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The Future of Nematology: Integration of New and Improved Management Strategies[1]

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Abstract: The potential for managing plant-parasitic nematodes by combining two or more control strategies in an integrated program is examined. Advantages of this approach include the use of partially effective strategies and protection of highly effective ones vulnerable from nematode adaptation or environmental risk. Strategies can be combined sequentially from season to season or applied simultaneously. Programs that have several strategies available but that are limited in the true integration of control components are used as examples of current management procedures and the potential for their improvement. These include potato cyst nematodes in northern Europe, soybean cyst nematode in North Carolina, and root-knot nematodes on vegetable and field crops in California. A simplified model of the impact of component strategies on the nematode damage function indicates the potential for combining control measures with different efficacies to give acceptable nematode population reduction and crop protection. The likelihood for additive, synergistic, or antagonistic effects from combining strategies is considered with respect to the biological target and component compatibility.
Key words: crop loss, cyst nematode, damage function, efficacy, *Globodera pallida, G. rostochiensis, Heterodera glycines,* integrated pest management, *Meloidogyne* spp., population density, root-knot nematode.

The integration of control strategies for managing plant-parasitic nematodes is not a novel concept. Sixty years ago, Tyler (30) proposed that the combination of two or more control strategies into an overall management program is the only sound, sustainable approach to effective root-knot nematode control. She stated that "a well-planned combination of practices will go much farther toward control of nematodes than any of the recommended treatments alone. The value and permanence of any chemical or cultural treatment will be increased if it is followed up by a wet fallow, or by a resistant crop, with particular attention to the control of weeds." This statement has been substantiated generally by subsequent worldwide programs directed at nematode management. The rationale for combining two or more strategies is twofold: i) most present and future control tactics are partially effective and must be combined with additional strategies to be fully effective and acceptable; and ii) most present and future strategies with close to 100% efficacy have poor longevity. This loss in efficacy may arise through nematode adaptability by selection to circumvent the action of control procedures or effects, or through unrelated problems such as environmental imbalance or risk. Because of these potential problems, the need exists to preserve and protect the highly efficacious protocols through combining and integrating control treatments and procedures.

One of the key elements of integrated pest management (IPM) is the systems approach, which addresses different levels of IPM. Using one well-recognized set of definition guidelines for IPM, Level 1 systems research concerns the combining of two or more control strategies to manage one or more species in the same pest group (4).

In this brief discussion, I propose that, despite the considerable research and extension interest and funding in IPM programs, we have advanced little in researching, designing, and implementing nematode management protocol based on combinations of two or more control tactics. Further, because of this shortcoming, effective alternatives to chemical nematicides are limited at best, at a time when nematicide options are diminishing and critical needs exist for alternatives.

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Recent Advances in Nematode IPM

The focus of plant nematode IPM has been a systems science approach to the population biology of these pests. The thrust of this effort has been to research, and in some cases to implement, nematode–crop ecosystem models as inputs for the pest management decision-making process (4,9). The central theme of relating nematode population density (especially initial or preplant densities [Pi]) to relative yield or crop loss has provided the basis for interpreting nematode count data from soil sampling procedures. Such critical point models, when adapted for specific regions, agricultural systems, and local edaphic conditions, have enabled a more rational selection of appropriate nematode control inputs. Thus, treatments can be applied only when justified economically to prevent or limit crop loss. The coupling of economic considerations to damage functions, using crop value and production and nematode control costs, has provided economic threshold information that has been implemented in a few instances (8). Additional research has been conducted on aspects of nematode population biology, including seasonal multiplication rates, winter survival, impact of host plant status, and level of resistance (9 and references therein, 28,33). On perennial crop systems, nematode population–host damage models remain mostly at a theoretical and nonimplementable stage of development (9). One exception, however, is the coupling of nematode population dynamics and infectivity with the seasonal cycles of tree and vine root growth that occur typically in periodic flushes, the timing of which can be used to target nematode control inputs (19).

The predictive modeling of nematode population biology and host phenology has been an important and well-directed effort that has formalized our approach to pest management decision-making. However, during the IPM era, we have avoided requisite research into the actual integration of the control options. Although the need for and the optimal timing of control inputs are critical, what do we have available that is effective? While considerable basic and applied research has been directed at the development of novel control tactics and improvement of existing ones, the approach in almost all cases has been to examine the efficacy of a single, isolated control strategy. Only a few examples exist about the combination of two or more strategies (1,2,8,10,14,16,24,25,28,30,33,35). These shortcomings are further emphasized because the majority of the few studies that have addressed the efficacy of combined strategies were based on individual components previously developed in isolation.

Combined Control Strategies and Tactics

For the most part, the development of control strategies in combinations of two or more, as an integrated management approach, has not been addressed from the outset. Reasons for this failure include reliance on highly effective nematicide treatments and the cumbersome practical difficulty in researching and then implementing combined or integrated management systems. Important consequences have resulted from this lack of a holistic approach to nematode management. A growing gap in availability of effective control programs has appeared, as highly effective soil fumigants and other nematicides have been lost. In the future, this gap will widen and greater yield losses from nematodes will have to be tolerated. Reliance on highly effective single control tactics risks the loss of efficacy because of strong directional selection pressure exerted upon the nematode population. This threat exists for single gene resistance, which is vulnerable to breakdown because of selection for nematode virulence (20,25,29,33,34), and for cultural control tactics such as changing planting and harvest dates (6,28). Chemical treatments at high dosage rates, which are vulnerable because of human safety and environmental risk concerns, are also threatened by selection for resistance in the target nematodes and by selection for enhanced biodegradation by soil microorganisms (19,31). Integration of strategies in combinations should reduce the potential for breakdown in efficacy or for environmental risk.

Application approach: Multiple management strategies can be applied sequentially or simultaneously. The first, temporal approach includes the season-to-season or year-to-year integration of strategies, and is particularly relevant to annual cropping cycles. This approach centers on crop rotation with nonhosts or resistant cultivars or both, to which other control strategies can be added, whether chemical, cultural, or biological. Temporal integration usually involves different control strategies applied in different years and often to different crops vulnerable to the predominant nematode pest. This season-to-season framework often includes a spatial component, because of the rotation and alternation of the primary vulnerable crops on adjacent fields or sites. The few examples of successful attempts at nematode management through combined strategies have been of this type, as discussed subsequently.

The second major approach to integrating control components involves simultaneous application of two or more strategies. This approach may fit the management requirements of both annual and perennial crop production systems. Few examples of this approach have been reported (e.g., 1,16), and studies into its potential have been limited. The research requirements for this approach are significant because they should encompass specific considerations early in the development of control agents and procedures. Although much future research is perhaps more urgently needed in the simultaneous combination approach (because of the unique issues that require resolution, such as compatibility and degree of efficacy), the temporal approach also requires considerable research input.

Current examples

Potato cyst nematodes: Management in northern Europe of the two potato cyst nematode species, *Globodera pallida* and *G. rostochiensis,* has included elements of integrating control strategies with some success (1,28,33). Although the program is one of the best examples of the combined treatment approach, its development has been piecemeal rather than a directed effort from its inception. This disjointed development reflects the emergence of control agents and procedures over many years; the controls were added to the system as they became available, and others were added in when existing controls lost efficacy or failed. As an example, the three strategies of resistance, rotation, and nonfumigant nematicide treatment have been effectively combined in managing potato cyst nematodes in British potato production (1,28,33). Potato cultivars (e.g., Maris Piper) with the major gene *H1* conferring a high level of resistance to *G. rostochiensis* but not to *G. pallida* were incorporated into nonhost rotations with considerable success. Three crops over 9 years decreased the nematode Pi in soil from 100 to <1 egg/g. The first two resistant potato crops required protection with an at-plant application of nonfumigant nematicide (aldicarb or oxamyl) to sustain acceptable yield (28). In related studies, susceptible and resistant (Maris Piper) potato cultivars were alternated in the rotation. Although the susceptible crop required protection with nematicide treatment, nematicide treatment was limited to every second potato crop. An additional benefit was in reducing selection pressure on the nematode population for the virulent *G. pallida* that was present in the field and that increased when Maris Piper was the only potato crop in rotation (28).

The selection of *G. pallida* in areas cropped to *H1* cultivars resistant to *G. rostochiensis* has occurred, and unfortunately

G. pallida is more difficult to control than *G. rostochiensis* (33,35). The few available resistant cultivars vary in their tolerance to injury and are partially resistant rather than highly resistant, thus allowing nematode populations to maintain or increase (7,14,28). In addition, *G. pallida* is more difficult to control with the standard treatments of aldicarb or oxamyl, perhaps because of the prolonged period of egg hatch that extends well into the growing season, beyond the time that toxic concentrations of nematicides occur (35).

Additional potato cyst nematode management strategies include the early harvesting of potatoes in the less frost-prone areas to prevent the completion of the nematode life cycle (28) and trap cropping to reduce nematode populations (13). Double trap crops combined with ethoprop treatment were highly effective in France for seed potato production, providing *G. pallida* population reduction of 98.5%, a level that would have required 21 years of continuous cropping with nonhosts to achieve (13). Other studies evaluated the effects on potato yield and nematode population dynamics of cultivars with different levels of resistance or tolerance in various combinations, when exposed to full, half, or quarter rates of standard aldicarb treatment (28). These data demonstrated that half or even quarter rates of aldicarb sustained yield and prevented nematode population increase on partially resistant, tolerant cultivars. Field experiments demonstrated that increasing input of compound fertilizer (14:14:22 N-P-K) reduced potato yield loss from *G. rostochiensis;* less aldicarb was required with increased fertilizer rates to protect an intolerant cultivar, and aldicarb was unnecessary to protect a tolerant cultivar (27). However, it was necessary to prevent increased final populations and problems for subsequent crops in the rotation.

In summary, a successful integrated management program with prolonged lives of resistance and nematicide results from combinations of resistance and tolerance, low rate of nematicide, and rotation alternating resistant and susceptible potato crops with nonhost rotation breaks between potato crops. Trap cropping and planting and harvest time manipulation are additional options in some regions. With such an integrated management framework in place, opportunity exists to develop and implement additional component strategies, such as a reasonably effective biological control agent or other cultural manipulation. The shift in prevalence from *G. rostochiensis* to *G. pallida* in some areas underscores the potential problems in reliance on single control inputs, in this case due to the early use of cultivars resistant only to *G. rostochiensis.*

Soybean cyst nematode: A 1988 colloquium summarized several decades of research on rotation and cropping systems for nematode management in North Carolina (2). Two papers focused on management of the soybean cyst nematode, *Heterodera glycines* (24,25). Sasser (24) demonstrated the value of 2-year or 3-year nonhost corn rotation breaks between susceptible soybean crops to increase soybean yield and decrease *H. glycines* populations. A combination of nematicide and resistant soybean followed by the nonhost rotation break limited nematode population densities to nondamaging levels for susceptible soybean cultivars. Schmitt (25) provided supporting data for this approach. The shift in nematicide availability from soil fumigants to aldicarb has left this production system with a chemical control that is ineffective on high population densities (because it fails to reduce the population to nondamaging levels) and only partially effective on lower population densities, with a positive net return to the grower but with lower yield than in uninfested fields (25). A similar scenario occurs for aldicarb use on sugarbeet for control of the sugarbeet cyst nematode, *H. schachtii* (10), where other control strategies must be combined (e.g., nonhost rotation or trap cropping) to reduce nematode populations to manageable levels. Both *H. glycines* and *H. schachtii* produce multiple generations in a single season, making them difficult to control with aldicarb (which is effective only for about 6 weeks after application at planting) compared to the potato cyst nematodes, which usually produce only one generation per season. The value of avoiding the intensive planting of resistant soybean cultivars was emphasized by analysis of survey data showing *H. glycines* race distribution from 1976–86 (25). During this period, a dramatic shift occurred in the prevalence of race 1 (resistance-controlled) from a dominant 80% of the *H. glycines* populations in North Carolina down to 18% in 1986, with a concomitant increase in frequency of other races uncontrollable with resistant germ plasm. This population shift has limited resistant cultivar use and is a result of biological management that should have incorporated integrated control.

Other biologically based control strategies have received limited investigation, including the late planting of early-maturing soybean genotypes that reduce the period of host-root availability to 3 months, compared to 6 months for early planted late-maturing types (25). The delay in planting from May to June can reduce initial nematode population density by 50% because of egg hatch in the absence of host roots, and the shorter growing season reduces the time during which nematodes multiply. There was no indication, however, that this process has been properly integrated with the other strategies. This integration could lower selection pressure for virulent races on resistant cultivars by reducing the required frequency of resistant crops. Resistance and rotation could allow infrequent use of delayed planting of early-maturing soybeans, which would lower the potential for selection of nematodes adapted to enhanced spring survival and reproduction on shorter-season soybean crops. Field research is required to develop this fully integrated system of combined strategies. A somewhat similar situation exists with the Australian program to control cereal cyst nematode, *H. avenae,* in which decades of research and implementation have resulted in the independent development of several control strategies of various efficacy, but these have not been integrated into a multiple component management program (5).

Root-knot nematodes: Integrated management is lacking for control of root-knot nematodes (*Meloidogyne incognita, M. javanica,* and *M. arenaria*) on annual field and vegetable crops in the warm interior valleys of California. This situation has been exacerbated by the suspension of the fumigant 1,3-dichloropropene (1,3-D), which has been used extensively for root-knot control in this diversified crop production system (15). Without 1,3-D, growers are faced with a range of mostly less effective or less practical alternatives, which in most cases have not been studied or implemented as components of an integrated multiple-strategy program. This system is representative of many other warm and hot climate vegetable production areas worldwide with endemic infestations of root-knot nematode.

In this system, the use of nematicidal formulations of metam sodium has become the primary alternative chemical control strategy and is partially to highly effective, depending on application method. The most practical applications, based on shank injection or through overhead sprinkler-irrigation systems, are only partially effective because of inadequate distribution in the target soil zone or loss to the atmosphere, whereas the highly effective application through drip-irrigation systems is rarely used because most crops are not produced under drip-irrigation (21). Development of drip-application technology and increased use of drip-irrigation in crop production could expand this mode of application and provide a future means of delivering biological control agents (3). However, effective use of metam sodium will require integration with additional strategies to provide economically acceptable nematode control in a total management program.

Resistant cultivars of some *Meloidogyne*-susceptible crops are available, including tomato, cowpea, lima bean, and sweet potato, although these represent few choices. Resistant tomato and cowpea cultivars have had the most utility and have allowed the expansion of rotation options between susceptible crops. The resistant cultivars of tomato and cowpea are highly tolerant, yielding well under high levels of infection, and they are highly (tomato) or partially (cowpea) effective in suppressing nematode multiplication, depending on the initial level of infestation (18,23). The near immunity of resistant tomato genotypes reduces population densities to nondamaging levels on subsequent plantings of susceptible cotton and bean cultivars, as demonstrated by a lack of response to fumigation with 1,3-D on those crops (Roberts, unpubl.). The resistant cultivars are especially important in rotation schedules because the extensive host ranges of the three *Meloidogyne* spp. limit the number of available nonhost cash crops. However, this importance places added pressure for a high frequency of resistant cultivar use and increases the potential for selection of virulent root-knot field populations. Recently, fields have been identified in central California with *M. incognita* populations virulent on cowpea cultivars possessing the *Rk* gene, which confers resistance to *M. incognita* (22).

Certain cultural controls have been examined for this production system, including manipulation of planting and harvest dates. Because of cosmetic damage to taproots, carrot (*Daucus carota*) is one of the most sensitive crops to root-knot nematode-induced injury. Studies on wheat and carrot (17) revealed a strategy that could protect the schedule-adjusted susceptible crop and limit nematode reproduction, thereby lowering the extent of yield loss on the following crop. Infested carrot fields are being planted later in the autumn and winter, when nematode activity in soil and root infection are diminished. The efficacy of this strategy varies with lateness of planting (Fig. 1) and never reaches 100% (17). The utility of rescheduling for root-knot management will be maximized only as a component strategy combined with

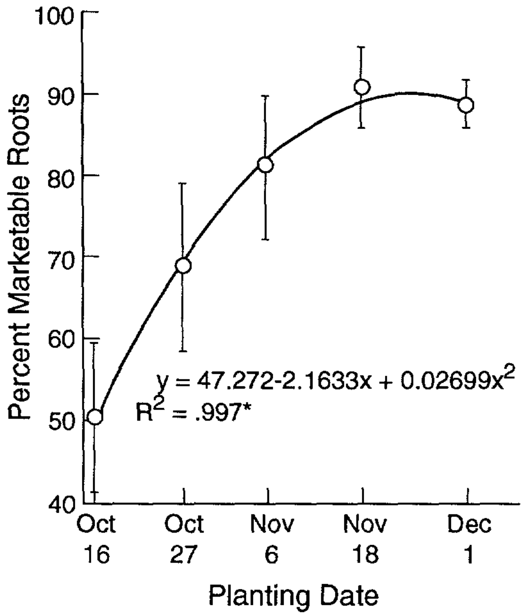

FIG. 1. Percentages (±SD) of marketable (nematode undamaged) carrot (*Daucus carota*) taproots in five plantings in a *Meloidogyne incognita*-infested field site (after 17).

one or more additional, compatible control tactics. Candidate components include a partially effective metam sodium treatment, low concentration of 1,3-D (if reintroduced), rotation with resistant tomato, cowpea or other crop, summer fallow, cover or trap cropping, and organic amendments or green manuring.

Although planting date scheduling combined with nematicide and resistant tomato rotation is beginning to be tested as an integrated approach, the other components have not yet been researched adequately, either singly, or more appropriately as part of a multiple strategy program. Attempts are underway to transfer root-knot (*M. incognita, M. javanica, M. arenaria*) resistance from 'Brazilia' carrot germplasm into California fresh market carrots. Though a fairly high level of heritability has been found, the breeding program probably will require 7 to 10 years. Incorporation of resistant carrot cultivars into an existing integrated management program would be highly desirable, as would any novel future control agent or strategy. If an effective integrated management program can be developed for carrot, it could provide a working model program for many other susceptible vegetables grown in this system.

Efficacy

Some control agents and procedures have a spectrum of efficacy from low to high, for example, based on dosage of a chemical treatment or biological agent or the length of planting time delay (Fig. 1) or earliness of harvest. These control components may provide flexibility when combined because their individual contribution to the total program can be adjusted according to requirements of the system. However, because an objective of combining treatments is to reduce reliance on high input of any one component, a management contribution made with moderate effect would be desirable. Because most growers are focused on maximizing short-term benefits rather than long-term maintenance of efficacy, they may accept an integrated approach with reluctance. Control strategies with a fixed high efficacy (e.g., major gene resistance) could be safeguarded by periodic use in a temporally based program (e.g., by alternation with susceptible cultivars of potato or soybean to reduce selection of virulent nematode species [*G. pallida*] or races [*H. glycines*]). Alternatively, highly effective controls could be applied with others that provide some level of nematode population reduction on their own and thus reduce the nematode population density to which the resistant crop will be exposed. The sum efficacy of this approach may contribute more than is actually needed for maximizing yield or net economic return.

In contrast to control strategies with adjustable efficacy or fixed high efficacy are partially effective strategies that are not sufficient by themselves to manage the nematode problem. Many existing and probably most future control agents and procedures will fall into this group. Adequate efficacy of the total management program will be achieved by contributions of the individual control agents and procedures. Research on the potential of these partially effective controls within the context of a multiple strategy approach is vital to their development and implementation. The current tendency to reject partially effective controls is based on their inadequacy as single treatments and, as a result, their questionable economic value. No doubt this attitude has been influenced by the legacy of highly profitable and effective chemical treatments such as the halogenated hydrocarbon soil fumigants, and possibly by the effectiveness of easily implemented major gene resistance in a few crops.

The questions to be researched are complex and in some cases will necessitate evaluation over many years in multifactorial experiments. Combinations of partially effective controls in an integrated program for insect control were discussed by Wheatley (32). He used an example of cultural control, resistance, and chemical treatment to control cabbage root fly in brassica crops and suggested that overall efficacy could be high but very difficult to demonstrate. Two objectives should be considered when integrating control strategies. The primary short-term objective is to reduce the Pi to a level (the economic threshold of the damage function) that maximizes net return on the current crop. This can be achieved by reducing nematode numbers or reducing their infectivity before growing the crop (e.g., with a nematicidal agent or cultural practice), or by shifting the damage function curve to the right (e.g., by substituting a resistant and tolerant cultivar so that the same Pi is less damaging). The second objective is to reduce the multiplication rate of nematodes so that fewer nematodes remain (Pf) in the soil after applying the control program for one season (i.e., $Pf/Pi < 1$). Population reduction has long-term, multiple-year significance because it decreases the damage potential of the population on succeeding susceptible crops. The two objectives are interrelated because each can influence the other significantly. Reduction of Pi to a level ≤ the economic threshold for the current crop will influence the nematode Pf but does not ensure a low Pf. Nematicide-treated crops may yield well, but high Pf levels (where Pf > Pi) can develop on the undamaged root systems (33). Tolerant, non-resistant or partially resistant cultivars have a similar effect (1,7,14, 18).

For the first objective, a simple compounding of efficacy percentages of the component strategies can be used as a working hypothesis for reducing Pi (actual reduction or equivalent effect). How many strategies and of what efficacy are required to achieve acceptable control? In applying two or more component strategies to reduce Pi, one can visualize a damage function (the relationship of Pi to relative crop yield) in which the Pi (independent variable), simplified here as a percentage of the density present before inputs are applied, is inversely linearly related to relative yield of the crop (the dependent variable), except at very high and very low Pi levels (26). Relative yield is based on the percentage of yield in the absence of nematodes. Each effective input will shift Pi to the left and raise the relative yield.

Table 1 provides hypothetical examples of the cumulative levels of efficacy for different control inputs. Example 1 describes a scenario in which each of four control strategies, A–D, has been assigned arbitrarily an efficacy of 66%. Each strategy is considered to act independently of the others and is added sequentially in effect, but not necessarily in time. Thus the first strategy (A) has a target Pi of 100% and leaves a residual nematode density of 34% (Table 1). The second strategy (B) acts on a target Pi now at 34% and leaves a residual nematode density of 11.6%. Application of all four strategies leaves a final residual nematode density at 1.3% of the original Pi. Example 2 is based on three strategies, each assigned arbitrarily an 80%

TABLE 1. Calculated values of the residual target nematode population density (% Pi) following the sequential application of control strategies of arbitrarily assigned efficacies, and an indication of the single and multiple-year economic feasibility of applied strategies.

				Impact for moderate Pi			Impact for high Pi		
		Nematode initial population density (% Pi)			Positive net return†			Positive net return†	
Strategy	Efficacy‡ (%)	Target	Residual	Pf/Pi	Current year	Multiple years	Pf/Pi	Current year	Multiple years
				Example 1					
A	66	100	34	>1	no	no	>1	no	no
B	66	34	11.6	>1	yes	no	>1	no	no
C	66	11.6	3.9	<1	no	yes	>1	yes	no
D	66	3.9	1.3	<1	no	yes	<1	no	yes
				Example 2					
A	80	100	20	>1	no	no	>1	no	no
B	80	20	4	<1	yes	yes	>1	no	no
C	80	4	0.8	<1	no	yes	<1	yes	yes
				Example 3					
A	85	100	15	>1	no	no	>1	no	no
B	66	15	5	>1	yes	no	>1	no	no
C	50	5	2.5	>1	no	no	>1	yes	no
D	40	2.5	1.5	<1	no	yes	>1	no	no
E	30	1.5	1.05	<1	no	yes	<1	no	yes
F	30	1.05	0.74	<1	no	no	<1	no	no

† Achievement (yes) or not (no) of positive net return to grower in the current year and in multiple years, based on control input effectiveness to decrease Pi ≤ an assigned economic threshold (12% of moderate Pi and 4% of high Pi) and to result in Pf/Pi <1. See text for explanation.

‡ Defined as the ability of a strategy to decrease (actual or its equivalence in effect) the target nematode population density (% Pi) by a given percentage.

efficacy, that reduce the nematode density to <1% of the original Pi (Table 1). Example 3 is based on six strategies with different efficacies assigned, which reduce the nematode density to 0.7% of the original Pi (Table 1). A situation in which control strategies have different efficacies is probably closer to reality.

Assessment of the economic feasibility of the scenarios in these examples (Table 1) must include the objective of reducing nematode seasonal multiplication rates in addition to reducing Pi. The hypothetical working model is extended in Table 1 to include tentative assignments for achieving positive net return on use of one or more strategies in the current year and after multiple (subsequent) years. The assignments are based on reduction of Pi relative to an economic threshold, and on suppressing multiplication rate to Pf/Pi < 1. In example 1 (Table 1), an economic threshold of 12% of a moderate Pi would be reached by applying any two strategies (in this example A and B) with 66% efficacy, and positive net return would be achieved in the current year by use of two (but not one, three, or four) component strategies. However, three or more strategies are required to attain Pf/Pi < 1; thus, positive net return over multiple years would be achieved by use of three or four strategies. For a high Pi, an economic threshold of 4% Pi would require three strategies and a Pf/Pi < 1 would require four strategies to achieve positive net return in the current and in multiple years, respectively (Table 1).

In example 3 (Table 1), application of strategies A (85% efficacy) and B (66% efficacy) would reduce Pi by 95%, satisfying the economic threshold requirements (12% Pi) for a moderate Pi and maximizing the current year net return compared to adding another four components (C–F). Adding strategy C would not achieve a positive net return in the current year nor provide multiple-year benefit because Pf/Pi remains >1. Applying four strategies (A–D) would give Pf/Pi < 1 and achieve positive net return over multiple years, as would addition of the fifth component, strategy E. In this example, addition of a sixth strategy (F) would become too costly and negate economic benefit of the total management program. The cost of each component would influence this decision. If significant reductions in nematode multiplication were achieved by the additional inputs (i.e., Pf/Pi < 1), the economic advantage for subsequent years may provide the justification for the additional inputs in the current season. The original target Pi, whether moderate or high, will influence the overall constraints, requirements, and success of such a system, hence the importance of controlling nematode multiplication to suppress subsequent-year Pi targets. Aldicarb use on a tolerant potato cultivar (grown with high inputs of compound fertilizer) to prevent increased final populations of *G. rostochiensis* and resultant problems for subsequent crops in the rotation is an example of a component strategy that was not needed to protect the current crop (27).

Simple relationships of independent action of strategies do exist, and a well researched system such as that for potato cyst nematode management has good quantitative data for nematode population densities and relative yields in response to rotation, resistant cultivars, and nematicides. Thus, efficacy levels could be assigned for predictive management purposes. For example, the annual percentage decrease in populations under nonhost rotation can be estimated, and a partially effective aldicarb treatment could be added to the rotation to drop the Pi below the economic threshold. Likewise, a resistant cultivar could be used in a similar manner to lower the Pi.

The simplified, conceptual framework (Table 1) becomes greatly complicated by synergism and antagonism between different strategies. These interactions require careful research into the effects of one strategy on another under a specific set of environmental conditions and level of nematode infestation. These interactions could be influenced by several factors, including timing of application, density-dependent action of strategies, and the biological target. For example, two strategies may attack the same, different, or overlapping portions of the nematode-infested soil zone; one input such as solarization may show high efficacy on the upper soil profile only (top 15–20 cm), whereas a water-applied biological or chemical agent might be effective to a 60–90 cm depth but have poor efficacy near the soil surface. This combined action may produce a higher than expected total efficacy, whereas two strategies operating only in the upper 15–20 cm would have a combined efficacy lower than expected, resulting in significant nematode populations remaining in the deeper soil profile. Similarly, strategies may have efficacies determined by a mode of action that is life-stage specific. Biological control agents are often stage specific, and experimentation would be needed to assess the combined impact of using a biological agent that is an obligate parasite of sedentary females on roots with a cultural or chemical control that targets only vermiform stages in the soil. It is readily apparent from these examples that efficacy of the total program will be determined by the interaction, overlap, and complementarity of the various components.

Compatibility

A nematode management program based on combinations of two or more control strategies requires compatibility of each component with the overall production system, and compatibility between individual components. Component compatibilities will determine the total efficacy of the combined program, and incompatibilities must be avoided. An example of extreme incompatibility would be a high level of fungal toxicity of a synthetic or natural chemical nematicide, which could thus not be used in a program with a fungal biological control agent. Change in planting or harvest date to reduce or avoid nematode activity may be incompatible with the seasonal schedule of another key crop in the nonhost rotation. Similarly, a resistant cultivar may have a time-to-maturation requirement that is incompatible with a nonhost rotation schedule or with a delayed planting time or early harvesting cultural control tactic. These examples of major incompatibility should be fairly obvious to avoid, whereas their converse compatibility would facilitate their potential as appropriate control combinations. More difficult to resolve are the less obviously incompatible combinations of partially negative impact or negative interactions that may appear only with time. Hence combination research is warranted at an early stage of systems development.

Summary of Key Considerations

The issues of efficacy and compatibility present a formidable challenge to research for new ways to control nematodes. Attention must be focused on the integration of a partially effective control strategy or agent into an overall program. This integration should be considered as early in the research program as possible, preferably from the outset. Biological control is one area where most research has identified organisms with partial efficacies, with some ranging from 50–80% reduction in levels of nematode infection of plants under artificial conditions (11,12). There is a perception that such levels are inadequate and unacceptable, which is true if a partially effective strategy is used singly; but important management potential may be overlooked without testing in a combined-strategy program.

Several factors will affect the direction of this approach to nematode management. Economic considerations include net cost to the producer (cost–benefit relationships), the commercial potential in developing component strategies (which may be viewed with some skepticism compared to developing control agents or genotypes of major effect), the economic support for research in public programs, and the cost for research and development in the private sector. Research and implementation efforts will have to address issues of availability of expertise, the requirement for team-based programs, and the involvement in long-term multifactorial experimentation, all of which are central to addressing the multiple-strategy management approach.

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