Infestation of *Sesbania* species by root-knot nematode (*Meloidogyne javanica*) and its effects on the soil nematode population in western Tanzania

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Abstract

Sixteen accessions of Sesbania sesban and 4 of S. macrantha were assessed for susceptibility to root-knot nematode (Meloidogyne javanica) under glasshouse and field conditions and the effect of Sesbania on the build-up of soil rootknot nematodes. In the field, Sesbania was planted on either ridges or flat land. All accessions were attacked by the nematode but at varied rates of infestation. Sesbanias planted on ridges were infected later than those on flat land; at the 3-month harvest, some accessions were still free of nematodes when grown on ridges. In general, accessions grown on ridges had lower galling and a smaller second-stage juvenile population in the roots than those on flat land. Overall, accessions 15036, 15024 and SR18B had the smallest numbers of second-stage juveniles on both ridges and flat land. All tomato test plants grown in soil from Sesbania plots were infected by the nematode but the level of infestation did not reflect that of Sesbania growing in the field. The data indicate that planting Sesbania would provide a medium for perennating the root-knot nematode.

The implications of the results are discussed in the context of planting *Sesbania* in smallholder crop production systems found in east and southern Africa.

Introduction

Damage from plant-parasitic nematodes is one of the principal yield-limiting factors in crop production in the tropics (Sasser 1980). In the Tabora region of Tanzania, losses caused by rootknot nematode (Meloidogyne javanica) on tobacco and groundnuts is often so severe that continued production is not possible without appropriate management of the pest (Anon 1981). Sesbania species are currently among the high priority multi-purpose shrubs being evaluated by the Southern Africa Agroforestry Research Network for use in agroforestry technologies in the unimodal rainfall plateau of east and southern Africa. This is a region where tobacco is often the major cash crop and usually a grain legume component is found in a maize-dominated cropping system. Whitehead (1969) reported that Sesbania species supported growth of the root-knot nematode; therefore, their introduction into the crop fields could contribute to the soil nematode load.

In a previous glasshouse study with germplasm collected from Kenya and Tanzania (Karachi 1995), considerable variation in the nematode infestation rates between and within *Sesbania* species was observed. This indicated that it was possible to select *Sesbania* accessions that act as poor hosts. In the present study, germplasm from a wider range of environments was evaluated for susceptibility to attack by the nematode under glasshouse and field conditions and the effect of *Sesbania* on the soil nematode population.

Materials and methods

The trials were conducted at the Tumbi Agricultural Research and Training Institute, Tabora, western Tanzania (5° 02' S, 30° 39' E; 1150 m above sea level). The 20 accessions used in all experiments are shown in Table 1.

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Table 1. Effect of inoculation with *Meloidogyne javanica* juveniles on root galling (RGI), egg mass production (EMI) and reproductive rating (R) in *Sesbania* accessions grown in the glasshouse.

Accession ¹	RGI ²	EMI ³	\mathbb{R}^4
S. sesban			
9043	1.0	0.7	0.1
15036	1.7	2.0	0.4
15022	2.0	2.7	0.6
15077	2.0	3.0	0.6
SR10	2.3	2.7	0.5
10693	2.3	3.3	0.7
10521	2.7	3.7	0.7
15024	2.7	3.0	0.7
15020	3.0	2.7	0.5
13144	3.0	3.7	0.7
13887	3.0	3.3	0.7
SR18B	3.3	3.7	0.7
15021	3.3	3.3	0.6
S026	3.7	3.0	0.7
15018	3.7	3.3	0.7
NRB2	4.0	3.3	0.7
S. macrantha			
SR22	2.0	2.7	0.6
SM020	4.0	3.7	0.7
SM069B	4.7	4.0	0.8
S067	6.3	4.0	0.8
Tomato	5.0	5.0	1.0
Mean	3.1	3.2	
ISD (P <0.05)	0.9	0.8	

¹Accessions 9043 to 15036 were obtained from the International Livestock Centre for Africa (ILCA). Those with code numbers starting with S and N were collections from Kenya and Tanzania, respectively.

 20 = no knots on roots; 5 = 50% roots infested, knotting on parts of main roots, reduced root system; and 10 = all roots severely knotted, plants usually dead.

 ${}^{3}0$ = no egg masses; 2 = 3–10 egg masses; and 5 = 31–100 egg masses per root system.

 ${}^{4}R$ >1.0 = good hosts; > 0.5–1 = moderate hosts; > 0.1–0.5 = poor hosts; and \leq 0.1= non-hosts.

Experiment 1: Infestation under glasshouse conditions

A heat-sterilised (80 °C for 30 min) 2:2:1 mixture (volume basis) of sandy loam, forest clay loam and sand (78% sand, 11% silt and 11% clay) was added to 12.5 cm diameter plastic pots (1 kg/pot) and sown with 2 pre-germinated seeds of each accession with tomato as the control. Pots were watered twice daily to 80% soil water holding capacity and seedlings were thinned to a single plant per pot 1 week after seed germination.

Nematode eggs were extracted from infected tomato (*Lycopersicon esculentum* cv. Money maker) plants in the field, and single egg mass cultures were increased on tomato seedlings in the glasshouse. Egg inoculum was extracted from 60-day-old tomato roots (Hussey and Baker 1973) and placed on nitex (Tetko Inc., NY) fibre fabric (20 micro pores). Hatched nematodes were collected over 12 h and standardised to 2000 second-stage infective juveniles (J2). Each seed-ling was inoculated with 1000 juveniles 15 days after seed germination. Experimental design was completely randomised with 3 replications.

At 35 days after inoculation, plants were harvested. Roots were washed to remove soil and rated for root gall indices (RGI) (Bridge and Page 1980). The egg masses were extracted and counted (Dickson and Struble 1965) from 3 randomly selected roots per plant representing the top, mid and bottom fractions of the plant root system. Egg mass indices (EMI) were assessed as described by Sasser and Carter (1982). A reproductive rating (R) was determined by dividing the average EMI for a Sesbania accession by the average EMI for tomato. Based on the R rating, hosts were rated as good (R = >1.0), moderate (R = >0.5-1.0), poor (R = >0.1-0.5) or non-hosts $(R = \le 0.1)$ (Tedford and Fortnum 1988). All data except R were subjected to analysis of variance. Least squares differences were calculated using SAS package (SAS 1985) for all experiments.

Experiment 2: Infestation under field conditions

The soil at the site was a sandy loam (pH 4.3 [1:1.25 soil: water]; 80% sand, 16% silt and 4% clay). The field had been cropped with maize in the previous season.

Seedlings were raised in the glasshouse in heat-sterilised sand contained in 10 cm deep trays for 6 weeks before planting in the field on November 12, 1992. Field blocks (20 m × 6.75 m) were laid out on either flat land or on ridged land; ridges were 25-30 cm high spaced at 1 m apart. These are the common land-preparation methods used in eastern and southern Africa. Each plot consisted of a single row of 10 plants. Seedlings were planted at 10 cm depth, 75 cm apart with 1 m between rows. A guard row of a local annual landrace was planted 2 m away surrounding each block and the plots were maintained free of weeds by hand weeding throughout the trial period. Plants were grown for 3-5 months in a completely randomised block design with 3 replications. A single clean-weeded plot was included in each block as the second control.

Harvests were made at 3, 4 and 5 months after planting. Sampling was systematic from one end of the row: harvests at 3 months, plants 2 and 3; at 4 months, plants 5 and 6; and at 5 months,

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plants 8 and 9. Soil from a ring with 50 cm diameter and 1 m depth around each plant was carefully removed by hand to ensure complete recovery of the root systems within the ring. Roots were then washed in water and transported to the laboratory in polythene bags for assessment of galling and extraction of infective juveniles. Galling was assessed as in Experiment 1. The numbers of J2 were estimated by the modified Baerman funnel technique described by Hooper (1969). All data were subjected to analysis of variance. Data on juvenile counts were square root-transformed before analysis.

Experiment 3: Infestation of tomato test plants grown in soil collected before and after growing Sesbania

Infestation in soil collected before growing Sesbania. Soil samples were collected on November 7,1992 prior to planting Experiment 2. Five 1 kg soil samples were dug using a 2.5 cm diameter auger along the length of each plot using a 15 cm sampling depth. Samples were thoroughly mixed, sieved to remove large particles and debris and a single subsample (1 kg) for each plot added to a 12.5 cm plastic pot and sown with 2 pre-germinated tomato seeds. Experimental management and design were as in Experiment 1 and measurements as in Experiment 2.

Infestation in soil collected after growing Sesbania. A circle with a radius of 25 cm was marked around the root collar of each plant to be harvested and 5 soil cores (2.5 cm diameter \times 15 cm depth) dug randomly around the perimeter. Five soil cores were also dug randomly from each of the clean-weeded blocks. The soil was bulked, thoroughly mixed and sieved, and a 1 kg subsample taken and used for growing the tomato test crop. The management of the experiment and design were as in Experiment 1 and measurements and data management as in Experiment 2.

Results

Glasshouse study

All accessions supported growth of the nematode (Table 1). However, significant differences (P < 0.01) in galling and egg mass production were observed. Based on the R rating, Accessions 9043, 15036, SR10 and 15020 were poor hosts

and the other accessions were moderate hosts. None of the *Sesbania* accessions was a better host than tomato.

Infestation in the field

As in the glasshouse study, all accessions were attacked by the nematode (Table 2). Significant (P<0.01) differences in galling and J2 populations were recorded between accessions. These differences varied with time of sampling and method of planting. The early infestation in plants on flat land resulted in a higher root gall formation and J2 populations at the 3-month harvest than those on ridges except in Accessions 15024, SM020 and SM069B. Accessions 9043, 15036 13144 and 15021 on ridges and 15020 on both flat land and ridges were not infected at this harvest. The delay in infestation on ridges resulted in most root galls and J2 populations at the 5-month harvest with the exception of galling in Accessions 9043, 15077, 13887 and 15018 and J2 populations in 9043, 15036, 15077 and SR22 which were highest at the 4-month harvest. However, root gall formation and J2 populations in Accessions 15022, 10521, 15020, 13144, 15021 and S026 increased up to the 5-month harvest on both flat land and ridges. Infective juveniles exceeding 40/plant were recorded only on flat land in Accessions 13887 and 15021 at the 4 and 5-month harvests, respectively. Overall, Accessions 15024, 15077, and SR18B roots contained the lowest numbers of J2 on both ridges and flat land. At the initial harvest, tomato roots contained more J2 than Sesbania but by the 5-month harvest, many accessions carried at least as many J2 as tomato.

Soil nematode population and infestation of the tomato test crop

As assessed by the infection of the tomato test crop, the initial soil population of nematodes was low and galling was recorded on only 4 plants (mean of 2 galls/plant) from which two J2 were extracted from 63 test plants (data not shown). No galling was recorded on plants grown in soil from the clean-weeded plots (data not shown). After growing *Sesbania*, all test plants grown in soil from the experimental plots were attacked by the nematode (Table 3). Significant (P <0.05) differences were recorded in galling and J2 populations attributable to growing the different

Accession	Method of	Time of harvest (months)						
planting		3			4		5	
		RGI ²	J2 ³	RGI	J2	RGI	J2	
S. sesban								
9043	F	1.5	17.7	1.9	24.4	1.8	17.9	
	R	0.0	0.0	1.5	11.1	1.1	6.3	
15036	F	1.3	5.4	1.5	23.1	1.5	13.3	
	R	0.0	0.0	1.5	8.4	1.8	1.5	
15022	F	1.7	12.8	2.0	17.2	2.3	28.2	
	R	1.1	4.5	1.9	5.3	2.0	28.8	
15077	F	1.5	6.8	1.8	14.8	1.6	5.2	
	R	1.1	5.4	1.9	18.3	1.6	16.4	
SR10	F	1.7	11.0	2.1	34.0	1.4	3.7	
	R	1.1	1.6	1.6	13.5	2.0	31.3	
10693	F	1.5	6.1	1.9	26.4	1.8	4.6	
	R	0.6	2.3	1.9	4.1	2.3	33.3	
10521	F	1.6	6.5	1.7	11.3	1.8	11.5	
	R	1.0	1.6	1.3	6.4	2.1	25.9	
15024	F	1.0	1.0	1.8	18.5	1.9	17.3	
	R	1.0	1.3	1.4	11.0	1.8	13.4	
15020	F	0.0	0.0	1.1	4.9	1.7	34.8	
	R	0.0	0.0	1.4	6.2	1.8	13.4	
13144	F	1.7	3.6	2.2	30.1	2.4	32.6	
12007	R	0.0	0.0	1.5	6.0	1.6	9.6	
13887	F	1.6	9.3	2.4	41.8	2.3	25.1	
CD 10D	R	1.0	4.2	1.9	12.6	1.9	21.5	
SR18B	F	1./	14.6	1.9	8.3	2.2	11./	
15021	ĸ	1.0	3.4	1.1	2.5	1.0	6.9	
15021	F	2.1	14.2	1.6	24.2	2.2	43.6	
5026	K	0.0	0.0	1.4	0.8	2.3	25.6	
5026	F D	1.4	12.9	1.5	15.0	2.2	25.7	
15019	K	1.0	5.9	1.1	0./	1./	24.1	
15018	Г D	1./	5.8	1.9	23.0	1.8	4.1	
NDDO	K E	1.0	1.4	2.1	65	1.9	25.5	
INKD2	Г Р	1.0	0.5	1.0	0.5	2.2	55.7	
S macrantha	K	1.0	2.0	1.0	2.1	1.0	5.9	
SP22	F	17	8.8	1.8	21.3	1.8	10.5	
3K22	P	1.7	2.0	1.0	21.3	1.0	19.5	
SM020	F	1.0	2.0	2.1	18.7	1.0	21.1	
5101020	P	2.1	16.1	1.8	0.1	1.9	21.1	
SM060B	F	2.1	18	1.0	9.1 27.6	1.9	24.9	
514100915	R	1.0	7.4	1.3	5.1	1.9	11.2	
\$067	F	2.2	37.4	2.1	33.4	1.5	14.2	
5007	R	14	4.8	15	13.7	2.5	24.1	
Tomato	F	27	36.6	2.6	22.6	2.3	16.7	
10mato	R	2.5	33.9	2.8	25.7	3.1	33.2	
Mean	F	1.6	9.7	1.9	20.7	1.8	17.8	
	R	0.9	3.8	1.6	9.6	1.8	19.1	
LSD (P < 0.05)	F	0.3	1.3	0.3	1.9	0.3	1.3	
	R	0.2	0.5	0.2	0.8	0.3	0.9	

 Table 2. Effect of method of planting and time of harvest on root galling (RGI) and infective juvenile (J2) populations in Sesbania grown in the field at Tumbi-Tabora, western Tanzania.

¹ F = planted on flat land; and R = planted on ridges.
 ² 0=no knots on roots; 5 = 50% roots infested, knotting on parts of main roots, reduced root system; and 10 = all roots severely knotted, plants usually dead.
 ³ Original data square root-transformed.

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Accession	Method of planting ¹ –	Time of harvest (months)				
		4		5		
	_	RGI ²	J2 ³	RGI	J2	
S. sesban						
9043	F	1.1	3.5	1.2	3.9	
	R	1.1	3.8	1.3	4.1	
15036	F	1.4	3.5	1.1	2.7	
15022	R	1.1	3.4	1.4	9.7	
	F	1.4	5.3	1.8	5.2	
	R	1.7	5.4	1.8	6.3	
15077	F	1.6	12.4	1.5	3.6	
CD 10	R	1.5	7.3	1.3	3.7	
SRIU	F D	1.8	/.8	1.0	2.3	
10603	K E	1.4	4.9	1.9	5.7	
10095	Г Р	1.7	11.1	1.9	4.9	
10521	F	1.4	4.4	1.5	4.7	
10521	R	1.4	2.8	2.0	8.1	
15024	F	1.3	14.3	1.8	5.0	
	R	1.3	3.7	2.5	7.5	
15020	F	1.0	1.7	1.3	4.1	
	R	0.6	1.6	1.0	1.7	
13144	F	1.5	8.8	2.3	4.7	
	R	1.4	5.5	1.8	6.8	
13887	F	1.6	5.7	1.8	4.2	
	R	1.4	7.3	1.8	3.6	
SR18B	F	2.0	7.1	1.3	3.6	
	R	1.0	2.2	1.8	4.1	
15021	F	1.1	3.9	1.3	2.5	
5026	R	1.1	5.6	1.3	2.6	
5026	F	1.4	7.0	1.5	5.2	
15019	K	1.4	10.0	1.0	1.5	
13018	Г	1.4	10.0	1.9	5.0	
NPB2	F	1.7	15	1.7	4.0	
INKD2	R	1.0	4.0	0.0	0.0	
S. macrantha	R	1.0	1.0	0.0	0.0	
SR22	F	1.1	3.9	1.4	2.3	
	R	0.3	0.5	1.3	3.6	
SM020	F	1.6	8.0	1.6	3.5	
	R	1.5	5.3	1.6	4.6	
SM069B	F	1.4	3.5	1.9	8.0	
S067	R	1.7	4.8	1.8	5.7	
	F	1.9	7.7	1.8	5.7	
Tomato	R	1.7	9.9	2.0	6.0	
	F	2.7	15.3	2.4	7.4	
	К	2.4	13.0	2.8	11.6	
Mean	F	1.5	7.4	1.6	4.4	
	R	1.3	5.3	1.6	5.3	
LSD (P < 0.05)	F	0.3	0.9	0.4	0.9	
	R	0.4	0.7	0.4	0.7	

Table 3. Effect of method of planting and time of harvesting Sesbania on root galling (RGI) and infective juvenile (J2) populations in tomato plants grown in the glasshouse in soil from Sesbania plots at Tumbi-Tabora, western Tanzania.

¹ Test soil collected from plots on flat land (F) and plots on ridges (R).
 ² 0 = no knots on roots; 5 = 50% roots infested, knotting on parts of main roots, reduced root system; and 10 = all roots severely knotted, plants usually dead.
 ³ Original data square root-transformed.

accessions and the methods of planting. However, the level of infestation in tomato was lower than that of *Sesbania* growing in the field.

Discussion

The studies demonstrate the potential of Sesbania to sustain reproduction of the root-knot nematode as evidenced by root galling, egg mass indices, numbers of juveniles in roots and the subsequent build-up of soil nematode inoculum during and after the Sesbania crop. The survival of the nematode is reported to be low when exposed to soil temperatures exceeding 33°C and low soil moisture (Daulton and Nausbaun 1961; Wallace 1968; Jain and Bhatti 1987). Similar soil conditions are attained at the site in August-November, which may partly explain the results obtained in this study. The delay in the infestation of plants growing on ridges was probably due to a greater reduction in the initial soil inoculum through solarisation. Jain and Bhatti (1987) reported that multiple ploughings in summer reduced soil rootknot nematode populations and infestation in tomato plants. In this study, soil was turned over twice in ridged plots (ploughing alone vs ploughing then ridging about one month later) under high temperature conditions. The infection at 4- and 5-month harvests reflects increased sites for infection through both well developed and spread root systems and an increased soil nematode population.

The rate of infection as reflected in galling was different between the accessions. Griffin and Waite (1971) reported that susceptible lucerne varieties attracted J2 of M. hapla more than resistant lines. In this study, plants of Accession 15020 were not infected at the 3-month harvest on either ridges or flat land. If this is an expression of a pre-infection resistance mechanism which delays infestation, it would affect nematode reproduction and provide a nematodefree environment for a short-lived annual for 3 months. The lack of infection at the 3-month harvest in 9043, 15036, 13144 and 15021 planted on ridges may relate to the unavailability of J2. The high level of infestation in the glasshouse study with inoculated plants was probably due to the level of available inoculum.

The success of the nematode in infesting roots as reflected in the number of J2 recovered varied between accessions. This again may suggest a presence of pre-infection resistance mechanisms that controlled the rates of penetration of J2 into the roots. In particular, Accessions 15036 and SR18B, which had the lowest mean nematode counts, could be assumed to be exhibiting more pre-infection resistance than the other accessions. However, it is unclear why the numbers of J2 were consistently lower in some entries when planted on ridges than on flat land even though root galling was similar. Further studies on the reaction of Sesbania spp. to attack by nematodes seem warranted. The pattern of infestation, i.e., early infestation resulting in the highest nematode counts at the 4-month harvest followed by a decline at the 5-month harvest and a substantial death of roots that were infected, is similar to earlier observations (Karachi 1995). New root developments were found mainly on accessions that exhibit biennial/perennial growth habit at the site (15022, 15021, S026, 15020, 10521 and 13144) and in which the nematode population tended to increase up to the 5-month harvest irrespective of the method of planting. The decline in nematode counts may therefore relate to reduction in sites for infection as well as indicating the potential of long-lived Sesbania to sustain growth of nematodes for an extended period.

The lack of infection of tomato plants grown in soil from clean-weeded plots may again be due to the effects of high soil temperatures and low moisture on the survival of the nematode; clean fallowing is one of the recommended cultural practices for control of the nematode in tobacco fields. However, the soil nematode inoculum levels as assessed by galling and the J2 populations in the tomato test crop did not reflect the rate at which Sesbania was infected in the field. The reasons for this are not clear. The sources of inoculum could have been the initial soil population or those migrating from the Sesbania root systems or both. The contribution to the soil inoculum by each of these potential sources was not examined in this study; therefore, that due to Sesbania cannot be ascertained.

Implications for the use of Sesbania in cropping systems

This study demonstrates that *Sesbania* accessions support growth and reproduction of the root-knot nematode and that, in the presence of *Sesbania*, there is potential for an increase in the soil nematode population within one cropping season.

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Planting perennial *Sesbania* accessions would provide a medium for perennating the nematode over a long period of time. Since a wide range of suitable food crops are susceptible to nematode attack (Whitehead 1969), planting *Sesbania*, which would contribute to the soil nematode load, would impact negatively on crop production in the smallholder low input/output mixed cropping systems prevalent in eastern and southern Africa. There is clearly a need for additional studies over a wide range of environmental sites where *Sesbania* may be planted, to identify materials that are non-hosts/poor hosts and management systems that will minimise the impact of the nematode on crop production.

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References

- ANON (1981) Tumbi Agricultural Research and Training Institute. Annual Report 1981. pp. 35–38. (Ministry of Agriculture: Tanzania).
- BRIDGE, J. and PAGE, S.L.J. (1980) Estimation of root-knot nematode infestation on roots using a rating chart. *Tropical Pest Management*, 26, 296–298.

- DAULTON, R.A.C. and NAUSBAUN, C.J. (1961) The effect of soil temperature on survival of the root-knot nematodes, *Meloidogyne javanica* and *M. hapla. Nematologica*, 6, 280–294.
- DICKSON, D.W. and STRUBLE, F.B. (1965) A sieving-straining technique for extraction of egg masses of *Meloidogyne* incognita from soil. *Phytopathology*, 55, 497 (abstr.).
- GRIFFIN, G.D. and WAITE, W.W. (1971) Attraction of Ditylenchus dipsaci and Meloidogyne hapla by resistant and susceptible alfalfa seedlings. Journal of Nematology, 3, 215–219.
- HOOPER, D.J. (1969) Extraction and handling of plant and soil nematodes. In: Peachey, J.E. (ed.) Nematodes of Tropical Crops. pp. 21–22. Technical Communication No. 40, Commonwealth Bureau of Helminthology, U.K.
- HUSSEY, R.S. and BAKER, K.R. (1973) A comparison of methods of collecting inocula of *Meloidogyne* spp. including a new technique. *Plant Disease Reporter*, **57**, 1025–1028.JAIN, R.K. and BHATTI, D.S. (1987) Population and develop-
- JAIN, R.K. and BHATTI, D.S. (1987) Population and development of root-knot nematode (*Meloidogyne javanica*) and tomato yield influence by summer ploughings. *Tropical Pest Management*, 33, 122–124.
- KARACHI, M. (1995) Sesbania species as potential hosts to root-knot nematode (*Meloidogyne javanica*) in Tanzania. *Agroforestry Systems*, **32**, 119–125.
- SAS. (1985) SAS Users Guide. (Statistical Analysis Systems Institute: Cary NC).
- SASSER, J.N. (1980) Root-knot nematode: a global menace to crop production. *Plant Diseases*, **64**, 38–41.
- SASSER, J.N. and CARTER, C.C. (1982) Root-knot nematodes (Meloidogyne spp.) identification, morphological variation, host range, ecology and control. In: Riggs, R.D. (ed.) Nematology in the southern region of the United States. pp. 21–23. Southern Co-operative Series Bulletin 276, Arkansas Agricultural Experiment Station, Fayettevile.
- TEDFORD, E.C. and FORTNUM, B.A. (1988) Weed hosts of *Meloidogyne arenaria* and *M. incognita* common in tobacco fields in South Carolina. *Annals of Applied Nematology*, 2, 102–105.
- WALLACE, H.R. (1968) The influence of soil moisture on survival and hatch of *Meloidogyne javanica*. *Nematologica*, 14, 231–242.
- WHITEHEAD, A.G. (1969) The distribution of root-knot nematodes (*Meloidogyne* spp.) in Tropical Africa. *Nematologica*, 15, 315–333.

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