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Ecological Considerations in evolving Strategies for Nematode Control in 2000 AD

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Crop losses caused by nematodes are a function of the interaction among plants, nematodes and environmental factors. A number of biotic and abiotic factors play a vital role in determining the activities and population densities of nematodes, and their impact on crop performance. Certain factors like host status, soil temperature, soil moisture, soil structure, organic matter, fertility level, biological enemies etc. are amenable to suitable modification/adaptation by alterations in cultural practices so as to shift the ecological resultant in favour of the plant and against the target nematode species. With the available information on the effects of some of these factors, a number of basic mathematical models have been evolved to depict the nematode population — crop yield relations and population growth patterns, though these are far from perfect. A few systems simulation models have been evolved for management of some nematodes, particularly the root-knot and cyst nematodes incorporating the effects of environmental factors. However, adequate information is still lacking on the exact nature of the interaction of the multiplicity of factors influencing the plant-nematode relations and on the effects of fluctuating factors as they operate in nature. Research in these directions has to be intensified so as to collect valuable information of relevance to nematode management by the year 2000 AD.

In order to evolve strategies for nematode management with long-term objectives, ecological considerations will be essential. A step-wise scheme for research in this direction is given.

Complete eradication of the target nematode species is neither easy nor ecologically desirable. The aim should be at maintenance of equilibrium populations at sub-economic levels on long term basis. Drastic control measures like use of nematicides cannot altogether be dispensed with. These may infact be essential to create instability in established nematode populations so that destabilized populations can be controlled by cultural and biological methods with or without minimum use of nematicides. Nematode control must not be viewed in isolation, but a multi-disciplinary integrated approach aimed at control of the complex of all major pests, diseases and weeds in a given area and preservation of beneficial microbial activity should be looked for.

Key Words: Nematode control, Ecological considerations

Introduction

Nematodes are a part of the complex of organisms inhabiting the earth's biosphere. They are quite diverse in their forms and feeding habits, and so numerous that a cm^3 of almost any soil may contain several hundreds of their kind. Being heterotrophs they hold position as consumers at various levels of the food chain in a given community. Many of their species are primary consumers feeding on flora right from the unicellular bacteria to the highly-evolved angiosperms, while the remaining may feed on fauna ranging from protozoans to mammals including man. Yet, nematodes are only a part of the complex of organisms that feed similarly.

The plant-parasitic nematodes along with other pests and pathogens compete with humanity for a share of the harvest of crops, many of them also opening ways for other pathogens, and are now recognised as an important limiting factor in agricultural production. Though first recognised directly as pathogens of plants in 1743 with Needham discovering *Anguina tritici* in wheat seed galls, the importance of nematodes became evident in the latter half of the nineteenth century with the discovery of the root-knot (Berkeley 1855) and cyst (Schacht 1859, Kühn, 1874, 1881) nematodes infesting commercially vital crops. By now, it is well understood that all kinds of crops throughout the world are attacked by one or more species of nematodes, at times so severely that the total crop fails.

Efforts have been made to control nematodes by chemical, physical, cultural, biological and genetic means with varying degrees of success. However, economically viable and practically feasible control methods have evaded discovery. A large number of environmental factors influence the crop growth as well as nematode activities and numbers, and consequently determine the efficacy of any control practice. No effective control measure can be devised without understanding such relationships. A concensus has now evolved in favour of developing integrated nematode management (INM) strategies combining the use of more than one approach keeping in view the environmental influences on the nematodes and the host. Webster (1982) and Bird (1981) have stressed control of nematodes as an integral part of the integrated pest management (IPM) system.

Nematode Population–Crop-yield Relations and Nematode Management

For most plant-parasitic nematodes, excluding perhaps those transmitting virus or reproducing very fast, it is possible to find out direct relationships between the population densities of nematodes and crop performance. The negative linear regressions such as $Y=a-b \log x$ or quadratic equations like $Y=a-b \log x-c (\log x)^2$ generally give good fit with observed data (Oostenbrink 1966, Peters 1961). Seinhorst's (1965) model $y=m+(1-m)Z^{P-T}$ *for* $P \geqslant T$, based on Nicholson's competition curve, is also quite suitable. This model incorporates a factor 'tolerance level'—(T) recognizing that plants have a capacity to bear some extent of nematode-induced stress without expressing detriment in growth or yield. Just above this is the 'injury threshold', the population density at which discernible damage occurs. However, in view of the fact that some investment has to be made directly or indirectly to control the pathogenic organism and the aim of the grower will be to get some economic gain by resorting to the control method, the population density which causes damage equivalent to the cost of control measure will be more relevant (Headley 1972). This population level is called the 'economic injury threshold' which is a dynamic concept since it will change with the costs of production and protection, as well as with the environmental influences (Ferris 1981).

Gaur (1975) defined integrated pest management as a philosophy aimed at combining the beneficial effects of a number of artificial and/or natural controlling or prophylactic measures or forces, either applied together or in a sequence, against pests, ideally against the whole pest-disease complex, on the same area or crop to maintain the equilibrium of pest populations below the economic threshold but above the maintenance threshold of natural enemies, leaving minimum of harmful effects on the environment. This definition, though a little too long, encompasses most of the principles of integrated management as laid down by NAS (1969). Smith (1978) defined integrated pest control concisely as 'a multidisciplinary ecological approach to the management of pest populations, which utilizes a variety of control tactics compatibly in a single coordinated pest management system'.

Wiese (1982) has stressed that if crop management decisions are to be rational, i.e. based on sound data rather than intuition, it is essential to survey, quantify, inter-relate and manipulate the principal yield determinant variables to avoid yield losses and to meet production objectives, practically and economically. The relative importance of these variables, once clearly discerned, will permit intelligent guidance of management alternatives, knowledgeable alteration of production designs and efficient focussing of problem-solving research.

Biotic and Abiotic Factors influencing Nematodes

Efforts have been made by various workers to study the effects of various biotic and abiotic factors on nematodes and their relations with plants. These have been reviewed extensively from time to time (Winslow 1960, Wallace 1963, 1971, 1973, Sayre 1971, Webster 1972, Norton 1978, 1979, Mankau 1981, Yeates 1981, Andersson 1982, Jones 1983, Sethi & Gaur 1984, etc.). A reading of literature gives a frightening impression of extreme complexity of the system and reveals important knowledge gaps. However, by developing a few simplistic notions and generalizations, it should be possible to use available data on nematode damage functions, nematode biology and crop production economics to make rational management decisions (figure 1). Use of best available biological evidence and experience-based intuition will allow immediate implementation with possibilities of fine tuning of the system in due course (Ferris 1980).

The biotic and abiotic components of the ecosystem may result in changes in the nematode and host characteristics. Certain factors like host status, soil temperature, soil moisture, soil structure, organic matter, fertility level, biological enemies, etc., are amenable to suitable modification or adaptation by alterations in cultural practices so as to shift the ecological resultant in favour of the plant and against the target nematode species. This forms the basis of a number of control tactics currently in vogue and offers good prospects for the future. Such ecological considerations have been employed in a number of successful control programmes.

Host Characteristics

In order to be a good host, a plant must be able to allow invasion externally or internally, provide food, permit nematode growth and reproduction and also support certain of its population while still surviving. It must be able to respond to the nematode's stimulus to develop intimate relationship in the form of cellular changes like hypertrophy and hyperplasia if such is necessary for the nematode. The host characteristics can be defined in terms of:

a, the maximum rate of reproduction of the nematode on the host;

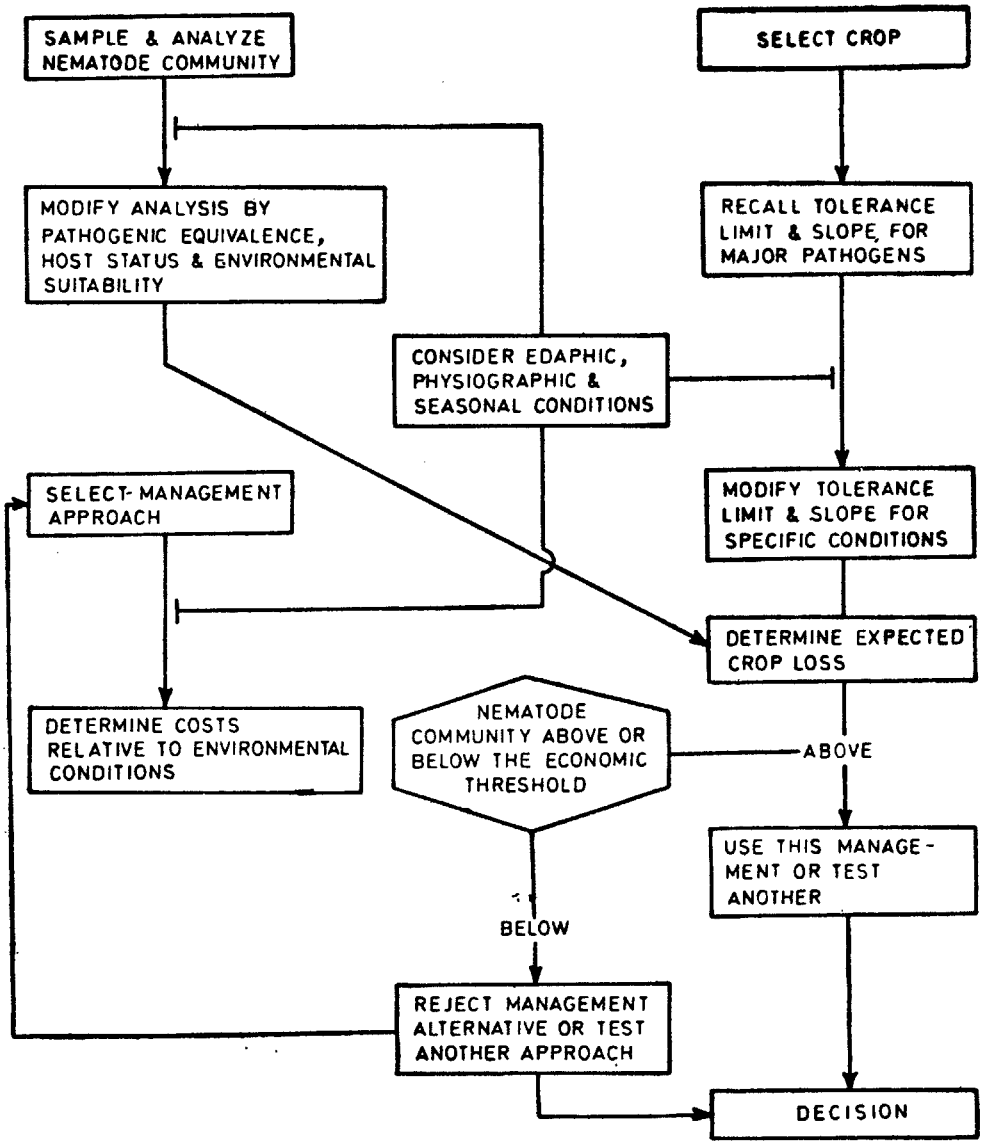

Figure 1 A simplified flow chart of the decision-making process in nematode population management (*after Ferris 1980*)

T, the tolerance level, i.e., the maximum population density up to which the plant does not express the nematode stress; and

E, the highest equilibrium nematode population that the plant can support.

These characteristics define the status of the plant (figure 2) as good, poor, tolerant, intolerant, resistant host, or as immune or non-host, or as antagonistic plant (Dropkin & Nelson 1960, Rhode 1972). The values of *a*, *T* and *E* can be modified genetically by plant breeding techniques as well as to a great extent by environmental manipulations. Generally, a plant with high *T* value and low *a* and *E* values is suitable from the grower's point of view. A tolerant host with high *a*, *T* and *E* values may not suffer damage itself but will leave very high post-harvest populations which will serve as initial population for the subsequent crop (Gaur 1975, Sethi & Gaur 1984).

The tolerance level of a crop to a nematode varies with the growing conditions and edaphic factors. It gives an idea of the relative susceptibility. Barker and Olthof (1976) have compiled the tolerance level of a number of crops. The tolerance level is generally higher when the plant is attacked after attaining some growth. This is an important consideration showing that in transplanted crops it is economical to control the nematodes in nursery to have nematode-free seedlings which can tolerate higher populations in the field.

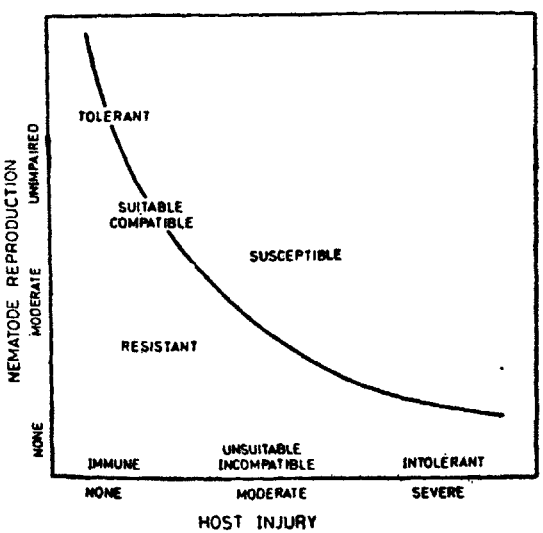

Figure 2 Host characteristics relative to host injury and nematode reproduction (*after Dropkin & Nelson 1960, Rhode 1972*)

Consideration of such host characteristics is essential for planning of crop rotation schemes and selection of resistant cultivars of crops. It is often possible to reduce nematode populations appreciably by growing non-hosts, resistant hosts or antagonistic crops during the period intervening susceptible host crops. Some problem is faced due to the susceptibility of crops to more than one species of nematodes present, the economic unsuitability of the alternate crops and the long periods of survival of certain nematodes in the absence of host.

However, it may be possible to find crop varieties bearing resistance against more than one nematode, for instance, the varieties C-152 of cowpea and ML-80 of '*mung*' (*Vigna radiata*) exhibit good degree of resistance against the root-knot and reniform nematodes (Mishra & Gaur, unpublished). Certain crops besides being non-hosts also suppress nematode population through the antagonistic effects of their root exudates, e.g., *Tagetes patula*, *T. erecta*, *Asparagus*, sesamum, mustard, etc. (Suatmadji 1969, Prasad & Dasgupta 1969, Atwal & Mangar 1969, Khan et al. 1971, Prasad & Haque 1982). Some crops trap nematodes by allowing massive invasion without permitting further development, e.g., *Crotalaria spectabilis*. Growing of crops which allow massive invasion and also reproduction, e.g., Oats for *Heterodera avenae*, are not safe to use as trap crops since delay in their destruction might be hazardous and uneconomical (Oostenbrink 1972).

Crop rotation has been one of the principal methods of nematode control in annual crops, and has been successfully used against a number of serious nematode pests, particularly when nematicides have proved too costly. Host range studies and screening for resistance are of great significance in planning rotations. Nematode's survival mechanisms and capacity for quiescence are the other important considerations. Most cyst nematodes including *Globodera rostochiensis*, *G. pallida*, *Heterodera schachtii*, *H. glycines*, *H. avenae* and some species of the root-knot and stem nematodes, wheat gall nematode, etc. have comparatively narrow host ranges in the field. For control of *H. schachtii* on sugarbeets, Konnecke (1967) recommended long-term crop rotations of 7-8 years, like: Sugarbeet + stable manure—green oats + alfalfa as undercrop—alfalfa-potato + stable manure—winter wheat—winter rye—sugarbeet etc., or sugarbeet + stable manure—pea—winter barley + alfalfa as undercrop—alfalfa—alfalfa— potato — rye-sugarbeet, etc.

The populations of *H. avenae* are known to decrease by 50–75% per year in the absence of host (Hesling 1958, Meagher & Rooney 1966). Thus, an interval of two years between susceptible crops would be sufficient to manage this nematode. The golden nematode of potato requires perhaps the longest rotations of 4–8 years depending upon the population density. The root-knot nematodes, particularly those prevalent in the tropics, generally have very wide host range and thus are the most difficult to control by crop rotation due to difficulty in finding suitable non-host crops. Similar is the case with the stem and bulb nematode, *Ditylenchus dipsaci*. The genetic variability and presence of biological races further adds to the complexity. But once a suitable non-host is found these nematodes can be controlled by relatively short rotations of one to two years (Norton 1969, Brodie et al. 1970, Johnson et al. 1975, Alam et al. 1977, 1981).

Varietal selection coupled with one to two years' crop rotation, application of nitrogenous fertilizer and planting in cool soil has been found to be the most successful management practice against *Pratylenchus thornei* on wheat (Van Gundy et al. 1974). Crop rotation, however, must be accompanied by proper weed control since many weeds are alternate hosts of nematodes and support heavy nematode populations in the absence of the main host crop (Rossner 1979).

Nematode Characteristics

The principal characteristics of nematodes requiring consideration are their distribution and dispersal in different physiographic regions, seasonal adaptations, host ranges, biological races, nature of damage caused, type of host response necessary for establishment, intraspecific competition, rate of population increase, survival potential in the absence of host and under adverse conditions, etc. Certain nematodes, like *G. rostochiensis*, *G. palida*, *Meloidogyne hapla*, etc., are confined to temperate regions and their absence in hotter physiographic regions are the factors that must be considered in planning national cropping patterns and quarantine measures. Some nematodes like *H. avenae*, even though present in hotter regions are active only in cooler months. Most nematodes require a minimum threshold temperature for development and other activities. Slight differences in seasonal adaptations of the host and the nematode may be considered in deciding planting periods.

Most of the endoparasitic nematodes require specific cellular changes like hypertrophy, hyperplasia, cell wall dissolution, etc. in the host in order to be able to feed and establish. The host response to the nematode's stimulus is an intricate biochemical mechanism, mostly controlled genetically.

Understanding of this mechanism can direct suitable genetic alterations in breeding programmes. Chemical inhibition at some stage of the chain of reactions, such as through the use of plant-growth regulators may also find greater importance. The failure of the nematode to evoke suitable response or occurrence of hypersensitive reaction in the plant may form the basis of resistance.

The presence of biological races in several species of nematodes and their evolution in response to intense selection pressure requires caution while growing, continuously, varieties resistant to only one of the races when others are also present concomitantly, though in low numbers (Jones et al. 1967). If the variety is susceptible to a fraction of the population the competition faced by it is much less and this fraction can soon rise to high populations. Also, there is a possibility of the nematode breaking resistance by adapting itself to the variety. Hence, in order to maintain the resistance and to avoid evolution of new biological races, it is not advisable to grow a resistant variety year after year on the same land.

Nematodes, characteristically, have low rates of reproduction compared to fungi and bacteria. Generally, only one to four generations are completed in a single crop season. The consideration of their fecundity is necessary. Nematodes like *Meloidogyne* spp, *Rotylenchulus reniformis*, *Pratylenchus* spp, *Ditylenchus* spp. and some *Heterodera* spp may produce large numbers of eggs in relatively short generations and thus may build up from very low to alarming levels of population in a short period such as a crop season with a good host. They are also active almost throughout the year in the tropical soils. Others, like many cyst nematodes, have high fecundity but fewer generations/year with special surviving mechanisms to face adverse conditions of temperature and moisture in the absence of a host. A few species like those of *Scutellonema*, *Xiphinema*, etc. have low fecundity and long life cycles resulting in rather slow build up of their population. Others like *Tylenchorhynchus* spp may have short life cycles which help them build up high populations in a given time.

A number of nematodes like *Globodera* spp, *Heterodera schachtii*, etc. require hatching factors secreted by the host roots in their exudates. Chemical identification of such factors and their synthesis will be valuable. The nematodes can be induced to hatch before subjecting them to a control method such as crop rotation, nematicide, etc., since the eggs are more difficult to kill than free juveniles.

The rate of population increase is density-dependent and can be used to predict the final populations on a crop (figure 3), mathematically through models such as

$$Pf = Piuy\ \{(b + c\ Piuy)^{-1} - S\}$$

(Oostenbrink 1966)

or

$$Pf = ay\ Epi\ \{(a-1)\ Pi + YE\}^{-1}\ for\ P \geqslant T$$

(Seinhorst 1968, 1970).

The rate of reduction in nematode population in the absence of host is usually

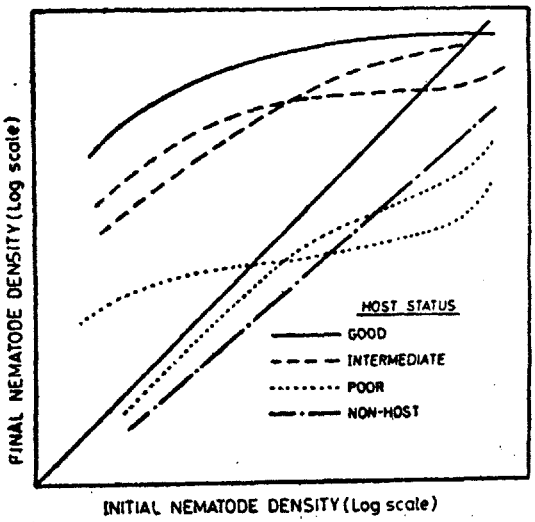

Figure 3 Host status in relation to nematode population growth (*after Seinhorst 1970*)

independent of density, but in some cases only part of the eggs may hatch successively. Population decreases @ 30–33 %/year have been reported for the golden nematode. According to Seinhorst (1970) if a, is the rate of population change; b the proportion of the population at the beginning of the year; and x the number of years in which no host is available, then

$$x = -\log a / \log b.$$

However, the rates of decline depend upon the agroclimatic conditions such as temperature, moisture, natural enemies, tillage disturbances and weed flora in the absence of the host crop. In the event of extreme adversities the population decrease may tend to be density independent.

Prediction of Crop Losses

Since nematode population growth can be predicted and relationships can be established between pre-plant population densities and crop performance, it is possible to predict crop losses likely to be caused by a particular nematode at densities present. This is mainly possible due to:

(*i*) the relatively slow mobility, so that the population present in the field prior to planting is generally the one that attacks the plant, and

(*ii*) the relatively slow rates of population increase.

The potential losses, likely to be caused to a crop, can thus be determined by establishing relationship called 'damage function' (Ferris 1980). This can be first done for the most predominant nematode pest on the principal host crop. Different species of nematodes present differ in their pathogenicity in terms of losses induced. For instance, the vascular feeders like root-knot, reniform, cyst nematodes, etc. cause more damage than cortical feeders like lesion, burrowing, lance nematode, etc., which in turn cause more damage than ectoparasites feeding on epiblema and root hairs. The pathogenicity indices can be worked out or presumed from experience-based intuition on a 0–1 scale. From these the effective initial population of the nematode community relative to the major nematode pest can be computed as weighted total and used as the independent variable in the damage function for the major species as suggested by Ferris (1980).

Similarly, since the different crops and their varieties differ in their susceptibility to the same nematode, the susceptibility indices can be computed relative to the principal crop. The damage function has again to be extrapolated to predict the possible losses to any crop under the conditions of the principal crop. The effects of important environmental factors and management practices on the damage function are also to be quantified and used for extrapolating the damage function to determine the possible losses to any crop by any combination of the species under a given set of conditions. This procedure will reduce the need to experimentally determine the damage function for every combination of hosts, nematodes and environmental factors.

Considerable data are already available in the literature to enable such exercises (Barker & Olthof 1976, Norton 1978). The gaps in knowledge can be filled up tentatively with experience-based intuition and subsequently with pointed experimentation. On these lines Ferris (1980) was able to develop simulation which help in nematode management decision-making (figure 1).

Cost of Control and Optimization

The expenditure that a grower is expected to make towards nematode control can not and should not be more than the value of crop loss that can be avoided by using the control method or management alternative.

In other words, one can profitably aim to reduce nematode populations to levels above which the damage caused exceeds the cost of control (Khan 1972, Headley 1972, Ferris 1978, 1980). The cost of control C increases exponentially with the degree of population reduction (ϕ) aimed at:

i.e., $C = e^{k\phi - 1}$, where k is scaling constant and e the base of natural logarithm.

Complete extermination of a nematode community would involve huge costs. The optimization of the cost of control and degree of population reduction in order to get maximum returns can be done with the following equations:

(*i*) *the cost function*:

$$dC/d\,Pm = -(K/P)\, e^{K(P-Pm)/P}$$

Where P is the initial population reduced to P_m at a management cost C, and

(*ii*) *the Nematode damage function*:

$$d\,Va/d\,P_m = V\,(1-m)\,ln\,z(z^{Pm-T})$$

Where V is potential crop value, Va the crop value at reduced population level P_m and z the damage potential of one nematode

The intersection of the lines of these two equations gives the extent to which the population should be reduced to maximize the returns to the grower (Ferris 1978, 1981). Such a model would enable to fix the targets for the level of nematode control using a particular control strategy.

Edaphic Factors and Nematode Control

A large number of edaphic and cultural factors influence the activities of nematodes and crop growth, and thus also the nematode damage function. The efficiency of various control methods also varies with such factors. Though a large number of factors are involved, a few that lend themselves to suitable alteration or adaptation are: host status, soil structure, soil temperature, soil moisture, organic matter content, fertility level, biological enemies etc. The environmental factors, besides affecting the damage function also influence the efficiency of a control method.

Soil Texture and Structure

These factors determine the soil pore spaces and pore neck diameters affecting nematode movement and root growth. These also control the moisture retention, aeration, thermal conductivity, osmotic potential etc. Specific growth rates of population of the same species of nematodes may vary greatly with soil structure and texture (Norton 1979, Sethi & Gaur 1984). In Netherlands, the tolerance levels of wheat and oat to *H. avenae* were 2 eggs/g of soil in sandy and peat but 8 eggs/g of soil in heavier soils, while for barley these were 3 and 10–12 eggs/g of soil, respectively (Kort 1972). Much higher dose of nematicides is required to achieve the same degree of control as the soil shifts towards finer particle size, or when the soil is too compacted, since the efficient dispersion of the nematicide is inhibited. Deep ploughing and summer fallowing are more effective in the lighter soil (Seshadri & Sethi 1978) compared to heavier soils which lose moisture more slowly and allow slower thermal changes due to the high specific heat of water held in the pore spaces.

Tillage practices chiefly influence the moisture and temperature by modifying soil structure. Besides, these can cause dispersal and disturbances of the established loci of population. One important effect is the creation of instability resulting in increased amplitude of oscillations even though the overall growth rates may not be appreciably changed (Sethi & Gaur 1984). The ultimate magnitude of nematode stress on the crop is determined by the manner of overlapping of the population waves with the plant growth cycle catering to the demands

of metabolic sinks at various stages of plant growth (Ferris 1981).

Soil Moisture

As nematodes in soil inhabit the moisture film around the soil crumbs or in the water lenses in pore necks, their movement is largely controlled by surface tension, suction, moisture characteristics and hysteresis in a particular soil. Aeration and osmotic potential as also temperature fluctuations are also directly controlled by moisture content. Besides, the concentration of soluble chemicals, especially the root exudates, biodecomposition products etc. are dependent on moisture. Wallace (1971, 1973) and Norton (1979) have discussed such interactions at length. Since most nematodes feeding on roots impair the water uptake and conduction, the plant suffers greater moisture stress as damage to root increases. Nematodes like root-knot, reniform, cyst and sheath nematodes, etc., which prefer well aerated soils are, generally, not a problem on crops able to tolerate waterlogging. Van Gundy et al. (1968) observed that *Hemicycliophora arenaria* populations were reduced in citrus irrigated after every 7 days.

Most of the above ground parasites like *Ditylenchus dipsaci, Anguina tritici, Aphelenchoides ritzemabosi, A. fragariae, A. besseyi,* etc. are more prevalent or active when humidity is high. In soil-inhabiting forms there is usually a spurt in population immediately following rainfall or irrigation as a result of increased hatching and activation of quiescent stages. A dry period in the ascending phase of population, or at the time of invasion usually results in sudden decline in population. Many species of nematodes, like *Aphelenchoides* spp, *Anguina tritici, D. dipsaci, Heterodera cajani, H. zeae, H. avenae, Meloidogyne* spp, *Rotylenchulus reniformis, Tylenchulus semipenetrans,* etc. have some stage in their life cycle which can withstand desiccation by going into complete or incomplete anabiosis which, however, can be broken by providing moisture even without any hatching factor. If the dry spell is suddenly broken for a brief period the revived nematodes would be less efficient to readapt to dry condition. Thus, alternate wetting and drying of soil in summer may prove to be more effective than continuous dry periods in reducing populations (Sethi & Gaur 1984.

In the case of *H. avenae,* a correlation existed between rainfall and disease intensity (Fidler & Bevan 1963). Maximum damage occurred in years with moist and cool period at the time of larval hatching. The increased population of infective juveniles and their easy mobility in the water-filled pores increase the intensity of invasion. If this is followed by drought in the season the damage is even more. However, if adequate moisture is provided in the season through rainfall or irrigation the crop might tolerate higher populations and perform well despite nematode attack, if the populations are low to moderate. In case of severe infestation the sprinkler irrigation is more beneficial (Kort 1972). Improving the water-holding capacity of the soil such as by adding organic matter, may also help.

Temperature

It is one of the vital factors determining the rates of biological processes of host and parasites, evaporation and other biological and chemical processes in the soil. The nematodes and host both have their optimum temperatures for different activities and rates of development (table 1). It is natural that most plant-parasitic nematodes are so adapted that the optima for the host are also the optima or at least supporting temperatures for them. Still the study of the effects of temperature is important from two points of view (Sethi & Gaur 1984):

(*i*) The extremes of temperature tend to kill or reduce nematode populations

Table 1 *Relation between soil temperature and nematode activity (after Wallace 1963)*

Nematode	Activity	Low inhibition temp. (°C)	Optimum temp. (°C)	High inhibition temp. (°C)
Meloidogyne incognita & M. javanica	Infection	10–12	20–35	
	Reproduction	9–16	27	
	Hatching		27	
Globodera rostochiensis & G. pallida	Activity	9–16	25	30–35
	Development	11	18–24	29
	Emergence		21–25	30–37
	Invasion		15–16	
Heterodera schachtii	Activity	5–10	25	30–35
	Emergence	10	25	35
H. glycines	Emergence	16	24	36
	Development	10	23	
Ditylenchus dipsaci	Activity	15	10–21	38
Pratylenchus projectus	Moulting	10	19–30	35

and this fact is useful for reducing the populations in the absence of host e.g., by insolation, steam treatment etc., or in the dormant stages of plant tissue by hot water treatment, and

(*ii*) The relationship between nematode numbers and crop yield is modified for the same species of nematode on the same host crop in a way that the damage threshold varies with temperature, due to slight differences in the temperature requirements of the crop and nematodes at various stages.

The detailed studies on temperature-time combinations are important for determining suitable hot water treatments so that the nematodes are killed while still leaving the disinfested tissue viable. The knowledge of (ii) above, finds use in determining the effect on the nematode damage function. It is also the cardinal principle for adjusting the dates of sowing or planting the crop in such a way that the crop attains some growth before the nematodes find suitable temperature for invasion, hatching, development or reproduction. Growing crops in the low temperature periods, when soil temperature is below the threshold temperature for nematode, helps in avoiding extensive nematode stress. For instance, Jones (1956) found that early sowing of sugarbeet usually escaped attack by *H. schachtii.* Van Gundy et al. (1974) observed that sowing wheat in cool soil (15°C) avoided early attack of *Pratylenchus thornei.* Gaur et al. (1979) and Mishra and Gaur (1979) found that '*rabi*' pulses like chickpea (*Cicer arietinum*) and lentil (*Lens culinaris*) could tolerate much higher populations of *M. incognita* with late sowings in mid-November compared to the normal mid-October sowings. They also found that different cultivars of these crops differed in growth according to the sowing date. Roberts et al. (1981) also noticed escape from *M. incognita* damage when winter wheat was sown late in cool soil. Thus, detailed study of temperature requirements of the nematode and host, and selection of varieties of crops suitable for growing at temperatures unsuitable to nematodes would be of immense value in planning of planting schedules.

Temperature also plays an important role in triggering on or off the dormancy in nema-

todes. For instance, Rao (1984) found that higher temperature of 30°C could induce dormancy in *H. avenae* and exposure to lower temperatures of 7–10°C with moisture could break it.

Organic Matter

The organic matter in soil in the form of crop residues in various stages of decomposition, humus and organic amendments has great importance in determining the physico-chemical properties of soil, particularly the soil structure, water holding capacity, *p*H and availability of nutrients as also acting as substrate for micro-organisms in soil. Most bacterial and fungal feeders and predatory organisms including nematodes are positively correlated with soil organic matter, while most plant parasites like some dorylaims and most tylenchids are negatively correlated (Norton et al. 1971).

Incorporation of various kinds of organic amendments to soil has some promise for effective long term nematode control. Use of chopped shoots, straw, sawdust, complete or deoiled seed cakes, animal manure etc. have resulted in significant population reductions of nematodes and increased crop yields (Singh & Sitaramaiah 1970, Norton 1978). Muller and Gooch (1982) have recently reviewed this aspect and conclude that oil cakes are most popularly experimented, while sawdust, compost, green manure and chicken manure have also shown some promise. In India the leaves and deoiled cakes of '*neem*' (*Azadirachta indica*) have proved very effective (Singh & Sitaramaiah 1970, Ram & Gupta 1982, Vijayalakshmi et al. 1984). The action of organic amendments is multifold, involving release of toxic degradation products, promoting biological enemies, improving soil properties and nutrient availability, favouring better plant growth and increase in tolerance levels. Further research on identification and synthesis of toxins released and on improving the organic matter status of soil by modified cropping practices will go a long way in developing control methods.

Fertility Level

The direct effects of mineral fertilizers through the action of ions or increased osmotic potential are trivial at the normally recommended dosages. The indirect effects via the host are more important. Mostly, application of fertilizers increases the tolerance level of the crop at the same time providing more feeding sites on the increased root system causing some increase in the nematode population (Hesling 1959, Ross 1959, Fidler & Bevan 1963, Bird 1970, Gour & Prasad 1970, Chawla & Prasad 1973).

Usually, deficiencies of N, P, K, Ca, Mg, Zn, Fe, B etc. appear in heavily infested plants, and control of nematodes alone often results in cure of such deficiences (Wilfrath & Wimmer 1903, Good 1968, Haque et al. 1972, Norton 1979). The effect of increase in nematode population is usually shortlived without much effect on equilibrium population even though the amplitude of oscillation is reduced (Gaur 1975). In case of standing crops and perennial trees when direct nematode control is not feasible, the spray applications of nutrients on the plant may help it to recover.

The source of nutrients is all important. Usually, the organic nitrogen in the form of compost, sludge, animal waste etc. releases toxic degradation products like ammonium ions killing or inhibiting nematodes (Heald & Burton 1968, Singh & Sitaramaiah 1970, Khan et al. 1974, Guiran & Bonnel 1979, Muller & Gooch 1982). Thus, management practices providing for sufficient organic matter would decrease demands of mineral fertilizers as well as help in reducing nematode populations and crop damage.

Biological Enemies

The natural habitat of nematodes usually has in it a number of fauna and flora antagonistic

to nematodes as have been reviewed by Sayre (1971), Mankau (1980), Webster (1972) and Norton (1978). Among the soil microfauna predating or parasitizing nematodes, protozoans like *Theratomyxa weberi* (Weber et al. 1952), *Dubosquia penetrans* (Thorne 1940, Prasad & Mankau 1969); Tardigrades—*Hypsobius myrops* (Sayre 1969); mites—*Macrocheles muscaedomesticae* (Rodriguez et al. 1962), collembola—*Onychyurus armatus* (Murphy & Doncaster 1957); predacious nematodes—species of *Sectonema, Nygolaimus, Mononchus, Mylonchulus, Seinura,* (Webster 1972, Norton 1978, Mankau 1980) have shown good promise in laboratory trials.

Similarly, virus (Loewenberg et al. 1959), rickettsias (Shepherd & Clark 1973, Endo 1979); bacteria—*Pseudomonas denitrificans* (Adams & Eichenmuller 1963); *Clostridium butyricum* (Johnston 1959) *Bacillus penetrans* (Mankau 1975), and a large number of nematophagous fungi like species of *Dactylaria, Dactylella, Arthrobotrys, Catenaria, Trichothecium, Harposporium, Phialophora* (Sayre 1971, Mankau 1980, Norton 1978), etc., have been proved effective in killing plant-parasitic nematodes.

However, the populations of the above natural enemies in soil, individually, may not be adequate enough to cause sufficient reduction in nematode populations, but a large number of organisms, each destroying a small percentage of nematode population, may exert significant biological control (Mankau 1980). At least such organisms constitute an important component of the environmental resistance against nematode population increase, which is proved by the fact that the build up of residual nematode populations is quite fast after the applications of broad spectrum pesticides.

Inundation of field with natural enemies is not feasible practically. The organism, so introduced, may also find it difficult to establish. However, preserving the natural populations of enemies present in the soil community and encouraging their build up, such as through improving the organic matter status of the soil, will be a practical approach. Knowledge of the conditions that maintain large and diversified predator populations is important (Mankau 1980).

Our perception of biological enemies immediately discourages us from using broad spectrum pesticides. It can also not be forgotten that nematodes other than the parasitic ones also have their own roles to play in soil communities, such as in regulation of the rates of decomposition affecting nutrient status of the soil (Whitford et al. 1982), or as enemies of other pests including insects (Nickle 1984). However, the growing trend is towards finding multiple pest control methods which may require application of pesticides capable of killing nematodes, insects, fungi, etc. (Webster 1982). For instance, use of DD+MECNS or Methyl bromide+Chloropicrin (2 : 1) with film mulch were used against nematodes and fungi in okra (Johnson et al. 1977). In such cases the overall effect on the community must be noted and caution is necessary against indiscriminate use of broad spectrum pesticides.

The ecological considerations discussed above will have to be borne in mind in formulating any nematode control strategy. The paucity of knowledge in several areas is evident, particularly, as regards the exact nature of interactions of the multiplicity of factors influencing the plant-nematode relations and on the effects of fluctuating factors as they operate in nature. Research in these directions has to be intensified so as to collect valuable information of relevance to nematode management by the year 2000 AD. Interdisciplinary team work involving nematologist, plant-pathologist, entomologist, weed scientist, soil scientist, soil microbiologist, plant-physiologist, plant breeder and agronomist, is necessary to arrive at really

practical and economical means of pest management.

The knowledge gained on the effects of such ecological factors on the nematode damage function, plant growth function and control efficiency function will enable to fix the economic thresholds rationally (Ferris 1980) and to select suitable nematode management alternatives, with the principal objective of increasing crop production on long-term basis. Complete eradication of the target nematode species is neither easy nor ecologically desirable. Drastic control measures like use of nematicides cannot altogether be dispensed with. These may in fact be necessary to destabilize established populations and the residual populations should then be easy to control by cultural, biological and genetic methods (Oostenbrink 1972).

More systematic research efforts will have to be made and better use made of the existing information scattered throughout the literature. The following stepwise scheme is suggested for future research:

(i) to develop unified standard methods for estimation of nematode populations and egg densities,

(ii) to study the distribution and dominance of pathogenic species,

(iii) to set up a centralized data bank on the effect of biotic and abiotic factors on the nematode population–plant yield relationships,

(iv) to compile the tolerance levels of various crop cultivars and pathogenicity indices of various nematodes,

(v) to identify the manageable limiting environmental factors,

(vi) to determine the economics and compatibility of nematode control measures with control of other pests and pathogens,

(vii) to study the effects of pest control methods on useful microbial activity,

(viii) to develop systems algorithms for the selection and combination of compatible practices keeping in view the avoidable crop losses, economic and practical suitability etc., and

(ix) to collect feed-back information to help in recombinations and revised recommendations if necessary.

References

Adams R E and Eichenmuller J J 1963 A bacterial infection of *Xiphinema americanum* (Abst.); *Phytopathology* **53** 745

Alam M M, Saxena S K and Khan A M 1977 Influence of different cropping sequences on soil populations of plant parasitic nematodes; *Nematologia Mediterranea* **5** 65–72

——, —— and —— 1981 Soil population of plant-parasitic nematodes under various cropping sequences; *Nematologia Mediterranea* **9** 49–56

Andersson S 1982 Population dynamics and control of *Heterodera avenae* — A review with some original results; *Bull. OEPP* **12** 463–475

Atawal A S and Mangar A 1969 Repellant action of root exudates of *Sesamum orientale* against the root-knot nematode, *Meloidogyne incognita* (Heteroderidae: Nematoda); *Indian J. Ent.* **31** 286

Barker K R and Olthof T H A 1976 Relationships between nematode population densities and crop responses; *Ann. Rev. Phytopath.* **14** 327–353

Berkeley M J 1855 Vibrio forming excrescence on the roots of cucumber plants; *Gardeners Chronicle* Apr. 220

Bird A F 1970 The effect of nitrogen deficiency on growth of *Meloidogyne javanica* at different population levels; *Nematologica* **16** 13–21

Bird G W 1981 Integrated nematode management for plant protection; in *Plant Parasitic Nematodes* Vol. III pp 355–375 eds B M Zuckermann and R A Rohde (New York : Academic Press)

Brodie B B, Good J M and Merchant W H 1970 Population dynamics of plant-parasitic nematodes in cultivated soil : Effect of sod-based rotations in Tifton sandy loam; *J. Nematol.* **2** 135–138

Chawla M L and Prasad S K 1973 Multiple cropping and nematodes. I. Effect of fertility management and intensive rotations on nematode populations and crop yield; *Indian J. Nematol.* 3 34–49

Dropkin V H and Nelson P E 1960 The histopathology of root knot nematode infestations in soybeans; *Phytopathology* 50 442–447

Endo B Y 1979 The ultrastructure and distribution of an intra-cellular bacterium like microorganism in tissues of larvae of soybean cyst nematode, *Heterodera glycines*; *J. Ultrastruct. Res.* 67 1–14

Ferris H 1978 Nematode economic thresholds, derivation, requirements and theoretical considerations; *J. Nematol.* 10 341–350

—— 1980 Nematology — Status and prospects: Practical implementation of quantitative approaches to nematology; *J. Nematol.* 12 164–170

—— 1981 Dynamic action thresholds for diseases induced by nematodes; *Ann. Rev. Phytopath.* 19 427–436

Fidler J H and Bevan W J 1963 Some soil factors influencing the density of cereal root eelworm (*Heterodera avanae* Woll.) populations and their damage to the oat crop; *Nematologica* 9 412–420

Gaur H S 1975 Crop Damage in Relation to the Density of Nematode Population and an Integrated Approach to Nematode Population Management; Ph.D. Thesis, IARI, New Delhi, 184 pp.

——, Mishra S D and Sud U C 1979 Effect of date of sowing on the relation between the population density of the root-knot nematode, *Meloidogyne incognita* and the growth of three varieties of chickpea, *Cicer arietinum*; *Indian J. Nematol.* 9 152–159

Good J M 1968 Relation of plant parasitic nematode to soil management practices; in *Tropical Nematology* eds G C Smart and P V G Perry 113–118 (Gainsville : Univ Florida) 153 pp

Gour A C and Prasad S K 1970 Effect of organic and inorganic fertilizer on plant and soil nematodes; *Indian J. Ent.* 32 186–188

Guiran G DE and Bonnel L 1979 Effect of soil organic matter on the infection of tomato by *Meloidogyne incognita* and on the multiplication and survival of the parasite; *Medid. Facult. Landb. Rijks. Gent.* 44 289–297

Haque Q A, Khan A M and Saxena S K 1972 Studies on the effect of different levels of certain elements on the development of root-knot. I. Effect of N, P, K levels on growth of okra and root-knot development; *Indian J. Nematol.* 2 35–41

Headley J C 1972 Economics of agricultural pest control; *Ann. Rev. Ent.* 17 273–286

Heald C M and Burton G W 1968 Effect of organic and inorganic nitrogen on nematode populations on turf; *Pl. Dis. Rep.* 52 46–48

Hesling J J 1958 *Heterodera major* O. Schmidt 1930. Population changes in the field and in pots of fallow soils; *Nematologica* 3 274–282

—— 1959 Some observations on the cereal root eelworm population of field plots of cereals with different sowing times and fertilizer treatments; *Ann. Appl. Biol.* 47 402–409

Johnson A W, Dowler C C and Hauser E W 1975 Crop rotation and herbicide effects on population densities of plant parasitic nematodes; *J. Nematol.* 7 158–168

——, Sumner D R, Jaworski C A and Chalfant R B 1977 Effects of management practices on nematode and fungi populations and okra yields; *J. Nematol.* 9 136–142

Johnston T M 1959 Effect of fatty acid mixtures on the rice stunt nematode (*Tylenchorhynchus martini* Fielding 1956); *Nature* 183 1392

Jones F G W 1956 Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. II. Microplot and field plot results; *Ann. Appl. Biol.* 44 25–26

—— 1983 Weather and plant parasitic nematodes; *Bull. OEPP* 13 103–110

——, Parrott D M and Ross G J S 1967 The population genetics of the potato cyst nematode, *Heterodera rostochiensis* : mathematical models to simulate the effects of growing eelworm resistant potatoes bred from *Solanum tuberosum* sp. *andigena*; *Ann. Appl. Biol.* 60 151–171

Khan A M, Saxena S K and Siddiqi Z A 1971 Efficacy of *Tagetes erecta* in reducing root infecting nematodes of tomato and okra; *Indian Phytopath.* 24 166–169

——, Alam M S and Ahmed R 1974 Mechanism of the control of plant-parasitic nematodes as a result of the application of oil cakes to the soil; *Indian J. Nematol.* 4 93–96

Khan M H 1972 Economic aspects of crop losses and disease control; in *Economic Nematology* ed. J M Webster (London: Acad. Press) pp 1–16

Konnecke G 1967 Fruchtvolgen VEB Deutscher Landwirt., Berlin.

Kort J 1972 Nematode diseases of cereals of temperate climates; in *Economic Nematology* ed. J M Webster (London: Acad. Press) pp 97–126

Kuhn J 1874 Uber das vorkommen von ruben — Nematoden an den wurzelen der halmfruchte; *Landwirts. Jahrb.* 3 47–50

—— 1881 Die Ergebnisse der Versuche zur Ermittelung der Ursache der Rubenmudigkeit und zur Erforschung der Natur der Nematoden; *Ber. Physiol. Lab. Univ. Hal.* 3 1–153

Loewenberg J R, Sullivan T and Schuster M L 1959 A virus disease of *Meloidogyne incognita incognita*, the southern root-knot nematode; *Nature* 184 1896

Mankau R 1975 *Bacillus penetrans* n. comb. causing a virulent disease of plant parasitic nematodes; *J. Invert. Pathol.* 26 333–339

—— 1980 Biological control of nematode pests by natural enemies; *Ann. Rev. Phytopath.* 18 415–440

—— 1981 Microbial control of nematodes; in *Plant Parastitic Nematodes* Vol. III eds. B M Zuckermann and R A Rohde (New York : Acad. Press) pp 475–494

Meagher J W and Rooney D R 1966 The effect of crop rotations in the Victorian Wimmera on the cereal cyst nematode (*Heterodera avenae*), nitrogen fertility and wheat yield; *Aust. J. Exp. Agric. Anim. Husb.* 6 425–431

Mishra S D and Gaur H S 1979 Effect of planting schedules on population density of *Meloidogyne incognita* and growth of *Lens culinaris*; *Bull. Ent.* 20 71–74

Muller R and Gooch P S 1982 Organic amendments in nematode control: An examination of literature; *Nematropica* 12 319–326

Murphy P W and Doncaster C C 1957 A culture method for soil microfauna and its application to the study of nematode predators; *Nematologica* 2 202–214

N A S 1969 Principles of plant and animal pest control Vol. III. Insect pest management and control; *Nat. Acad. Sci.* Washington 508 pp.

Needham T 1743 A letter concerning chalking tubulous concretions called malm : with some microscopical observations on the fauna of the red lily, and worms discovered in smutty corn; *Philos. Trans. of R. Soc.* 42 173–174, 634–641

Nickle W R 1984 Plant and Insect Nematodes (New York and Basel: Marcel Dekker, Inc.) 925 pp.

Norton D C 1969 *Meloidogyne hapla* as a factor in alfalfa decline in Iowa; *Phytopathology* 59 1824–1828

—— 1978 *Ecology of Plant Parasitic Nematodes* (New York : John Willey & Sons) 268 pp.

—— 1978 Relationships of physical and chemical factors to populations of plant parasitic nematodes; *Ann. Rev. Phytopath.* 17 279–299

——, Frederick L R , Ponchillia P E and Nyhan J W 1971 Correlations of nematodes and soil properties in soybean fields; *J. Nematol.* 3 154–163

Oostenbrink M 1966 Vermeerdering van plantanaaltjes op de geschade plant; *Tijdscher Plantenziekten* 72 208–209

—— 1972 Evaluation and integration of nematode control methods; in *Economic Nematology* ed. J M Webster (London: Acad. Press) pp 497–514

Peters B G 1961 *Heterodera rostochiensis* population densities in relation to potato growth; *J. Helminth.* R T Leiper Suppl. 141–150

Prasad D and Haque M M 1982 Reaction of varieties of marigold against root-knot nematode, *Meilodogyne incognita*; *Indian J. Nematol.* 12 35–41

Prasad N and Mankau R 1969 Studies on a sporozoan parasite of nematodes; *J. Nematol.* 1 141–150

Prasad S K and Dasgupta D R 1969 A preliminary field trial on the effect of sesamum intercropping on the population development of plant-parasitic nematodes; (Abst.) *First All India Nematol. Symp.*, New Delhi, India p 66

Ram K and Gupta D C 1982 Efficiency of plant leaves, nematicides and fertilizers alone and in combination against *Meloidogyne javanica* infecting chickpea (*Cicer arietinum* L.); *Indian J. Nematol.* 11 221–225

Rao M S 1984 Studies on the survival of *Heterodera avenae* cysts under different storage conditions. M.Sc. Thesis, IARI, New Delhi 43 pp

Rohde R A 1972 Expression of resistance in plants to nematodes; *Ann. Rev. Phytopath.* 10 233–252

Roberts P A, Van Gundy S D and M C Kinnerey H E 1981 Effect of soil temperature and planting date of wheat on *Meloidogyne incognita* reproduction, soil populations and grain yield; *J. Nematol.* 13 338–345

Rodriguez J G, Wade C F and Wells C N 1962 Nematodes as a natural food of *Macrocheles muscaedomesticae* (Acarina: Macrochelidae), a predator of the housefly egg; *Ann. Ent. Soc. Am.* 55 507–511

Ross J P 1959 Influence of resistance to *Heterodera glycines* on soybean yield and nematode population; *Phytopathology*, 49 319

Rossner J 1979 Influence of continuous monoculture and weed control measures on population density of migratory root nematodes; *Zeits. Pflanzen. Pflanzenschutz.* 86 257–265

Sayre R M 1969 A method of culturing a predaceous tardigrade on the nematode, *Panagrellus redivivus*; *Trans. Am. Microsc. Soc.* 88 226–274

—— 1971 Biotic influences in soil environment; in *Plant Parasitic Nematodes Vol. I.* eds. B M Zuckermann, W F Mai and R A Rohde (New York : Acad. Press) pp 235–256

Schacht H 1859 Ueber einige Feinde und Krankheithen der Zuckeriibe; *Zeitscher ver Rubenzerker Ind Zoolver* **9** 390

Seinhorst J W 1965 The relation between nematode density and damage to plants; *Nematologica* **11** 137–154

—— 1968 A model for the relation between nematode density and yield of attacked plants including stimulation at low densities; (Abst.) *Int. Symp. Nematol.* (8th) Antibes, Sept. 8–14, 1965 p 83

—— 1970 Dynamics of population of plant parasitic nematodes; *Ann. Rev. Phytopath.* **8** 131–156

Seshadri A R and Sethi C L 1978 Nematode problems; in *Wheat Research in India* 1966–1976 ed. P L Jaiswal (New Delhi : ICAR) 244 pp

Sethi C L and Gaur H S 1984 Role of ecology in nematode population management tactics in agricultural production systems; in *Progress in Microbial Ecology* eds K G Mukerji, V P Agnihotri and R P Singh (Lucknow: Print House (India)) pp. 413–428

Shepherd A M and Clark S K 1973 An intracellular microorganism associated with tissues of *Heterodera* spp; *Nematologica* **19** 31–34

Singh R S and Sitaramaiah K 1970 Control of plant parasitic nematodes with organic amendments; *PANS* **16** 287–297

Smith R F 1978 History and complexity of integrated pest management; in *Pest Control Strategies* eds. E H Smith and D Pimental (London·/New York: Acad. Press) pp. 41–53

Suatmadji R W 1969 Studies on the effect of *Tagetes* species on plant parasitic nematodes; *Sticht. Fonds Landbouw. Export Bur. Publ.* **47** Veenman and Zonen NV, Wageningen. 132 pp.

Thorne G 1940 *Dubosquia penetrans* n. sp. (Sporozoa, Microsporidia Nosematidae), a parasite of the nematode *Pratylenchus pratensis* (de Man) Filipjev; *Proc. Helminth. Soc. Wash.* **7** 51–53

Van Gundy S D, Mc Elroy F D, Cooper A F and Stolzy L H 1968 Influence of soil temperature, irrigation and aeration on *Hemicycliophora arenaria*; *Soil Sci.* **106** 270–274

——, Perez J G B, Stolzy L H and Thomason I J 1974 A pest management approach to the control of *Pratylenchus thornei* on wheat in Mexico; *J. Nematol.* **6** 107–116

Vijayalakshmi K, Gaur H S , Goswami B K and Mishra S D 1984 Effect of soaking seed in extracts of oil-seed cakes and plant leaves on the germination of chickpea and its vulnerability to the root-knot nematode; (Abst.) *Nat. Symp. Soil Pest and Soil Organ.*, BHU., Varanasi, India, Oct. 29–31, 1984. pp. 71-72

Wallace H R 1963 *The Biology of Plant Parasitic Nematodes* (London: Arnold)

—— 1971 The influence of the density of nematode population on plants; *Nematologica* **17** 154

—— 1973 *Nematode Ecology and Plant Disease* (London : Edward Arnold) 228 pp

Weber A P, Zwillenberg, L O and Van der Laan 1952 A predaceous amoeboid organism destroying larvae of the potato root eelworm and other nematodes; *Nature* **169** 384–385

Webster J M 1972 Nematodes and biological control; in *Economic Nematology* ed. J M Webster (London: Acad. Press) pp. 469–496

—— 1982 Not nematodes alone — or, integrated pest management to a nematologist; *Agric. Forestry Bull.* **5** 31–35

Whitford W G, Freckman D W, Santos P F, Elkins N Z and Parker L W 1982 The role of nematodes in decomposition in desert ecosystems; in *Nematodes in Soil Ecosystems* eds. D W Freckman and J A Wallwork (Univ. of Texas Press) pp 98–116

Wiese M V 1982 Crop management by comprehensive appraisal of yield determining variables; *Ann. Rev. Phytopath.* **20** 419–432

Wilfrath N and Wimmer G 1903 Untersuchurgen tiber die Wirkung der Nematoden auf Etrag and Zusammen setzung der Zuckerruben *Ztschr*; *Deusche Zuckerindustrie* **53** 1–41

Winslow R D 1960 Nematode ecology; in *Nematology* eds. J N Sasser and W R Jenkins (Univ. North Carolina Press, pp. 341–415

Yeates G W 1981 Nematode populations in relation to soil environmental factors —A review; *Pedobiologia* **22** 312–388