Tribunes

A THEORETICAL MODEL FOR PLANT-NEMATODE INTERACTION (1)

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The importance of studies on the biochemistry of plant-nematode relationships has been fairly welldocumented in recent reviews (Webster, 1975; Dropkin, 1976; Kaplan & Keen, 1980; Gommers, 1981). These studies have essentially been aimed at unmasking the biochemistry of plant resistance to the invading nematode pathogen. The existence of a gene-for-gene mechanism operating in the plantnematode combination has been suggested by Jones (1974) followed by Sidhu (1975).

In 1974, Giebel proposed a scheme to depict the biochemical mechanism of plant resistance to nematodes wherein he indicated the inducer effect of β-glucosidase from the nematode saliva on the physiology of the host. This was one of enzymes suggested to interact with plant growth hormones and phenols resulting in expressions of susceptibility or resistance. The need was felt to elucidate the role of enzymes like IAA-oxidase, peroxidase, phenylalanine ammonia lyase, polyphenol oxidase and ribonuclease in the resistance phenomenon and studies with this objective led us to suggest that root-knot nematodes elicit the latent biosynthetic potential of the plant host (Ganguly & Dasgupta, 1979; Mote & Dasgupta, 1979; Ganguly, 1979; Premachandran, 1980; Dasgupta et al., 1981). Through our series of investigations, involving time-course analysis emphasizing the initial stages of plant pathogenesis, we are now convinced that the early events after nematization decide the course of disease development. Information on the role of phytoalexins in plant-nematode interaction (Abawi, Van Etten & Mai, 1971; Rich, Keen & Thomason, 1977; Veech, 1978; Kaplan & Keen, 1980) gives further support to our views on the importance of the early crucial events in pathogenesis. Evidence from the available literature and the results of our own studies lead us to suggest a theoretical scheme operating at the molecular level in the plant-nematode pathosystem, particularly in the case of plant-Meloidogyne interaction.

The theoretical model substantiating our views is presented in Figure 1. The central theme of the scheme is the role of the host, besides that of the parasite, in deciding the course of disease development. It is well-known that the initial step in any host-parasite relationship is mutual recognition between the host and the parasite. A report of the shared antigens of Meloidogyne incognita and its hosts cotton and soybean (McClure, Misaghi & Nigh, 1973) is indicative of similar recognition mechanisms operating in other plant-nematode combinations too. Also, it is possible that there may be some receptor components on the surface involved in the recognition mechanism. When a plant tissue is penetrated by a parasite, combination of receptor components on the outer part of the plant tissue with that of the parasite gives a biochemical stimulus to both the plant tissue and the parasite thereby inducing metabolic and cytologic changes in both the organisms (Uritani, 1978). The specificity observed in plant-nematode combinations may possibly be attributed to the molecular mechanisms operating as has been demonstrated by Nordbring-Hertz and Mattias-

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son (1979) in a fungus-nematode combination. According to this scheme, it is envisaged that after the initial recognition phenomenon, there is an exchange of signals at the molecular level (Dropkin, Helgeson & Upper, 1969) resulting in the release of inducer molecules from the parasite thereby altering the synthetic pathways leading to the changes in the biochemical constitution of the plant tissue. Although the nature and constitution of these inducer molecules are yet to be elucidated, basic proteins like



Fig. 1. Hypothetical scheme depicting plant-nematode interaction with particular emphasis on tomato-*Meloidogyne* combination. (1): Mc Clure, Misaghi & Niqh (1973); (2): Misaghi, McClure & Kuk (1975); (3): Bird (1968); (4): Yu & Viglierchio (1964); (5): Premachandran & Dasgupta (1982); (6): Mote & Dasgupta (1979); (7): Ganguly & Dasgupta (1979); (8): Keen & Kaplan (1977); (9): Giebel (1974); (10): Dasgupta & Ganguly (1975); (11): Vanderplank (1978; (12): Arrigoni *et al.* (1981).

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histones (Bird, 1968) or plant growth regulators (Yu & Viglierchio, 1964) or hydrolases emanating from the nematode may act on the host genome, or bring about modifications of the different RNA species.

The present scheme takes into account the relationship between the co-polymerization of proteins and the successful establishment of an host-parasite relationship under the influence of an endothermic reaction. Root-knot nematode infection lays great stress on the energy levels of the cells of both resistant and susceptible plants (Misaghi, McClure & Kruk, 1975). Susceptibility of plants to pathogens, in general, is an endothermic reaction (Vanderplank, 1978) and in the case of phytoparasitic nematodes this has been experimentally confirmed by the heat treatment experiments of Dropkin (1969). Protein copolymerization, *i.e.* polymerization of possibly dissimilar protein molecules from the host and the pathogen, necessary for the successful establishment of a compatible host-parasite relationship (Vanderplank, 1978) necessitates energy utilization. The increased concentration of adenylates observed after nematode invasion of the susceptible plants (Premachandran, 1980) is probably utilized herein. Where incompatibility occurs there is no protein co-polymerization and the energy taken up is diverted for the hypersensitive reactions or similar other host responses.

The genome modified by the inducer molecules turns out, in its turn, increased concentrations of RNA polymerases or RNases besides being directly involved in the de novo synthesis of isozymes (Premachandran & Dasgupta, 1983). The macro-molecules have their respective roles in the processing of RNA molecules and are directly involved in the synthesis of newer proteins including enzymes. At this juncture, the afore-mentioned initial events, *i.e.* recognition, induction and genome modification, energy changes and protein co-polymerization, are taken over by the secondary events including the breakdown of proteins by the enzymes of nematode origin, especially by the hydrolases (Giebel, 1974; Dasgupta & Ganguly, 1975). The amino acids phenyl alanine and tyrosine are known to have significant roles in lignification and hence the resistant reaction, while growth regulators, depending on their concentration dictate expressions of resistance/susceptibility. The recently hypothesised Ascorbic acid-Hydroxy proline-Cyanide-resistant respiration pathway, now proved to be directly involved in the biological defence mechanism (Arrigoni, Arrigoni-Liso & Calbrese, 1977; Zacheo et al., 1977; Arrigoni, 1979) and also the findings on the role of enzymes as peroxidase and superoxide dismutase in the resistance phenomenon (Ganguly & Dasgupta, 1979; Arrigoni et al., 1981) may probably be considered to be taking

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place at a secondary level consequent to and dependant upon the earlier mentioned primary responses.

We conclude that all the changes that occur in a plant after nematization are merely consequences of these early events. The end result of plant-nematode interaction is the production of polypeptides related either to a resistant or susceptible response. The suggestion that there occurs a complementation of host-specific and pathogen-specific polypeptides is supported by the experimental evidence for the appearance of enzymes with catalytically different properties.

Chakravorty (1977) suggested a possible molecular basis for obligate host-pathogen interaction and gave evidence for a similar phenomenon occurring in the case of other pathogens like fungi, bacteria, etc... Our data lead us to suggest a protein-for-protein relationship in the susceptible combinations and probably a gene-for-gene mechanism operating in the tomato-*Meloidogyne* interaction. We suggest that interactions between the root-knot nematode, *Meloidogyne incognita* and its host plants result in derepression of genes, subsequently leading to *de novo* synthesis of molecules of RNA and proteins, under the influence of inducer molecules emanating from the nematode.

Future investigations will aim at unmasking the role of RNA polymerases and *de novo* synthesis of mRNA in nematode-infected plants. Furthermore, investigations on the molecular biology of resistance, use of micro-analytical methods for localization and quantification of the different macromolecules and studies on the inter-relationships between the various macromolecules should go a long way in drawing up a final picture.

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