Plant Resistance in Nematode Pest Management[1]

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Abstract: Plant resistance is a primary component in the development of nematode pest management programs. A survey of resistant cultivar and rootstock implementation in 75 annual and perennial crops grown in California provides an insight into the current status of plant resistance in modern agriculture. As new sources of commercially suitable resistant germplasm are made available, their successful implementation will require information on quantitative relationships of injury tolerance and hosting ability, and on relationships to intraspecific pathotypes or races present in the major agricultural regions of implementation. Computer simulation and modeling as an aid in developing these programs is discussed. A format for the implementation of a resistant line with good agronomic potential is outlined. *Key words:* review, California crops, pest management, population dynamics, damage functions, tolerance.

Recent discussions on status and prospects of nematology provide a good indication of the current emphasis and importance attached to research in, and development of, plant resistance to nematodes (4,36). In response to a 1979 request from the U.S. Secretary of Agriculture, the Society of Nematologists identified five major priority research areas which included plant breeding for resistance to nematodes (36). A 1979 Integrated Pest Management Research Priority Report (4) identified plant resistance over chemical, biological, cultural, and regulatory control components as the highest research priority in management procedures. Recommended increases in scientific-year-effort for plant resistance studies in 1980–89 were double those for the other control components. Bird (4) recognized this may necessitate a reorientation of existing Agricultural Experiment Station personnel to fulfill some of the research needs in this area.

The increasing environmental and cost limitations of chemical control methods have contributed to the renewed interest in plant resistance. In less developed countries where chemical control is difficult to implement, plant resistance has been considered repeatedly as the most promising component of nematode pest management. With the imminent resurgence in plant resistance development, it is important to consider its current status in nematode pest management and to combine the present level of practical experience with the requirements for developing programs that can maximize and preserve the effectiveness of this natural resource. This paper addresses some of these considerations and requirements.

AVAILABILITY AND USAGE

A relationship seems to exist between the level of nematode specialization and the availability of resistant crop plants (Fig. 1). Plant resistance has been found and developed predominantly to the highly specialized parasitic nematodes such as *Globodera*, *Heterodera*, *Meloidogyne*, *Rotylenchulus*, *Tylenchulus*, and *Ditylenchus*; i.e., nematodes that have a sedentary endoparasitic relationship with their host for at least a portion of their life cycle. In these groups, resistance in a given cultivar or rootstock may be conferred to nematode species belonging to separate genera, to several species from the same genus, to a single species, or to particular pathotypes or host races of a single species. Resistance to these specialized endoparasitic forms is usually limited within a crop by confinement of resistance genes to just one or a few cultivars

Fig. 1. Plant resistance availability and development in relation to host range and parasitic specialization for various phytoparasitic nematode groups (see text).

or rootstocks of that crop. In some crops that are severely damaged by endoparasitic nematodes, for example cucurbitaceous crops infected by *Meloidogyne* spp. and sugarbeets and crucifers infected by *Heterodera schachtii*, resistance is not available. On the other hand, crop plant resistance to nematodes that have a less specialized parasitic relationship with their host, such as some migratory endoparasites (e.g., *Pratylenchus* and *Aphelenchoides*) is generally undeveloped. *Pratylenchus scribneri* resistance in lima beans (29) and *Aphelenchoides* resistance in *Chrysanthemum* (18) provide isolated examples. Resistance to ectoparasitic nematodes (e.g., the Dorylaimida genera *Longidorus, Paratrichodorus, Trichodorus,* and *Xiphinema*) has not been developed in cultivars or breeding lines nor located in wild germplasm sources of any major crops, although many examples of nonhosts (immunity) exist.

From an evolutionary standpoint, this pattern of resistance to different parasitic groups is to be expected. Natural selection of resistance genes is more likely to have occurred in the most highly specialized host-parasite relationships where a co-evolutionary development of host and parasite has produced a highly specific interaction in which host and parasite compete for a genetic advantage (35). The root browsing

ectoparasitic nematodes have less specific feeding requirements and characteristically wider host ranges. Selection of resistance to these ectoparasites has not occurred in plants, presumably because selection pressure from the parasite is low and little advantage is gained by the host plant (unless resistance genes are linked to gene loci that improve plant fitness through other characters).

Table 1 lists the major crop and nematode combinations in which nematode resistant cultivars and rootstocks are available and in use.

Status in California: California is a good example of intensive diversified agriculture. About 75 food and fiber crops are grown in a range of soil and climatic types and where many of the important phytoparasitic nematode genera are represented by one or more species (34).

Of the nematode-resistant crops available, relatively few are used in California (Table 1). In 45 or so annual field and vegetable crops, *Meloidogyne* resistance in beans (large lima), cowpeas, sweet potatoes, and tomatoes are the only cases where plant resistance is currently used as a nematode management tactic, and resistant cultivars, especially of sweet potatoes and tomatoes, are mostly used in conjunction with a preplant fumigation treatment. The scope of

Table 1. Major annual and perennial crops in which resistance to nematodes is available and used for nematode pest management.

Crop	Nematode
Beans	*Meloidogyne incognita*, M. javanica*, Pratylenchus scribneri*
Cowpea	*M. incognita**
Cotton	*M. incognita*
Potato	*Globodera pallida, G. rostochiensis*
Soybean	*M. incognita, M. javanica, Heterodera glycines, Rotylenchulus reniformis*
Sweet potato	*M. incognita*, M. javanica*, M. arenaria**
Small grains (wheat, barley, oats)	*Heterodera avenae, Ditylenchus dipsaci*
Tobacco	*M. incognita, M. arenaria, Globodera* spp.
Tomato	*M. incognita*, M. javanica*, M. arenaria**
Alfalfa	*M. incognita*, D. dipsaci**
Apricot	*Meloidogyne* spp.*
Citrus	*Tylenchulus semipenetrans**
Grape	*Meloidogyne* spp.*
Walnut	*Meloidogyne* spp.*
Prunus rootstock—Nemaguard: (almond, nectarine, peach, plum)	*M. incognita*, M. javanica*, M. arenaria**

*Nematode-crop combinations in which resistance is used in California.

implementation is limited by cultivar suitability for commercial characteristics. For example, of the some 279,000 acres of tomatoes grown in California in 1979 (1), representing more than 80% of the U.S. total tomato production, 250,000 acres were of processing types in which *Meloidogyne*-resistant cultivars were not available. The remaining 29,000 acres were fresh market tomatoes of which two of the popular cultivars ('Jackpot' and 'Royal Flush') are resistant to *Meloidogyne incognita, M. javanica,* and *M. arenaria;* other leading fresh market cultivars like 'Castlemart' are susceptible to *Meloidogyne* spp. Importantly, in 1981, for the first time, a good yielding processing cultivar ('Goldsmith GS27') has been released which contains resistance to *Meloidogyne* spp. together with the fruit attachment characters required for machine harvesting. The tomato example illustrates the very limited implementation of nematode resistance in a highly susceptible crop where our overall knowledge of resistance can be considered advanced. The acreage planted with resistant cultivars of the other annual crops in which resistance is available is also small. Commercial cotton cultivars with resistance to *Meloidogyne incognita* are available, but they are not used in California because the "one variety law" limits major San Joaquin Valley plantings to susceptible 'Acala' cultivars (SJ2, SJ4, SJ5).

Of the 30 or so perennial crops in California, resistance has been implemented extensively in some crops and not at all in others. Citrus rootstocks (e.g., *Poncirus trifoliata* and its citrange hybrids), resistant to citrus nematode *(Tylenchulus semipenetrans)*, have been used extensively and successfully for some 25 yr, although certain *T. semipenetrans* pathotypes are now known to circumvent this resistance and reduce yield (3). *Meloidogyne*-resistant grapevine rootstocks (e.g., 'Dog Ridge,' 'Salt Creek,' 'Harmony,' 'Freedom') are available (12), but they are not preferred due to a tendency to promote vegetative growth. However, some commercial plantings on the last two rootstocks are being made (27). Partial resistance and tolerance in some grape cultivars such as 'Thompson Seedless' are used in sandy soils in the interior San Joaquin

and Coachella Valleys, where problems are likely from *Meloidogyne* spp. (12,27). Probably the most successful plant resistance implementation program in California involved the use of *Meloidogyne*-resistant 'Nemaguard' rootstock (derived from *Prunus davidiana*) for *Prunus* crops. Approximately 75% of the almond, nectarine, peach, and plum plantings—approximately 500,000 acres in 1979 (2)—are on Nemaguard rootstocks. After 20 yr of use, there is no evidence of selection of *Meloidogyne* populations that can circumvent resistance in Nemaguard (M. V. McKenry, personal communication). Alfalfa cultivars resistant to *Meloidogyne* (e.g., cv. Moapa) and *Ditylenchus dipsaci* (e.g., cv. Lahontan) are used on a limited scale in California; however, the *Meloidogyne* resistant germplasm has been incorporated into commercial lines. *Meloidogyne* resistance in walnut (cv. California Black) is also utilized in 95% of the walnut acreage. Thus, apart from *Prunus* and citrus and walnut rootstocks, the implementation of nematode-resistant cultivar and rootstock plantings of California crops is limited, especially in annual crops. Examples of nematode resistance implementation in world agriculture that are not common to California will be used in the following sections.

TOLERANCE AND QUANTITATIVE RELATIONSHIPS

In the present context, tolerance refers to the ability of a plant to grow and yield during injury from nematode parasite attack, and it is independent of resistance-susceptibility that is used herein in a non-epidemiological sense referring to the ability of a plant to support nematode reproduction (31). Thus, tolerant cultivars yield better than intolerant cultivars under similar nematode attack.

Two factors are critical when considering the implementation of resistant cultivars in nematode pest management: one is the tolerance level and, therefore, the yield potential of the cultivar in infested soil, and the second is the effect of that cultivar on the population dynamics of the nematode species in question. The second factor is a more important consideration in annual than in perennial crops, because seasonal

Table 2. Yield comparisons of resistant and susceptible cultivars of annual crops on nematode infested and noninfested land.

Nematode	Crop	Cultivar		Unit	Yield		Yield ratio (infested/ uninfested) × 100	Reference
					Infested	Uninfested (or treated)		
G. rostochiensis	potato	Maris piper	R*	kg/ha	17,100	28,400	60	(8)
	tuber	Record	S	"	7,600	31,000	25	
H. glycines	soybean	Centennial	R	kg/ha	6,400	7,529	85	(25)
	seed	Bragg	S	"	2,310	—	—	
M. incognita	soybean	Bragg	R	kg/ha	1,642	2,536	65	(24)
	seed	Hood	S	"	209	1,675	12	
M. incognita	tobacco	NC 95	R	g/plant	31	60	52	(16)
	leaf	McNair 30	S	"	7	70	10	
M. incognita	sweet	Eureka	R	bu/ha	470	555	84	†
	potato	Jewel	R	"	381	534	71	
	tuber							
M. incognita	cotton	N6072	R	kg/ha	1,638	2,333	70	(17)
	lint	Auburn 56	S	"	1,342	2,444	55	
H. avenae	barley	Proctor-	R	kg/ha	4,569	7,559	60	(6)
	seed	type	S	"	3,827	7,571	51	

*R = resistant cv.; S = susceptible cv.
†Roberts and Scheuerman, unpublished data.

population changes must be considered in planning rotations containing different cultivars of the same or other crops. Table 2 compares yield of resistant and susceptible cultivars of the same crop in nematode infested and uninfested (or nematicide treated) soil. In all cases, resistant cultivars show reduced yield under heavy nematode attack, with yield reductions ranging from 15 to 48 percent. Resistance and tolerance in tobacco to *Globodera solanacearum* were shown to be genetically independent characters (13). However, in a range of crops (Table 2), resistant cultivars generally yield better than susceptible cultivars under nematode attack, and in lightly and moderately infested soils, resistant cultivars may show no significant yield reduction. Comparisons of grain yields of resistant and susceptible barley genotypes on cereal cyst nematode (*Heterodera avenae*) infested soils at 18 different sites in Britain (of which 13 sites compared near-isogenic resistant and susceptible lines) revealed that resistant lines out-yielded comparable susceptible lines by a mean of 8.6 percent (18).

Yield reduction in resistant cultivars results from root injury by invading juveniles of root endoparasites; when the mechanism for resistance is postinfectional, roots of resistant cultivars can be invaded as much as susceptible cultivars (38), and root injury may be particularly severe where a hypersensitivity response in the host is induced by the nematode (9). Indications that some tolerant cultivars have mechanism(s) that reduce numbers of juveniles able to penetrate into roots are found in both annual and perennial crops (8,12). A positive correlation between tolerance to cyst nematode injury and water use efficiency, including stomatal opening regulation in the plant, has been noted in potatoes (7,8).

The quantification of the relationship between pest density and crop yield is a necessary basis for rational decision making in an integrated pest management program in which appropriate, reliable pest sampling and assay procedures are developed (5,10, 11). The yield of the resistant cultivar in relation to the preplant nematode population density (the damage function) must be determined, preferably from field data. How
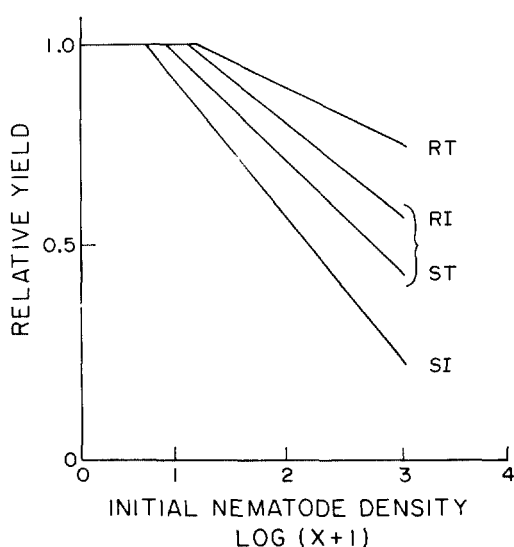

Fig. 2. Hypothetical damage functions (relationship between yield and initial nematode populations) for cultivars of an annual crop possessing different nematode resistance and damage tolerance characteristics. RT = resistant, tolerant; RI = resistant, intolerant; ST = susceptible, tolerant; SI = susceptible, intolerant.

the possession of resistance and tolerance characteristics by a cultivar might influence this relationship is shown in Fig. 2. The curve, developed from Seinhorst (33), generally shows a linear relationship except at very low or very high population densities. Both the position and the slope of the curve will be governed by the relative tolerance of the particular cultivar, as well as by edaphic, environmental, and cultural factors (10). Field studies have shown that yields of resistant potatoes were inversely proportional to preplant population densities of potato cyst nematode unable to reproduce on them (23). Similarly, comparisons of *Meloidogyne incognita* damage to resistant and susceptible tobacco cultivars over a range of initial densities conform to the Seinhorst (33) equation, although maximum yield of the two cultivars differed (16). Ferris (10) noted that the relative tolerance of a cultivar to the nematode pest might be a problem in a quantitative management approach to a particular nematode-crop relationship. As part of the damage function derivation, he suggested that all cultivars for which no data were available be regarded as intolerant to the particular nematode species and given a max-

imum "pathogenic equivalence" rating of 1; those cultivars where a level of tolerance was known would be given a rating of some factor less than 1. In relationships with a minimum yield at the highest nematode densities, a measure of yields at least two densities above the tolerance level are necessary to determine the position of the yield curve in relation to nematode densities (33).

Where good yield of the primary crop is the main objective, and long-term nematode management is not considered, then in some nematode-crop situations the tolerance of the cultivar to damage may be considered more important than the possession of resistance factors that inhibit nematode reproduction. Such situations might include nematode pests that complete a single generation during the growing season and where secondary infections by other organisms are not prevalent; for example, root-knot and cyst nematodes in cool climates. However, if multiple nematode generations occur, if secondary infections such as those with root-rot fungi are a yield determinant, or if nematode infection predisposes the crop plant to a fungal wilt or rot infection in a disease complex, then the possession of resistance is very important because it may limit these negative effects on yield. *Meloidogyne* infections on vegetables in warm climates (14) and the *Meloidogyne-Fusarium* disease complex on cotton (17) are examples of these situations.

In practice, a nematode management program must consider long-term trends of nematode population dynamics under crop rotations. Resistant cultivars reduce the pre-plant population densities that will affect the next crop, and often more so than non-host or immune plants because they may promote hatching and attract invasive juveniles to roots. For example, a susceptible cotton (cv. Acala SJ2 or SJ5) is rotated with resistant cowpea (cv. Blackeye 5) by some growers in California to manage *Meloidogyne incognita*. Resistant cultivars can, therefore, increase the frequency with which infested land can be planted with susceptible cultivars of the same or other crops, and they can reduce the dependence on other management options such as chemical nematicides. Rotations can be developed to maximize resistance usage in annual crops, as exemplified by current population modelling work.

Rotations are not a major consideration for nematode management on perennial crops. Resistance may be more desirable than tolerance, because roots of susceptible perennial cultivars or rootstocks support nematode reproduction in successive years and heavily infected roots are more vulnerable to secondary infections.

MODELLING AND IMPLEMENTATION

The use of interactive computer programs is increasing in research and implementation efforts directed towards integrated nematode pest management. This is particularly true in Europe for cyst nematodes and in the United States for root-knot nematodes (11,20,21,22). Computer programs which aid in resistant cultivar implementation include cultivar selection in quantitative nematode management, planning of rotations to optimize resistant cultivar effectiveness, understanding such processes as genetic selection and intra- and inter-specific competitions in parasite relations.

The development of profiles on susceptible and resistant cultivars and rootstocks through applied research will be the key to successful implementation of management programs that utilize plant resistance to nematodes. A feasible, conceptual framework has been developed (11) for the derivation and implementation of quantitative nematode management decisions. This concept relies on the use of interactive computer programs to manipulate the data files of those parameters that may influence the management decision. The complexity of the decision process necessitates the use of these computer programs. Cultivar or rootstock selection is a primary component in such a system, and the data files used to make these selections must include a profile of each available cultivar or rootstock in terms of its nematode species and pathotype hosting ability and its tolerance to nematode damage. Therefore, the breadth and accuracy of this information on the cultivar or rootstock will be a limiting factor in the selection process.

Jones and co-workers (20,21) in Europe

have applied computer simulation and population models to potato cyst nematodes (*Globodera pallida* and *G. rostochiensis*) on potatoes, where data on population dynamics and host parasite relationships are probably most advanced in nematology. A population model has been developed to investigate the influence of potato cultivars bearing major dominant gene H_1 (from *Solanum tuberosum* spp. *andigena* Juz. and Buk.), conferring resistance to *G. rostochiensis* pathotype Ro1, on nematode populations under different rotations and when used in combination with other management strategies such as chemical nematicides.

Goodness of fit of the model prediction to field data, where the model is compared both with and without an amendment to incorporate interspecific competition between *G. rostochiensis* and *G. pallida,* confirms that on fields with mixed populations of the two species continuously cropped with potatoes resistant to *G. rostochiensis* Ro1 only, the characteristic delay in the increase of *G. pallida* densities is caused by competition with *G. rostochiensis,* which until it has fallen to a low level, suppresses the *G. pallida* population (21). Earlier versions of the model (23) compared rotations in which susceptible and/or resistant potatoes were grown in various rotation frequencies (from continuous susceptible or resistant cultivars to alternating the two with up to three other crops in between); model predictions led the authors to suggest that the best policy for potato growers with fields suitable for resistant cultivars is to alternate resistant and susceptible cultivars in a crop rotation growing potatoes every 3–4 yr.

Simulation on the increase in frequency of a resistance breaking gene in a potato cyst nematode population when resistant cultivars are grown enabled predictions of gene selection based on two hypotheses for nematode genotype background: females are double recessives (aa), or they are double dominants and heterozygotes (AA and Aa) for that character (21). The model confirmed that, over a wide range of initial genotype frequencies, if genes able to circumvent resistance are present, selection of these genes does take place when a resistant cultivar is grown continuously, and that

selection is faster for the hypothesis of recessive females. Predictions on the rate of gene selection are loosely validated by the lack of field evidence so far that growing potatoes with gene H_1 has selected from *G. rostochiensis* Ro1 populations able to circumvent gene H_1 resistance (21). Field trials with susceptible and resistant cultivars and fumigated and nonfumigated plots, suggest that nematicides that kill 70–90% of the nematode population may expedite rather than prevent selection of a race or species of potato cyst nematode able to reproduce on a resistant cultivar (21).

The cyst nematode models apply to species with one generation per season, and they would require adaptation for multigeneration species such as *Heterodera* and *Meloidogyne* in warm climates. These models are based currently on incomplete data. However, the programs can be updated as new information becomes available, and although information gaps exist in important practical areas, these examples illustrate the undoubted potential of simulation and modelling work in developing nematode management programs that utilize plant resistance.

INTRASPECIFIC VARIATION

Intraspecific variation in ability to reproduce on resistant cultivars and rootstocks occurs in many nematode-crop combinations. These variants are referred to most commonly as pathotypes, biotypes, or races. Schemes for their identification and classification have been developed for several important species using differential hosts that possess key resistance genes. Pathotypes have been identified in potato cyst nematodes on potatoes (26), in cereal cyst nematodes on barley (18), in soybean cyst nematode on soybeans (30), on root-knot nematodes on a range of crop plants (28), in citrus nematode on citrus (19), and so on. The numbers of variants that can be differentiated varies with both the number of host differentials and the method of assessment used. For example, Riggs et al. (30) differentiated six *Heterodera glycines* variant groups on five differentials, and 25 and 36 variant groups on 13 differentials, from a collection of 38 geographical isolates. For practical purposes, the commercially im-

portant resistant cultivars can be used as differentials in an open-ended scheme that includes cultivars with new resistance characters as differentials and designates isolates able to reproduce on them as new races. Therefore, only the variants that relate directly to decisions on growing a particular cultivar on infested land are considered.

Although it is not practical to determine the predominant pathotype in every infested field, limited testing of nematode isolates from selected fields may provide a guideline for cultivar choice in a given area. For widespread species with continental or global distributions like *Meloidogyne incognita*, the identification of variants on a regional rather than on a total basis is more meaningful for resistance development and implementation, both in advanced and in developing agriculture. Attempts at such programs in less developed countries are in progress (28). With reference to tomato production in the United States, California isolates of *Meloidogyne* spp. would be the most practical test criteria for developing and implementing resistant cultivars of this crop in North America. Tests with 10 California isolates of *M. incognita* indicated that intraspecific variation in ability to develop on resistant tomatoes does occur (37).

Although incomplete, our understanding of resistance usage is developed enough that new sources of resistance can be used more effectively than in the past. For example, the development of a commercial sugarbeet with resistance to *Heterodera schachtii* is now a realistic possibility (32), and the existence of pathotype variants in *H. schachtii* has already been observed (15). Nevertheless, sugarbeet growers and processors are keenly awaiting the availability of resistant sugarbeets to replace, rather than integrate with, the current management options of long rotations and expensive nematicides. It is, therefore, of utmost importance that the nematology community, through education and advisory networks, makes a concerted effort to ensure full integration of resistant cultivars into properly planned rotations that might include judicious nematicide usage and other cultural or biological tactics.

Resistance-breaking pathotypes on perennial crops present a different management problem because a resistant cultivar or rootstock may be continually exposed to a nematode population for many years. The selection of *Tylenchulus semipenetrans* pathotypes able to circumvent resistance bred from the *Poncirus trifoliata* gene pool is a good example (3,19); the full impact of this selection will be felt when present plantings are replaced with a new generation of citrus stock after 40–50 yr. New sources of resistance in commercial citrus germplasm are a pressing requirement. The development of stable forms of resistance that are multigenic in nature may be most appropriate in perennial crops.

FIELD DEVELOPMENT

The plant breeder or genetic engineer is primarily responsible for developing commercially acceptable resistant germplasm. The field development and implementation of this resistance is the second phase of the resistance program, and it will determine the overall success of that breeding effort. A format for the implementation of a resistant line with good agronomic potential could be as follows:

1. Preliminary testing for resistance to major pathogenic species and pathotypes.
2. Testing for resistance to a range of nematode isolates from the region of implementation.
3. Testing for tolerance and resistance in the field that could include evaluation of combined use with a nematicide (e.g., where a nematicide could provide control plots).
4. Testing to a nematode-disease interaction or complex where applicable (e.g., rootknot nematode—fungal wilt complex).
5. Planning of effective rotations that are consistent with acceptable cropping practices.
6. Education and advisory program for growers, processors, pest control advisors, etc., to promote proper implementation.

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