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Nematodes and other soilborne pathogens of cowpea

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Abstract
Since the First World Cowpea Conference was held in 1984, over 200 papers have been published on soilborne organisms parasitizing cowpea,*Vigna unguiculata* (L.) Walp. More than a dozen nematode genera and numerous soilborne fungi—including *Rhizoctonia solani*, *Sclerotium rolfsii*, *Phytophthora* spp., *Macrophomina phaseolina*, *Fusarium* spp., and *Pythium* spp.—have been implicated in root rot, seed rot, damping off, and basal stem canker of cowpea. Most of these papers have reported on the control of nematodes and fungal pathogens. A few studies have attempted to elucidate the mechanisms of resistance to these pathogens. Several authors investigated interactions of nematodes with soilborne fungi, mycorrhizae, and *Rhizobium* spp. This paper summarizes pertinent information from many of those published reports.

Nematodes

New species

Caveness and Ogunfowora (1985) listed 51 species in 23 genera of nematodes associated with cowpea. Cowpea has since been cited as a host for nine further species. *Pratylenchus scribneri*, *Criconemella sphaerocephala*, *Paratylenchus* spp. (Gallaher and McSorley 1993), *Hemicycliophora poranga* (Chitambar 1993), and *Tylenchorhynchus germanii* (Baujard and Martiny 1991a) reproduced well on cowpea. *Ditylenchus destructor* (Basson et al. 1990), *Paralongidorus bullatus* (Baujard et al. 1993), *Hoplolaimus galeatus* (Rhoades 1984), and *Xiphinema longicaudatum* (Lamberti et al. 1992) were reported to survive on cowpea but were not considered serious pathogens of the crop. The pathogenicity of *X. ifacolum*, however, was confirmed; the nematode formed a coenocyte in the swollen root tips of cowpea and reduced growth by 37% (Lamberti et al. 1992).

Studies of *T. germanii* explained its impact as a pathogen in West Africa. As few as 250 nematodes per plant damaged root systems of cowpea, millet, sorghum, and groundnut (Baujard and Martiny 1991b). The nematode became anhydrobiotic during the 9-month long dry season (Baujard and Martiny 1991a) and multiplied at high soil temperatures (30–36 °C) and low soil moisture levels (5–11%) (Baujard and Martiny 1991b).

Controlling nematodes using cowpea in cropping systems

In various cropping systems tested, cowpea reduced population densities of several nematodes. Rodríguez-Kábana et al. (1988a,b) concluded that 'Iron,' a cowpea cultivar,

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could be grown in rotation with soybean because it had no root-knot galls and very low root and soil population densities of *Meloidogyne arenaria*, *M. incognita*, *Heterodera glycines* (race 4), *Paratrichodorus christiei*, *Pratylenchus brachyurus*, and *Helicotylenchus dihystera* in greenhouse trials. In field trials at seven locations in Florida, lower soil population densities of *M. incognita* resulted after cowpea cultivar California Blackeye No. 5 than after maize cultivar Pioneer 3098 or sorghum cultivar Asgrow Chaparral (McSorley and Gallaher 1993). Both microplot and field trials showed that a 3-month summer cover crop of the cultivar California Blackeye No. 5 reduced population densities of *Belonolaimus longicaudatus*, *Hoplolaimus galeatus*, and *P. christiei* more than a sorghum-sudangrass cover crop (Rhoades 1984; Rhoades and Forbes 1986), bare fallow, weedy fallow plus nematicide, or a cover crop of *Sesbania exalata* (Rhoades and Forbes 1986). Despite these results, cowpea was not recommended as a summer cover crop because the few *B. longicaudatus* which developed on cowpea were able to build up to damaging levels on later maize crops (Rhoades 1984). Similarly, although cowpea was a poor host for *Paralongidorus bullatus* (Baujard et al. 1993) and *Ditylenchus destructor* (Basson et al. 1990), the few nematodes which survived on cowpea could be potentially damaging to groundnuts in a rotation.

Intercropping maize and cowpea was recommended to provide some control of nematodes on each crop. Maize and cowpea growth was reduced by *Pratylenchus sefaensis* and *M. javanica*, respectively, but intercropping maize and cowpea significantly reduced population densities of *P. sefaensis* compared to maize monoculture, and of *M. javanica* and *R. reniformis* compared to monocropped cowpea (Egunjobi et al. 1986).

Controlling nematodes with organic products

Mulches and soil amendments have often been tested as methods to control soilborne pathogens. Population densities of *M. incognita*, *Helicotylenchus* sp., and *Pratylenchus* sp. were lower on cowpea when 1 t/ha of dried pulverized kolanut (*Cola nitida*) pod was applied to ridges 5 weeks after planting (Oyedunmade et al. 1995). Amending the soil with 6 t/ha of partially decayed, flaked, dry cocoa pod husks reduced root-knot galling by 27% in field trials and increased dry grain yield by 7% (Egunjobi 1985); while larger yield increases were obtained in greenhouse and microplot trials, the amount of husks used was impractical. In field trials, although the lowest population densities of *M. incognita* were found in plots treated with the nematicide carbofuran, the highest net revenue per hectare and the best crop growth were obtained by adding 10 t/ha of cocoa pod husks or cassava peels to soil (Egunjobi and Olaitan 1986). Microplot studies showed that amending soil with a mixture of 4 t/ha soybean meal, 2 t/ha urea, and 2 t/ha Clandosan 601 (a chitinous material from blue crabs) was more effective than the nematicide aldicarb in reducing juvenile *M. incognita* populations in soil at harvest and increasing crop yield (Rodríguez-Kábana et al. 1990). Several mechanisms seemed to explain the effect of this soil amendment: (1) increased soil chitobiase activity which correlated with fewer nematode galls, and (2) increased soil urease activity, indicating that soil microorganisms produced ammonia that is toxic to nematodes. Soil amendments, however, are not always beneficial. Although rice hulls reduced the population densities of *M. incognita* in field trials, many plants died prematurely from *Fusarium semitectum*, *Colletotrichum linde-muthianum*, and *Phoma* spp., which were stimulated by the rice hulls (Egunjobi and Olaitan 1986).

Controlling nematodes with host plant resistance

Many cowpea cultivars have been screened for resistance to nematodes. Characterization of new resistance to root-knot nematodes is reported in this volume (Roberts et al. 1997) and references in that paper will not be repeated here. Criteria used to assess resistance to nematodes include galling, numbers of eggs or juveniles produced, the reproductive ratio (final nematode population densities divided by initial population densities), and plant yield or damage.

A gall index or the actual number of galls per root system are often used to rate resistance of many cultivars. Of eight cowpea cultivars tested, only IT82E-77 had few galls per plant 36 days after inoculation and so was considered resistant to *M. javanica* in pot tests (Onyeigwe and Ogbuji 1991). Cultivar IC 20447 was classified as highly resistant to *M. incognita* and *M. javanica* because it had no galls after 45 days (Patel et al. 1990). Neither the gall index nor the number of galls per root system, however, accounts for differences in the size of a plant's root system. Counting the number of galls per gram of root took longer than using a gall index, but Witcher and Ogle (1987) felt the counts distinguished biologically significant differences among cultivars. Eight of 16 cultivars they tested were resistant to both *M. incognita* race 3 and *M. arenaria* race 1.

Galling does not always predict the reproductive efficiency of root-knot nematodes on a particular host, so many researchers count the numbers of egg masses, eggs, and/or juveniles produced from infected root systems. Based on galling and the number of eggs produced, cultivars IT89KD-288 and IT90K-76 (M.S. Gaya, B.B. Singh, D.A. Florini, IITA, Kano, unpublished) as well as 33 of 76 cowpea cultivars or germplasm accessions (Idowu and Diboh 1987) were rated highly resistant to *M. incognita* in Nigeria. For pot studies, Khan and Husain (1989b) used three criteria to characterize a cultivar's level of resistance: number of galls per root system, nematode reproduction ratio, and reduction in plant growth. Using their index, they rated only cultivar IC-503 to be moderately resistant.

Unfortunately, this rigorous index has no simple terms for cases in which a cultivar is susceptible but tolerant or when a cultivar is resistant but intolerant. A tolerant cultivar should show no growth reduction even when infected. For example, yield losses on cowpea cultivars Tennessee Brown and California Blackeye No. 5 suggested that these resistant cultivars are not tolerant to infection by *M. incognita* race 1 (Gallaher and McSorley 1993).

Pathogenic variability in nematode populations and genetic variability in seedlots of cowpea cultivars have been cited as reasons for susceptible reactions of resistant cultivars. *M. incognita* races differed in their ability to reproduce on 2 of the 12 cultivars tested by Swanson and Van Gundy (1984); California Blackeye No. 3 was resistant to races 3 and 4 but Queen Ann was resistant only to race 2. Although not described as a race, population J7c54 of *M. javanica* was virulent on cultivar Mississippi Silver, which was resistant to most *M. javanica* populations. Interestingly, plants from one seedlot of California Blackeye No. 5 were resistant to races 1, 2, 3, and 4 of *M. incognita*, but plants of the same cultivar from another seed source were susceptible (Swanson and Van Gundy 1984).

Mechanisms of resistance to nematodes

Mechanisms of resistance to root-knot nematodes were studied in several cowpea cultivars. As for many cultivars, resistance to *M. incognita* in cowpea cultivars IC 9642-B and TVu 2430-P is controlled by a single dominant gene (Singh and Reddy 1986). Their

resistance was associated with reduced juvenile penetration, root galling, and fecundity, with delayed development of juveniles to adult females. Resistant cultivars had fewer and smaller giant cells than susceptible lines (Singh et al. 1984). Cells around root-knot nematode larvae died in the roots of the resistant line IC 9642-B before feeding sites could be established (Singh et al. 1984). In resistant cultivars, the cork layer was thicker than in susceptible cultivars and sclereids were present in the cortex. Within 96 h of inoculation with *M. incognita*, plants of the resistant cowpea cultivar C-152 synthesized mRNA six times more rapidly than uninoculated plants (Raja and Dasgupta 1986). In the susceptible cultivar, mRNA was produced more slowly than in the resistant cultivar and a second type of mRNA was produced that blocked the synthesis of some polypeptides which could activate host plant defenses (Raja and Dasgupta 1986).

Soilborne pathogens

New species

So many fungal pathogens had previously been reported from cowpea that new reports of pathogens in the crop have been rare in the past 10 years. Root infection in cowpea was recorded for *Fusarium equiseti* (Ramachandran et al. 1982), *Pythium myriotylum* (Croft 1988), and *Phytophthora dreschleri* (Erwin et al. 1991). In addition to *P. dreschleri*, many other pathogens including *M. phaseolina*, *R. solani*, two *Pythium* spp., *Thielaviopsis basicola,* and *Fusarium solani* f. sp. *phaseoli* were isolated from rotting cowpea roots in California fields, but only the latter two caused early dying of plants in the field and yield loss (30–50%) in pot studies. *Fusarium oxysporum*, was surprisingly not associated with the early dying of cowpea plants, although it was present in 74% of the fields surveyed. Unfortunately, the effect of joint inoculation with the pathogens was not studied.

Macrophomina

Macrophomina phaseolina is not a new pathogen of cowpea, but, since 1984, there have been many studies on its biology and the conditions for infection. *M. phaseolina* was reported to be the most important single fungal pathogen in the Bay region of Somalia (Gray et al. 1990). Temperature studies confirmed why it is one of the major pathogens of cowpea in such hot, arid zones. An Indian isolate grew best and formed most sclerotia on potato dextrose agar (PDA) at 30–35 °C (Ratnoo and Bhatnagar 1991). An isolate from Niger grew best at 35 °C on PDA, with poor growth occurring < 10 °C and > 40 °C (Adam 1990). Soil samples from a survey conducted in Niger had up to 139 sclerotia per gram of soil, while soil collected in France had none (Adam 1990). In India, 42–71% of plants died and there was no grain yield in plots containing 46–148 sclerotia per gram of soil at the time of symptom appearance (Lodha and Singh 1984).

Both the age of the plant at inoculation and drought stress affect the susceptibility of cowpea to *Macrophomina*. Plants younger than 45 days were found to be most susceptible, but only 30% were infected following inoculation at 60 days (Ratnoo and Bhatnagar 1993a). Senescing plants and drought-stressed plants of all ages, however, are commonly colonized by the fungus (Burke et al. 1986). More plants are infected in areas of low annual rainfall and without irrigation in Niger (Adam 1990) and Botswana (de Mooy et al. 1986). Seed is easily infected. *M. phaseolina* was found in 64% of seed samples collected in Niger; some seedlots had as much as 100% of the seeds infected (Adam 1990).

When cowpeas were grown in soil infested with *Macrophomina* sclerotia, infection occurred underground in emerging cotyledons and hypocotyls; roots were colonized but appeared healthy (de Mooy and Burke 1990). When young plants were inoculated, the pathogen spread more rapidly downwards to the roots and upwards in the stems, causing rapid wilting (Ratnoo and Bhatnagar 1993a). In another study, de Mooy and Burke (1990) postulated that ashy stem blight symptoms that appear in the field when plants approach maturity or are under drought stress may be due to activation of dormant hypocotyl lesions; they found no evidence of internal growth of the fungus from the cortical lesions or from the roots, and they did not detect mycelium in microscopic examinations of stem pith, phloem, and xylem. Adam et al. (1991), however, found mycelium around cells of the vascular bundles 96 h after seedlings were inoculated.

Macrophomina phaseolina has a very wide host range, but two studies suggested that isolates may differ in pathogenicity. Burke et al. (1986) found that some cowpea genotypes were infected more often than others, but suggested that the Botswana strain was specific to legumes since sorghum intercropped in the same fields was not susceptible. Byadgi and Hegde (1985) reported variation in virulence, morphology, and pycnidial production. They found that isolates of *M. phaseolina* obtained from *Phaseolus vulgaris*, *Cicer arietinum*, and cowpea grew faster, and were more virulent than those from sorghum, soybean, or *Gliricidia*. In another study, isolates of *M. phaseolina* and *R. solani* from cowpea were more virulent on cowpea than on tomato or *Lagenaria siceraria*; however, modifications in the pathogenic behavior of the isolates were attributed to sucrose as the carbon source and L-asparagine as the nitrogen source in culture media (Naresh et al. 1992).

Sources of resistance to many soilborne pathogens have been identified, but highly resistant cultivars are often not available for generalist pathogens such as *M. phaseolina*. Moderate levels of resistance were reported in 5 of 33 cowpea cultivars (Singh and Lodha 1986) and in 4 of 141 cultivars (Sohi and Rawal 1983) in India. None of the 89 varieties was resistant to *Macrophomina* in Niger, but 30% were regarded as tolerant because 20% or fewer of their plants were infected (Adam 1990). Better cowpea stands were attributed to moderate resistance of one cultivar in Senegal (Gaikwad and Sokhi 1987).

Phytophthora

Races and formae speciales of *Phytophthora vignae* were identified in two reports. Previously reported as a problem on cowpea in Australia and Tanzania, *P. vignae* was detected in Sri Lanka in a greenhouse (Sivakadadcham and Fernando 1991) and was later found in many of the 25 fields surveyed (Fernando and Linderman 1993) even though the symptoms of Phytophthora wilt were seen in only one of the fields. Different races of the fungus were identified using differential cultivars (Fernando and Linderman 1993). Tsuchiya et al. (1986) found that isolates of *P. vignae* from *Vigna radiata* were virulent to *V. radiata* but not to cowpea, while isolates from cowpea were virulent only to cowpea. The isolates could be distinguished by pathogenicity tests and not by soluble protein and isoenzyme patterns. The authors, therefore, proposed two formae speciales: *P. vignae* f. sp. *adzukicola* Tsuchiya, Yanagawa, and Ogoshi for that on *V. radiata*, and *P. vignae* f. sp. *vignae* for that on cowpea (Tsuchiya et al. 1986).

Host plant resistance is the preferred method of controlling *P. vignae*, and several sources of resistance have been identified. Of the 1781 cowpea lines planted in an infested

field and sprayed with a spore suspension of *P. vignae*, only KU235 and TVu 3861 were moderately resistant after the third inoculation (Mligo 1988). In a root inoculation assay using 0.01 g mycelium/kg of potting mix, cultivar CPI 84853 expressed partial resistance to races 1, 2, 3, and 4 of *P. vignae* although this cultivar was highly susceptible to race 4 following hypocotyl inoculation (Davis et al. 1993). Resistance to *P. vignae* race 2 was found to be dominant and controlled by a single gene or gene complex (Bateman et al. 1989). The resistance was mediated by phenylalanine ammonia-lyase (PAL) (Ralton et al. 1988). Only low levels of PAL were produced by the near-isogenic cultivars, Poona and Caloona, in response to inoculation with race 3, which was virulent on both cultivars. Race 2 invaded the susceptible cultivar, Poona, faster than PAL levels could build up except at high temperatures (35 °C), at which Poona seemed resistant. Enzyme activity increased rapidly in the resistant cultivar which became susceptible if compounds which inhibited the production of PAL were applied to the cut bases of hypocotyls (Ralton et al. 1988).

Chemicals that did not control *Phytophthora* spp. in vitro induced defense reactions in cowpea plants which helped in controlling the pathogen (Guest and Bompeix 1990). Phosphite (a breakdown product of Fosetyl-Al) stimulated the production of several phytoalexins in cowpea susceptible to *Phytophthora cryptogea* (Saindrenan and Bompeix 1986). Within 24 hours of inoculation with *P. cryptogea*, enough kievitone accumulated in lesions treated with phosphite to inhibit *P. cryptogea* growth. Phosphite treatment also induced high levels of phaseollidin at inoculation sites, which reached levels inhibitory to fungal growth by 48 h after inoculation (Saindrenan et al. 1988).

Pythium

Koleosho et al. (1987) found that production of oxalic acid and polygalacturonase coincided with decreased pH in hypocotyls of the susceptible cultivars IT 81D-1020 and VITA 5 infected with *Pythium aphanidermatum*, whereas resistant cultivars IT 82E-32 and TVx 3236 had only low levels of oxalic acid and polygalacturonase with little change in pH. They postulated that the oxalic acid chelated calcium and magnesium ions and reduced the pH enough to permit polygalacturonase to degrade the middle lamella of plant cell walls. They suggested that oxalic acid levels in cowpea cultivars 8–10 days after inoculation could be indicative of resistance to *P. aphanidermatum*. Cowpea cultivars with dark seeds were more resistant to *Pythium* spp. than those with cream-colored or beige seeds, perhaps because light-colored seeds imbibed water more rapidly and leaked more solutes which could favor infection (Legesse and Powell 1992).

Fusarium

The severity of Fusarium root and stem rot in cowpea varied with host genotype and plant age, but not with the different levels of inoculum tested. Cultivar CES 42-2 showed less infection than TVx 289-4G or VCS 6-1. The percentage of infected plants was highest in 22-day-old plants, while 5-day-old seedlings were not infected (Sajise 1988). Cowpea cultivars Blackeye, TVu 1330, and TVx 3236-01G were susceptible to Fusarium wilt, while TVu 1560 was resistant (Shihata et al. 1988). Xylem extracts of TVu 1560 were more toxic to *F. oxysporum* than those of Blackeye, the susceptible cultivar, and may explain why the xylem vessels of Blackeye but not TVu 1560 were extensively colonized by the pathogen (Shihata et al. 1989). In the wilt-susceptible cowpea cultivar California Blackeye

No. 5, *F. oxysporum* f. sp. *tracheiphilum* spread quickly upward in plants, colonized most tissues within 6 weeks, and caused severe wilt (Harris and Ferris 1991c). In wilt-resistant cultivar California Blackeye No. 3, however, there was little proliferation of *F. oxysporum* in any tissue whether or not plants were infected by *M. javanica*. Split-root experiments provided no evidence that infection by *M. javanica* results in a translocatable factor that reduces wilt resistance (Harris and Ferris 1991c).

Sclerotium

Field trials conducted from 1982 to 1985 revealed genetic variability in cowpea for resistance to *Sclerotium rolfsii*. The accessions Carolina Cream and CR61N exhibited good levels of resistance (Fery and Dukes 1986). Screening in pots also showed large varietal differences in resistance to *S. rolfsii*. When two sclerotia were set against wounded cowpea stems, symptoms ranged from the enlargement of the initial wound with no further disease development for cultivars IT 82D-699 and IAR-339-1 to wilting and death of plants for cultivar K-59 (Nwakpa and Ikotun 1988).

Control of fungal diseases

Weed mulch (Gupta and Gupta 1986), wheat straw, and neem cake (Ratnoo and Bhatnagar 1993b) controlled *Macrophomina phaseolina*. Neem cake improved growth of plants inoculated with *R. solani* or *M. incognita*, but not with *R. reniformis*; while groundnut cake only improved growth of plants inoculated with *R. solani* (Khan and Husain 1988c). Leaf extracts of *Adhatoda vasica* suppressed mycelial growth of *S. rolfsii*, *R. solani*, *Phytophthora vignae*, and *Pythium* spp., and also suppressed sexual reproduction of the latter two when incorporated into PDA (Sivakadadcham 1988). Cowpea and neem extracts enhanced oospore production in *Pythium butleri* and *Phytophthora vignae*, respectively, while none of the leaf extracts tested controlled *F. solani*. (Sivakadadcham 1988). Green manure, farmyard manure, and biogas sludge all increased seedling rot induced by *R. solani* in growth chamber experiments (Kataria and Grover 1987).

Over the past 10 years, there have been many reports of fungicide efficacy, often based on in vitro or pot tests, but few studies found a correlation between such tests and field results (Adam 1990; Ramadoss and Sivaprakasam 1988; Singh and Lodha 1986). Efficacy of fungicides can be modified by the inoculum ratio and virulence of different pathogens (Gangopadhyay and Grover 1984, 1986); by temperature, moisture, and soil nutrients (Gangopadhyay and Grover 1984; Kataria and Sunder 1985); by soil type (Gangopadhyay and Grover 1984; Kataria and Sunder 1987, 1988); and by soil amendments (Bandyopadhyay et al. 1982; Gangopadhyay and Grover 1984; Kataria and Grover 1987; Kataria and Sunder 1988). Insecticides and herbicides were occasionally reported to have fungicidal or nematicidal activity in vitro (Kataria et al. 1989) but not in vivo (Ramadoss and Sivaprakasam 1989).

Biological control of *M. phaseolina*, *S. rolfsii*, and *R. solani* was demonstrated in pot studies. *T. viride* reduced *M. phaseolina* growth in vitro both alone and in combination with carbendazim, but pelleting seed with the fungicide plus *T. viride* increased germination, reduced postemergence mortality, and increased shoot and root length and dry matter of cowpea (Alagarsamy and Sivaprakasam 1988). *Trichoderma* spp. isolated from sclerotia successfully controlled *S. rolfsii* both in culture and in the greenhouse (Almeida and

Landim 1981). Another biocontrol agent, *Paecilomyces lilacinus*, was antagonistic to *R. solani*, reduced the multiplication of *R. reniformis* and *M. incognita,* and reduced the damage to cowpea. *P. lilacinus* was more effective on single pathogens than on combinations of the pathogens (Khan and Husain 1988b; Khan and Husain 1990).

Pathogen interactions

Many papers have reported interactions among nematodes, pathogenic fungi, mycorrhizal fungi, and *Rhizobium* spp. Examples of five general trends are given below.

Trend 1. A pathogen which first infects a root usually suppresses reproduction of the second pathogen. For both *M. incognita* and *R. reniformis*, inoculation of one nematode before the other reduced the multiplication of the second (Khan and Husain 1988a). Furthermore, the nematode reproduction factor on cowpea was highest when nematodes were inoculated alone, lower when they were inoculated concomitantly with *Rhizoctonia solani,* and lowest when the fungus was inoculated 15 days before the nematodes (Khan and Husain 1988a). Culture filtrates from *R. solani* reduced hatching of *M. javanica* eggs, leading Singh et al. (1986) to postulate that infection of roots by *R. solani* prior to nematode infection permits a buildup of fungal metabolites detrimental to hatching. When *R. solani* or *M. phaseolina* were inoculated on cowpea 7 days prior to *H. cajani,* nematode multiplication was inhibited, resulting in few or no cysts (Walia and Gupta 1986a,b). *M. javanica* inhibited penetration into the roots of cowpea and maize by *Pratylenchus sefaensis* and *R. reniformis* (Egunjobi et al. 1986).

Trend 2. Plant damage is greater and fewer nodules are formed when *Meloidogyne* spp. or *Heterodera* spp. are inoculated before pathogenic fungi or *Rhizobium* spp. When *H. cajani* was inoculated on cowpea 2 weeks before *R. solani,* there was a significant reduction in the top growth of plants (Walia and Gupta 1986a). Vascular discoloration was greatest when *M. javanica* was added 4 weeks before *F. oxysporum* f. sp. *tracheiphilum* (Harris and Ferris 1991c). Fewer nodules were produced on cowpea when *H. cajani* was added before *M. phaseolina* (Walia and Gupta 1986b).

Trend 3. Fungi can suppress multiplication of nematodes when inoculated at the same time as the nematodes. The number of *M. javanica* galls was decreased when *R. solani* was present, especially when the two pathogens were inoculated simultaneously (Kanwar et al. 1988). Concomitant inoculation of *F. solani* and *H. cajani* resulted in lower populations of the nematode and greater shoot weight of cowpea than when the pathogens were inoculated alone (Varaprasad et al. 1987). The low nematode population may have been due to toxic substances produced by *F. solani*. Mani and Sethi (1984) found that high concentrations of culture filtrates of *F. solani* and *F. oxysporum* f. sp. *ciceri* killed eggs and immobilized juveniles of *M. incognita*, and low concentrations inhibited egg hatch.

Trend 4. Vesicular-arbuscular mycorrhizae and/or *Rhizobium* spp. increase plant growth, decrease nematode population densities, and reduce fungal infection when inoculated before or simultaneously with nematodes or fungi. *M. incognita* and *R. reniformis* reproduced least when cowpea was inoculated with *Rhizobium* sp. before inoculation with

nematodes (Khan and Husain 1988a). The best cowpea growth and nodulation were recorded in treatments containing both mycorrhizae and *Rhizobium* sp. without nematodes; however, plant growth was good and nematode multiplication suppressed in *M. incognita*-infested treatments containing the endomycorrhizal fungus *Glomus etunicatum* (Sivaprasad et al. 1990). In roots highly colonized by mycorrhizae, Sivaprasad et al. (1990) postulated that reduced penetration and slower development of *M. incognita* juveniles led to fewer nematodes, fewer roots with galls, and fewer galls per length of root. Sundaresan et al. (1993) found that *F. oxysporum* infection of roots and resulting disease severity were reduced when roots were previously colonized by *Glomus fasciculatum*. The degree of root colonization by mycorrhizae was correlated with the quantity of three phytoalexins, one of which inhibited germination of *Fusarium* conidia (Sundaresan et al. 1993).

Trend 5. Host plant resistance may not be effective when two or more pathogens are inoculated together on cowpea cultivars resistant to one of the pathogens. *M. incognita* and *R. reniformis* reduced the resistance of cultivar IC-244 to *R. solani* when either nematode was inoculated at the same time as *R. solani* (Khan and Husain 1989a). In the same study, cultivars RC-8 and EC-4213A were found to be resistant to *R. solani* and moderately resistant to *R. reniformis* when inoculated with each pathogen individually or simultaneously; however, the resistance was not expressed when either pathogen was inoculated in combination with *M. incognita*. Similarly, cultivar S488 was no longer resistant to *R. reniformis* and cultivar CO-4 was no longer resistant to *R. solani* when *M. incognita* was inoculated with either pathogen. Interestingly, cultivar IC-503, which was moderately resistant to *M. incognita*, did not become more susceptible to this pathogen even when the other pathogens were present (Khan and Husain 1989a). *M. javanica* increased the wilt symptoms caused by three races of *F. oxysporum* f. sp. *tracheiphilum* in the wilt-resistant cultivar California Blackeye No. 3, but did not similarly increase the wilt caused by two isolates of race 3 of the fungus in the wilt-resistant cultivar CB7977 (Harris and Ferris 1991a, 1991b). As for many experiments on pathogen interactions, root-knot nematodes seem more able to disrupt the mechanisms of resistance to other pathogens.

Looking ahead

Soilborne pathogens of cowpea have been studied alone and in various combinations over the past 10 years. Although good information on pathogens, control measures, and mechanisms of resistance has come from work on individual pathogens, experiments in which several pathogens were inoculated together have provided exciting new insights into pathogen-host interactions. More studies of this type will improve the deployment of cowpea cultivars resistant to many pathogens. Inoculation of cowpea with *Rhizobium* spp. and mycorrhizal fungi may become an integral part of integrated pest management practices because these organisms mitigate the effects of pathogenic fungi and nematodes. Studies on the effect of organic amendments on pathogen survival and pesticide efficacy will contribute to the development of control packages that minimize the use of chemical pesticides. Research is still needed on cropping systems and biocontrol agents to explain why certain combinations of crops and microorganisms suppress plant diseases. If undertaken, such complex studies should help formulate strategies for controlling most soilborne pathogens in the next 10 years of cowpea research.

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