Resistance/Tolerance and Related Concepts/Terminology in Plant Nematology

Clarification of concepts and terms is essential for communication among scientists; it is especially important to the goal of developing acceptable nematode-resistant cultivars. Much progress in standardization of terms and concepts in plant pathology is being made through the development of a specialized dictionary (8) and other related treatments (2,12,13,17). The fact that nematodes are primarily parasitic and secondarily pathogenic causes problems in adapting terminology that was initially established for fungi and bacteria (27). Researchers working on nematodes have traditionally been assigned to diverse disciplines; thus, discipline-specific diversity in concepts and terminology has evolved. The ensuing discussion provides a potential framework that should facilitate more effective communication between nematologists and related disciplines. Special emphasis is placed on overall responses of both nematode and plant as related to resistance and tolerance and on the concepts of nematode biotype, pathotype, and race.

Even with our diverse concepts and viewpoints, considerable success has been achieved in incorporating resistance to plant-parasitic nematodes into crop cultivars that have high quality and yield. Primary target nematodes are those that induce readily observable symptoms (root or other tissue galls) and/or visible reproductive "structures" (egg masses or cysts). Thus, research on resistance has focused largely on the sedentary endoparasites, i.e., root-knot species (*Meloidogyne* spp.), cyst formers (*Heterodera* and *Globodera* spp.), the reniform nematode (*Rotylenchulus reniformis*), and a few migratory endoparasites, such as the stem nematode (*Ditylenchus dipsaci*) and the burrowing nematode (*Radopholus* spp.) (4). Some sources of resistance to other migratory endoparasites, such as lesion nematodes (*Pratylenchus* spp.) and the ectoparasite *Xiphinema index*, also have been identified (4). Numerous reviews on nematode-crop resistance are available (4,12–15,27–29). This treatment focuses on the terminology and concepts used by nematologists. Suggestions are offered that might facilitate enhanced communication within and among other plant-protection disciplines.

Practical resistance to nematodes depends on the suppression of both disease development and parasite reproduction (4). A disease- or pest-resistant cultivar must be agronomically or horticulturally acceptable to justify its release. Still, growers may reject resistant cultivars. For example, about 100 root-knot–resistant tomato cultivars have been developed (14), but few of these are widely grown because of a range of factors. In contrast, *Meloidogyne incognita*–resistant tobacco cultivars are grown on more than 60% of the hectarage in many regions. Resistant cultivars acceptable for one region may fail in other environments or be unsuitable because of cultural practices. This situation has developed with the peach cultivar Nemaguard; when used as "rootstock" resistant to *M. incognita*, Nemaguard performs well in California but is associated with widespread winter injury of trees in the southeastern United States.

Variation in terminology: Resistance and tolerance

Russell (13) indicates that any inherited characteristic of a host that lessens the effects of parasitism results in resistance. The availability of rapid population assays enables nematologists to evaluate many potentially resistant plants. However, some scientists working on *Meloidogyne* spp. (which induce readily measurable root galls on most hosts) continue to use only the traditional root-gall index for assessing host resistance. Still, nematode reproduction, root-gall development, and host growth should all be assessed in evaluating resistance to *Meloidogyne* spp. (7). Numerous researchers focusing on cyst nematodes (*Heterodera* and *Globodera* spp.) often initially assess the resistance of a cultivar or line exclusively by its effect on nematode development and/or reproduction (4,9,28, 29). These scientists (4,9,28,29) use the term "tolerance" to describe the general plant response to nematode infection. Tolerance also continues to be used to describe the capacity of a host to withstand infection and rapid nematode reproduction without significant damage, as initially envisioned by N. A. Cobb (3). Table 1 presents the terms used by Dropkin and Nelson (6) and by Trudgill (28) to describe ranges of resistance and host tolerance to nematodes. The single terms offered by Dropkin and Nelson (6) have been used widely, but host growth or yield responses are not determined readily in many plant-breeding programs.

The level of resistance (based on nematode reproduction) may be complete, intermediate (partial), or nonresistant (susceptible) (4). Cook and Evans (4) indicated that tolerance is not a type of resistance. They suggested that this term be used exclusively to describe the amount of host injury or yield suppression. Tolerance and resistance may occur simultaneously, but Trudgill (28) concluded that they are independent. This independence, however, may not be clearly discerned for many root-knot-resistant cultivars that also are moderately tolerant. Invasion of roots of resistant plants by juveniles of *Meloidogyne* spp. and the often associated hypersensitive responses (19) may result in short-term stunting of plants, but most recover (1).

Thus, the concept of tolerance to nematode parasites is frequently used to describe two distinct biological phenomena: 1) the traditional use as conceived by N. A. Cobb (3), working with "rust-enduring" plants, and described by Dropkin and Nelson (6), i.e., the ability of plants to support parasite (nematode) reproduction without being damaged significantly, and 2) general plant response to infections. Wallace (31) argues that host tolerance to nematodes is a general nonspecific phenomenon, evolving from long-term abiotic stresses. He further suggests that plants that are tolerant to particular stresses caused by abiotic factors may also be tolerant to nematodes that induce similar stresses. The striking impact of environmental stress factors on plant growth responses during the expression of partial, reproductive resistance (11,28) tends to support this hypothesis. In contrast, the second type of "tolerance" (such as that involving the genetically controlled hypersensitive resistance response) more closely reflects the host's ability to suppress nematode reproduction and regenerate tissues or compensate for death of root cells. This capacity is generally a function of inoculum density (16) and/or level of resistance.

In addition to placing the highest priority on developing nematode-resistant and nematode-tolerant cultivars (limited nematode reproduction and host damage), considerable effort is being directed toward identifying and deploying "tolerant-susceptible" cultivars (limited host damage and uninhibited high nematode reproduction) (9,28). Wallace (31) contends that most native host plants are tolerant and

Table 1. Terms used by Dropkin and Nelson (6) and by Trudgill (28) to describe ranges of resistance and host tolerance to nematodes

Parasite reproduction	Host growth: Good		Host growth: Poor	
	Reference 6	Reference 28	Reference 6	Reference 28
Good	Tolerant	Tolerant/nonresistant	Susceptible	Nontolerant/nonresistant
Poor	Resistant	Tolerant/resistant	Intolerant	Nontolerant/resistant

susceptible (suitable hosts) to the nematodes with which they are associated. The suggestion offered by Wallace (31) that "tolerance should be maximized and resistance minimized" warrants greater consideration. The approach to include tolerance, presently employed by Hussey and Boerma (9), should result in a reduction of selection pressure for the development of new pathotypes or races. Nevertheless, problems may be encountered in selecting and breeding for tolerance, as numerous genes are likely involved. Additionally, research may need to address how tolerant cultivars are deployed and their impact on yields, since they may support high nematode equilibrium population densities.

Techniques in molecular biology offer much potential for facilitating the development of resistance to plant-parasitic nematodes. Currently, transgenic plants with unique genes are being evaluated for host resistance that sensitize certain root tissues to *Meloidogyne* spp. (23), and this approach has much promise. Insertion of selected bacterial genes into plants also has potential as a biocontrol of nematodes (21). This new technology likely will require continuing evolution of our concepts of host resistance.

Nematologists need to be able to communicate more effectively with each other, with other plant-protection scientists, and with growers. Terminology should be clear to our colleagues and clientele without having to repeatedly define each term. Although this goal is unlikely to be fully achieved, adaptation of terminology similar to that offered by Clarke (2) has promise for bridging some of the key gaps. Terminology should reflect the facets or processes impacted by resistance and tolerance. Resistance and tolerance can be partitioned to include: 1) host response, 2) parasite response, and 3) overall response.

Three possible basic "interactions" may occur between nematodes and plants: 1) *neutral (immune)*, with no infection; 2) *compatible* (suitable host), with a susceptible or tolerant reaction; and 3) *incompatible* (unsuitable host) with a hypersensitive (resistant) or intolerant reaction. As discussed earlier, many nematologists focus primarily on relative host suitability in terms of nematode reproduction ("resistance") and on host sensitivity in reference to pathogenicity ("tolerance"). For new resistant or tolerant cultivars to be accepted at the grower level, both reactions must be included. The partitioning of tolerance as well as resistance into three types, as proposed by Clarke (2) for tolerance, provides a framework for more definitive communication and research in these increasingly important areas.

The concept of tolerance can be effectively employed in clear definitions with slight modifications of the three divisions offered by Clarke (2):

- *Tolerance to the parasite*: The ability of a plant to endure the effects of levels of parasitic infection (including nematode reproduction) that would cause greater damage or disease if they occurred in other plants of the same or similar species.
- *Tolerance to disease*: The ability of a plant to endure the effects of levels of disease (i.e., host physiological damage, etc.) that would cause greater impairment of growth or yield if they developed in other plants of the same or similar species.
- *Overall (general) tolerance*: The ability of a plant to endure the levels of parasitic infection and disease that would cause greater impairment of growth and yield if they occurred in other plants of the same or similar species.

A similar partitioning of resistance could encompass the current approach of several nematologists—focusing primarily on nematode reproduction. It also would provide the option for assessing resistance to associated pathogens in disease complexes induced by multiple parasites. The key divisions of resistance and specific definitions are:

- *Resistance to the parasite*: Any feature(s) or property(ies) of a host that prevents, reduces, or delays the development of a parasite (2).
- *Resistance to the disease*: Any feature(s) or property(ies) of a host that prevents, reduces, or delays the development of a disease and/or damage.
- *Overall (general) resistance*: Any feature(s) or property(ies) of a host that prevents, reduces, or delays the development of a parasite and associated disease.

Overall resistance, like overall tolerance, would involve resistance to the parasite and resistance to the disease and/or damage.

These rather simple but clear divisions allow the researcher to focus on the host or pathogen or both. Most plants resistant to a parasite also are resistant to the disease, and this overall or general resistance is usually the goal for effective nematode management. Still, other parasite-resistant lines are intolerant as described by Dropkin and Nelson (6). Clarke (2) emphasizes that partial resistance and tolerance may be misused or confused. To avoid this problem, the degree of infection (biomass of parasite) and amount of disease (galling, growth and yield inhibition) should be assessed. For some nematodes, such as *Heterodera* and *Globodera* spp. (which typically induce few or no definitive disease symptoms), the focus for early screening may be limited to resistance to the parasite or tolerance to parasitism. These definitions also should contribute to clarifying the confusion that has developed in nematology in using the term "tolerance" to refer to resistance to disease or damage (resistant and tolerant cultivar) and "true tolerance" (susceptible host, little disease) to damage (9,28). The term "intolerant" also should be retained to describe cultivars/plants that are highly sensitive to the nematode (stunting, etc.) upon infection even if there is little or no parasite reproduction (resistant to parasite but with high host sensitivity).

Many comparisons of relative host suitability (nematode reproduction) and susceptibility for the types of tolerance and resistance, and susceptible and intolerant interactions for nematodes/hosts, could be considered. The inclusion of partial resistance reflects the continuum of these host/parasite relationships rather than the sometimes implied, strictly differential categories. Thus, compatible and relatively incompatible relationships may develop with some partially resistant cultivars. For example, tobacco resistant to *M. incognita* races 1 and 3 shows a slight hypersensitive reaction to *M. arenaria* and *M. javanica*, compared with a very severe tissue response to the target species (19). Some tobacco breeding lines show resistance to root-gall (disease) induction by *M. arenaria* but support a high level of reproduction of this parasite (Ng'ambi, Rufty, and Barker, *unpublished*). Corn typically gives this type of response to *Meloidogyne* spp.

Pathotype, biotype, and race

Numerous schemes have been offered to classify nematodes according to their parasitic capabilities (27). "Pathotype," especially in Europe, refers to a biological entity (nematode population) that is distinguished by its inherent capacity (or inability) to multiply on a given host genotype with one or more genes for resistance (4,28). The term "race" generally is used in this context for the soybean cyst nematode in the United States (15). Another proposal includes "biotype" for parthenogenetic nematode populations with different host preferences and "pathotype" for equivalent populations of amphimictic species (18). Others use race to refer to populations of a nematode species distinguished by their inherited ability to reproduce on designated species of plants (4,28). These so-called races, however, may simply be heterogenous nematode populations (such as *Ditylenchus dipsaci*) from which homogenous strains can be selected through monoculture (4). Dropkin (5) recommended that nematologists use pathotypes to designate any intraspecific variant, based on variables such as a differential host test, instead of race, biotype, or strain. In contrast, Triantaphyllou (27) suggested that biotype could be recognized as the basic unit for characterizing nematodes in reference to their parasitic capabilities. He redefined biotype as a "group of genetically closely related individuals sharing a common biological feature such as specified parasitic capability, preferably restricted to a single differential host with simple genetic basis for resistance." This view of biotype is similar to the race concept utilized in plant pathology for genetic variants of plant-pathogenic fungi (30). Triantaphyllou (27) also indicated that the term "pathotype" is equivalent to biotype and, as usually used for the potato cyst nematode, becomes equivalent to a race. Combinations of biotypes, commonly found in field populations, could be referred to as races (one race per field), but this approach is currently used for *Heterodera glycines* and is interpreted differently by various scientists.

The mode of nematode reproduction must be considered in reviewing the usage of the terms pathotype, biotype, and race. The proposal by Sidhu and Webster (18) to designate "pathotype" for host-specific variants of amphimictic species and "biotype" for such variants in parthenogenetic species has been practiced by few scientists. Among the parthenogenetic *Meloidogyne* species, both host and cytological races have been designated. For example, *M. hapla* and *M. incognita* have cytological races (A and B) that differ little as to host reactions (26,27). In contrast, the host races 1-4 of *M. incognita* and host races 1 and 2 of *M. arenaria* are identified via reproduction responses on differential plant species/cultivars (22). Thus, the letter designation implies a cytological race, whereas a numerical ranking infers a host race for this genus. The responses to the differential hosts for *Meloidogyne* species and races, however, are not always consistent (20). For example, many populations of *M. arenaria* race 1 often reproduce little on *M. incognita*-resistant tobacco, a designated positive host (1). DNA analyses should effect a more useful characterization of the biotypes and genotypes of these types of parthenogenetic nematodes. The race concept, as applied to the amphimictic nematode *H. glycines*, has numerous inherent problems (10,20,24,25). Because of their diverse genetic makeup, Niblack (10) concluded that the race designation of *H. glycines* should be used only for applied research and extension purposes. Thus, the determination of biotypes (27) or genotypes is becoming more essential for genetic studies of amphimictic species.

Conclusions

A parallel extension of Clarke's (2) three-part definitions of tolerance has much potential for providing more definitive concepts and framework for enhanced communication among plant protection disciplines in response to resistance and tolerance. He described three aspects of tolerance: to parasite, to disease, and overall. I endorse Clarke's definitions. A parallel proposal herein includes three divisions of resistance: to parasite, to disease, and overall (general). The diversity of concepts, including resistance and tolerance, will likely receive increased attention in nematology and related disciplines. For example, because of legal issues, terms used by extension workers and/or representatives of seed companies in communicating with growers may differ from those used by scientists. Hopefully, greater commonality in these concepts can be achieved, regardless of discipline or interest.

How should the intraspecific variants of nematodes be labeled: race, strain, biotype, or pathotype? The recommendation by Dropkin (5) that plant nematologists drop the use of race, biotype, and strain and use "pathotype" to refer to intraspecific variants (populations), delimited by a differential host test, has not been widely adopted. This usage of pathotype has no implications as to the genetic determinants in the nematode or host plant (5). Triantaphyllou (27) offered the most logical solution to this issue. He proposed that "biotype" be used to refer to the basic unit, typically identified on differential hosts, and "race" be used for cultivar-specific combinations of biotypes found in field populations. A definitive genetic designation will be essential as progress is made in investigations of nematode genetics, especially for amphimictic species. As suggested by Dropkin (5), the term "strain" should become applicable as molecular biology techniques are employed to characterize the genetic variations in species of plant-parasitic nematodes. Schmitt and Shannon (15) recommend that the current race scheme for *H. glycines* be retained and that soybean cultivars be characterized by naming their source of resistance. Although diverse usage of these terms may continue, use of the single term "race" to refer to either level of variant should be discontinued.

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