THE ROLE OF CROPPING SYSTEMS IN NEMATODE POPULATION MANAGEMENT

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Introduction

Crop rotation is one of the oldest and most important approaches to the control of nematodes that feed on the roots of annual crop plants. The value of rotations often was recognized long before their effects upon the dynamics of nematode populations and communities were considered. As specific nematode problems were identified and their economic importance demonstrated, attention usually was given to crop rotations as a means of either preventing or reducing crop losses attributed to these pests. In many cases, crop rotation became the conventional method for nematode control and was readily accepted by growers because they previously had been introduced to such management practices as a means of improving soil fertility and crop productivity.

Early rotation schemes were aimed at the control of a single nematode species on a susceptible main crop. They were developed empirically on the basis of knowledge of nematode life histories and host ranges. Field experiments involved the selection of suitable alternate crops and determination of the number of seasons between main crops needed to obtain the desired degree of control. Evaluation of cropping systems was based mainly upon measurements of root disease severity in, and performance of, the main crop at the end of its growth season. Little, if any, attention was given either to the performance of rotation crops or to effects upon nematode populations. Bessey (5) found certain cropping systems to be effective in controlling root knot in susceptible vegetable crops. He concluded that success depended upon how well the rotation crops met these requirements: (*a*) prevent development and reproduction of the parasite; (*b*) at least pay the expense of working the land, as well as rent, taxes, etc.; (*c*) enrich the land or at least not impoverish it; and (*d*) make such vigorous, dense growth as to choke out root-knot susceptible weed hosts. He also recognized certain difficulties and limitations. Because of the wide host range of root-knot nematodes, the choice of alternate crops was limited and many of the most effective crops available could contribute little to farm income. Although these concepts were formulated over 60 years ago, they still apply to the development and evaluation cropping systems for specific nematode problems and land use practices.

In principle, crop rotations are adaptable to a wide variety of nematode problems and offer great flexibility in application. Potential benefits, however, have not always been fully achieved in farming practice. The endemic, complex, variable, and insidious nature of nematode problems often made it very difficult for the farmer to assess their importance and to take proper remedial measures. Crop rotation is only one of the several approaches to control, and its popularity with growers tends to wane as crop production methods intensify due to advances in agricultural technology. For example, when the use of nematicides becomes economical, rotation may be abandoned (53). The development and use of nematode-resistant cultivars may have a similar effect. Crop rotation, chemical treatment, and host resistance are complementary methods. If one should prove to be adequate, however, the others may seem to be superfluous. Reliance upon single methods and limitation of options may have certain temporary economic advantages but can hardly be expected to provide a satisfactory long-range solution. Consequently, increasing attention is being given to the integration of control methods designed for efficiency, reliability, and stability.

Modern concepts of pest management (59), ecosystem analysis (82), nematode population dynamics (68), and nematode control strategy (83) reflect the current trend toward improved pest control within the context of a productive and wholesome environment. Communities of plant parasitic nematodes, as an integral part of the ecosystem, are responsive to environmental factors including those influenced by man. The roots and/or rhizospheres of suitable host plants comprise the ecological niches in which plant-parasitic nematodes develop and reproduce. Food supply, therefore, is one of the most important determinants of seasonal and annual changes in the population structure, density, and distribution (49). In agroecosystems, the food supply is governed largely by the cropping practices employed by the grower and is subject to periodic manipulation. Hence, consideration of cropping effects is basic to any scheme of nematode-population management regardless of the nematode species or crops involved. Management, as used here, implies the integration of various man-imposed actions with those of the ecosystem (60) in reducing and regulating nematode populations. As additional, precise knowledge is acquired on the dynamics of nematode populations in relation to the epidemiology of root diseases involving these pests, effective use of cropping systems in integrated control programs will be enhanced. The term "cropping system" covers all kinds of crop sequences, including continuous monoculture, whereas, "crop rotation" implies an inflexible cycle or a fixed series of crops.

Nematodes Populations and Communities

Root-feeding nematodes of a given species exist and function as members of a reproducing population. Most soils, especially cultivated soils, harbor a mixture of nematode species. The species comprising each community may represent a broad spectrum of types with respect to their behavior, parasitic habits, and effects upon their hosts. Several descriptive categories are recognized. Some species are sedentary during developmental and reproductive periods, whereas others are migratory. Endoparasites enter the roots, ectoparasites remain outside the roots and feed in epidermal and cortical tissues, others are intermediate. Like other kinds of parasites, nematodes cause injury to their hosts by their feeding activities. Many nematodes, however, alter host metabolism and, acting either alone or in combination with other kinds of root pathogens, cause far greater damage than can be accounted for by the mere withdrawal of food substances (49). Some species multiply continuously during active periods, whereas others reproduce in separate generations. In addition to these diverse characteristics, efficient dispersal, polyphagy, relatively weak interspecific competition, and great persistence largely account for the occurrence of nematodes in complex, dynamic communities (46, 51, 52).

The community of plant-parasitic nematodes is an integral part of a complex of soil-inhabiting microorganisms which forms a vital subsystem within the whole ecosystem. Since the individual populations comprising the community occupy the same microhabitat and often rely upon the same sources of food, they tend to coexist in either the same or overlapping ecological niches. Odum (50) defined a niche as a position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior. According to Gause's Principle (22) species occupying the same niche are competitively exclusive; one species would be better adapted to exploit the niche and the other eliminated. An endo- and an ecto-parasitic nematode feeding upon the same root system occupy niches that are spatially separated; however, they could influence each other since both are dependent upon the same food source. Oostenbrink (52) noted that the concept of the niche may be broad or limited and that the principle of competitive exclusion does not always hold for nematodes. Even so, there is evidence that interactions between species occur in various ways and to varying degrees (12, 13, 20, 21, 29, 31, 32, 43, 44, 64, 69). In general, the highly specialized, sedentary endoparasites appear to occupy niches that are more narrowly defined than those occupied by the migratory ectoparasites which have relatively broad host ranges and tend to provoke less host response. When mixed populations of root-knot nematodes occupy the same niche, one may be better adapted to exploit it than the others (12, 37). Although the interaction mechanisms and the ecological significance of the associations among nematode species are not well understood, the cropping systems employed largely determine the structure of the communities in which they occur.

Ecosystem Stability

The composition of nematode communities and the dynamics of populations comprising them are related to the degree of stability of the ecosystems in which they function. Stability implies the capacity of the system to return to a mean position following disturbance, the mean itself moving in a direction consistent with the development of the system (72). The greater the stability, the more rapid is the return. An absolutely stable ecosystem would remain constant. Preston (58) considers the stability of pest populations in terms of extinction of a species on the one hand and its rise to plague proportions on the other. Fluctuations between these limits represent a more or less stable system. In natural or undisturbed ecosystems, stability is achieved by genetic, structural, and functional diversity of component communities; equilibrium or homeostasis is maintained effectively because of the variety of ecological niches available to species of organisms at all trophic levels (41, 72). Thus the more numerous the kinds of organisms, the greater their numbers and the shorter their generation time, the more associative, competitive, and antagonistic interactions will occur to check unrestrained multiplication and to maintain balance (86). In such ecosystems, therefore, populations of the various species comprising the nematode community should exhibit stability in terms of density fluctuations and genetic constitution, being buffered and governed by dynamic interactions with other components of the system (45).

Agroecosystems, in contrast to natural ecosystems, lack continuity, diversity, and stability (71, 86). Uniformity is usually the goal in agroecosystems. Most cultivated crops consist of the same or similar genotypes within a single species; thus they lack intraspecific diversity. Plant population density is regulated. All plants are of about the same age, nutrients are supplied, and weeds are controlled. Continuous monoculture, lacking both inter- and intra-specific diversity, is the least complex of agroecosystems and is, therefore, the least stable. The latter practice tends to narrow the community spectrum of plant parasitic nematodes to those species most favored by the host (46, 49, 70). Conversely, the abundance of free-living saprophagous nematodes often is more closely related to the amount of organic matter in the soil than to the type of crop (23). There is considerable evidence that the number of species, biomass, and population densities of plant-parasitic nematodes are greater in cultivated than in noncultivated soils (33, 52, 56, 87). A farm survey in the Netherlands revealed that all cultivated fields were infested with four to six genera of plant-parasitic nematodes (54). Parasitic species tend to flourish in cultivated soils where a vigorously growing food source is available, whereas predaceous and buffering species are more sensitive to the disturbances involved. For example, species of predaceous Mononchidae are abundant in forests, fence rows, and stream banks in Oregon, but they tend to disappear from intensely cultivated areas (30).

Outbreaks of pests and diseases, where the population of the pest or pathogen species fluctuates beyond the bounds of dynamic equilibrium, are a common feature of agroecosystems (27, 71). Moreover, unstable ecosystems are more responsive to environmental changes than stable ones. It appears that the nematode communities in cultivated soils lack the biological checks that govern them in undisturbed ecosystems (34, 45).

Although intensive agriculture invites upsets in ecological balance and increases the threat of ubiquitous soil-borne pathogens, crop production would be impossible without the complexity of soil microbial communities even in these disturbed ecosystems (86). Moreover, agroecosystems are stabilized to varying degrees by human inputs. Skillful labor, powerful machines, financial resources, and an array of management systems are employed to modify certain environmental factors and to reduce the danger of pest and disease outbreaks (23, 41, 42, 72, 73). Thus it is possible to maintain or increase crop productivity while encouraging suitable diversity and stability in the ecosystem. In many modern agricultural regimes, stability is being approached, but the cost of man's inputs and their ecological consequences often are limiting factors. When arable lands are not cropped they revert to natural vegetation and the pest communities become increasingly complex and stable (41), but return to a balanced state may require a period of several years.

The attainment and maintenance of stability of root-knot nematode (*Meloidogyne* spp.) populations by human input is well illustrated by the culture of flue-cured tobacco in North Carolina during the past 20 years. In the early 1950s estimates of annual losses due to root knot in this intensively cultivated, high-value crop exceeded $50 million or approximately 10% of the value of the crop. Crop failures due to root knot were not uncommon. An intensive survey by counties showed that an average of 54% of the growers practiced continuous monoculture, whereas 27% used rotation crops occasionally, and the remaining 19% rotated consistently. The use of nematicides was just beginning; fewer than 1000 acres were fumigated in 1951. Yields averaged about 1200 Kg per hectare (= lbs. per acre). The situation has changed drastically since that time. Tobacco is rotated with other crops on more than 85% of the acreage and over 65% of the crop is grown in fields treated with nematicides. Losses due to root knot have declined to less than $5 million annually (76). Average yields have nearly doubled due to improved disease control and production technology. These gains were achieved, however, by considerable investment in both research and educational programs and by increased production costs. Even so, root knot is still a major problem requiring continued, costly inputs by man just to maintain the gains that have been made. Crop production may become unprofitable when yields are limited by a nematode population that is favored by intensive culture (36). It may become profitable, however, where the crop is valuable enough to justify costly control procedures (15).

Nematode-Host Relationships

In considering the use of cropping systems for nematode population management, the interactions between the various nematode species and host plants involved is of primary importance. In each parasite-host combination, characteristics of the nematode may be defined in terms of its parasitic efficiency, i.e. its ability to obtain food from its host, and its ability to cause damage, i.e. its pathogenicity. Host status refers to the suitability of the plant to serve as a substrate for the parasite and its relative vulnerability to damage. All features of this interaction, being interrelated and influenced by environmental factors, comprise a complex, dynamic system. In a recent review, Seinhorst (68) presented the status of quantitative research on the populational aspects of these systems. He has developed concepts and mathematical models that describe the dynamics of nematode population increase and the relationships between nematode density at the time of planting and plant yield.

The status of a crop with respect to a particular nematode species may be defined (67) in terms of a (the maximum reproduction rate of the nematode on that crop) and E (the equilibrium density). The multiplication rate slows with increasing population density until an equilibrium density is reached at which multiplication just suffices to maintain the population density. Relative vulnerability to damage may be determined experimentally by subjecting test plants to a wide range of initial population densities and recording the threshold of tolerance (T), i.e. the density below which no apparent yield reduction occurs. These concepts, considered together, encompass both the susceptibility and tolerance of the crop to a nematode species or pathotype. They are thus indicative of the nematode population changes and crop damage which might be expected under a particular set of environmental conditions. The characterization of crop cultivars in terms of E and a for each nematode species and under various environmental situations then becomes invaluable in planning cropping systems for nematode population management. Since E and a are not necessarily correlated with T, knowledge of the latter is also important (68).

Basically the principles of crop rotation for population management are: (*a*) the reduction of the initial or preplant population densities (P_i) of nematodes to levels that allow the subsequent crop to become established and to complete its early growth before being heavily attacked, and (*b*) to preserve competitive, antagonistic, and predaceous nematodes and other organisms at population densities effective in buffering the pathogenic species. The rate of population increase and damage caused by a nematode species is influenced by P_i, a and E for the particular crop, soil community structure, environmental conditions, and time. The initial population density (P_i) is determined by the final density (P_f) of that species at the end of the preceding crop and the mortality rate between crops. Time alone may account for a considerable population reduction through starvation; however, many species are very persistent even over long periods in fallow soil; also in modern intensive agriculture the period between crops is being reduced progressively (7, 61). A low P_i may be achieved by the use of a preceding crop that either is not a host or has a low a or E, and/or by cultural practices and chemical treatments applied between crops. Thus, turning roots onto the soil surface (48, 75), flooding (15, 23), repeated discing to expose the nematodes to the elements (23) are often effective in decreasing nematode populations.

Also, P_i may be reduced by growing cultivars with vertical resistance to the pathogen (80). Vertical resistance is the type involved in most crop varieties into which nematode resistance has been incorporated (26, 28, 63). In this case the initial population is unable to establish a successful relationship with the host plants and is thus reduced. There is a need for caution with this type of resistance due to the intense selection pressure for a vertical pathotype (62, 80). Reduction of the multiplication rate (a) of the pathogen can be achieved through the use of cultivars with effective levels of horizontal resistance (62, 80). Thus, corn hybrids differ in their suitability for species of root-knot nematodes and *Meloidogyne* populations vary in their ability to reproduce in corn roots (1, 2, 47). Because nematodes respond to selection pressure there is a need for caution when horizontally resistant cultivars are used frequently (2, 65) but the danger is not as great as with vertical resistance (35, 62, 81).

The equilibrium density (E) should be considered in conjunction with a, as the overall host status is the determinant of the value of a particular cultivar in a cropping system. Using the categories of host status of Dropkin & Nelson (19) a tolerant host would have a high E value; even if a is low due to horizontal resistance, a crop may be able to support a large nematode population. In this case density-dependent factors governing population increase would not markedly suppress the rate of increase until high densities have been reached. Alternatively, in a susceptible crop where a is large,
is intolerant, i.e. has a low E value,
the multiplication rate at low densities so that the rate of population increase slows down early in the season and P_f is low.
considered in relation to subsequent crops in the rotation.
crop with a low E would result in a lower P_f than a tolerant crop with high E value and so favor the subsequent crop.
rotation system would be economically unsound. The effect of a crop on nematode population densities is also governed by time of exposure.
planting, and the use of early varieties that can become established before conditions are suitable for nematode activity, are frequently recommended (16, 24, 25, 79, 83). Similarly the removal of roots from the soil immediately after harvest may prevent continued reproduction of the nematode and result in a lower P_f, thus favoring the subsequent crop (48, 75).

Although environmental conditions affect nematode populations directly in many ways, indirect effects of host plants on nematode population are perhaps even more profound. Such factors affect plant vigor and thus influence the values a and E which, in turn, are reflected in P_f and plant damage. This may be explained in terms of stress. The plant as a whole is a complex organism comprised of several kinds of organs each of which performs specific functions. All functions, however, are interrelated and interdependent. Root dysfunction caused by nematode attack often impairs the functioning of other organs, thus creating internal stresses. Such stresses may be either ameliorated by environmental conditions favorable for plant growth (85) or intensified by external environmental stresses. Bessey (5) noted that yields of root-knot susceptible crops were markedly increased following certain rotation crops even though the incidence of root galling was not reduced appreciably.

Man has considerable influence on the environment in agroecosystems. The nutrient status of the soil may be altered by the addition of fertilizer. Large amounts of potassium allow cotton to withstand root-knot stress even though the P_f is increased (55). Similarly Bird (6) showed that the P_i at which the plant growth rate was slowed was greater on plants grown with full nutrients than on nitrogen-deficient plants. But *Pratylenchus scribneri* populations were higher in soybean and cotton plots receiving no fertilization than in plots receiving all major elements (14). The rate of development of *M. incognita* was retarded in plants with nutrient deficiencies (18). Man is able to influence soil temperature by plant spacing and soil shading, as well as by irrigation. The amount of oxygen present under *Eragrostis curvula* may be decreased to cause inhibition of *Meloidogyne javanica* (38). Some crops may rapidly deplete the soil of moisture, directly affecting nematode populations; others form a dense cover and reduce evaporation from the soil surface. Soil moisture may be further regulated by irrigation and land drainage, thus reduced irrigation may prevent hatching of root-knot eggs and so reduce reinvasion of the host (83).

Epidemiological Considerations

Root-feeding nematodes damage their hosts and produce symptoms of disease in various ways and to varying degrees. Through their pathogenic activities they also may change the reaction of the host to secondary pathogens (57) which in turn may alter the disease syndrome. When disease increases in a population of host plants, an epidemic is in progress, and theoretically its course is subject to epidemiological analysis. Van der Plank (80) has quantified the science of plant disease epidemiology. He has described mathematically the dynamics of disease increase and spread where appropriate measurements can be made throughout the course of an epidemic, particularly during the early logarithmic phase of the epidemic curve. The number of lesions increases logarithmically until the available infection sites are reduced to an extent that slows the infection rate or results in significant reinfection of established lesions. In the case of systemic infection the individual diseased plant is considered a lesion and the group of infected plants in an area is a focus of disease. Similar concepts of logarithmic increase apply to foci, again until they begin to expand into each other. The dynamics of these increases depend not only on the initial amount of viable inoculum, but also upon the number of available infection sites at the time of initial exposure and at times of reinfection, i.e. the proportion of noninfected tissue (1-x) where x is the proportion of tissue already infected. The quantity (1-x) will increase or decrease depending upon whether the tissue is being infected faster than it is being produced by the growing crop.

In the case of nematodes, the host-parasite interaction takes place below the soil surface and, with some exceptions, pathological processes do not occur in easily recognizable, measurable lesions or units. Even so, it is often possible to study the dynamic aspects of such interactions by periodic measurement of nematode population densities and plant growth responses. Much progress has been made in the development of methods for determining the relationships between P_i and crop performance (68) and information thus obtained is the basis for the establishment of nematode diagnostic and advisory services (4). Van der Plank (82) emphasized the need for measuring the whole epidemic or population dynamic process from start to finish. Although this presents many difficult problems for the phytonematologist, Van der Plank's system of quantitative epidemiology provides certain concepts that are important in developing strategies for nematode population management. A better understanding of the complex patterns of root development and the effects of nematodes upon root morphology and function is needed. The development of roots and shoots is clearly interdependent but not necessarily parallel (40).

Application of modern epidemiological concepts in nematology may be illustrated by situations in which the nematodes invade and develop in specific infection sites (such as root tips), establish specialized relationships with host tissues, and cause discrete lesions. Increase in numbers of foci from a single source occurs so slowly that the individual plant can be considered as a noninfectious or slightly infectious focus. The lesions are then the infected sites within the focus (root) and a given problem area is a group of such foci. If P_i is low, then (1-x) at the beginning of the season will be large and the plant will grow vigorously. If the plant growth rate is greater than the rate of production of propagules by the nematode, (1-x) will remain large and growth will not be inhibited. As root growth ceases with senescence, so (1-x) will become smaller until all available sites are infected or intraspecific competition decreases to a minimum the rate of increase of the nematode population. By this stage the crop may have reached maturity.

The value (1-x) affects not only the dynamics of crop growth, being the amount of root available to supply the plant with nutrients and water, but also the nematode population dynamics as a measure of the number of sites available for infection. Increase in lesion number ceases to be logarithmic once reinfection of established lesions is occurring. This reduction is probably also influenced by decreased growth rate and reproduction by the competing nematodes, and by increased production of males in some nematode species (17, 39, 77, 78). The number of available infection sites and the initial population density both will be involved in determining the initial value of (*1-x*). Anything that can be done to increase (*1-x*) will favor the plant. Thus, the establishment of healthy seedlings with vigorous root systems, the use of horizontally resistant cultivars in which the rate of infection and nematode development is reduced, use of fertilizer and irrigation, enhancement of nematode competitors and antagonists, or the use of nematicides, will all allow (*1-x*) to remain large and the plant to grow vigorously. Conversely, if conditions favor the nematode, (*1-x*) will decrease, and although this will slow nematode increase it will also depress plant growth rate and yield.

A simplified equation for the rate of increase of infected areas on the root would be $dx/dt = rP(1-x)$ where dx/dt is the rate of increase of infected tissue at any point in time, *t;* r is the maximum infection rate of the nematodes under ideal conditions; P is the number of nematodes available for infection at time *t:* (*1-x*) is the proportion of root tissue still available for infection. At the beginning of the season the seedling has no infected tissue, thus, $x = 0$ and infection will occur at a maximum rate if environmental conditions are ideal. As x increases, (*1-x*) will be less than unity and have a slowing effect on the infection rate dx/dt. If the root is still able to grow rapidly, the proportion x may remain small so that the effect of (*1-x*) on the infection rate is negligible. If the proportion of the root infected increases, (*1-x*) will decrease so that the rate of subsequent infection will decrease. The factor (*1-x*) can also be considered as having a direct effect on the plant growth rate and on the nematode reproduction rate. When $x = 0$, plant growth will proceed at a maximum under prevailing conditions; it will slow down if (*1-x*) decreases appreciably. Subsequently, reproduction also will decrease. Thus there are two dynamically interacting components in this simplified system, the nematode population and the roots, each reciprocally affecting the other through the amount of root tissue infected. If conditions are sub-optimal for the nematodes but favorable to the plant, (*1-x*) will remain large and plant growth rapid. Nematode increase will be limited by environmental conditions rather than availability of infection sites. If environmental conditions favor the nematode, reproduction and infection by the nematode will be influenced only by the size of (*1-x*) as it affects infection site availability and plant growth vigor. Integrated control seeks to maximize (*1-x*) by providing conditions optimal for plant growth and sub-optimal for the nematode population.

Knowledge of the sequence and timing of events can be employed to determine the critical periods during the course of an epidemic. Using studies of root knot of flue-cured tobacco in North Carolina as an example, the following pattern emerges. In most infested fields, preplant densities of infective larvae are too low to damage young transplants appreciably and the value (*1-x*) remains near unity during May and June. During the first two months the host plants grow rapidly while the increase in numbers of galls declines as the initial inoculum becomes exhausted. In early July the situation begins to change as reproduction by first generation females reaches a peak resulting in about a 1000-fold increase in nematode numbers. Thus, it appears that this is a critical period in the epidemiology of root-knot because it comes at a time when the value (1-x) is reduced due to natural decline in host plant vigor and to a great increase in nematode population density. It is the time when the future course and the final outcome of the epidemic are determined by whether the threshold of host tolerance (66) is exceeded and, if so, to what extent. This emphasizes the importance of P_i, the initial population (inoculum) from which the epidemic starts. Presumably, under conditions favorable for larval penetration and nematode development, initial infections x_0 will be proportional to P_i and subsequent increases in x will be related to the value of x_0. Traditional nematode control strategy, therefore, has been aimed at reducing P_i below the economic threshold. Although considerable progress has been made in applying knowledge of nematode population dynamics to the determination of economic threshold values (52, 68), this remains one of the major challenges in population management. When complex cropping systems are employed, especially those involving several kinds of crops, this problem becomes magnified. The occurrence of plant parasitic nematodes in mixed communities, changes in community composition, and fluctuations in population densities of the individual species must be taken into account.

The magnitude of the fluctuations about the mean is important to agroecosystems. Pest or pathogen populations may oscillate above economic threshold densities in unstable situations. With continuous cropping of potatoes, population oscillations of *Heterodera rostochiensis* were large at first but decreased to an equilibrium at which intermediate root size was balanced by intermediate density and P_f/P_i approached unity (36). Thus, a stable situation was reached with plant growth limited by the nematode population and vice versa. Relief of other stresses on crop growth, e.g. soil moisture or fertility, might again unbalance the system by allowing increased plant growth and hence fluctuation of the nematode population above the equilibrium density for the next season (6, 85). The economic threshold density will vary with the amount of stress the plants are under and with their age, more vigorous plants being able to support more nematodes (6, 85). It is probably unnecessary to keep the population low throughout the season; the financial and environmental costs involved would outweigh the benefits derived. A more efficient practice would be to keep densities low while the crop is young and intolerant by using crop rotation, cultural manipulations, and changes in planting time (10, 83).

Crop Selection

Species of plant-parasitic nematodes generally have overlapping host ranges and differ in their sensitivity to environmental manipulation. Many of the ecological features of agroecosystems can be altered by cultural practices and cropping systems, such alterations having both direct and indirect effects upon nematode populations and communities. Although such practices usually provide considerable flexibility in most agricultural regimes, selection of crops may be limited by land use and economic considerations (11). Thus compromises often are dictated by knowledge of both the advantages and limitations of any particular course of action. The achievement of as much intra- and interspecific diversity as possible either in space or in time, is desirable. This may be accomplished by growing multiline varieties, rotating crops, changing cultivars, or "rotating the rotation" to different alternate crops. Multiple cropping in areas having long growing seasons adds organic matter to the soil, increases the cycling of nutrients, and improves soil structure. All of these practices tend to decrease population densities of nematodes on a crop of a particular genotype.

A cropping system should be selected so that one crop does not produce a population of nematodes larger than the economic threshold density of the succeeding crop in the system. Thus, Brodie et al (9), in studying grass-sod and row crop sequences, determined that corn and cotton should not follow each other in soils infested with the sting nematode, *Belonolaimus longicaudatus.* In a tobacco rotation experiment conducted at Rocky Mount, North Carolina from 1954 to 1966, six crops were used in various combinations and sequences based upon 4-year cycles. In each cycle, two different alternate crops were used with tobacco, such as tobacco-corn-tobacco-peanut. The overall nematode community included 9 plant-parasitic species representing 7 genera. After the first cycle of cropping was completed, patterns of community spectra within each system were fairly well established. Although the community structure within each system changed each year, the spectrum was stable and fluctuations of populations within each community were somewhat predictable. Although the community spectrum in each rotation system remained fairly broad (5 to 6 species of plant parasites), that within continuous monoculture plots of either tobacco, cotton, corn, or peanut had only 2 or 3 species. In all cases the stabilizing effects of the rotations benefited the alternate crops as well as tobacco.

Another factor to be considered in crop selection pertains to the effects of crops upon genetic variability within populations of plant parasitic nematodes. The problem of "genetic vulnerability" is beyond the scope of this review, but brief mention seems appropriate. Cropping systems can exert selection pressures upon nematode populations to such an extent that "resistance-breaking" pathotypes can emerge and reduce the effectiveness of the system. Jones et al (35) advocate the rotation of resistant and susceptible cultivars of potato to avoid an intense selection for resistance-breaking pathotypes of *Heterodera rostochiensis.* Populations of *Meloidogyne incognita* initially were suppressed by corn in a tobacco-corn rotation; later they responded to the selection pressure and reached high densities on both crops, negating the value of the cropping system (2, 65). When resistance-breaking pathotypes emerge as the result of selection pressures favoring them, they still may remain at low levels for a period of years as a minority component of the population, gradually building up to damaging proportions. Thus, although the problem of genetic vulnerability with nematodes may not be as serious as with pathogens that spread far and fast, nevertheless, valuable sources of resistance may inadvertently be lost through the continued use of injudicious cropping systems.

Outlook

Concepts of pest management provide a wide variety of options in devising long-range solutions to pest problems (59). They are aimed at the regulation rather than the elimination of pest populations. Strategies and approaches are based upon an understanding of the life systems of pests and upon predictable ecologic and economic consequences (59). Crop rotation is one of the options in regulating nematode populations, but its greatest potential undoubtedly lies in the role it may play in integrated control programs of the future (83). As crop production becomes more intensive, empirical approaches of the past no longer will suffice. Use of crop rotations will be determined by their relative value in complementing other practices in total management systems that are effective, economical, and ecologically sound. Within this context, an appraisal of the present status and future prospects seems appropriate.

POPULATION DYNAMICS The characteristics and behavior of the major species of plant-parasitic nematodes are well understood. Seinhorst (68) has indicated, however, that studies of nematode population dynamics have been minimal. This also applies to the epidemiology of root diseases caused by nematodes and allied root-infecting pathogens. Last (40) observed that the reasons for our inadequate knowledge of soil-borne pathogens can be found in the root pathologists' prediliction for single, end-of-the-season observations; and that, to an extent, such investigators have adopted a fixed attitude to their problems and have not developed with the times. In phytonematology, marked changes in attitudes and approaches are evident (68, 83) and encouraging but they also bring deficiencies and difficulties into sharper focus. As Van Gundy (83) observed, predictions of disease potential are based upon knowledge of pathogen population dynamics and the techniques for establishing economic thresholds. This can be done in the relatively few nematode problem areas where advisory services are well established (4). Accuracy of predictions depends largely upon the reliability of the nematode assay data on which they are based. Wide variations in horizontal (3) and vertical distribution of nematodes in the soil create serious sampling problems (4). Assay procedures are often too insensitive to measure populations prior to planting or the infectivity of the nematodes present. Thus, refinement of sampling and assay techniques will play a major role in the determination of economic thresholds.

ECOLOGICAL CONSEQUENCES Crop rotations, in contrast to continuous monocultures, would be expected to have desirable effects upon agroecosystems because they tend to increase diversity and stability. Although reduction and regulation of nematode populations may be the primary purpose, rotations also may have many intangible side effects. In general, the greater the diversity of crops, particularly if sod crops are interspersed with row crops, and the longer the interval between main crops, the greater the stability. Thus, the need for other kinds of stabilizing inputs is reduced. Where relatively short rotation cycles (2 or 3 crops) are used, stability can be increased by changing periodically either the alternate crops or the cultivars of the main crop, or both. Without careful selection of a cropping system, soil-improvement benefits may be negated by increases in nematode populations (8). Thus the selection of the proper sequence is as important as the choice of the crops. From the viewpoint of soil conservation and the efficient use of land resources as well as pest control practices, available options should be flexible enough to employ a prescription approach to decision making (74).

ECONOMIC CONSEQUENCES In many nematode problem areas, crop rotation is the best, if not the only, economic means of control, largely because nematode-resistant cultivars are not available and crop values are too low to justify costly treatments. In areas of intensive crop culture, however, this practice is in jeopardy for economic reasons. Most nematologists undoubtedly agree with Van Gundy (83) that regardless of how successful crop rotation is and can be, it may never survive the technological revolution in agriculture unless grower attitudes can be changed. Where farms are located near major urban areas, some of the best agricultural lands are taken out of production as they are diverted to other uses. Because of shortages of skilled farm labor, increased wages, and increased consumer demands for farm products there is a marked trend toward consolidation and centralization of operations into more productive and efficient units. Plant breeders have developed high-yielding cultivars of major food and fiber crops, but, in doing so, they have reduced genetic and cytoplasmic diversity. If these trends continue, long-range management of populations of nematodes and other soil-borne pathogens will require increasingly large inputs in terms of machines, energy, and chemicals at the risk of compromising still further the stability of agroecosystems.

INTEGRATED CONTROL Because the cropping system is the dominant feature of agroecosystems, it is the foundation upon which integrated pest management systems rest. In the selection of crops and their sequence, ranging from continuous monoculture of a single cultivar to complex, long-term rotations, various degrees of ecosystem diversity in time and space can be obtained. In a broad sense, cropping systems exert a major influence on the dynamics of the whole complex of pests detrimental to plant health and crop productivity. For example, a well designed crop-rotation experiment may provide material for analytical study not only of nematode populations but also of other soil pathogens, soil insects, and weeds. This emphasizes the interdisciplinary nature of pest management, especially where different kinds of pests interact with each other and where a given management practice affects more than one target organism. Hence, the concept of integrated control need not be limited to a combination of complementary practices directed at a single target but rather can be expanded to include pest complexes of varying dimensions. Much progress is being made in breaking down the barriers that impede cooperation between disciplines and agencies. The emergence of broad concepts of pest management and the interest and involvement of all sectors, not only of research and educational institutions, but also of the agribusiness community and the public at large, justify an optimistic outlook.

The ecosystem approach to pest management presents great challenges and opportunities for the future. A stage is being reached where quantification of information on population dynamics of plant parasitic nematodes and the epidemiology of root diseases is possible. Techniques of systems analysis are now being employed in plant pathology (84, 88) and provide a means for synthesizing the wealth of complex information available on integrated control. Models of biological systems are simplifications of the real world and are constructed to assist in its understanding. Simulations based on these models are usually imperfect in predicting the behavior of the system because of knowledge gaps (72, 84). Simulations call attention to these gaps, however, and to interactions between components which formerly were not perceived. The application of systems analysis and simulation in predicting nematode population behavior will provide a better understanding of their role in crop production. It will also aid in planning and evaluating integrated control programs fitting harmoniously into systems of land management designed to maintain the productive capability of the soil (49, 83).

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