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Interactions between *Fusarium oxysporum* f. sp. *tracheiphilum* and *Meloidogyne* spp. in *Vigna unguiculata*. 2. Specificity of different taxa

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A California isolate of *Meloidogyne javanica* increased Fusarium wilt symptoms in cowpea cultivars California Blackeye No. 3 (CB3) (resistant to wilt) and Grant (tolerant) inoculated with each of the three races of *Fusarium oxysporum* f. sp. *tracheiphilum*. The same isolate of *M. javanica* did not similarly increase wilt in wilt-resistant cultivar CB7977 inoculated with two isolates of race 3 of *F. o. tracheiphilum*. Six of seven isolates of *M. javanica* caused similar increases in vascular discoloration in cultivar CB3, but one isolate of *M. javanica* and seven of *M. incognita* did not. Vascular discoloration rating was positively correlated with galling severity. However, increasing the initial inoculum density, and thus galling index, of one isolate of *M. incognita* did not increase vascular discoloration. The vascular discoloration ratings for the wilt-susceptible CB5 controls in each experiment were higher than those for the wilt-resistant cultivars infected with *M. javanica*. It is hypothesized that *M. javanica* but not *M. incognita* reduces, but does not eliminate, resistance to all races of *F. o. tracheiphilum* in cultivars CB3 and Grant.

INTRODUCTION

Wilt of cowpeas (*Vigna unguiculata*) was known to be closely associated with root-knot nematodes in the field over 70 years ago (Barre, 1912). Nearly half a century later, Thomason *et al.* (1959) reported that *Meloidogyne javanica* increased xylem necrosis in stems of the 'wilt-tolerant' cultivar Grant and the wilt-susceptible cultivar Chino 3 when grown in soil infested with *Fusarium oxysporum* f. sp. *tracheiphilum*.

Three races of *F. o. tracheiphilum* have been reported (Armstrong & Armstrong, 1950; Hare, 1953), based on virulence to differential cultivars of cowpea. Races 2 and 3 occur in California, and race 3 probably predominates (Swanson, 1984; Harris, 1989).

California Blackeye No. 3 (CB3) and CB7977 are resistant to all three races of *F. o. tracheiphilum*, but CB5 is susceptible to races 2 and 3. CB3 has a single incompletely dominant gene for race 2 resistance and a single completely dominant gene for race 3 resistance (Rigert & Foster, 1987). Some scientists reported that resistance to Fusarium wilt conferred by single dominant genes was not broken by *Meloidogyne* spp. (Jones *et al.*, 1976; Abawi & Barker, 1984; Caperton *et al.*, 1986). Both CB3 and CB5 are susceptible to a California isolate of *M. javanica* (Swanson & Van Gundy, 1984). Swanson (1984) showed that this isolate of *M. javanica* increased the vascular discoloration caused by races 1 and 3, but not by race 2, of *F. o. tracheiphilum* in both cultivars.

Different species of *Meloidogyne* enhance Fusarium wilt in different crops, e.g., *M. incognita* and *M. hapla* on tomato (Jenkins & Coursen, 1957), and *M. incognita*, *M. arenaria* and *M. javanica* on tobacco (Porter & Powell, 1967). All four species of root-knot nematode can attack cowpea, but *M. incognita* is the predominant species damaging this crop (Fery & Dukes, 1980). *M. incognita* also can enhance Fusarium wilt in cotton (Martin *et al.*, 1956), alfalfa (McGuire *et al.*, 1958), watermelon (Sumner & Johnson, 1973), and summer squash (Caperton *et al.*, 1986). In southern California, however, *M. javanica* predominated in cowpea fields in the 1950s (Thomason *et al.*, 1959). Only one isolate of *M. javanica* has been reported to increase Fusarium wilt symptoms in cowpea (Thomason *et al.*, 1959; Swanson, 1984). This isolate was collected in 1954 by I. J. Thomason from a cowpea field in southern California and is maintained at the University of California, Riverside as culture J-7c-54. It is reported to be a particularly virulent

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parasite on several hosts (Thomason & McKinney, 1960; Swanson & Van Gundy, 1984) and may be atypical. It was not known whether *M. incognita* could also increase susceptibility to Fusarium wilt in cowpeas, although race 1 of *M. incognita* did not affect wilt severity in cultivar CB5 in an earlier experiment (Harris & Ferris, 1991a). The specificity of the interaction between different *Meloidogyne* species and *F. oxysporum* on cowpea is unknown.

The objectives of this study were: to determine the effects of a California isolate of *M. javanica* on resistance to different races and isolates of *F. o. tracheiphilum* in three California cowpea cultivars; and to determine whether different taxa and isolates of *M. incognita* and *M. javanica* reduce resistance of cowpea cultivar CB3 to *F. o. tracheiphilum* race 3.

In this research (see also Harris, 1989; Harris & Ferris, 1991a, b) we define resistance as the ability of a host to suppress or retard the activity of a pathogen; tolerance as the ability of a host to endure infection by a pathogen; and susceptibility as the inability of a host to oppose the operation or to overcome the effects of a pathogen.

MATERIALS AND METHODS

In all experiments, seeds were surface-disinfested (Harris, 1989; Harris & Ferris, 1991a), then sown in coarse sand previously treated with aerated steam at 82 C for 30 min. Single-egg-mass cultures of *Meloidogyne* spp. were maintained on tomato (*Lycopersicon esculentum*) cultivars Rutgers or UC82 in aerated-steam-treated sand in 16·5-cm-diameter clay pots in a glasshouse. Eggs were extracted by the NaOCl technique (Hussey & Barker, 1973).

Interactions between *M. javanica* and races of *F. o. tracheiphilum* in five cultivars of cowpea

Two experiments were conducted to compare the effects of the virulent California isolate of *M. javanica* on Fusarium wilt in five cultivars of cowpea inoculated with two isolates of race 3 of *F. o. tracheiphilum*, or one isolate of races 1 and 2. The experiments were conducted in controlled-environment growth chambers at 27/21 C day/night temperatures with a 12-h photoperiod and daytime illuminance of approximately 400 μ Em $^{-2}$s $^{-1}$ (16 lux). In the first experiment, cowpea cultivars CB3 and CB7977, which are resistant to all three races of *F. o. tracheiphilum*, were inoculated with either of the race 3 isolates Perry CB5 or 160/s128, with or without *M. javanica* (isolate J255). Both fungal isolates were collected from fields of cowpea cultivar CB5 with Fusarium wilt symptoms in 1985 in Tulare County (Harris & Ferris, 1991a). Isolate J255 of *M. javanica* is a single-egg-mass culture subcultured in a glasshouse in about 1978 from culture J-7c-54 described above. Cowpea cultivar Mississippi Silver was inoculated with isolate 160/s128 (with and without *M. javanica*) as control resistant to *Fusarium* and *M. javanica*, and CB5 was inoculated with isolate 160/s128 (without *M. javanica*) as a control susceptible to *Fusarium*. Plastic pots (500 cm^3, 10-cm diameter) were filled with sand, watered with deionized water, and 2500 eggs of *M. javanica* were pipetted into each of five seed-planting holes in each of half of the pots. One seed was planted immediately in each hole. Each treatment (pot) was replicated three times, and splash barriers were placed between treatments to prevent cross-contamination. After 3 weeks, each seedling was inoculated with 10^7 conidia of the appropriate isolate of *F. o. tracheiphilum* by pipetting a spore suspension into a hole in the sand at the base of each seedling. Conidia were washed from potato-dextrose agar (PDA) slant cultures and the concentrations of the conidial suspensions were adjusted with sterile water with the aid of a haemacytometer. Plants were watered five times with half-strength Hoagland's solution (Hoagland & Arnon, 1950), or with deionized water on other days. After an additional 3 weeks, each plant was rated for Fusarium wilt symptoms according to two rating systems described in the preceding paper (Harris & Ferris, 1991a) (Table 1).

The second experiment was conducted to compare the effect of isolate J-7c-54 of *M. javanica* on the cowpea cultivars CB3, CB5, and Grant inoculated with each of the three races of *F. o. tracheiphilum*. The cultivar Grant is moderately to highly resistant (or tolerant) to different isolates of *F. o. tracheiphilum* (Thomason *et al.*, 1959), and susceptible to *M. javanica* and *M. incognita* (Swanson, 1984). Isolate 0923 (race 1) of *F. o. tracheiphilum* originated from P. N. Patel, University of California, Riverside, isolate 058 (race 2) from Pennsylvania State University, and isolate 160/s128 (race 3) was described earlier. Dry chlamydospore-infested straw was mixed with aerated-steam-treated sand to give a density of 2×10^4 colony forming units (c.f.u.) per cm^3 of sand (Harris & Ferris, 1991a). This infested sand was placed in 460-cm^3 polystyrene cups, and one seed was sown in each cup. Immediately after sowing seeds, 1000 eggs of *M. javanica* were

Table 1. Effect of *Meloidogyne javanica* (*M.j.*) on mean Fusarium wilt disease ratings and vascular discoloration ratings of cowpea cultivars 3 weeks after inoculation with two isolates of *Fusarium oxysporum* f. sp. *tracheiphilum* race 3

		Isolate of *F. o. tracheiphilum* race 3					
		Perry CB5		160 s128		Control (none)	
Cowpea cultivar[a]	Fusarium wilt rating[b]	−*M.j.*	+*M.j.*	−*M.j.*	+*M.j.*	−*M.j.*	+*M.j.*
CB3	DR	0·53	2·33	0·50	2·27*[c]	0·00	0·00
	VD	0·20	1·08	0·40	1·60	0·00	0·00
CB7977	DR	0·40	0·36	0·00	0·40*	0·00	0·00
	VD	0·00	0·00	0·00	0·00	0·00	0·00
CB5	DR	NT[d]	NT	1·07	NT	NT	NT
	VD	NT	NT	0·47	NT	NT	NT
Mississippi	DR	NT	NT	0·00	0·47	NT	NT
Silver	VD	NT	NT	0·00	0·00	NT	NT

[a] Reaction to *F. o. tracheiphilum* race 3: CB3, CB7977 and Mississippi Silver, resistant; CB5, susceptible.
[b] DR = disease rating; VD = vascular discoloration.
[c] Within cultivar fungal isolate treatments, means (+*M.j.*) followed by an asterisk are significantly greater ($P<0·05$) than the corresponding control (−*M.j.*), according to a *t*-test.
[d] NT = not tested.

Table 2. Effect of *Meloidogyne javanica* (*M.j.*) on mean vascular discoloration ratings of cowpea cultivars 8 weeks after inoculation with three races of *Fusarium oxysporum* f. sp. *tracheiphilum*

	Race and isolate of *F. o. tracheiphilum*							
	Race 1 Isolate 0923		Race 2 Isolate 058		Race 3 Isolate 160 s128		Control (none)	
Cowpea cultivar[a]	−*M.j.*	+*M.j.*	−*M.j.*	+*M.j.*	−*M.j.*	+*M.j.*	−*M.j.*	+*M.j.*
Grant	0·00	0·87*[b]	1·07	2·60*	1·33	2·80*	0·00	0·36
CB3	0·07	2·87*	1·87	3·27*	0·60	2·80*	0·00	0·26
CB5	0·47	1·73*	4·73	4·67	4·87	4·93	0·60	1·13

[a] Reaction to *F. o. tracheiphilum*: Grant, tolerant; CB3, resistant; CB5, susceptible.
[b] Within cultivar fungal race treatments, means (+*M.j.*) followed by an asterisk are significantly greater ($P<0·05$) than the corresponding control (−*M.j.*), according to a *t*-test.

pipetted into each planting hole. Control treatments had sterilized straw and/or sterile distilled water added to the sand instead of chlamydospores of *Fusarium* and/or *M. javanica*. Each treatment was replicated 15 times in a completely randomized design. Plants were watered on alternate days with half-strength Hoagland's solution. After 8 weeks, each plant was rated for Fusarium wilt symptoms as described previously (Harris & Ferris, 1991a) (Table 2).

Results were subjected to analysis of variance, by weighted least-squares regression in SAS

Table 3. Identity and origin of isolates of *Meloidogyne* used in experiments

Species	Race	Isolate	Origin (and supplier)
M. javanica		J-7c-54	Cowpea, Chino, San Bernadino Co. (I. J. Thomason)
M. javanica		J255	Subculture from J-7c-54 (H. Ferris)
M. javanica		PRJc-18	Tomato, Tulare Co. (I. J. Thomason)
M. javanica		Minton	(N. A. Minton, Georgia)
M. javanica		Dinuba	Grapevine, Dinuba, Fresno Co. (M. V. McKenry)
M. javanica		Wells	Tomato, Westley, Stanislaus Co., 1988 (W.C. Matthews)
M. javanica		IMP 7	North Carolina (P. R. Esbenshade)
M. incognita	1	Call	Cowpea cultivar CB3, Poplar, Tulare Co., 1988 (F. Workneh)
M. incognita	1	Den	Cowpea cv. CB3, Denair, Stanislaus Co., 1988 (A. R. Harris)
M. incognita	1	IMP E152	Nigeria (P. R. Esbenshade)
M. incognita	1	I 265	Orange Co. (H. Ferris)
M. incognita	3	Jeffers	Cotton, Shafter, Kern Co., 1986 (D. Jeffers)
M. incognita	3	Roberts	California (P. A. Roberts)
M. incognita	3	Shafter	Cowpea, Shafter, Kern Co., 1987 (A. H. C. van Bruggen)
M. incognita	4(3?)	8046	Cowpea cv. 8046, Poplar, Tulare Co., 1986 (C. Frate)
(test could not be completed because of insufficient nematodes in the culture)			
M. incognita	4	Frate	Cowpea cv. CB3, Poplar, Tulare Co., 1986 (C. Frate)

(Statistical Analysis System; SAS Institute Inc., 1985) to minimize the residual sum of squares. Treatment means were compared by *t*-tests.

Effect of different taxa of *Meloidogyne* on Fusarium wilt

Sixteen isolates of *Meloidogyne* (including seven from California cowpea fields) (Table 3) were identified by differential host test and perineal-pattern morphology (Hartman & Sasser, 1985). Two experiments were conducted to compare the effect of 14 different taxa and isolates of *Meloidogyne* (listed in Table 4) on Fusarium wilt resistance in cowpeas. The cultivar CB3 was used because it is resistant to all three races of *F. o. tracheiphilum*, and susceptible to *M. javanica* and *M. incognita* races 1 and 3, and possibly to races 2 and 4 (Swanson, 1984). Race 3 of *F. o. tracheiphilum* was used because earlier research suggested that it predominates in California (Harris, 1989).

In the first of two experiments, seeds were surface-disinfested and germinated in humid chambers, then sown in aerated-steam-treated sand in 5·7-cm-square plastic pots (one plant per pot). For each of the five treatments with an isolate of *Meloidogyne*, 1000 nematode eggs were pipetted into a hole in the sand just above the seed, 1–3 days after planting. Three and a half weeks after inoculation with *Meloidogyne*, each seedling was transplanted carefully into 460-cm^3 polystyrene cups that contained aerated-steam-treated sand mixed with dry chlamydospore-infested straw at a concentration of 2×10^4 c.f.u. per cm^3 of sand. Galls were visible on roots from all *Meloidogyne* treatments during transplanting.

Polystyrene cups were placed in 6000-cm^3 plastic tubs (three cups per tub) of aerated-steam-treated sand. The tubs had no drainage holes, and were immersed in constant-temperature water baths so that the plant root zone was maintained at 27 C (range 24–34 C), which is optimal for Fusarium wilt development (Swanson & Van Gundy, 1985). Each tub was treated as an experimental unit, and was replicated five times in a randomized complete block design, using water baths as blocks. Two control treatments were used: one was inoculated with *F. o. tracheiphilum* alone (no *Meloidogyne*); the other control was inoculated with sterilized straw (no pathogens), and data were excluded from statistical analysis. Plants were watered on alternate days with deionized water or half-strength Hoagland's solution (Hoagland & Arnon, 1950). Plants were assessed for Fusarium wilt as described earlier, 5 weeks after inoculation with *F. o. tracheiphilum*. Root galling was rated on a scale of 0–100 according to the system of Daulton & Nusbaum (1961) (Table 4). Results were subjected to analysis of variance as described earlier, and treatment means were compared by protected least significant difference (Fisher, 1935).

In the second experiment, the virulent J-7c-54 isolate of *M. javanica* was compared with five other isolates of *M. javanica* and four of *M. incognita* for ability to enhance Fusarium wilt.

Table 4. Mean Fusarium wilt disease ratings, vascular discoloration ratings and galling index values of cowpea cultivar CB3 after inoculation with *Fusarium oxysporum* f. sp. *tracheiphilum* race 3 (isolate 160/s128) and different isolates of *Meloidogyne*

Meloidogyne species, race and isolate	Disease rating	Vascular discoloration	Galling index
First experiment:			
M. javanica J-7c-54	3·02	3·13	87
M. javanica J255	2·46	3·53	89
M. incognita R1 1265	0·67	0·27	59
M. incognita R3 ex cotton, Shafter	0·00	0·00	72
M. incognita R4 Frate, ex CB3, Poplar	0·33	0·13	73
None (control, with *F. o. tracheiphilum*)	0·33	0·00	0
None (control, no *F. o. tracheiphilum*)	0·00	0·00	0
PLSD ($P<0·05$)	0·57	1·02	12
Second experiment:			
M. javanica IMP 7		2·94	76
M. javanica J-7c-54		2·85	70
M. javanica Dinuba		2·60	89
M. javanica Wells		2·16	84
M. javanica Minton		1·79	82
None (control, with *F. o. tracheiphilum*)		0·60	0
M. javanica PRJc-18		0·47	28
M. incognita R1 IMP E152		0·47	57
M. incognita R1 Call (1000 eggs per plant)		0·33	63
M. javanica J-7c-54 control (no *F. o. tracheiphilum*)		0·27	85
M. incognita R3 Roberts		0·27	50
M. incognita R1 Call (10,000 eggs per plant)		0·13	78
M. incognita R1 Den		0·00	52
None (control, no *F. o. tracheiphilum*)		0·00	0
PLSD ($P<0·05$)		0·70	11

The same methods were used, except as follows. Seeds were planted directly into *Fusarium*-infested sand in 460-cm^3 cups, and nematode eggs were added immediately. *M. javanica* J-7c-54 without *F. o. tracheiphilum* was also included, and all the control treatments were duplicated on CB5. To determine whether level of nematode infection or severity of galling affects Fusarium wilt in cultivar CB3, a higher inoculum density (10^4 eggs per plant) of *M. incognita* race 1 Call was also included, for comparison with the standard inoculum level. A completely randomized design was used for the five replicates of the 14 treatments, and plants were assessed for Fusarium wilt 11 weeks after inoculation.

RESULTS

Interactions between *M. javanica* and races of *F. o. tracheiphilum* in five cultivars of cowpea

In the first experiment, addition of *M. javanica* to cultivar CB3, before inoculation with either of two race 3 isolates of *F. o. tracheiphilum*, resulted in similar increases in Fusarium wilt ratings, but the increase was significant for only disease rating for isolate 160/s128 ($P<0·05$). None of the treatments showed a highly susceptible reaction (i.e., ratings > 3) (Table 1). CB7977 was resistant to both isolates of *F. o. tracheiphilum*, irrespective of the presence of *M. javanica*. All Mississippi Silver plants inoculated with *M. javanica* were heavily galled, but remained resistant to *F. o. tracheiphilum* race 3.

In the second experiment, *M. javanica* increased vascular discoloration ratings in all Grant and CB3/*F. o. tracheiphilum* race treatments ($P<0·05$) (Table 2). In wilt-susceptible CB5, *F. o. tracheiphilum* races 2 and 3 caused maximum wilting and death in all but one plant in each treatment, even in the absence of *M. javanica*. Disease rating was not considered a reliable measure of Fusarium wilt in this experiment

because foliar symptoms were masked by the effects of *M. javanica*, leaf abscission, and natural senescence in these 8-week-old plants. CB3 had the highest, and CB5 the lowest, mean galling index value ($P < 0.0001$). Neither *F. o. tracheiphilum* treatments nor vascular discoloration rating had any effect on nematode galling index values ($P < 0.05$).

Effect of different taxa of *Meloidogyne* on Fusarium wilt

In the first experiment, there were differences in disease rating and vascular discoloration rating between isolates of *Meloidogyne* (Table 4) ($P < 0.0001$). The two isolates of *M. javanica* (J-7c-54 and J255) resulted in higher ($P < 0.05$) disease ratings and vascular discoloration ratings than any of the isolates of *M. incognita*. The treatments with *M. incognita* had no more wilt disease ($P < 0.05$) than the controls (*F. o. tracheiphilum*, no *Meloidogyne*). The galling indices were higher ($P < 0.01$) for the two isolates of *M. javanica* than for any of the isolates of *M. incognita*.

In the second experiment, disease rating was not a reliable measure of Fusarium wilt, because foliar wilt symptoms were masked by natural senescence and the effects of nematode damage in the 11-week-old plants. The different *Meloidogyne* taxa resulted in differences in vascular discoloration rating and galling index (Table 4). The overall F values for the two ratings were significant at $P = 0.0001$. Five of the six isolates of *M. javanica* resulted in higher ($P < 0.05$) vascular discoloration ratings than any of the other treatments, which were not significantly different from each other. The same five treatments with *M. javanica*, plus the higher inoculum density of *M. incognita* race 1 Call, and the control with *M. javanica* J-7c-54 (no *F. o. tracheiphilum*), had the highest galling indices. The small vascular discoloration rating in the latter control treatment was due to a susceptible reaction in only one plant. In the control with *F. o. tracheiphilum* but no *Meloidogyne*, six of 15 plants had slight vascular discoloration at the primary node. In the two CB5 control treatments inoculated with *F. o. tracheiphilum*, all but one plant died of Fusarium wilt, whether or not *Meloidogyne* was present. The vascular discoloration ratings were 4·93 and 4·87, respectively. There was a positive correlation between vascular discoloration rating and galling index when data were analysed either from all 11 *Meloidogyne* + *Fusarium* treatments ($r = 0.48$, $P < 0.001$), or from only the six *M. javanica* + *Fusarium* treatments ($r = 0.50$, $P < 0.001$). The 10-fold increase in the inoculum density of *M. incognita* race 1 Call increased ($P < 0.05$) the galling index, but not the vascular discoloration rating.

DISCUSSION

M. javanica apparently reduced resistance in cultivar CB3 to *F. o. tracheiphilum* races 1 and 2, and two isolates of *F. o. tracheiphilum* race 3 (Tables 1 and 2). These results confirmed that Fusarium wilt symptoms in CB3 increase when *M. javanica* is added to soil in addition to *F. o. tracheiphilum* race 3 (Harris, 1989; Harris & Ferris, 1991a, b). CB3 has a dominant resistance gene to race 3, and an incompletely dominant one to race 2 (Rigert & Foster, 1987). There are contradictory reports on the ability of *M. incognita* to break monogenic resistance to *F. oxysporum*, especially in tomato (Caperton *et al.*, 1986; Mai & Abawi, 1987). The low levels of Fusarium wilt in our first experiment reported here, even in susceptible CB5, may have been due to poor survival of conidia in the soil (Harris, 1989; Harris & Ferris, 1991a). Chlamydospores are the normal resting stage (Booth, 1971), and were used in subsequent experiments (Harris, 1989; Harris & Ferris, 1991b). Addition of *M. javanica* to Grant and CB5 planted in sand infested with race 1 of *F. o. tracheiphilum* resulted in increases ($P < 0.05$) in vascular discoloration (Table 2), but the low ratings still indicate resistance (only one and three plants, respectively, showed susceptible reactions). The increased vascular discoloration ratings with the addition of *M. javanica* to the three cultivars (Table 2) also reflect an increase in the number of plants rated as susceptible (i.e. rating > 2). The mean ratings, however, are much lower than those of susceptible CB5 with race 2 or 3. CB5 is resistant to race 1 (Swanson, 1984), but also isolate 0923 is only weakly pathogenic on cultivars CB3, Grant (Table 2), and PI 115683 (Harris, 1989). The low vascular discoloration ratings in some of the control treatments (no *F. o. tracheiphilum*) were due to susceptible reactions in one to three plants, which may have been caused by airborne contamination (Burgess, 1981). With the exception of CB5, all cowpea cultivars inoculated with *M. javanica* were heavily galled, including Mississippi Silver, which is reported to be resistant to this nematode in Mississippi (Hare, 1967). Our results confirm that CB3 is a suitable commercial cultivar in which to study the reduc-

tion of Fusarium wilt resistance induced by *Meloidogyne*, and so this cultivar was used in subsequent experiments (Harris, 1989; Harris & Ferris, 1991b).

Single-egg-mass cultures of root-knot nematodes generated from cowpea crops in central and southern California were identified as *M. javanica*, and *M. incognita* races 1, 3, and 4 (Harris, 1989). Although *M. javanica* predominated in southern California cowpea fields in the 1950s (Thomason & McKinney, 1960), little cowpea is now grown in those areas. Most California cowpea production is now in the southern San Joaquin Valley (Fresno, Tulare and Kern Counties), and the crop commonly is rotated with cotton, which is not a host of *M. javanica* or *M. incognita* races 1 and 2 (Hartman & Sasser, 1985). These rotations may suppress *M. javanica* populations, and allow increase of *M. incognita* races 3 and 4. No *M. javanica* was recovered from eight root or soil samples collected between 1985 and 1987 in southern San Joaquin Valley cowpea fields showing Fusarium wilt symptoms (Harris, 1989). *M. incognita* was recovered from three of these fields, and no root-knot nematodes were recovered from the other five samples. Similarly, P. A. Roberts and A. E. Hall (personal communication) found *M. incognita*, but not *M. javanica*, in four cowpea varietal trial sites widely separated in the San Joaquin Valley. Susceptible cultivars in these sites showed Fusarium wilt symptoms.

Although all isolates of *M. incognita* (races 1, 3, and 4) caused considerable galling on cultivar CB3, none caused an increase in Fusarium wilt symptoms. It is interesting that the two subcultures of *M. javanica* (J-7c-54 and J255) did not differ in their effects on either galling index or Fusarium wilt ratings, despite having been maintained in separate greenhouse cultures for at least 9 years. Isolate J-7c-54 was typical of the isolates of *M. javanica* in the incidence and severity of galling and vascular discoloration induced in cultivar CB3. The only atypical isolate of *M. javanica* was PRJc-18, which caused only moderate galling and slight vascular discoloration. Isolate J-7c-54 caused less galling ($P < 0{\cdot}05$) than the Minton isolate, which came from the same cultures as the isolate used by Fery & Dukes (1980). This observation does not support the hypothesis that the California isolate, J-7c-54, is more pathogenic on cowpea than the isolate from the south-eastern USA (Swanson, 1984; Swanson & Van Gundy, 1984).

CB3 was susceptible to all *Meloidogyne* tested, but galling generally was more severe with *M. javanica* than with *M. incognita*. This was expected, because *M. javanica* reproduces more than *M. incognita* on this cultivar (Swanson, 1984). Resistance to all four common *Meloidogyne* species (including *M. javanica*) has been reported in cowpea in the USA (Hare, 1967; Hadisoeganda & Sasser, 1982; Swanson & Van Gundy, 1984), and Ferry & Dukes (1980) believe it to be determined by a single dominant gene. This resistance has been reported to be ineffective against *M. javanica* J-7c-54 (Swanson & Van Gundy, 1984). Further, J-7c-54 increases Fusarium wilt symptoms in wilt-resistant cultivars (Thomason *et al.*, 1959; Swanson, 1984). In our experiments, the vascular discoloration ratings in CB3 with isolate J-7c-54 were only 3·13 and 2·85 (Table 4), in contrast to a rating of 4·93 in the wilt-susceptible cultivar CB5 inoculated with the same nematode and fungus. Thus, resistance apparently is lowered but not completely overcome. Further, there is a quantitative relationship between severity of galling and Fusarium wilt symptoms, but an increase in inoculum density of *M. incognita* to produce galling equal to that caused by *M. javanica* did not increase Fusarium wilt. Therefore, it is hypothesized that *M. javanica*, but not *M. incognita*, increases the incidence and severity of Fusarium wilt in CB3.

If *M. javanica* is uncommon in California cowpea fields, the incidence of nematode-enhanced Fusarium wilt may be lower than suggested previously (Thomason *et al.*, 1959; Swanson, 1984). A comprehensive survey is needed to determine the distribution of species and races of *Meloidogyne*, particularly *M. javanica*. Also, the occurrence and importance of nematode-enhanced Fusarium wilt needs to be determined before setting priorities for breeding programmes for disease resistance in cowpea.

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