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The Biochemistry and Molecular Biology of Plant Resistance to Pathogens: An Introduction[1]

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During the past two decades, the development of new technologies in biochemistry and molecular genetics had provided new approaches for investigating plant–pathogen interactions, for exploring the genetics of resistance, tolerance, and susceptibility, and for moving resistance genes between plant varieties by mechanisms other than those of conventional breeding. This symposium on the biochemistry and molecular biology of resistance of plants to plant pathogens was designed to bring together scientists who use molecular approaches to study the response of resistant plants to pathogens. An attempt also was made to include scientists developing management strategies based upon molecular or mechanical transfer of germplasm from resistant or tolerant plants to varieties or species of economically important agricultural plants susceptible to specific pathogens. Therefore, in assembling this symposium, little attention was given to the system being studied by the participants; instead, emphasis was placed on putting together a series of papers that would familiarize nematologists with the new technologies, model systems, and approaches for studying plant–pathogen interactions and for transferring resistance between plants. An additional goal of this symposium was to encourage nematologists to apply new biochemical, molecular, and genetic techniques to studies on the reaction of plants to plant-parasitic nematodes and perhaps to develop new model systems to facilitate studies on biochemical and molecular mechanisms used by plants to respond to nematode invasion. If nematologists are to understand fully the mechanisms by which nematodes successfully infect plants or the mechanisms that plants use to prevent establishment of nematode infections, a simple model laboratory system must be found that mimics as closely as possible the field environment for invasion and establishment of nematode infections of natural hosts.

Plant-parasitic nematodes are major pathogens of cereal, grain, and grass crops world-wide. They significantly damage horticultural and forest plantings and reduce fruit production in several areas of the world as well. The impact of these organisms on global agriculture is becoming even more important as the 21st century approaches, with an increased need for greater crop yields to feed the populations of both developing and developed countries (8,10,19). This production increase must be achieved without further environmental damage caused by destruction of natural habitats to create tillable agricultural lands or by using chemical pesticides that eventually collect in and pollute the environment.

Few if any crops are immune to nematode attack, and those crops often described as resistant to specific nematode populations in actuality are tolerant and

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sustain some level of infection without affecting yield or growth (4,8,23). Thus, nematode populations establish in these plants, but establishment and reproduction are poor (4,23). The stress on these resistant or tolerant plants, or damage induced by their invasion by parasitic nematodes, may decrease the plants' ability to fend off other pathogens, may open pathways for other pathogens to enter the plant, or may induce physiological changes negatively affecting plant growth, yield, or survival (11,23). Resistance is not always complete, and a plant variety resistant to one nematode pathotype, race, or species may be highly susceptible to a different pathotype, race, or species. This situation is particularly evident in the reactions of soybean cultivars to races of the soybean cyst nematode (*Heterodera glycines*) and the responses of many plant species to races or species or root-knot nematodes (*Meloidogyne* spp.), two major nematode pathogens of agricultural crops world-wide (1,5,8,23). The varied resistance of different potato varieties to races or species of potato cyst nematode (*Globodera rostochiensis* and *G. pallida*) significantly affects the yield of potatoes throughout Europe. The genetics and mechanisms of this resistance and susceptibility have been subjects of intensive research (2,5,7).

At present, control of plant-parasitic nematodes relies on application of fumigant or nonfumigant nematicides to nematode-infested fields before or during planting, on crop rotation methods, or on use of resistant or tolerant plant varieties bred by conventional genetic methods (9). Although each of these management strategies has some positive features, there are negative aspects that reduce their effectiveness and value. Nematicides often are highly toxic or expensive, and their use requires proper application, handling, and cleanup to minimize their environmental effects. During the last decade, compelling evidence has been collected to show that many nematicides accumulate in the environment and become toxic pollutants (12). Because of the prohibition of the use of many effective nematicides, some agricultural systems are left with few means of controlling plant-parasitic nematodes (9,12). The deregistration of ethylene dibromide (EDB) and 1,2-dibromo-3-chloropropane (DBCP) fumigant nematicides has significantly affected agriculture and forced producers in some areas to rethink the planting of certain nematode-susceptible crops (4,12). The remaining nematicides are expensive, have potential health risks to the user, and are not particularly effective in many cases (12,19). Fumigant nematicides cost $50 to $60 per acre to apply and nonfumigant nematicides about $30 per acre. In soybean production, because nematicides provide only ca. 50 to 75% of the yield potential of *H. glycines*-susceptible soybean cultivars, the maximum yield following nematicide treatment often falls short of the yield needed for economic success of the producer (19).

Although crop rotation and breeding resistant varieties are effective measures of control alone or in combination, they often have significant disadvantages (9,10). Crop rotation frequently involves 3 to 5 years of alternative crop production and often includes a fallow year. In single crop or marginal agricultural systems, or in forest or fruit production, this method may not be feasible.

The benefit-to-cost ratio of breeding varieties of nematode-resistant plants is economically advantageous to the producer (4); however, nematode populations rapidly break resistance, and new resistant varieties must be continually sought. Breeding resistant varieties of a grain or cereal crop by conventional genetic methods is a long-term undertaking, requiring as many as 10 years; production of nematode-resistant fruit, forest, or ornamental trees takes considerably longer (4,9). For some crops, such as *Cucumis* species, no known source from which resistance can be captured into productive domestic varieties is available (24). Beyond the continual need to search for new resistance sources, breeding for resistance has other problems. Often, positive agricultural traits as yield or seed quality must be sacrificed to obtain nematode resistance.

There have been several attempts at biological control of phytoparasitic nematodes, including utilization of nematode-antagonistic fungi and soil amendments that change the physical or biological properties of the soil (13–16,21,22). Because these efforts have not had tremendous success, it may be time for nematologists to investigate other ways of moving resistance among plant species or of introducing a systemic resistance response into a particular plant that then allows the plant to fend off or tolerate nematode attack. This challenging approach requires discovering fundamental knowledge about the nature of plant resistance to nematodes and putting into practice some modern methods of gene capture and transfer.

This symposium addresses several approaches to studying resistance and for applying this knowledge to the transfer of resistance among plant varieties. The work of Cramer et al. (6) involves methods for investigating the molecular mechanisms of the genetic control of plant defense genes in response to pathogen attack. Their work utilizes an approach that nematologists might consider in studying molecular regulation of nematode–host interactions. The work of Bent et al. (3) with *Arabidopsis* presents a simple model system that is just beginning to find application for study of the interaction of plants with plant-parasitic nematodes (20). Punja and Zhang (17) offer a look at one class of pathogenesis-related proteins, the chitinases, that might be involved in resistance of plants to disease. Their work presents some interesting ideas about how to investigate the involvement of pathogenesis-related proteins in nematode–host interactions. Finally, Reimann-Phillip and Beachy (18) introduce nematologists to techniques, model systems, pitfalls, and practicality of genetic transfer of resistance genes between plant varieties. Taken together, these papers should provide nematologists with the tools to look anew at the biochemistry of nematode resistance and to begin considering how molecular approaches might be exploited either to study resistance responses of plants to parasitic nematodes or as control strategies.

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