera schachtii* has been reported as representing up 94% of the nematodes in fields in Utah, USA (Thorne, 1927). The vast numbers of bacterial-feeding nematodes reported from decomposing plant material (Wasilewska *et al.*, 1981) and animal dung (Sachs, 1950) shows how soil management can influence the nematode assemblage.

Reducing the relative contribution of nematode species to an assemblage to a manageable expression, usually an index, is a challenge. The Shannon-Weiner diversity index (H') is widely applied to nematodes. Also, Bongers (1990) 'nematode maturity index' is of considerable value when assessing the effects of pollution on nematode assemblages. However, recent work in Welsh grasslands indicates that management regimes may greatly influence particular feeding groups and this may be useful when investigating the sustainability of various land uses.

Soil processes

Originally it was accepted that increasing nematode populations were directly related to reducing crop yields (Fig. 1A). Subsequently, it has been shown that a positive relationship exists between total nematode abundance and plant yield (Fig. 1B). The earlier relationship involved the occurrence only of the 'pest' species whereas currently interactions between the 'free-living' nematodes and other soil organisms are included in the relationship between nematodes and plant yield. The influence of nematodes in increasing the turnover of soil bacteria and fungi and consequently the cycling of plant nutrients is integral to this new approach (Wardle *et al.*, 1993; Yeates *et al.*, 1993).

Discovering such a critical role for nematodes in soil processes emphasises the current level of understanding of basic nematode ecology. More recently, however, fundamental studies on life histories of bacterial-feeding nematodes have begun to be reported (Ferris *et al.*, 1995). A further recent advance is that of relating populations of predatory

mononchids to bacterial-feeding cephalobids and thus to soil bacterial populations and nutrient cycling (Yeates & Wardle, 1996). It appears that this mechanism has greater benefits for plant and crop yield than does any predation on 'plant-pathogenic' nematodes.

The future

Many new techniques which can be applied to better understand ecological interactions of nematodes have become available. Defining a problem and then using suitable techniques to solve it provides scientific advance to knowledge. With the gradual increase of understanding in all the traditional areas of nematode ecology in its broadest sense the principal problem which needs to be addressed is **determining the duration of nematode activity as temperature and moisture fluctuate in real soils**. This would give better information on migration activity towards roots; more information on dispersal and survival of entomophilic nematodes; a better ability to relate activity to diversity with nematodes as bioindicators; with marine nematodes, a better appreciation of short-scale variation in substrate texture; and insight on the proportion of the time microbial-feeding nematodes actively contribute to soil processes.

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Yeates G.W. Экология нематод.

Резюме. Обитающие в растениях и почве нематоды относятся к царству животных, а потому для пополнения энергетического баланса (потребление = дыхание + отходы жизнедеятельности + рост тела + размножение) каждый вид нуждается в поступлении достаточного количества пищи. Для обеспечения этого баланса нематоды должны взаимодействовать с другими организмами и другими компонентами среды. По своему типу эти взаимодействия могут быть отнесены к нескольким большим классам: пища, температурный и влажностный режимы, физические особенности субстрата, биологическая конкуренция, стадия развития, показатели биологического разнообразия сообщества, динамика процессов в почве или другом субстрате. Хотя с использованием новой техники становится возможным привлечение ранее недоступных данных, очевидна и необходимость четкого определения самой сути проблемы, что сфокусировало бы научный поиск. Представляется, что доминантной проблемой, стоящей в настоящее время перед экологией нематод, является оценка параметров жизнедеятельности нематод на фоне флуктуаций температурного и влажностного режимов в реальных субстратах. Интеграция уже имеющихся по этой теме данных в концептуальные или математические модели способствовала бы, вероятно, более совершенному пониманию миграций фитопатогенных нематод к корням, распространения и выживания энтомофильных нематод, связи между активностью и биоразнообразием, важности микрониз и микрораспределений и такого фактора, как продолжительность активного питания нематод микроорганизмами почвы.