

17 Resistance to Plant-parasitic Nematodes

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17.1 Introduction

In plant nematology, the most widely used definition of resistance is based on a measurable effect on nematode reproduction: a resistant plant inhibits the reproduction of a nematode species relative to reproduction on a plant lacking such resistance (Cook and Evans, 1987). Resistance of plants to pathogens is usually defined as the ability of the plant to lessen, inhibit or overcome the attack by the pathogen (Wingard, 1953). Entomologists frequently use a broader definition, defining resistance as the amount of heritable characteristics of the plant that influences the damage done by insect pests (Painter, 1951), with non-preference, antibiosis, and tolerance as types of resistance.

Tolerance is used by nematologists to characterize plant response to nematode parasitism and is distinct from the ability of the plant to support nematode reproduction. Thus, a susceptible plant may be intolerant with a relatively large degree of growth suppression due to nematode parasitism or it may be tolerant with limited growth suppression due to parasitism (Cook and Evans, 1987). Likewise, a resistant host can be either tolerant or intolerant of nematode parasitism. Several reports document differences in tolerance of susceptible plant species (Cook, et al., 1997; Hussey and Boerma, 1989), but relatively few document differences in tolerance in species that are also resistant to nematode reproduction, for example, in sweet potato (Roberts and Schuurman, 1984). In most cases, resistant plants are tolerant of nematode attack, even though resistance is typically a post-infection process. The few examples of intolerance of resistant plants relate to root injury resulting from elicitation of a severe hypersensitivity reaction as part of the resistance response during initial root infection, such as is the case for *Globodera tabacum solanacearum* on resistant *Nicotiana* species (Baalaway and Fox, 1971; Johnson, et al., 1989).

These differences in definition among the various disciplines reflect how resistance is expressed in the plant to pathogens, insects and nematodes, the

17 Resistance to Plant-parasitic Nematodes

nature of the interaction of the pest or pathogen with the host, and also the methods used to measure resistance. The resistance and tolerance terminology is useful in defining the two important ways in which these traits are of critical value as management strategies for plant-parasitic nematodes. Resistance, because it is usually associated with tolerance, provides protection of crop yield potential and, in most cases, suppresses nematode population densities in soil, thereby easing the pest pressure on the following crop. In nematology, the emphasis on nematode reproduction to some extent reflects the general lack of discrete symptoms upon which assessment of resistance is often based when dealing with microbial plant pathogens. Nematode reproduction can be measured with sufficient ease, accuracy, and precision to be a practical alternative to measurement of symptom development. However, most important is the proven ability of resistance to protect plants from nematode parasitism, again emphasizing that resistant plants are usually tolerant and yield well under nematode pressure. Disease incited by nematodes is strongly influenced by initial population densities (Seinhorst, 1965), especially when compared to many foliar diseases or insect pests for which the rate of increase is of primary importance to the final amount of crop damage. Therefore, the suppressive effect of resistance on nematode population densities becomes an important aspect of the use of resistance in crop management systems.

Numerous recent reviews are available that discuss definitions and availability of resistance (Cook and Evans, 1987; Roberts, 1992; Trudgill, 1991), the genetic basis for resistance (Roberts, et al., 1998), mechanisms of resistance (Williamson, 1998; Williamson and Hussey, 1996), breeding for resistance (Young, 1998), bioengineering resistance (Opperman and Conkling, 1998; Vrain, 1999) and protocols for screening for resistance (Starr, et al., 2002a). In this chapter we will discuss why nematode resistance is not currently utilized to its fullest potential, the need for greater emphasis to be given to the development of nematode-resistant crop genotypes, and also where opportunities exist for increased use of resistance.

17.2 Background of Resistance to Plant-parasitic Nematodes

Among the first reports of resistance to nematodes was that of Webber and Orton (1902), who described resistance of a cowpea variety "Iron" to root-knot nematodes based on reduced root-galling in field plots. They cited reports by Zimmerman (1897) for observations of resistance to root-knot in coffee, and Wilfarth (1900) on selection of sugarbeets with resistance to nematodes.

17.3 Resistance as a Component of Nematode Management

In these early reports, the authors do not consider the possibility of crossing resistant plants with susceptible genotypes to move the resistance into improved genotypes, but speculated on the possibilities of making selections from within the resistant populations for individuals with good agronomic characteristics and resistance. Ware (1936) reported that Orton made selections in 1905 from the cotton line “Jackson Limbless” that had good resistance to *Fusarium* wilt and noted that it was “somewhat resistant to root-knot but had little else to recommend it.” Moore (1960) cited Nilsson-Ehle (1920) as being the first to study heritability of resistance to nematodes and who identified resistance to *H. schachtii* in barley as being due to a single dominant gene. The lack of knowledge or appreciation for the importance of proper identification of the nematode population hampered early efforts to identify and characterize resistance in host species.

Barrons (1939) was one of the first to study the mechanisms of resistance to nematodes. Working with root-knot nematodes on cowpea, he distinguished resistance from tolerance and noted that resistance was not due to inhibition of root penetration. Barrons speculated resistance might be due to chemical inhibitors in the roots and that these inhibitors “may counteract or neutralize the giant cell inducing effect of salivary secretions of the nematode.”

A major achievement in resistance to nematodes was the introgression of the *Mi-1* gene for resistance to *M. arenaria*, *M. incognita*, and *M. javanica* from the wild tomato relative *Lycopersicon peruvianum* into *L. esculentum* (Smith, 1944). Today, root-knot resistant tomato cultivars with *Mi-1* are widely grown commercially. In addition, resistance conditioned by the *Mi-1* gene has been a valuable research model and has added greatly to the understanding of resistance in tomato (Williamson, 1998). With the cloning and determination of DNA sequences of *Mi-1* (Milligan, et al., 1998) and also the *HsI^{pro-1}* gene for resistance to *H. schachtii* in wild beet for use in sugarbeet (Cai, et al., 1997), the progress in the understanding of at least these two types of resistance will likely accelerate.

17.3 Resistance as a Component of Nematode Management

Hundreds of reports document crop yield suppression on a worldwide scale due to parasitism by plant-parasitic nematodes (see Evans, et al., 1993; Luc, et al., 1990; Sasser and Freckman, 1987). However, nematodes are often overlooked as crop pests, or they are considered to be pests of minor significance. Several factors contribute to the general underestimation of the

17 Resistance to Plant-parasitic Nematodes

impact of nematodes as crop pests. Most nematodes are soilborne pathogens that rarely cause diagnostic symptoms on the foliage. The typical non-specific symptoms of nematode parasitism in the form of general plant stress are often attributed to other causes. Further, although many soil environments that support plant growth are infested with plant-parasitic nematodes, most soils do not harbor sufficient nematodes to cause measurable yield suppression. Local and regional distribution patterns of nematodes also influence the perceived level of crop loss. For example, where more than 30% of the fields planted to a given crop in a region are infested with a potentially damaging nematode species (e. g., root-knot nematodes on cotton [Starr, et al., 1993] or cyst nematodes on soybean [Noel, 1992] in the USA), two thirds of the crop remains free of measurable damage. In addition, nematodes in infested fields are typically distributed in a highly aggregated pattern such that much of the field may be free of damaging population densities of the nematodes (Noe and Barker, 1985). This is not to argue that nematodes are unimportant as plant pathogens, because to lose 10% to 50% of ones yield on 30% of a field is a considerable burden, but rather to illustrate how easy it is to overlook such losses. Nevertheless, with the advent of successful management practices, starting with the soil fumigant nematicides over 50 years ago, and including the introduction of some highly effective resistant cultivars of major crops, the recognition of nematodes as important pathogens continues to increase. This is true both in high input intensive production systems, as well as in low input subsistence farming in developing countries.

Management of plant-parasitic nematodes to avoid crop losses is difficult, as is true for many crop pests. However, if resistance to nematodes was more widely available, crop productivity could be improved with little effort or direct cost to the producer. Resistance is one of several common tactics used to manage nematode pests of crops. Other tactics include use of nematicides, crop rotation and other cultural manipulations, biological control, and regulatory approaches. Use of resistant cultivars and rootstocks, like the other approaches, has both advantages and disadvantages that must be recognized and researched if viable management programs based on resistance are to be implemented. Still, host-plant resistance has been prioritized over chemical, biological, cultural, and regulatory control components as a major goal for pest management (Barker, et al., 1994). Several advantages and benefits can be achieved by breeding crop plants resistant to injurious parasitic nematodes for production on infested land. Resistant crops provide an effective and economical method for managing nematodes in both high and low value cropping systems. Assuming the resistance is coupled with tolerance to nematode infection, the resistant crop is "self-protected" and should yield well

17.3 Resistance as a Component of Nematode Management

on infested land. Furthermore, resistant crops in annual cropping systems can reduce or suppress nematode population densities to levels that are non-damaging to subsequent crops, thereby enabling shorter and more manageable rotations. Additional important benefits of resistant crops are their environmental compatibility, that they do not require specialized applications, and, apart from preference based on agronomic or horticultural desirability, usually they do not require an additional cost input or deficit. Because resistance and tolerance are amenable to integration with other management tactics, management systems can be developed that promote resistance durability or provide additional protection when resistance or tolerance is not expressed at high levels (Roberts, 1993).

In comparison, traditional nematicides such as the fumigant 1, 3-dichloropropene, the carbamates aldicarb and oxamyl, and the organophosphate fenamiphos, when applied correctly will increase crop yield if nematode population densities exceed damage thresholds, and they remain an important aspect of nematode management (see Whitehead, 1998). However, there is no long term suppression of nematode population densities with the use of nematicides. Additionally, the use of nematicides is frequently cost prohibitive, especially in subsistence agriculture, and environmental and human health concerns have resulted in withdrawal of or increased restrictions on the use of these toxic materials for many nematode-crop combinations. No new nematicide that has widespread use has been developed in the past 20 years. Approximately 10 years and tens of millions US\$ are required to develop and bring to market any new pesticide, and the nematicide market potential is relatively small (nematicide sales account for less than 1% of pesticide sales in the USA, whereas herbicides and insecticides account for 60% and 21%, respectively, of total pesticides sales for agriculture [Ware, 1994]). Thus, it is unlikely that any new nematicide based on currently available chemistry will be developed in the near future and nematicides are likely to have a diminished role in crop protection.

Crop rotations can decrease the potential for substantial yield losses due to nematodes (see Luc, et al., 1990; Whitehead, 1998) and provide at least short term suppression of nematode population densities. The magnitude of these benefits generally is positively correlated with the number of cropping seasons between the planting of susceptible crops. However, rotation systems are seldom adopted unless there are additional benefits to the producer beyond nematode management. Regardless of whether the producer is involved in intensive production agriculture or subsistence farming, many factors are involved in the decision about the most appropriate cropping system from the producer's standpoint. Overall, profitability and yield stability are the primary

17 Resistance to Plant-parasitic Nematodes

concern of the producer. Because many nematode species are polyphagous with wide host ranges and many fields have polyspecific communities of plant-parasitic nematodes, development of cropping systems that meet all of the needs of the producer and suppress nematode population densities is a formidable challenge. Nonetheless, there are numerous examples of effective nematode management with crop rotation (see Luc, et al., 1990; Whitehead, 1998). A further aspect of crop rotation is the role that resistant cultivars of susceptible crops can play. Many important nematodes, such as root-knot nematodes, have very wide host ranges and few non-host rotation crops are available. Thus, use of a resistant crop, with the same overall effect of suppressing nematode population densities, can be as effective as a non-host and may have greater economic appeal to the producer as a cash crop. Examples of resistant cultivars in crop rotation are given further on.

Biological control of nematodes through the use of parasites, predators, or antagonists holds some promise for the future (see Evans, et al., 1993), but with current knowledge it is difficult to promote or establish a microflora or fauna in soils that effectively suppress nematode population densities, especially in a relatively short period of time of a single growing season. In the foreseeable future, reliable and effective biological control systems are likely to be limited to specialized situations (e. g., intensely managed crop systems where the environment can be manipulated to promote biological activity).

17.4 Benefits of Resistance

Resistance is an effective management tool that improves crop yield (Table 17.1) in the presence of nematode population densities that exceed the damage threshold. Because resistance to nematodes is usually developed by selection of plants with reduced rates of nematode reproduction, nematode population densities are typically lower following a resistant cultivar than a susceptible cultivar. The use of the root-knot nematode resistance gene *Mi-1* in tomato on *Meloidogyne incognita* populations is an excellent example of this important effect (Roberts and May, 1986). However, the result may be different if the crop has only partial resistance. Niblack et al. (1986) demonstrated that at moderate to high initial population densities, *M. incognita* populations reach their maximum densities at about 90 days after planting on susceptible soybean cultivars (presumably the limited population development was due to extensive damage to the host), whereas on partially resistant cultivars that were less damaged by the nematodes the population densities were still increasing at 120 days after planting.

17.4 Benefits of Resistance

Table 17.1 Selected examples of the effect of resistance to plant-parasitic nematodes on crop yield in nematode-infested and non-infested fields.

Crop cultivar	Nematode species	Host status	Yield	
			Infested	Non-infested
soybean ¹	<i>Heterodera glycines</i>	S	2146 kg/ha	3183 kg/ha
		R	2919	3190
soybean ¹	<i>H. glycines</i>	S	2392	3825
		R	3180	3554
peanut ²	<i>Meloidogyne arenaria</i>	S	914 kg/ha	4678 kg/ha
		R	3771	5155
tobacco ³	<i>M. incognita</i>	S	301 g/plot	504 g/plot
		R	407	477
cotton ⁴	<i>M. incognita</i>	S	970 kg/ha	—
		R	1075	—

¹G. L. Tylka, personal communication; ²Starr, et al., 1998; ³Barker, et al., 1981; and ⁴Ogallo, et al., 1999. S = susceptible, R = resistant.

Resistance not only complements crop rotation for nematode management, but also improves the ease with which effective rotation systems can be developed. Ogallo et al. (1999) demonstrated that resistance to root-knot nematodes in cotton not only increased lint yields in nematode-infested fields compared to susceptible cultivars but also gave yield stability (Fig. 17.1). Additionally, they demonstrated that yield of susceptible lima beans was increased when planted in infested fields following two crops of resistant cotton relative to the yields following two crops of susceptible cotton (Fig. 17.2). This yield increase was due to suppression of population densities of *M. incognita* by the resistant cotton cultivar. Typically, the direct cost to the grower for the use of resistance is minimal, thus resistance fits all agricultural production systems. This low cost to the grower may change, however, with increasing use of transgenic systems by private industry for development of new cultivars. Private companies will expect to recover the high cost of development of resistant cultivars by transgenic methods through increased cost of seed. Beyond these agronomic and economic traits, a critical benefit of resistance is that it provides an ecologically sound approach to nematode management, especially relative to traditional nematicides, though there is concern by some that use of resistance developed by modern genetic engineering will have adverse effects on the environment and public health.

Resistance is not a panacea that will solve all nematode management problems. No resistance to important nematode species (especially migratory ectoparasites such as *Belonolaimus* and *Hoplolaimus*) is known for some crops

17 Resistance to Plant-parasitic Nematodes

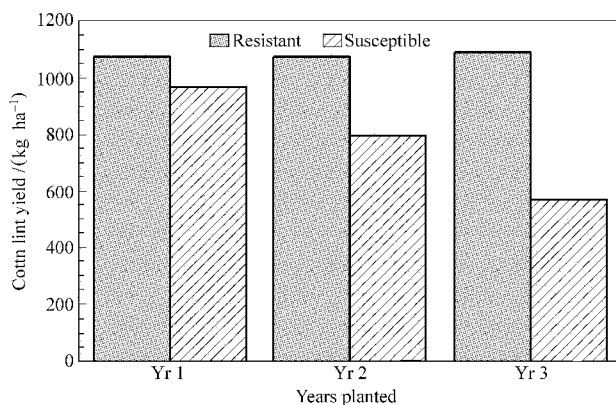


Figure 17.1 Cotton lint yields for three consecutive years for a root-knot resistant cultivar compared to yields of a susceptible cultivar in a field infested with *Meloidogyne incognita* (from Ogallo, et al., 1999).

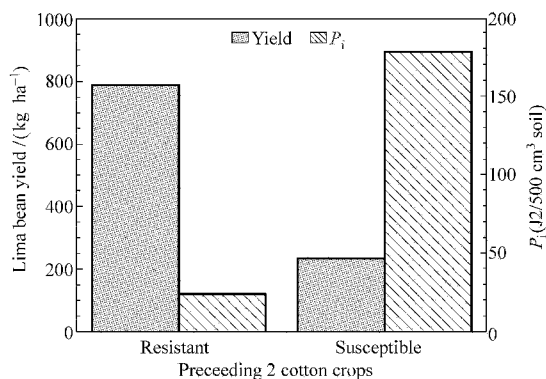


Figure 17.2 Illustration of the value of two years of a resistant host (cotton) on yield of a subsequent susceptible crop (lima bean) in *Meloidogyne incognita*-infested soil, compared to the yield following two years of susceptible cotton. The increased yields of lima bean following the resistant cotton are due to the lower initial nematode population densities (P_1) resulting from lower nematode reproduction on the resistant cultivar (from Ogallo et al., 1999).

or is present only in wild species or undeveloped genotypes. A major effort will be required to develop high yielding crop genotypes with desirable levels of resistance to these and other nematodes. The use of broad-spectrum fumigant nematicides probably will be further restricted. Consequently, the

17.4 Benefits of Resistance

importance of many plant-parasitic nematodes currently considered “non-target” relative to main “target” pest species of root-knot, cyst and some other nematode groups, may take on a greater significance as limiting factors in plant growth. Resistance to the “target” nematode species will not provide a similar broad-based protection against polyspecific nematode communities. Like crop rotation and biological control systems, resistance is typically a highly specific trait and is expected to be effective against only a single nematode species or even a subspecific race or pathotype.

A further consideration in resistance specificity is that after development of a resistant cultivar, the resistance may not be durable if the target nematode species has a high level of genetic variability (Bakker, et al., 1993; Kaloshian, et al., 1996; Roberts, 1995; Young and Hartwig, 1992). In fields where individuals in the nematode population carry virulence to specific resistance, the frequency of those individuals will usually increase in the presence of the resistant cultivar, especially if the resistant cultivar is grown frequently. Thus, a “resistance-breaking” population of nematodes may develop and render the resistance ineffective at that location. However, resistance can be made more durable by pyramiding multiple resistance genes to reduce the intensity of selection. For example, *Meloidogyne* spp. resistance in cowpea based on genes *Rk* plus *rk3* is expressed at a higher level, effective against a broader range of nematode populations and may be more durable than resistance conferred by gene *Rk* alone (Ehlers, et al., 2000). Nematodes with multiple virulence factors matching multiple resistance genes will require multiple mutation and selection events to occur, greatly increasing the probability for long-term durability of the resistance. Specific resistance deployment schemes based on frequency and combination of resistance in cropping systems can be designed that also increase the duration of selection pressure required for development of nematode populations virulent on specific resistance genes. Resistance to multiple nematode species, along with multiple diseases and arthropod pests, can be introgressed into one cultivar.

These limitations aside, resistance in many cases can be readily developed using proven technologies, requiring only that the effort to do so be expended. Transgenic approaches, while useful, are not needed in many cases. There are far more reports of resistance in various crop genotypes than there are resistant cultivars. A bibliography of resistance (Armstrong and Jensen, 1978) contains 1371 citations dealing with resistance in 119 crop species or genera. In the period of 1995 to 1998, Nematological Abstracts contained approximately 300 abstracts annually that dealt with some aspect of resistance. Young (1998) reported that the Crop Science Society of America (CSSA) has registered 143 nematode-resistant cultivars or germplasm lines for 15 field crops. Furthermore,

17 Resistance to Plant-parasitic Nematodes

in the texts by Luc et al. (1990) and Evans et al. (1993), resistant cultivars or the potential for their development from known resistant germplasm sources were discussed for nearly every crop. Nearly 90% of all reports involve *Meloidogyne*, *Globodera* or *Heterodera* species. This preponderance of effort on these genera reflects their overall importance as agricultural pests and the relative abundance of resistance to species of these genera.

17.5 Resistance and Crop Yields

Although resistance to plant-parasitic nematodes is usually identified and characterized based on inhibition of nematode reproduction, the primary objective for resistance development is to protect yield potential. As discussed previously, resistance can be an effective tool for management of nematode population densities and thus be of benefit in protecting subsequent susceptible crops, but this must be considered a supplemental benefit. Plant breeders are unlikely to introgress resistance into elite breeding lines or cultivars if the primary benefit will be to another crop through suppression of nematode population densities. It is doubtful if growers would be willing to plant a resistant cultivar if there was no yield benefit to that crop. Thus, when working with host resistance, yield must be the top priority. Ideally, a good yielding resistant cultivar that has the added benefit of suppressing nematode populations in the cropping system will be a strong incentive for crop improvement, particularly as nematicide availability and use decline.

As documented in Table 17.1, when nematode-resistant cultivars are planted in fields where initial nematode population densities exceed the damage threshold, resistant cultivars usually will yield more than susceptible cultivars. A few studies have examined the effects of resistance on the relationship between initial nematode population densities and crop yield. The Seinhorst (1965) model ($Y = m + (1 - m)Z^{P_i - T}$), where Y is the relative yield, m is the minimum yield at the highest possible nematode density, Z a constant, P_i the initial nematode population density, and T the damage threshold density) was used to examine this relationship for *M. incognita* on cotton (Zhou, 1999), pepper (DiVito, et al., 1992), and tomato (DiVito, et al., 1991). In each case, there was little or no change in the damage threshold population density T , but the minimum yield parameter m was increased (Fig. 17.3). Thus, the resistant cultivars were more tolerant (less yield loss) across a range of initial nematode densities. If the resistance of a crop approaches immunity, as with the *Mi-1* gene in tomato or the resistance in peanuts to *M. arenaria*, there may be no effect of initial nematode population density on yield (Fig. 17.4)

17.5 Resistance and Crop Yields

(Starr, et al. , 2002b). Different types and levels of resistance can be expected to have different effects on the relationship between initial nematode population densities and crop yields.

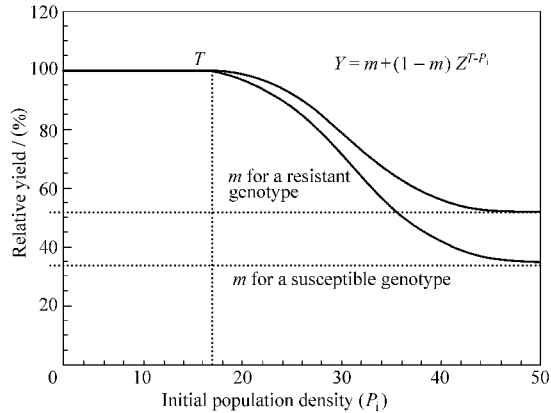


Figure 17.3 Schematic representation of the effect of resistance on the relationship between initial nematode population densities and crop yield based on the Seinhorst model. In some interactions the primary effect of resistance is to increase the value of m , the minimal yield value, with no effect on T , the damage threshold value.

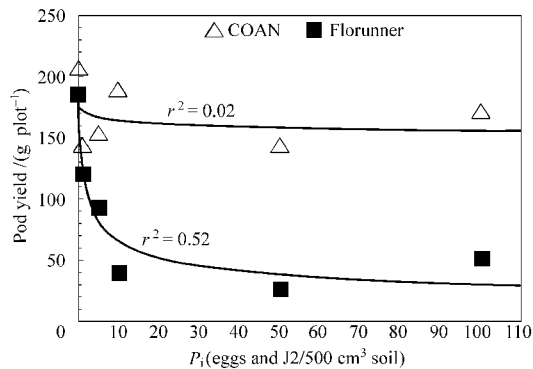


Figure 17.4 Effect of resistance in peanut to *Meloidogyne arenaria* race 1 on the relationship between initial nematode population densities and pod yield. In this case, the slope of response curve for the resistant cultivar “COAN” was not different from zero, indicating that there was no effect of increasing P_i on yield (Starr, et al. , 2002b).

17 Resistance to Plant-parasitic Nematodes

Regardless of the specific effect of resistance on the relationship between crop yield and initial nematode population densities, and assuming resistance confers tolerance, one expects greater yield loss at any given nematode population density for a susceptible cultivar than would be observed for a resistant cultivar. The end result is an increase in the economic threshold density (the nematode population density above which the potential economic loss exceeds the cost of implementing a specific management tactic [McSorley and Phillips, 1993]), for resistant cultivars relative to susceptible cultivars. If the direct cost of the resistance to the grower is minimal, then grower profits and (or) yield stability will increase. In many instances, e. g., cotton in the USA, producers are incurring unnecessary losses because nematodes are not recognized as crop pests and therefore are not targeted for management inputs. Improved host resistance, even if it is only partial resistance, will suppress overall crop losses due to nematodes.

Another way to view the benefits that can be derived from the use of resistance is to consider the effects on the portion of the field in which the nematode population density exceeds the damage threshold. Because of the usually clustered distribution of nematode populations, yield losses are seldom uniformly distributed over a field. Indeed, a field with more than 30% of the area exhibiting clear symptoms of nematode damage would be considered severely infested. In most situations where current management relies primarily on nematicides or crop rotation, these practices are applied to the entire field, not just the infested portions. Thus, the increased yield return expected from a portion of the field from these management practices must exceed the cost of treating the entire field. Resistance, which can be used with little or no increase in production costs, can be used to increase yield and profitability in situations where it is uneconomical to use more costly management practices, because the portion of the field infested is limited or the infestation level does not exceed the economic threshold for costly management practices. Even with partial resistance, the increase in yield may result in greater profitability than alternative management practices or no management. Studies that have critically examined the economic benefits of cultivars with partial resistance are lacking and are needed to fully document the benefits of resistance.

17.6 Examples of the Current Use of Resistance

Today, resistance is widely and effectively used in some crops for management of some nematodes. We have chosen a few examples of resistance to root-knot and cyst nematodes to illustrate various considerations and features of current

17.6 Examples of the Current Use of Resistance

successful resistance development and use. The reader is referred to other reviews for a broader description of examples, including use of resistance in perennial tree and vine crops (Cook and Evans, 1987; Evans, et al., 1993; Luc, et al., 1990; Roberts, 1992; Roberts, et al., 1998; Trudgill, 1991; Young, 1998).

17.6.1 *Meloidogyne*-tobacco

Resistance to root-knot nematodes in tobacco was first reported in the early part of the 20th century (see Clayton, et al., 1958), but resistant cultivars were not grown widely until the 1970s. In North Carolina, 97% of the 84,000 ha tobacco crop is planted with cultivars that are resistant to *M. incognita* (T. Melton, North Carolina State University, pers. comm.). Despite this high percentage use of resistance, more than 70% of the crop also is treated with a nematicide. This reflects the fact that even after more than 20 years of use and a highly effective grower education program, the producers of this high cash value crop are unwilling to put their complete trust in resistance. Factors that contribute to a lack of faith in resistance include the presence of races of *M. incognita* with virulence to the resistance, and the presence in some tobacco fields of *M. arenaria* and *M. javanica* against which the resistance is not effective, and the effectiveness of promotional efforts of the nematicide industry. Because of the value of the crop, growers are willing and able to treat the crop with a nematicide to ensure that root-knot nematodes do not damage the crop. Although the widespread use of this resistance resulted in an increased frequency of *M. arenaria* in North and South Carolina (Fortnum, et al., 1984; Schmitt and Barker, 1988), *M. incognita* remains the most frequently encountered species on tobacco and resistance is still highly effective in most fields.

17.6.2 *Meloidogyne*-tomato

The *Mi-1* gene for resistance to *M. arenaria*, *M. incognita*, and *M. javanica* has been used for many years in fresh market tomatoes with much success. However, because of *Mi-1* linkage to the undesirable trait of tough fruit attachment that made mechanical harvesting difficult, it was not widely used in commercial processing tomato production in the USA until the 1980s. Currently, many tomato cultivars in the different fruit quality and maturity classes are available with *Mi-1*, and the majority of the tomatoes grown commercially on infested fields in California carry this resistance. Despite the apparent success of the *Mi-1* gene in California, only recently have tomatoes carrying this resistance gene been widely grown in Florida. The recent use in Florida has been the result of the popularity of the cultivar Sanibell that carries

17 Resistance to Plant-parasitic Nematodes

the *Mi-1* gene, although its success is because of superior horticultural traits and not because of resistance to *Meloidogyne* spp. Virulence to the *Mi-1* gene can develop in Florida populations of *M. incognita* after as few as five plantings of Sanibell and breakdown of resistance at high soil temperatures also occurs (Noling, 2000). Even so, the *Mi-1* gene can be considered as quite durable, in that it has been overcome by virulence development in few field situations. In California, more than 20 years of intensive use has resulted in only a very few isolated cases of resistance breakdown (Kaloshian, et al., 1996).

Nevertheless, it is fortunate that additional genes for resistance to *M. incognita* and other root-knot species have been identified within the *Lycopersicon peruvianum* germplasm resources and, depending on the gene, several are heat stable or are effective against nematode populations virulent to *Mi-1* (Veremis and Roberts, 1996). Introgression of these genes into tomato cultivars is proving to be a challenging goal, because of problems associated with self- and cross-incompatibility in *L. peruvianum* and between *L. peruvianum* and *L. esculentum*, respectively (Veremis and Roberts, 2000). However, successful introgression of one or more of the novel *Mi* genes along with *Mi-1* may allow development of management systems that overcome problems associated with the use of *Mi-1* as a single gene for resistance.

17.6.3 *Heterodera-soybean*

Resistance to *Heterodera glycines* in soybean was first reported in 1957 (Ross and Brim), with resistant cultivars being widely grown by the mid-1970s. The *H. glycines*-soybean system is representative of cases where the effectiveness of resistance is compromised by virulence in the nematode populations. The race situation in *H. glycines* remains unsettled, with 16 races currently recognized (Riggs and Schmitt, 1983), but debate continues over the appropriate choice of both differential soybean genotypes and the basis of indexing resistant and susceptible reactions. Numerous high yielding soybean cultivars have resistance to races 1 and 3 of *H. glycines*, and a few good cultivars have resistance to races 6 and 14. The cultivar Hartwig has the broadest base of resistance, being resistant to races 1 to 6, 8 and 14, but it has relatively poor yield potential. Hartwig has proved useful as a parent for the development of additional cyst-resistant cultivars. Fortunately, of the 16 described races, eight are rarely encountered. Races 1 and 3 predominate in the northern portion of the USA, whereas races 2 to 6, 9 and 14 predominate in the southern states. In North Carolina, approximately 48% of the soybean crop of 573, 000 ha was planted to cyst nematode-resistant cultivars in 1998

17.6 Examples of the Current Use of Resistance

(J. Dunphy, North Carolina State University, pers. comm.), but 60% of the infestations are races against which resistance is not effective.

17.6.4 *Globodera*-potato

Resistance to the potato cyst nematodes was first reported in 1954 (Ellenby). Similar to the genetic variability in *H. glycines*, multiple pathotypes of *G. pallida* and *G. rostochiensis* have been described. However, these remain somewhat controversial, especially those of *G. pallida* for which pathotype differentiation is not clear-cut, due to incomplete data on the genetics of resistance in the host and virulence in the nematodes (Trudgill, 1985). None the less, resistance to *G. rostochiensis* has been widely used in several countries, including The Netherlands and the UK. Currently in The Netherlands about 55% of the ware potatoes (those for human consumption) and 99% of the starch potatoes are resistant to one or more pathotypes of the potato cyst nematodes (F. Gommers, Wageningen Agricultural University, pers. comm.). In the UK, approximately 45% of the potato crop carries the major resistance gene *H1* derived from *Solanum tuberosum* ssp. *andigena* that confers resistance to *G. rostochiensis* pathotype Ro1 and thus is effective against most populations of *G. rostochiensis* in that country (K. Evans, IRAC Rothamsted, pers. comm.). The *H1* gene has remained very effective against the Ro1 pathotype and can be considered a durable resistance, in that few examples exist of *H1* resistance causing emergence of virulent *G. rostochiensis* populations over some 40 years of use. However, a negative consequence of using *H1* resistance is that the frequency of *G. pallida*, which is not controlled by *H1*, is increasing in the UK and only about 1.5% of the potato crop carries effective resistance against prevalent pathotypes of *G. pallida*. Resistance to *G. rostochiensis* was quite effective in managing cyst nematodes until the appearance of *G. pallida* in the late 1970s. Resistance to *G. pallida*, based on resistance genes *Pa2* and *Pa3* from *Solanum vernei*, was then introduced during the 1980s with limited success. The resistance to *G. pallida* from both *S. vernei* and *S. spegazzini* is quantitative in nature based on multiple genes with partial resistance expression. This type of resistance coupled with a high level of genetic variability for virulence in field populations has made it difficult to achieve an adequate level of resistance, and screening for genotypes with tolerance to *G. pallida* has been given priority in some programs (Brodie, et al., 1993). Despite these problems in maintaining effective resistance deployment against such variable pathogens as cyst nematodes, resistance has been useful in alleviating crop losses. Fortunately, the limited host range of these cyst nematodes has made the use of crop rotations that include non-host crops an effective complement to the use of resistance.

17.6.5 *Meloidogyne*-cotton

Cotton is a major crop worldwide and is widely grown in the southern and southwestern regions of the USA. *Meloidogyne incognita* has long been recognized as an important pathogen of cotton (Starr, 1998), because of its damaging effects directly and also because it forms a disease complex with the vascular wilt pathogen *Fusarium oxysporum* f. sp. *vasinfectum* (DeVay, et al., 1997). Resistance to *M. incognita* has been researched since the early part of the 20th century (see Ware, 1936). The first germplasm with a high level of resistance was the transgressive resistance in Auburn 623 RNR, which was selected from the F9 generation of Cleve wilt 6 x Wild Mexico Jack Jones (Shepherd, 1974). This early generation material was poorly adapted commercially but Shepherd and his coworkers made substantial improvements in the agronomic traits of this material and eventually released nine germplasm lines with high levels of resistance and good yield potential (Shepherd, et al., 1996). However, this excellent source of resistance has yet to be introgressed into widely grown cotton cultivars.

In the 1990s three cotton cultivars (Acala NemX, Stoneville LA887, and Paymaster 1560) with moderate to good levels of resistance to *M. incognita* were released. Stoneville LA887 and Paymaster 1560 have resistance derived from Cleve wilt 6 (Robinson, et al., 1997) whereas the source of resistance in NemX is uncertain. Despite the value of these cultivars in increasing cotton yields in nematode infested fields and in reducing population densities of *M. incognita* (Ogallal, et al., 1999; Zhou, 1999), they accounted for less than 1% of all cotton planted in the USA in 1999 (Anon., 1999). Why these cultivars are not more widely accepted for use in nematode infested fields is unknown, especially given the recent increase in the understanding of nematodes as important pests of cotton. Unfortunately, highly effective cotton IPM programs that have been developed over the past 20 years are focused primarily on insect pests and provide little information to growers on effective strategies for nematode management. With the recent effort in development and sales of the highly profitable transgenic cotton cultivars, the private cotton breeding industry has had little incentive to work with nematode resistance. In California, a reduction in the total cotton acreage in recent years has meant that some of the poorer yielding ground, including that infested with *Fusarium* wilt and *M. incognita*, has been left out of production, impacting the use of Acala NemX. Another factor limiting current use of nematode resistance is the reluctance of grower education programs to promote or recommend the use of resistance. At least one extension specialist from a cotton producing state expressed reluctance to recommend one of these moderately resistant cultivars

17.6 Examples of the Current Use of Resistance

because he was concerned that some growers would not understand how to use the resistance, and without nematicide treatment growers may suffer substantial yield losses in severely infested fields. Also, he felt that many growers would continue to use nematicides in infested fields even though resistance was available. Clearly there is a need for improved grower education programs, in addition to expanding the choice of available resistant cultivars.

Rotylenchulus reniformis has become a widespread problem in the USA. In some regions, more than 50% of the cotton fields are infested with either *R. reniformis* or *M. incognita* (Blasingame, 1993). Effective resistance to *R. reniformis* has not been found within *G. hirsutum*, but resistance has been identified in other *Gossypium* species. However, efforts to introgress this resistance into *G. hirsutum* have been complicated by incompatibility barriers. No useful resistance to *R. reniformis* was identified among lines of *G. hirsutum* that carried a single monosomic addition from the highly resistant, but genetically incompatible *G. longicalyx* (Frerich, 1995). Several introgression pathways have been suggested to transfer *R. reniformis* resistance from the diploid species *G. arboreum* and *G. herbaceum* into *G. hirsutum*, including generation of fertile interspecific hexaploids, synthetic allotetraploids, and a 4x

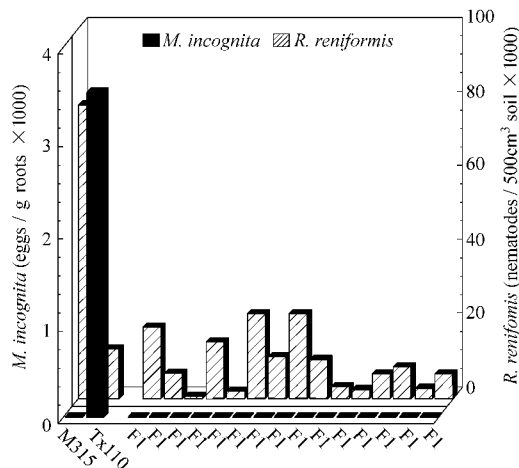


Figure 17.5 Resistance to *Rotylenchulus reniformis* and *Meloidogyne incognita* in F1 individuals from a cross between the reniform resistant *Gossypium barbadense* TX110 and the root-knot nematode resistant *G. hirsutum* M315. Resistance to each nematode species was measured separately on different F1 individuals and was based on nematode reproduction (Starr, unpubl. data).

triple hybrid from a resistant diploid by a 2(ADD) 6x genome cross (Stewart and Robbins, 1996). More recently, the moderately resistant *G. barbadense* line TX110 crossed with the *M. incognita*-resistant *G. hirsutum* genotype M315 resulted in fertile F1 progeny with high levels of resistance to *M. incognita* and moderate resistance to *R. reniformis* (Fig. 17.5) (Starr, unpubl. data). Substantial additional breeding efforts will be required before any resistance to the reniform nematode is available commercially.

17.6.6 *Meloidogyne*-peanut

Recently, success has been achieved in a long term effort to introgress resistance to *M. arenaria* from wild *Arachis* species into the cultivated peanut *A. hypogaea* (Simpson and Starr, 2000). Because *A. hypogaea* is an allotetraploid and the resistant species are diploid with differing genomes, a complex interspecific hybrid was developed first (Table 17.2), resulting in a synthetic tetraploid that was cross-compatible with *A. hypogaea* (Simpson, 1991). A backcross-breeding program was used to introgress the resistance into high yielding genotypes. The first nematode resistant cultivar, COAN, was released in 1999 (Simpson and Starr, 2000) and substantial education programs are in progress to demonstrate the value of the resistance to the growers. Because COAN does not have the yield potential of the best susceptible cultivars, it is only being recommended for nematode infested fields. COAN was a selection from the fifth backcross generation of the breeding program. Selections from the seventh backcross generation appear to have yield potential equal to that of the highest yielding susceptible cultivars (Fig. 17.6) (Church, et al., 2000) and should be more widely acceptable to peanut growers.

Table 17.2 Introgression of resistance to *Meloidogyne arenaria* from wild *Arachis* species into the cultivated peanut *A. hypogaea*.

1. *A. diogeni*, a diploid A genome species with nematode resistance is crossed with *A. cardenasii*, another diploid A genome, nematode-resistant species.
2. The progeny of the *A. diogeni* x *A. cardenasii* is crossed with *A. batizocoi*, which is a diploid B genome and nematode-resistant species.
3. The diploid AB genome progeny of *A. batizocoi* x (*A. diogeni* x *A. cardenasii*) are infertile. Fertility is restored by treatment with colchicine to create a synthetic tetraploid with an AB genome. The synthetic tetraploid (TxAG-6) is highly resistant to *M. arenaria*.
4. The synthetic AB tetraploid TxAG-6 is crossed with the cultivated peanut, *A. hypogaea*, which is also a tetraploid with the AB genome, to transfer nematode resistance to genotypes that can be readily crossed with cultivated peanut.
5. A backcross breeding program, with *A. hypogaea* "Florunner" as the susceptible recurrent parent, with selection for nematode resistance based on reproduction of *M. arenaria* in each generation.
6. The *M. arenaria*-resistant cultivar COAN is a selection from the fifth backcross generation.

17.7 Future Projections

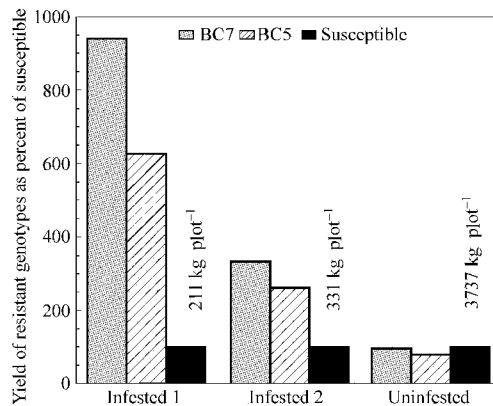


Figure 17.6 Improvement in yield potential of peanut resistant to *Meloidogyne arenaria* race 1 with continued backcrossing and selection for yield. Yield of a selection from the BC7 generation was greater than the selection from the BC5 generation and the susceptible cultivar in the two nematode-infested sites. In the uninfested field, the yield of the BC7 generation selection was equal to that of the susceptible standard, whereas the yield of the selection from the BC5 generation was only 70% of that of the susceptible standard. Note that the yield of the susceptible cultivar was suppressed by more than 85% in the infested fields (from Church, et al., 2000).

The resistance in COAN is due to a single dominant gene derived from *A. cardenasii* (Burow, et al., 1996; Choi, et al., 1999). Restriction fragment length polymorphism (RFLP) markers linked to the resistance loci have been identified and are being used for marker-assisted selection (MAS) in ongoing breeding efforts (Choi, et al., 1999; Church, et al., 2000). MAS is also being used to identify additional nematode-resistance genes within the available germplasm resources, including resistance to *M. javanica* populations parasitic on peanut (Abdel-Momen, et al., 1998). Nematode resistance is being combined with resistance to tomato spotted wilt virus, resistance to Sclerotinia blight, and high oleic to linoleic fatty acid ratio, a desired trait in the peanut industry. Introgression of additional resistance genes will increase the durability of the resistance and promote yield stability.

17.7 Future Projections

Host resistance is a management tactic that has much potential and needs to be utilized more effectively. Many of the problems associated with resistance can

be overcome or minimized with additional research, breeding effort, and effective grower education programs. Unfortunately, many nematologists believe or find that their responsibility ends with the research. This attitude may be the greatest impediment to more effective use of resistance.

Many of the available germplasm resources remain to be characterized with respect to resistance to nematodes. Holbrook et al. (2000) advocate the use of core collections, which are subgroupings of the entire germplasm collection representing major geographic regions or other bases for diversity, as a means of more effective screening of large germplasm collections. In this approach, one screens a set number of individuals from each subgroup, with the number being based on the proportion of the entire collection represented by that group. When the trait of interest (i. e., resistance) is identified within a subgroup, one concentrates further screening on that subgroup with corresponding less emphasis on other subgroups.

Even after resistant phenotypes have been identified, further research will be required to determine the number of unique genes for resistance that may be present in different resistant accessions. For example, Robinson and Percival (1997) recently identified accessions of *G. hirsutum* from the Yucatan peninsula of Mexico with resistance to *M. incognita* that is similar to the resistance in Cleve wilt 6 and Wild Mexico Jack Jones. However, it is not known whether these accessions carry unique genes for resistance or if their genes for resistance are identical to those already in use in breeding programs. As DNA-based markers (e. g., SSR, RFLP, and RAPDs) tightly linked to resistance loci become more readily available, they can be used to rapidly screen additional resistance phenotypes to identify novel resistance genes. Use of several MAS techniques may allow one to determine more rapidly if the resistance phenotypes are due to unique genes rather than the more time consuming traditional genetic analysis of each candidate.

Recent work on *M. javanica* and *M. incognita* resistance in carrot has demonstrated the utility of MAS (Boiteux, et al., 2000; Simon, et al., 2000; Boiteux, Roberts and Simon, unpubl. data). Analysis of two codominant RAPD-derived STS (sequence-tagged site) markers flanking the *Mj-1* resistance locus have revealed the expression of a weakened level of resistance in heterozygous individuals compared to homozygous individuals due to a gene dosage effect. This finding has important implications for carrot cultivar development, which typically is based on F1 hybrid carrots as the commercial type. Homozygous resistance will be necessary to provide full protection of carrots from *M. javanica*. Not only do these markers allow a rapid screening protocol for selection of homozygous individuals in the resistance breeding program, they also enable direct comparison of resistance

conferred by *Mj-1* with other resistance factors in the carrot genome. For example, an unanswered question is whether the more variable and weaker resistance to *M. incognita* in plants with *Mj-1* is due to a different interaction of *M. incognita* with *Mj-1* compared to *M. javanica*, or whether *M. incognita* resistance is conferred or modified by additional gene loci in carrot.

Genetic transformation of plants with cloned resistance genes is an exciting part of the future for resistance to nematodes. The recently cloned genes *Mi-1* from tomato and *Hs1^{pro-1}* from sugarbeet represent an essential first step toward that goal. Cloned genes present the opportunity to transfer resistance directly into elite genotypes of the same crop, or into cultivars of different crops. The benefits of this capability are obvious and include avoidance of linkage drag and also the expansion of the resistance utility, particularly in crops where natural genes for resistance have not been identified or are in genotype backgrounds that prohibit simple introgression by crossbreeding. Another opportunity emerging from molecular and genetic analysis of resistance is the common clustering of resistance genes or their effects, either by closely positioned gene loci, or by multiple resistance expression (Michelmore and Meyers, 1998). For example, a novel heat stable resistance gene is located in the *Mi-1* region of tomato (Veremis, et al., 1999), and *Mi-1* has been shown to have a dual resistance function, in that it confers not only nematode resistance but also resistance to potato aphids (Kaloshian, et al., 2000; Rossi, et al., 1998). Thus, quite different pathogens and pests, in this case a root-cell-feeding nematode and a leaf sieve element-feeding insect, are being blocked by at least some portion of the same resistance pathway.

The potential disadvantages of the innovative approaches to resistance usage also must be considered. For example, although *Mi-1* seems quite durable, virulence to this gene in *Meloidogyne* spp. has been documented (Kaloshian, et al., 1996), and an expansion of its use in other crops on the same infested fields would certainly increase the potential for selecting virulence in heterogeneous nematode populations. Other problems exist with cloned genes that must be resolved through research efforts. For example, *Mi-1* has been demonstrated to express resistance when inserted into eggplant, but not in some other solanaceous plants such as tobacco (Frijters, et al., 2000). Clearly, at the fundamental molecular level, there is much we do not understand about resistance gene function and expression in foreign genomes. Interestingly, transgenes for insect resistance (Bt toxin) have been introgressed into the nematode-resistant cotton cultivar Paymaster 1560, but the transgenic plants apparently lost the resistance to *M. incognita* (Colyer, et al., 2000). It remains unclear whether this loss of nematode resistance in transgenic cotton was due to a mutation caused by insertion of the transgene into the

17 Resistance to Plant-parasitic Nematodes

nematode-resistance gene. A more likely explanation is that during development of the cultivar subsequent to the insertion of the transgene there was insufficient screening of segregating populations to retain the nematode resistance.

Research has only begun to explore the possibilities for engineered resistance (Opperman and Conkling, 1998; Vrain, 1999) and as yet no cultivar with engineered resistance to nematodes is available for growers. The recent text by Fenoll et al. (1997) lists numerous possibilities for engineered resistance, including anti-nematode genes, anti-feedants, and plantibodies. Many researchers are confident that such sources of resistance will become valuable additions to our arsenal in the near future. It is expected that engineered resistance will help overcome fertility barriers that limit use of some native sources of resistance and will provide sources of resistance to nematodes such as *Belonolaimus* and *Hoplolaimus* spp. for which no resistance is currently known. A major question is whether engineered resistance will be more durable than many currently available resistance genes, especially with respect to *Globodera* and *Heterodera* spp. Based on present knowledge, we can assume that engineered resistance will have some similar and unique constraints with respect to durability compared with natural resistance.

Regardless of the source of resistance, it will be little more than a research tool if nematologists do not form an effective collaboration with plant breeders to move the resistance into appropriate crop genotypes that have the highest yield potentials and other important agronomic and horticultural characteristics. The nematology community has a responsibility to convince the public and private sector plant breeders that introgression of resistance to nematodes into the elite crop germplasm lines or cultivars will be beneficial. Plant breeders need expert input to identify appropriate sources of resistance and to develop or adopt effective screening systems that will permit timely introgression of resistance. The collaborative effort requires an active participation from the initial steps of resistance identification all the way through to the field assessment of the finished cultivar. One challenge is to overcome the common view that resistance frequently comes at the expense of yield. This is true in some cases, including the recently released COAN peanut with resistance to *M. arenaria*. However, there are no data that prove yield must be sacrificed to achieve resistance, and it is often only the first generation of released resistant cultivars that have suboptimal yield potential and later generations overcome this association. As has been recently demonstrated with cotton (Ogallo, et al., 1999), peanut (Church, et al., 2000), and soybean (see Table 17.1), the linkage between lower yield potential and resistance can be broken and resistant genotypes with yield potentials equal to those of the best yielding

References

susceptible genotypes are possible. Similarly, the use of the *Mi-1* gene in tomato was initially limited by problems of linkage drag with undesirable horticultural traits (Williamson, 1998), but this negative linkage has been broken and tomato cultivars carrying the *Mi-1* gene are now widely grown commercially.

Once high yielding cultivars with improved levels of resistance to nematodes are developed, effective grower-based education programs are required to successfully implement their use. Some forms of resistance will lack durability due to variability in the nematode population, or they will express only partial resistance such that some yield loss may occur at high initial nematode population densities. Thus, it is essential that the resistance be deployed in a responsible manner and be integrated with other nematode management tactics to achieve optimal benefits with respect to yield and to enhance durability. Because there are relatively few extension specialists or advisors with nematology as their primary responsibility, we must work in cooperation with extension personnel from a variety of disciplines to develop effective education programs. Often the first task is the education of the extension specialist or crop production advisor as to the value of nematode resistance in the crop and cropping system.

In summary, the identification, development, and deployment of resistance requires a long term and extensive effort, but as has been demonstrated repeatedly, the benefits justify the effort. In one of the few critical studies of the economic benefits of resistance, Brady and Duffy (1982) documented that a \$1 million expenditure to develop one soybean cultivar with resistance to *H. glycines* resulted in benefits in the amount of \$400 million. Host resistance will not be the solution to all problems caused by plant-parasitic nematodes, but resistance could and should play a bigger role in many nematode management systems. The era of nematicides is approaching an end and we must develop alternative management strategies. Clearly, the use of host plant resistance must be one of these alternatives, and it will play a priority role in many crop production systems, both directly and as a component of an integrated approach to nematode management.

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17 Resistance to Plant-parasitic Nematodes

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