INTER-RELATIONSHIPS BETWEEN NEMATODE AND PLANT COMMUNITIES IN AGRICULTURAL ECOSYSTEMS

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ABSTRACT


In a consideration of nematode and plant inter-relationships, five nematode trophic groups must be considered: microbivores, fungivores, parasites of higher plants, predators, and omnivores. In uncultivated areas, such as deciduous forests, many species of nematodes are likely to be present (often 100 to 200 species in temperate areas) with the trophic structure stable and dependent on topographic, edaphic, vegetative and climatic factors that characterize the habitat. When formerly uncultivated lands are placed in cultivation, some species build up, and other members of the nematode community decline and even disappear. Soils of perennial crops may have a nematode species diversity comparable to soils of undisturbed areas. Soils planted to annual crops, however, usually have a low species diversity although nematode densities may be high during certain seasons of the year. Nematode community structure depends on a number of factors including soil type and crop grown, and may shift from year to year depending on cropping history. In the tropics monocultures and their subsequent effect on nematode communities are an even greater departure from the natural state than they are in temperate zones. Primary control strategies for nematodes have included the use of nematicides and resistant varieties. Also used are crop rotation, summer or winter fallow, trap cropping, and other techniques. New strategies must be developed by which all biological and physical aspects of the feedback system can be managed.

INTRODUCTION

A popular expression in the vocabulary of modern agriculture is the phrase, "integrated pest management". In earlier years this expression meant simply a degree of cooperation between entomologists and plant pathologists (and later, perhaps, weed control experts as well), to assure that the needed agricultural chemicals were used in a complementary and economical fashion. Recently, however, the expression has acquired a more sophisticated and expanded meaning to imply the coordinated use of all possible control methods for pests, including biological, environmental, and cultural methods, within management techniques directed toward the fullest utilization of natural
pest mortality and other suppressive factors in any given agro-ecosystem (Chiarappa et al., 1972).

This kind of thinking has led to a feeling of "ecosystem awareness" among agriculturists which has drawn them toward the thinking of theoretical biologists. The climate, soils, bacteria, fungi, higher plants, and animals of all kinds, which occur together at any particular place comprise an ecosystem. The biotic components of an ecosystem, or all the organisms taken together, comprise an ecological community (Pianka, 1974). The relationships between communities of plants, and the communities of nematodes in the soils around those plants are the focus of the present paper. Because current thinking emphasizes the exploitation and utilization of factors present within natural ecosystems, it would be well to review what we know of relationships between nematode and plant communities in natural, or relatively undisturbed, ecosystems before assessing our knowledge with respect to agricultural systems, in temperate and tropical areas. Finally, the outlook for control of nematode pests by "integrated management" based on a knowledge of ecological communities must be examined.

Pianka (1974) points out that the concept of a natural community is an abstraction, because natural communities nearly always grade into each other, and are seldom clear-cut entities. The community can be represented by a food web, comprised of food chains, each of which represents a single pathway up the food web. As is the case with all plant and animal communities, the green plants constitute the producers or autotrophs. The nematodes are all consumers or heterotrophs. Contrary to much popular belief, not all soil nematodes feed directly on green plants — many nematodes feed on bacteria and fungi, the decomposers within the system which break down plant and animal material, returning nutrients to the soil. Other kinds of nematodes feed on small soil fauna, including other kinds of nematodes (Fig.1). In such an ecosystem there may be several levels of trophic activity. It is important to remember that the ability of each individual to perpetuate itself is determined in part by its relationships to all of the other organisms within the community (Pianka, 1974).

Nematologists of Russia and the eastern European countries have developed a trophic classification of nematodes, which can be related to the usual systematic classifications; and they have slanted their thinking for some years toward a consideration of nematode and plant community inter-relationships (Paramonov, 1962; Wasilewska, 1967 b). Paramonov (1962) assumes that in the soil ecosystem the main source of nematode nutrition, directly or indirectly, is the plant root system, and this accounts for the fact that most nematodes occur in the plant rhizosphere. He suggests that a main source of nematode nutrition is the soil fungi, a view not generally held in other parts of the world (Yeates, 1973). Moreover, Paramonov and his followers suggest that a great many more nematode species than those usually thought of as plant parasites coexist in plant organs, forming complex biocoenoses.

This school of thought defined four ecological groups which they termed:
Fig. 1. Diagram showing relationships between nematodes and other soil microfauna and flora. Arrows point to prey in each instance.

(1) the eusaprobionts (or eusaprobionts) feeding on bacteria or fungi (Wasilewska, 1967 b); (2) the dyssaprobionts (Paramonov, 1962) or hemisaprobionts (Wasilewska, 1967 b), feeding partly as eusaprobionts and partly as parasites of higher plants; (3) the pararhizobionts (Paramonov, 1962) with mixed food habits; and (4) the plant parasites. Wasilewska (1971 b) simplified the terminology greatly by naming five trophic groups similar to the groupings used by various western authors (e.g. Yeates, 1971). Wasilewska's (1971 b) groups and the major taxa she included are: (1) the microbivores, which include the Rhabditidae, Diplogasteridae (many), Panagrolaimidae, Cephalobidae and many other taxa; (2) the fungivores, which include principally the fungus-feeding members of the Tylenchida; (3) the parasites of higher plants which include most Tylenchida and some Dorylaimida; (4) the omnivores, which include most of the Dorylaimida plus certain of the Enoplida and other taxa; and (5) the predators including Monochida, Seinura, and various dorylaimids known to be predators.

NEMATODE COMMUNITIES IN RELATIVELY UNDISTURBED OR NATURAL ECOSYSTEMS

Temperate areas

The pioneer work on nematode communities which inhabit uncultivated areas was that of Overgaard Nielsen (1949), and his findings are still being studied closely by present day workers. Nielsen surveyed the Danish nematode fauna both qualitatively and quantitatively from various localities and a variety of soils. His total numbers ranged from 175 000 to 20 000 000 m⁻² soil to a depth of 5–10 cm with a fresh weight of 0.7–17.8 g/m². The highest numbers were found in grass fields, and the lowest in extremely dry habitats. He concluded that nematodes probably play an important role in acting as a reservoir of easily available nutrients, which may be mobilized at their death. On account of their rapid succession of generations, the organic matter of
nematodes is returned to the soil several times a year. Nielsen calculated oxygen consumption at 16°C to be about 600–1 500 cc/kg/h. Because nematodes are essentially aquatic (living in a film of water), they use little energy for locomotion, and thus invest a greater proportion of their assimilated energy in producing new biomass, than do higher animals (Nielsen, 1949, 1967).

A recent study has been carried out in the authors' laboratory (Johnson et al., 1972, 1973, 1974) on nematode community structure in 18 Indiana (U.S.A.) mixed hardwood stands of varying composition, soils, physiography, and past management practices. During a period of sampling which extended over two years, a total of 175 species representing eight orders of nematodes were found in the soils. The nematode species composition in these sites of close geographical proximity showed a high degree of similarity, with 18 species occurring at all 18 sites, and approximately half the total species occurring in more than 50% of the sites. Several techniques were utilized to study the intersite relationships among the nematode communities, including a resemblance equation and community ordination. Both techniques showed good correlations of clusters of sites based on nematode species with dominant tree species and major soil types. The ordination technique produced clusters that correlated well with groupings based on forest types and successional stages of tree communities at the sites (Fig.2) and also with groups based on well-defined soil types. No single edaphic factor could adequately explain the relationships, but leaf litter, depth of the "A" horizon, pH, and kg of phosphorus and potassium/ha showed a general relationship when compared to the sequential position of each site on the main axis of the ordination plot. Since these factors are directly related to the topography, soil type and tree community, it is unlikely that any one factor would have a dominating influence over the whole community. Probably the community responds to the many factors that together characterize the habitat. Single features that are by themselves major characteristics of the habitat may show closer relationships, as indicated by the relationship between the nematode communities and the tree communities and soil types.

Disturbances within a habitat may have a marked influence on the nematode community, depending on the degree of the disturbance. In the study cited above, a site which had undergone heavy grazing, and a second site which had been completely cut over and permitted to grow back to an even-aged stand of black locust, were the most disturbed of the sites and had apparently undergone striking changes in their community structure, as evidenced by the dissimilarity between these two sites and all other sites in the ordination.

Ordination of the nematodes by taxonomic group (Johnson et al., 1974) revealed that the disturbances at some sites had drastically affected the dorylaimid fauna (the omnivores of Wasilewska, 1971 b), whereas there was less effect of site disturbance on the tylenchid fauna (the plant parasites and facultative plant parasites which are also fungivores). When nematodes of the remaining six orders were combined in an ordination, it was not possible to
correlate the position of the sites in this ordination with known physical or floristic factors. Undoubtedly, the many species represented in these diverse orders (principally the microbivores and predators) do not respond similarly to the same environmental factors. Many of them are bacterial feeders that fluctuate radically in numbers depending on available food material. An ordination which utilized the biomass of all nematode individuals was very similar to the ordination of the dorylaimid nematodes, indicating the influence of this group in all considerations based on biomass. Because dorylaimid nematodes as a group are much more sensitive to disturbances in the forest habitats than are tylenchid nematodes, they are valuable as indicators of ecological change in relatively natural habitats.

A mean number of $1.8 \times 10^6$ nematodes m$^{-2}$ was found in these hardwood stands. At the highly disturbed, cut over, black locust site tylenchids ac-
counted for 56% of the nematode population, and at one of the least
disturbed climax beech-sugar maple sites, dorylaimids were 35% of the total,
and tylenchids only 30%. The percentage of the total population comprised
of individuals of the other six orders (microbivores and some of the preda-
tors) varied greatly among the undisturbed sites from a high of 54% to a low
of 26%.

Further information has been collected on nematode communities of the
eastern deciduous forests of the U.S. (Ferris, 1972; Ausmus et al., 1974).
Monthly samples in a mesic hardwood stand near Oak Ridge, Tenn., ranged
from $1.1 \times 10^6$ to $6.9 \times 10^6$ nematodes/m$^2$ of soil to a depth of 15 cm.
Biomass (dw) ranged from 0.5 to 2.1 g/m$^2$ (dw calculated at 25% fw). The
proportions of the nematode biomass in several trophic groups were: 39%
primary consumers (the plant parasites plus some of the omnivores of
Wasilewska, 1971 b); 42% predators; 16% bacterial feeders (or microbivores);
and 3% fungus feeders. A comparison of these values with those obtained over
a 2-year period in Indiana (U.S.A.) deciduous woodlots is in Table I. Despite
the wide differences in absolute values for both density and biomass, the
proportions belonging to each trophic group are remarkably similar. Based on
annual fluxes of carbon, nitrogen, and potassium from roots to consumers,
and radio-tracer techniques to estimate nematode root consumption, Ausmus
et al. (1974) concluded from the Oak Ridge data that the phytophagous
nematodes consumed 8.5% of the root pool, more than any other group of
soil invertebrates found in these soils.

A recent study of a beech forest (Yeates, 1972) adds to the information
of Nielsen on nematodes of Danish soils. Yeates found a total of 75 species
and a mean number of individuals of $1 \times 10^6$ m$^{-2}$, with an average biomass
(dw) of 0.28 g/m$^2$ (dw calculated at 58.5% fw). Yuen (1966) recovered 62
species from a regenerated woodland in England; as compared to 65 species
found by Bassus (1962) in deciduous forests of central Germany.

**TABLE I**

<table>
<thead>
<tr>
<th>Percentage of nematode biomass belonging to the different trophic groups in deciduous forest habitats, Oak Ridge, Tenn. and Tippecanoe County, Ind. (U.S.A.). (Data given based on means for all samples.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak Ridge, Tenn.</td>
</tr>
<tr>
<td>Primary consumers</td>
</tr>
<tr>
<td>Fungal feeders</td>
</tr>
<tr>
<td>Bacterial feeders</td>
</tr>
<tr>
<td>Predators</td>
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<tr>
<td>Total biomass (range)</td>
</tr>
<tr>
<td>Total biomass (average)</td>
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<tr>
<td>Total density (range)</td>
</tr>
<tr>
<td>Total density (average)</td>
</tr>
</tbody>
</table>
Nematode communities of the forested sand dunes of the Kampinos forest in Poland, covered with xerophilous vegetation and scanty tree stands, were found by Wasilewska (1970, 1971 a) to have 107 species. Based on six samplings during 1 year, she found a range of 0.5—7 × 10⁶ m⁻² individuals, with a fresh weight of 0.2—0.7 g/m². More nematodes and a greater biomass were in mixed forest than in dry pine forest. In numbers, the microbivorous nematodes were highest, followed by the fungivorous, with the plant parasites third. If considered from the standpoint of biomass, the omnivorous group (chiefly Dorylaimida) were at the top, followed by the microbivores. She found two peaks in numbers and biomass, one in spring and one in autumn, and concluded that most species overwinter as juveniles. There was some difference among the trophic groups with respect to seasonal peaks. The microbivores fluctuated greatly and reached relatively high numbers and biomass, even in winter. The fungivores and higher plant parasites reached their maximum levels (in numbers) in the spring. Wasilewska (1971 a) found that as plant succession progressed, the numbers and biomass of the nematodes increased; and that with an increase in plant succession, the percentage of total numbers and biomass of the microbivorous groups increased with a concomitant decrease in the omnivorous group. Since the omnivores of Wasilewska correspond to the order Dorylaimida, this appears to be an important difference between her data on forested dunes and our data from U.S. deciduous forests, where dorylaimid numbers are greatest in undisturbed climax areas. She further found that the percentage of obligate parasites of higher plants decreased, and the numbers of facultative parasites increased as plant cover became more luxuriant and the habitat more complex.

In a study of complete nematode communities in three uncultivated field plots with different soil types in southern Manitoba (Canada), Kimpinski and Welch (1971) found nematodes more abundant in clay soils than in sand. They did not attribute this difference to differences in soil texture, however, but rather to a combination of factors such as lower moisture content in sand and possibly also a deficiency in nutrients, resulting in a reduced amount of plant material, which leads to a reduction in numbers of nematodes of all trophic categories.

Schmitt (1973) found that seasonal fluctuations of plant parasitic nematodes in an Iowa prairie exhibited similar patterns for similar habitats. In well-drained areas, the populations were high in the early spring, declined until midsummer, and increased by fall. Some of the species of plant parasitic nematodes overwintered as eggs, whereas others overwintered as vermiform nematodes. One species, *Helicotylenchus hydrophilus*, overwinters as eggs in well-drained areas, but as vermiform nematodes in pothole centers, suggesting that the habits and activities of nematodes can be manipulated by slight changes in the environment.
Practically no nematode data exist for uncultivated soils of tropical areas, although a considerable literature deals with surveys of parasitic species in cultivated soils. Coleman (1970) estimated the numbers and biomass of litter and soil nematodes in a Puerto Rican rain forest (El Verde) to be a maximum of $2 \times 10^4$ individuals/m$^2$, with an average biomass of 8–10 mg/m$^2$ (dw). These figures are much lower than figures for temperate mainland areas. Coleman (1970) commented that numbers of soil microarthropods are also lower per unit area in El Verde rain forest than in many temperate areas. According to Janzen (1973), tropical islands are known to have fewer insect species and lower biomass than mainland areas.

NEMATODE COMMUNITIES IN TEMPERATE AGROECOSYSTEMS

It has become apparent in recent years that many species of nematodes are very widespread, but present in natural communities in very low concentrations (Oostenbrink, 1966; Brodie et al., 1970). When lands are cleared and placed in agricultural production, certain species build up, depending on the crop sequence, whereas other members of the nematode community decline in numbers and perhaps even disappear. Oostenbrink (1966) has generalized that every root in the soil probably can serve as a host for some nematode species present, and thus nematodes must be considered an overall factor in crop husbandry and soil productivity. Paramonov (1962) expressed a similar view and lamented that some experts maintain that nematodes in cultivated soils are of no practical problem, simply because they do not observe them feeding as they do insects. Oostenbrink (1966) has compiled several reasons for the polyspecific communities of plant parasitic nematodes that are in nearly every cultivated field. An important factor is the efficiency with which man disperses nematodes as he moves them around with soil and plant parts. A second factor is the polyphagy of many plant parasitic species. A third factor is their great persistence. The overwintering habits of nematodes are quite different from those of many agricultural insects. Even in temperate climates there is usually a dense population of parasitic nematodes ready in the early spring to attack crops. Moreover, many investigators have shown that many nematode species can persist, at least in small numbers, over long periods of time in the absence of a favorable host crop, and in fallow soil. One seldom finds evidence of a complete collapse of populations of plant parasitic nematodes in agricultural ecosystems (Oostenbrink, 1966). A fourth factor cited by Oostenbrink, and a very interesting one, is the evidence that interspecific competition is not great among nematodes. Oostenbrink cites the many instances in which several species of Pratylenchus (lesion nematodes) are found to occur together in crop soils, and questions the validity for nematodes of Gause’s rule of competitive exclusion, which holds that two species with identical ecologies cannot live together. Since data are accumulating
which indicate that closely related nematode species are often found together in the same soil (Mukhopadhyaya and Prasad, 1969; Jones, 1972 b) and there is often great species diversity in nematode communities, Yeates (1970) is probably correct in his statement that this difference between nematode communities and communities of other soil animals probably reflects their small size and ecological specialization. The relevant question would be to ask how much ecological overlap can two similar nematode species tolerate and still co-exist (Pianka, 1974).

A bulging literature exists which describes population fluctuations over months or years of certain plant parasitic nematode species in fields planted to specific crop plants (Oostenbrink, 1966; Good, 1968; Brodie et al., 1969; Seinhorst, 1970; Ferris and Bernard, 1971 a; Nusbaum and Barker, 1971). The data are especially numerous for those nematode-crop interactions which result in great economic losses. Studies which include complete nematode communities in cultivated fields are much less numerous.

**Perennial crops**

A few studies on complete nematode communities of perennial crop soils are of particular interest. Such crops share certain characteristics of natural areas (they are not subject to the frequent disturbance of plowing and fitting the land) and characteristics of the usual agricultural ecosystem (usually a monoculture). Our data on the black locust stand cited above might be in this category. It will be recalled that this near-monoculture had the highest percentage of tylenchid nematodes of any of the sites studied. Studies in natural prairies such as that of Schmitt (1973) cited above, are similarly interesting.

Wasilewska (1967 a, b and c) reported on nematodes in two alfalfa fields in Poland, in which she found a total of 137 species in 34 genera, a figure which is comparable to the species count in natural areas such as our U.S. hardwood stands. Two peaks in soil populations occurred, one in spring or early summer and another in autumn. The lowest abundance of soil nematodes occurred in summer and winter, which she attributed to low temperatures in winter and high rainfall in the summer (Wasilewska, 1967 b).

She summarized her data on community structure in younger and older stands as follows (Wasilewska, 1967 b). In the younger crop, parasitic species plus a group of microbivores predominated in the soil. In the older stand, a group of microbivores and one facultative parasite were the soil predominants. The total abundance of nematodes in the soil increased slightly with consecutive years of culture. The number of species and also the number of predominants increased with the age of the stand. She noted that the percentages of the most numerous ecological groups were similar in the several habitats, although the absolute densities varied greatly, suggesting to her that reciprocal interactions occurred among the ecological groups of nematodes.
Annual crops

**Seasonal fluctuations.** — After following seasonal variations in components of plant parasitic nematode communities for many years in soils of corn and soybean fields, and of crops grown in rotation with soybeans, in midwest U.S.A., we find that most ectoparasitic species (*Helicotylenchus*, *Paratylenchus*, and *Tylenchorhynchus*, Fig.3) increase unevenly during a growing season to reach a peak soil population in late summer. It seems to be generally true that soil populations of ectoparasitic nematodes fluctuate mainly in response to the development of host plants present (Oostenbrink, 1966; Kimpinski and Welch, 1971). In the presence of a host crop, a soil population may rise to a high level, fall back to a much lower level within weeks after the harvest has occurred, and then decline only slowly until the next growing season (Simons, 1973). In our fields, the ectoparasitic species *Paratylenchus projectus* undergoes an interesting shift in proportions of active stage and resting-stage forms during a growing season. In the spring, most individuals of a population are in a resistant pre-adult resting form. By midseason the proportion has changed to favor the active stage; and by fall the resting stage is again predominant (Fig.4).

As the growing season progresses, examination of soil samples for endoparasitic nematodes such as *Pratylenchus* spp. may reveal a decline in numbers

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**Fig.3.** Seasonal changes of four genera of plant-parasitic nematodes in soybean fields, Urbana, Ill. (U.S.A.), (based on data for 3 years, two fields sampled each year). After Ferris and Bernard (1961).

**Fig.4.** Seasonal changes of *Paratylenchus projectus* in pre-adult and adult stages in check and two fumigated areas, Urbana, Ill. (U.S.A.). After Ferris and Bernard (1961).
(Fig. 3). We have contended that this apparent decline occurs as more nematodes enter roots, and that the total number present in a field is, in fact, increasing. As roots disintegrate during fall and winter months, these endoparasitic nematodes return to the soil, and this accounts for the large numbers usually found in the early spring months.

**Effect of soil type.** — A considerable body of information indicates that soil type may be very important for determining community composition of nematodes in a field, although it is recognized that this effect may result from a combination of factors related to soil type, such as moisture differences in different soil types (Wallace, 1963; Winslow, 1964; Geraert, 1967; Kable and Mai, 1968; Ferris and Bernard, 1971 b; Ferris et al., 1971; Norton et al., 1971; Kimpinski and Welch, 1971; Upadhyay et al., 1972; Simons, 1973). In our field crop rotation fields during a 5-year droughty period, *Helicotylenchus pseudorobustus* was not a predominant in light sandy soils (Fig. 5A), but was a predominant in heavier soils (Fig. 5B). During the same period of time, *Paratylenchus projectus* was present in low numbers in the

![Fig. 5. Relative abundance polygons showing nematodes recovered/473 cc soil in individual blocks of different soils, Urbana, Ill. (U.S.A.). Letters on horizontal axes show crop sequence (C, corn; S, soybeans; W, wheat; F, forage). Blocks in a given crop may be compared by reading vertically. Numbers of nematodes for each block in a given year may be compared by reading along diagonals. A, *Helicotylenchus pseudorobustus* in Urbana—Proctor silt loam blocks designated 1, 2, 3, and 4. B, *H. pseudorobustus* in Hartshurg—Illiopolis silty clay loam blocks designated 1, 2, and 3. C, *Paratylenchus projectus* in Toledo silt loam blocks designated 1, 2, 3, and 4. D, *P. projectus* in Urbana—Drummer silty clay loam blocks designated 1, 2, 3, and 4. After Ferris and Bernard (1971 b).]
heavy soils (Fig.5D) and was a predominant in the light-colored soils (Fig.5C). The facility (mentioned above) of *P. projectus* for remaining in the pre-adult resting stage during periods of adversity is probably a factor in its ability to thrive in drouthy areas.

Analysis by community ordination of the plant parasitic nematode communities at 14 soybean breeding locations maintained in Indiana and Illinois showed that the community structure tends to be similar on the dark-colored, highly productive soils throughout the two-state region. On lighter soils the community structures differ somewhat from the darker soils and from each other, possibly reflecting the more diverse nature of the lighter soils (Fig.6).

Norton et al. (1971) also found a correlation between soil type and popu-

![Fig.6. Three-dimensional model of ordination based on total density of plant parasitic species at 14 study sites in Illinois and Indiana (U.S.A.) soybean fields. Dark, highly productive soils are represented mainly by those sites clustered together at upper part of figure. After Ferris et al. (1971).](image-url)
lations of certain nematode species in Iowa soybeans, with *H. pseudorobustus* better adapted to the heavier soils. The highest percentages of Dorylaimida (excluding *Xiphinema americanum*) were found at soil texture extremes (i.e. clays and loamy sands). This suggested that the Dorylaimida as a group may thrive (or at least survive) under a wide diversity of moisture conditions. We have found *Xiphinema americanum* to be less sensitive than other parasitic species to soil moisture differences within the range provided by our experimental fields.

**Effect of crop grown.** — Within each soil type, the crop species grown affects community structure. It has been demonstrated that certain aggregations of species of plant parasitic nematodes frequently occur together; and the data indicate that population shifts occur among these species, which depend on the crop in the soil at any given time. We frequently found shifts in components of the *Pratylenchus* community during a 5-year period of field crop rotation sequences. In one field *P. scribneri* was the predominant *Pratylenchus* species during the first year of sampling when the field was planted to a forage mixture. 2 years later, after 2 years of corn, *P. hexincisus* predominated 10 : 1 over *P. scribneri*. Another shift occurred the next year when the two were co-predominants in the same soil planted to soybeans (Ferris and Bernard, 1967).

Some researchers have found no consistent correlation between nematode community structure and cropping history. Norton et al. (1971) concluded from field experiments that diversity of physical habitats, coupled with diverse cropping systems, probably masked any effects that might have been observed under more uniform conditions. They did find a positive correlation of facultative plant parasites (Tylenchinae—Psilenchinae) plus microbivores with percent organic matter of the soil, a reasonable finding as these groups are thought to feed on bacteria and/or fungi.

Wasilewska (1969) has provided some interesting data regarding nematode community changes when an annual crop (potato) follows a perennial crop (alfalfa) in Poland. Although the species composition did not differ, the percentage of Dorylaimida in the total population was greater in alfalfa; whereas the percentage of microbivores was greater in potatoes.

A comparison of typical proportions of nematode groups making up the total nematode community found in a variety of habitats of Indiana and Illinois (U.S.A.) is given in Table II. The Dorylaimida correspond to the omnivores of Wasilewska; the Tylenchida are the plant parasites (largely); and the third column includes the microbivores, plus some predators, particularly in the woodland habitats. In general, higher total counts were found in natural hardwood stands than in well-managed highly productive cultivated fields. The number of species likewise is higher in the uncultivated areas. Of the uncultivated areas, the cut-over black locust stand is the most similar to the monocultures of the cultivated fields. It should be noted that sizeable percentages of microbivores were present in all of the productive soybean fields. Poor growth was noted only in the field in which 96% of the nematodes were in the plant parasitic group.
TABLE II

Densities and percentage of individuals belonging to major taxonomic groupings in a variety of Indiana and Illinois (U.S.A.) habitats. See text for discussion of habitats

<table>
<thead>
<tr>
<th>Site</th>
<th>No. spp.</th>
<th>Total count/m²</th>
<th>% Dorylaimida</th>
<th>% Tylenchida</th>
<th>% other</th>
<th>Characteristics of habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stewart beech</td>
<td>86</td>
<td>2 020 000</td>
<td>33</td>
<td>30</td>
<td>37</td>
<td>Natural woodland</td>
</tr>
<tr>
<td>Livestock woods</td>
<td>66</td>
<td>2 203 740</td>
<td>4</td>
<td>44</td>
<td>52</td>
<td>Grazed woodland</td>
</tr>
<tr>
<td>Cut-over black locust wood lot Soybeans</td>
<td>58</td>
<td>1 365 390</td>
<td>5</td>
<td>56</td>
<td>39</td>
<td>Monoculture (near)</td>
</tr>
<tr>
<td>Greenfield Soybeans</td>
<td>19</td>
<td>717 660</td>
<td>12</td>
<td>58</td>
<td>30</td>
<td>Highly productive</td>
</tr>
<tr>
<td>Bluffton Soybeans</td>
<td>21</td>
<td>415 530</td>
<td>2</td>
<td>28</td>
<td>70</td>
<td>Highly productive</td>
</tr>
<tr>
<td>Reiser's Soybeans</td>
<td>19</td>
<td>1 768 770</td>
<td>6</td>
<td>68</td>
<td>26</td>
<td>Champion field</td>
</tr>
<tr>
<td>Carrollton</td>
<td>12</td>
<td>4 210 380</td>
<td>0.6</td>
<td>96</td>
<td>3.4</td>
<td>Very poor growth</td>
</tr>
</tbody>
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NEMATODE COMMUNITIES IN TROPICAL AGROECOSYSTEMS

Although limited investigation has been made of complete nematode communities of any tropical areas, it is evident from work with other organisms that forces different from those of temperate areas are at work in the tropics affecting interrelationships of organisms in cultivated ecosystems. Janzen (1973) has summarized the problems in managing agricultural pest communities. The kinds of pest communities will vary in important ways with elevation and location. Lowland areas may be seasonal or aseasonal, with a difference in the intensity and effects of the dry season. In all lowland areas, year round warmth results in rapid breakdown of litter and a leaching of soil nutrients. It is reasonable to assume that in many such areas, nematodes are able to reproduce the year around, if sustenance is available. It is known that even where there is a severe dry season, many insects persist as adults, and this is likely true of nematodes as well. Tropical lowlands support a complex natural biological system, and it is known from other groups of organisms that these complex systems are easily perturbed and cannot be easily reconstituted. Long distances in space and time between conspecific plants undoubtedly prevent large buildups of single species of plant parasitic nematodes just as they do of other plant pests. This situation would aid in keeping the nematode communities diverse. Thus monocultures and their subsequent effect on nematode communities are a much greater departure from the normal in the tropics than they are in temperate zones. The upper elevations of the tropics, where cooler weather slows down development, may be expected to
have different kinds of nematode communities than the lowland areas. Janzen (1973) noted for insect communities more species and a higher biomass at 500 to 1,000' elevation than in the lowlands. Marginal farmlands on very poor soils in the tropics probably support still different types of nematode communities.

Oostenbrink (1966) indicated that much lower nematode densities were found in arable soils of Venezuela at the end of the dry season than were customarily found in soils of The Netherlands. Smart and Perry (1968) suggest that densities of plant parasitic nematodes are generally lower in tropical areas than in northern temperate areas, although greater crop damage results in the warmer climates for a variety of reasons.

It has been customary in the shifting agriculture of the tropics to leave fields fallow after several years of cultivation. Although the usual explanation is exhaustion of nutrients, Janzen (1973) suggests that the real cause is lowered yield, probably as a result of increased pest populations of all kinds. He cites the magnificent stands of native weeds which grow in such abandoned fields as evidence for the supposition. According to Janzen, the literature of the tropics is replete with fertilizer trials, but with almost no information on the dynamics of pest faunas.

In a report on changes in plant parasitic nematode populations on newly cleared land in the Nigerian tropics, Caveness (1972) noted that the traditional farming system of shifting cultivation permits small numbers of plant parasitic nematodes to survive in small numbers in abandoned land. When modern farming practices are introduced into these areas, certain of these plant parasitic species, rarely found prior to cropping, may increase to become large percentages of the total population. Other species eventually disappear from the cultivated soils. Brodie et al. (1970) recommend selection and rotation of crop plants with varying abilities to support different species of plant parasitic nematodes to delay build-up to damaging levels in newly cleared agricultural lands of subtropical and tropical regions.

Kermarrec and LaMassese (1972) have worked recently on certain aspects of the dynamics of nematode populations in the French West Indies. They derived a statistic, "R", which is a ratio of the total nematode population to the population of phytophagous tylenchids. They found that when sugar cane follows a natural savannah, R decreases approaching 1. The internal equilibrium of the nematode community structure is destroyed by uprooting and replanting.

APPLICATION OF KNOWLEDGE OF NEMATODE COMMUNITIES TO INTEGRATED PEST MANAGEMENT CONCEPTS

One school of modern ecological thought, stemming largely from the work of MacArthur, has suggested that the stability of populations within a community should increase both with the number of trophic links between species and with the equitability of energy flow up the various food chains. Thus communities with many trophic links provide greater possibilities for
checks and balances to operate (Pianka, 1974). But argument still exists among ecologists as to whether community diversity necessarily leads to population stability.

It seems clear from many lines of work that the animal populations in natural (uncultivated) areas, at least in temperate regions, are relatively stable (Pimentel, 1969). The same species are usually found in the same habitats at the same seasons for many years in succession; and this seems to be generally true also for nematode populations. According to Pimentel (1969), with many animal communities, individuals of the species making up the community reoccur in subsequent seasons in numbers which are of the same order of magnitude as previously found, which is again generally true for nematodes if we exclude the microbivores (Johnson et al., 1974; Ferris et al., 1972). In natural areas, most species are rare in relative numbers, with few dominants. The interactions between species result in genetic feedback mechanisms which form a fully responsive, evolving system (Pimentel, 1969). Such a living system responds to changes within the community.

Pianka (1974) reminds us that in nature resources are not wasted. When life supports for most species are destroyed, the species which do remain generally expand their activities and exploit all the available resources. This is what is likely to happen in agricultural monocultures, which clearly are unstable systems. Once a pest population gets started, it can increase to large numbers in the absence of competing species, and spread to additional areas (Pianka, 1974).

Current strategies for control

To combat the effects of large populations of plant parasitic nematodes in monocultures, nematologists have increasingly turned to the use of pesticides in crops where their use is economically feasible; or to the use of resistant varieties when these are available. Nematicides often give dramatic reductions in nematode populations and in some cases the effect is comparatively long lasting. Data in Fig. 7 show soil and root populations in muck soils of Indiana (U.S.A.) following fumigation to control *Pratylenchus penetrans*, a species very injurious to onions, and the predominant member of the nematode community in these fields. Despite the fact that both crops used in the rotation are good hosts for the species, numbers remained low for a total of 3 years. Consistent periodic fumigation of these muck soil fields has proved to be an effective and economic control in this instance.

It often happens, however, that pest populations recover from the pesticide treatment soon after the application. When this occurs, the pest, now freed from competitive predators and parasites (also killed by the pesticide treatment) may expand more rapidly than was possible before the treatment. The data of Fig. 8 illustrate such an occurrence. Following soil treatment all test blocks were accidentally flooded during unusually heavy rainfall, and reinestation of the treated areas occurred. The target species began to build
up in them, and in one of the treated areas the final population exceeded that of the check blocks, where the population had fallen as the result of natural control by an unknown agent.

An enormous quantity of data has accumulated during the past 30 years showing fluctuations of target economically important nematode species in fumigated and unfumigated fields planted to susceptible or resistant crop varieties. Perhaps the most extensive work has been carried out with the potato cyst nematode, an important pest nematode indigenous to the Andes Mountains of South America and well established throughout Europe. In reviewing the work on this species in Great Britain, Jones (1972a) emphasized that the relationship between nematode parasite and host is like that between predator and prey, and that nematode numbers oscillate when potatoes are grown every year. With this particular species the oscillations are dampened because the cysts retain eggs that fail to hatch immediately. The graph of Fig.9 shows that when fumigants are used with susceptible varieties the remaining individuals multiply greatly and result in peak populations larger than those found in unfumigated fields. The use of resistant varieties is effective in keeping down populations, but may result in a genetic change in the nematode species as a result of selection by the resistant potato variety. Data from many sources indicate that other cyst formers behave in much the same way. In an Indiana (U.S.A.) test, cyst counts of soybean cyst nematode at the end of a single growing season were the same in fumigated and non-fumigated field plots where a susceptible soybean variety was grown. Cyst counts were much lower in non-fumigated plots where a resistant variety was grown (Fig.10).

In addition to pesticides and resistant varieties, a third technique for reducing losses to nematodes has been to utilize known facts regarding crop ef-
Fig. 8. Changes in populations of *Paratylenchus projectus* during one soybean growing season in check block and two blocks fumigated the previous November and subsequently reinfested by flooding. After Ferris and Bernard (1961).

Fig. 9. Population changes in a field trial (Great Britain) when a susceptible and a resistant potato variety were grown every year, with and without fumigation (DD = DD liquid injected, DAZ = Dazomet powder rotovated in). Initially the land was infested with *H. rostochiensis* pathotype A. After 6 years some plots that grew the resistant variety were almost wholly infested with a new species, pathotype E. After Jones (1972 a).

Fig. 10. Soybean yields and population changes at the end of a growing season of soybean cyst nematode (cysts/200 cc soil) in non-fumigated and fumigated Indiana (U.S.A.) fields planted to resistant and susceptible varieties. Initially cyst counts were similar in all plots (87 cysts/200 cc soil).
fect on buildup of various species, in rotations of varying kinds and lengths with or without the use of fumigation. Jones' diagrammatic presentation in Fig. 11 for potato cyst nematode in Great Britain illustrates the concepts involved. For this species, which forms viable cysts that may persist for many years, the nematode can return to damaging numbers after only one or two

![Diagram of potato cyst nematode population changes](image)

Fig. 11. Diagrammatic changes in populations of potato cyst nematode when susceptible potatoes are grown continuously with and without a nematicide or grown in a four or eight-course rotation. After Jones (1972 a).

potato crops (Jones, 1972 a). In practice British farmers usually plant potatoes every 5 or 6 years because the small loss in yield incurred is economically preferable to waiting until the numbers of cysts are reduced to the point where no loss in yield occurs.

Other management techniques have been effective in controlling certain nematode pests. Among these are the use of summer or winter fallow. Clean summer fallow may be accomplished by plowing or harrowing, or by the application of herbicides. Simons (1973) cautions that susceptibility of nematodes to drying may have been overrated, as vermiform stages appear to survive soil desiccation well. For effective eradication, a strong and longlasting drought is necessary, and the efficacy of the method should be field tested in many separate areas of the world. Flooding has also been used to control nematodes in special situations. Simons (1973) indicates that microbiological activity in saturated soil results in chemical properties of the soil solution unfavorable for most nematodes. Still other practices have included the use of nematode-resistant cover crops, manipulation of planting time, organic manuring, the removal or destruction of infected plant parts, the use of trap crops, the use of nematode-free planting stock, and attention to the general nutrition and care of the host plant (Thorne, 1961; Good, 1968, 1972; Mai, 1968).
Most of the research which might be used in attempting alternate strategies in nematode pest control has been carried out in temperate regions. Although it is recognized that nematode pests abound in tropical areas, as do insect and weed pests and plant diseases (Smart and Perry, 1968), Janzen (1973) comments that evaluation systems for losses to pests in these areas may cost too much to make them feasible for low value crops. Chiarappa (1969) noted that nematode figures are often not even included in loss data, although he estimates that these losses are very large. Many governments in tropical regions are not aware of nematodes and their losses, but this situation is changing with each year that passes. When they do become aware, the high costs of nematicides versus the relatively low value of many crops raised is an obstacle to their use. Even when the crops are of high value, hard currency for the purchase of nematicidal materials from abroad may be limiting. In recent years, however, well-trained tropical nematologists have been carrying out research on alternate strategies. A case in point is the recent investigation of the effect of fallowing on banana nematodes and on crop yields (Edmunds, 1970, 1971). The conclusion reached following this work was that fallowing is not an economically feasible control. Its use results in loss of production time, increased production costs, and no significant increases in yields.

New strategies for control

Many suggestions are currently being made for ingenious combinations of methods to manage pest populations in agricultural systems. Many of these are aimed at control of insect pests, but the principles can be applied to nematodes as well. Basically, in agriculture we have a change of the environment from the natural state to another, more useful state (Pimentel, 1970) and it takes energy to make and maintain the change. All biological and physical aspects of the system must be managed as an integrated system. Pimentel (1970) suggests that a number of practices should be reconsidered in this perspective. For instance, breeding programs should not sacrifice resistance to pests for yields; beneficial organisms as well as target species must be considered when applying pesticides; care must be taken not to introduce new pest species for which local crops have no resistance, or to introduce crops which lack resistance to certain indigenous pests. In addition, the monoculture concept versus the concept of increased species diversity must be rethought. Plant spacing and timing is another area for consideration. With certain insect pests, it has been found that more damage results in sparse growths of crops than in dense.

Some of these considerations are not new to nematologists. Others, such as a concern with plant spacing and timing, should be investigated more fully. Webster (1969) is optimistic that sophisticated manipulation of host physiology, based on greater knowledge of host parasite relationships, offers prospects for nematode control. The possibility of attempting to maintain a diversity
of nematode species in crop soils is another attractive possibility, although it is known that long food chains cannot be sustained in an unstable community because species at the ends of the chains are highly susceptible to fluctuations lower down in the food chains (Pimentel, 1970). The marked decrease of most of the Dorylaimida in disturbed forest stands and their paucity in cultivated fields (Table II), indicates that these may be nematodes at the ends of food chains difficult to sustain in cultivated fields. The microbivores on the other hand, are opportunistic species with rapid fluctuations and their presence could probably be encouraged in agricultural lands. In one experiment, nematologists found that an increase of microbivores in fungus-amended soil coincided with a decrease in three species of plant parasitic nematodes (Palmer and MacDonald, 1974). In experiments in India on control of plant parasitic nematodes with organic amendments to soil, Singh and Sitaramaiah (1973) found that a 2 inch-thick pine needle mulch reduced numbers of parasitic nematodes in soil with a concurrent increase in the numbers of free-living nematodes, especially of the predator genus Mononchus. Nematode species reacted differently to the amendments, with some reduced more by castor cake than with sawdust or margosa cake, whereas other species behaved in an opposite way. Populations of free-living nematodes were always higher in amended than in non-amended soil and were correlated with decreases in numbers of root knot nematode juveniles in most treatments.

Turnbull (1969) provides an interesting analysis of the difficulties inherent in attempting to change pest numbers by habitat manipulation. Since the application of pesticides often provokes community reactions which result in more severe damage than the difficulty they were supposed to alleviate, biological control appears to be a more sophisticated technique, wherein introduced biotic agents are intended to become an integral part of the community's regulative processes. Since pest problems are usually problems of numbers, regulation of population numbers becomes a necessity.

According to the concept of community homeostasis, all living things are components of self-regulatory communities in which the biological activities of each organism impinge on and interact with the activities of other organisms of the same area. Excessive numbers of a member organism are destroyed by other members of the community. Such homeostatic balance is commonly assumed to be a characteristic of natural communities. When communities are modified to meet agricultural needs, it is reasoned that man's interference has destroyed the self regulative potential, and a sort of non-community is created, the symptoms of which are said to be the increases of pests which destroy the crop. Biological control techniques would mandate a kind of management of the habitat that would enable it to become self-regulatory again.

According to Turnbull's analysis, it is not possible to restore natural regulation to part of the community and not to the whole. We want the pest species regulated, but the crop species to achieve its full productive potential, and no naturally occurring regulating system can achieve this sort of
discrimination. Thus such a system is not consistent with our purposes. Man's interference does not destroy community regulation, but aggravates the tendency of the cybernetic system to return the community to its original state. The farther the community is forced from its homeostatic course, the stronger are the forces of reaction, and pests are prominent among the reactive forces. Therefore the natural self-regulatory systems of communities cannot be looked on as allies in battles with pests, but instead as our chief antagonists. Effective controls must be designed either to exert continuous pressure on homeostatic systems to keep them permanently off course, or they must aim at erecting new systems designed by man to meet his special requirement (Turnbull, 1969).

Turnbull (1969) evaluates three strategies of control in terms of these concepts of community dynamics. The first strategy is that of applying controls from without, as with pesticides. This type of control, as we have seen, evolves the maximum homeostatic response and is likely to be self defeating in the long run. Moreover, the danger of environmental contamination is of increasing concern. The second strategy is the concept usually evoked by the phrase, "biological control", and includes attempts to restore the natural states of homeostasis by environmental manipulation. Unfortunately, since the objective of agriculture is to supply the crop species with overwhelming and permanent advantage, this strategy too ultimately will fail.

The third strategy suggested by Turnbull (1969) is to use the natural forces, and not to ignore them or to submit to them. We know what we want from communities and what forces are at work or should be. Then we modify, corrupt, mold, check, eliminate, or add to the forces to shape the community in the way we wish. Attempts at integrated pest management which incorporate the use of pesticides as an integral part of the system, to lend a bias, and not just as an emergency supplement, are an attempt in this direction. For the main pest controls, however, the system relies on natural phenomena and habitat modification. The newer autocidal controls of the entomologists fit nicely into this concept (Turnbull, 1969). The challenge to nematology, a relatively young science, is to achieve a greater understanding of nematode community dynamics so that new facts can be incorporated into models of natural phenomena; and their modification into systems of nematode pest management.

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