

# Reproduction of lectin-treated *Meloidogyne* spp. in two related soybean cultivars

Eric L. DAVIS\*, David T. KAPLAN\*, Donald W. DICKSON\*\*  
and David J. MITCHELL\*\*\*

\*U.S. Department of Agriculture, Agricultural Research Service, 2120 Camden Road, Orlando, FL 32803; \*\*Department of Entomology and Nematology, and \*\*\*Department of Plant Pathology, University of Florida, Gainesville, FL 32611, USA.

## SUMMARY

Second-stage juveniles of *Meloidogyne incognita* races 1 and 3, and *M. javanica* were incubated in various lectin and sugar solutions and added to soil in which one of two related soybean cultivars was growing. Compounds tested included soybean agglutinin, concanavalin A, wheat germ agglutinin, *Lotus tetragonolobus* agglutinin, *Limulus polyphemus* agglutinin, and their specific sugars. The number of egg masses per soybean root system was rated 60 days postinoculation to evaluate lectin and sugar effects on nematode reproduction. Treatment of all *Meloidogyne* spp. populations with sialic acid and sialic acid plus *Limulus polyphemus* agglutinin strongly suppressed nematode reproduction in soybean roots of both cultivars. Several concanavalin A treatments moderately reduced reproduction of *M. incognita* race 3 and *M. javanica* in compatible soybean plants, but results were not reproducible in a second experiment. Impairment of host-finding and penetration may be responsible for reduced reproduction of sialic acid-treated *Meloidogyne* spp. in soybean roots.

## RÉSUMÉ

### *Reproduction de Meloidogyne spp. traités avec des lectines sur deux cultivars voisins de soja*

Des juvéniles de deuxième stade de *Meloidogyne incognita* races 1 et 3 et de *M. javanica* ont été mis à incuber dans diverses solutions de sucres et de lectines, puis inoculés dans le sol où croissaient deux cultivars voisins de soja. Les composés testés comprennent : l'agglutinine du soja, la concanavaline A, les agglutinines du germe de blé, de *Lotus tetragonolobus* et de *Limulus polyphemus*, ainsi que leurs sucres spécifiques. Le nombre des masses d'œufs présentes sur le système racinaire des pieds de soja a été évalué 60 jours après l'inoculation afin de tester l'effet des lectines et des sucres sur la reproduction du nématode. Chez tous les *Meloidogyne*, le traitement à l'acide sialique, seul ou additionné d'agglutinine de *Limulus polyphemus*, réduit considérablement la reproduction du nématode sur les racines des deux cultivars de soja. Plusieurs traitements à l'aide de concanavaline A ne réduisent que modérément la reproduction de *M. incognita* race 3 et de *M. javanica* sur les sojas correspondants, mais ces résultats n'ont pu être reproduits lors d'une deuxième expérience. Une altération lors de la recherche de l'hôte et de la pénétration peut être la cause de la diminution de la reproduction, dans les racines du soja, des *Meloidogyne* spp. traités par l'acide sialique.

Interaction between nematodes and other organisms is influenced by chemosensory stimuli (Green, 1971; Ward, 1978; Prot, 1980; Croll & Sukhdeo, 1981; Dusenbery, 1983; Zuckerman & Jansson, 1984; Huetel, 1986). Researchers have postulated that intervention in host finding and recognition of nematodes may be achieved by blockage or obliteration of carbohydrates on nematode surfaces (Zuckerman, 1983; Zuckerman & Jansson, 1984). Proteins (lectins) that bind mannose, glucose, and sialic acids, and enzymes (glycohydrolases) that may cleave these carbohydrates from nematode surfaces have impaired nematode chemotaxis toward source attractants (Jansson *et al.*, 1984; Jeyaprakash *et al.*, 1985). Adhesion of conidia of *Meria coniospora* Drechsler to nematode chemosensory organs, nematode attraction to the fungus, and infection of nematodes by adhering conidia were inhibited by sialic acids, sialidase, or limulin (Jansson & Nordbring-Hertz, 1983, 1984;

Jansson, Jeyaprakash & Zuckerman, 1985). A lectin specific for mannose appeared to inhibit chemoreception necessary for the feeding and sexual attraction of males of *Trichostrongylus colubriformis* Giles (Bone & Bottjer, 1985). Capture of nematodes by *Arthrobotrys oligospora* Fres. appeared to involve interaction of lectin on fungal traps with N-acetylgalactosamine moieties present on the nematode surface (Nordbring-Hertz & Mattiasson, 1979; Borrebaeck, Mattiasson & Nordbring-Hertz, 1985).

Other studies have reported the presence of carbohydrates on the head region and surface of some phytoparasitic nematodes (McClure & Zuckerman, 1982; Spiegel, Cohn & Spiegel, 1982; Spiegel *et al.*, 1983; Forrest & Robertson, 1986; McClure & Stynes, 1988; Davis *et al.*, 1988; Robertson *et al.*, in press). Various lectins bound to carbohydrates present in amphidial exudates of second-stage juveniles (J2) of potato cyst

and root-knot nematodes (Forrest & Robertson, 1986; McClure & Styne, 1988; Davis *et al.*, 1988). Differences in structure and relative amount of carbohydrates present in amphidial carbohydrate complexes of several populations of *Meloidogyne* spp. have been reported (Davis *et al.*, 1988).

Nematode surface carbohydrates may be involved in plant-nematode interactions (Marban-Mendoza *et al.*, 1987; Davis, 1988). It has been reported that soil applications of concanavalin A (Con A : a mannose and glucose-specific lectin), and relatively high concentrations of *Limax flavus* agglutinin (LFA : a sialic acid-specific lectin), significantly suppressed galling of tomato roots induced by *Meloidogyne incognita* (Kofoid & White) Chitwood (Marban-Mendoza *et al.*, 1987). Treatment of J2 from a population of race 3 of *M. incognita* with various lectins and carbohydrates promoted hypersensitivity in an apparently compatible soybean-*M. incognita* interaction (Davis, 1988). Very few nematodes could be detected within soybean roots after inoculation of root tips with J2 of *Meloidogyne* spp. suspended in solutions of LFA and sialic acid. The objective of this research was to determine the effect of several lectins and carbohydrates on establishment and reproduction of three populations of *Meloidogyne* spp. in two related soybean [*Glycine max* (L.) Merr.] cultivars.

### Materials and methods

Populations of *Meloidogyne incognita* races 1 and 3 (Mi1 and Mi3) and *M. javanica* (Treb) Chitwood (Mj) were maintained in greenhouse culture on roots of "Rutgers" tomato (*Lycopersicon esculentum* Mill.) and "Black Beauty" eggplant (*Solanum melongena* L.). *Meloidogyne* spp. populations were identified by using adult female perineal patterns, J2 lengths, and development on differential host plants (Sasser & Carter, 1985). Species identifications were also confirmed by three independent nematode taxonomists (see acknowledgements). Eggs of each nematode population were extracted from host roots with 0.53 % NaOCl for 30 seconds (Hussey & Barker, 1973) and hatched at room temperature on a Baermann funnel. Preinfective J2 that had hatched within 48 hours were used as test organisms in each experiment.

Purified, unconjugated soybean agglutinin (SBA), wheat germ agglutinin (WGA), *Lotus tetragonolobus* agglutinin (LOT), Con A, and *Limulus polyphemus* agglutinin (LPA) (E-Y Labs, San Mateo, CA, USA) were individually bound to surface carbohydrates of *Meloidogyne* spp. J2 by incubating nematodes in separate solutions containing lectin. The sugar specificity of each lectin and corresponding competitive sugars are listed in Table 1. The procedure used to determine the specific hemagglutination activity for each lectin was

described by Davis *et al.* (1988). Buffer solutions included : 0.01 M phosphate-buffer saline (PBS) at pH 7.2 for SBA, WGA, and LOT; 0.05 M Tris-saline plus 0.01 M CaCl<sub>2</sub> at pH 7.5 for Con A; 0.05 M Tris-saline plus 0.01 M CaCl<sub>2</sub> at pH 8.0 for LPA.

Table 1

Sugar specificity and competitive sugars of soybean agglutinin (SBA), wheat germ agglutinin (WGA), *Lotus tetragonolobus* agglutinin (LOT), Concanavalin A (CON A), and *Limulus polyphemus* agglutinin (LPA).

Lectin	Sugar Specificity	Competitive Sugar <sup>a</sup>
SBA	α-D-galactose	D-galactose
WGA	N-acetyl- α-D-galactosamine	N-acetyl- D-glucosamine
	β-D-glucosamine	
LOT	α-L-fucose	L-fucose
CON A	α-D-mannose	D-mannose
LPA	α-D-glucose	N-acetylneuraminic acid
	neuraminic (sialic) acid	

<sup>a</sup> Corresponding competitive sugars (0.1 M) used for all assays of inhibition of lectin activity.

Preinfective J2 of Mi1, Mi3 and Mj were concentrated in the appropriate buffer or in distilled water by centrifugation at 1 000 g for 3 min. Treatments for each lectin included incubating J2 (ca. 16 000 J2) of each population in lectin solution (200 µg/ml), lectin (200 µg/ml) plus 0.1 M competitive sugar, and 0.01 M competitive sugar minus lectin for 2 hours at 4°. Control treatments included J2 in buffer and J2 in distilled water incubated for 2 hours at 4°. Suspensions of J2 in each treatment (1.0 ml total volume per treatment) were diluted to 16 ml (12.5 µg/ml lectin and/or 6.25 mM sugar) immediately before being added to soil in which soybeans were grown as described below.

Two related cultivars of soybean (cv. Pickett 71 and Centennial) were used for root challenge by J2 of *Meloidogyne* spp. Pickett 71 is compatible and Centennial is incompatible with *M. incognita*, and both soybean cultivars are compatible with *M. javanica* (Kaplan, Thomason, & Van Gundy, 1979). Individual soybean seedlings were grown in a greenhouse in 150-cm<sup>3</sup> conetainers<sup>®</sup> (Leach Nursery, Canby, OR) containing steam-pasteurized Astatula fine sand (hyperthermic, uncoated typic quartzipsamments). Approximately 2 000 J2 in 2-milliliter suspensions of each treatment combination were added to the soil in each conetainer using a syringe fitted with a 10-cm-long canulus (Davis & Rich, 1987). There were four replicates of each

treatment combination. Test plants were maintained in a glasshouse at  $27 \pm 3^\circ$ , watered daily, and fertilized once a week with a solution containing 10-6-10 (N-P-K) plus microelements. Experiment 1 was conducted in the spring and experiment 2 was conducted in the summer.

Soybean plants were removed from containers 60 days after soil was infested with J2 and the roots were rinsed free from soil. The number of *Meloidogyne* spp. egg masses per root system was rated on a 0-5 scale (Sasser & Carter, 1985). Data were subjected to analysis of variance procedure and treatment differences were determined by the Waller-Duncan *k*-ratio *t*-test with  $k = 100$  ( $P \leq 0.05$ ). This experiment was repeated once.

## Results

Hemagglutination assays indicated that the binding of pure lectins was relatively strong, except for LPA. Specific hemagglutination activities were 4 096, 4 096, 8 192, 8 192, and 16 units/mg lectin for SBA, Con A, WGA, LOT, and LPA, respectively. Hemagglutination activity of all lectins was completely inhibited in the presence of 0.1 M corresponding competitive sugar.

Pickett 71 soybean was highly compatible with Mi1 in two experiments, as indicated by the high egg mass ratings in buffer and water controls (Tab. 2). Little reduction in Mi1 reproduction in Pickett 71 compared to controls was demonstrated by any lectin or sugar treatment except LPA plus sialic acid and sialic acid alone in the second test. This was not, however, verified by the results of the first test. Reproduction of Mi1 in Pickett 71 in experiment 2 was significantly lower for LPA plus sialic acid compared to all other lectin-plus-sugar treatments. The rating for LPA plus sialic acid in the first experiment was only significantly lower than that of SBA plus galactose. Treatment with LPA alone in the first experiment significantly reduced reproduction of Mi1 in Pickett 71 compared to SBA and Con A alone. Sialic acid significantly reduced the egg mass rating in experiment 1 compared to N-acetylglucosamine and mannose. However, both buffer and water controls for LPA produced relatively low egg mass ratings compared to all other treatments in experiment 1. Centennial soybean was highly incompatible with Mi1, as indicated by poor nematode reproduction (mean egg mass rating  $\leq 2.25$ ) among all lectin, sugar, and control treatments in two experiments.

Table 2  
Reproduction of *Meloidogyne incognita* race 1 in "Pickett 71" soybean roots after treatment of second-stage juveniles with selected lectins and their competitive sugars.

Treatment	Egg mass rating <sup>a</sup> /lectin				
	SBA <sup>b</sup>	WGA	LOT	CON A	LPA
EXPERIMENT 1					
Lectin	4.50 $\alpha^*$	3.50 <i>abcde</i>	3.75 <i>abcd</i>	4.50 <i>a</i>	3.00 <i>cde</i>
Lectin + sugar	4.25 <i>ab</i>	3.50 <i>abcde</i>	3.00 <i>cde</i>	3.75 <i>abcd</i>	2.75 <i>de</i>
Sugar	3.25 <i>bcde</i>	3.75 <i>abcd</i>	3.25 <i>bcde</i>	4.25 <i>ab</i>	2.50 <i>e</i>
Buffer	4.00 <i>abc</i>	3.50 <i>abcde</i>	3.50 <i>abcde</i>	4.00 <i>abc</i>	2.50 <i>e</i>
Distilled water	4.00 <i>abc</i>	3.75 <i>abcd</i>	4.25 <i>ab</i>	4.25 <i>ab</i>	3.00 <i>cde</i>
EXPERIMENT 2					
Lectin	4.50 <i>abc</i>	4.25 <i>bcd</i>	4.50 <i>abc</i>	4.00 <i>cd</i>	4.50 <i>abc</i>
Lectin + sugar	4.25 <i>bcd</i>	4.75 <i>ab</i>	4.75 <i>ab</i>	5.00 <i>a</i>	1.00 <i>e</i>
Sugar	4.75 <i>ab</i>	3.75 <i>d</i>	4.50 <i>abc</i>	4.50 <i>abc</i>	3.75 <i>d</i>
Buffer	4.50 <i>abc</i>	4.00 <i>cd</i>	4.50 <i>abc</i>	5.00 <i>a</i>	4.75 <i>ab</i>
Distilled water	5.00 <i>a</i>	4.75 <i>ab</i>	4.25 <i>bcd</i>	4.75 <i>ab</i>	5.00 <i>a</i>

<sup>a</sup> Scale : 0 = 0; 1 = 1-2; 2 = 3-10; 3 = 11-30; 4 = 31-100; 5 = > 100 egg masses/root system.

<sup>b</sup> Lectins and corresponding competitive sugars included soybean agglutinin (SBA) and galactose; wheat germ agglutinin (WGA) and N-acetylglucosamine; *Lotus tetragonolobus* agglutinin (LOT) and fucose; Concanavalin A (CON A) and mannose; *Limulus polyphemus* agglutinin (LPA) and sialic acid.

\* Table values are the mean of four replicates. Means followed by the same letter for each experiment are not significantly different ( $P \leq 0.05$ ) according to the Waller-Duncan *k*-ratio *t*-test.

Race 3 of *M. incognita* was highly compatible with Pickett 71; almost all treatments and controls had high egg mass ratings (Tab. 3). Treatment with sialic acid alone and sialic acid plus LPA significantly reduced reproduction of Mi3 in Pickett 71 over that of the controls in both experiments. Moderate reduction in

Mi3 reproduction in Pickett 71 was observed for Con A plus mannose treatment, as compared to controls, in experiment 1 but not in experiment 2. Centennial soybean was incompatible with Mi3, as indicated by relatively low mean egg mass ratings ( $\leq 2.75$ ) for all treatments in two experiments.

Table 3

Reproduction of *Meloidogyne incognita* race 3 in "Pickett 71" soybean roots after treatment of second-stage juveniles with selected lectins and their competitive sugars.

Treatment	Egg mass rating <sup>a</sup> /lectin				
	SBA <sup>b</sup>	WGA	LOT	CON A	LPA
EXPERIMENT 1					
Lectin	4.75 ab*	4.75 ab	4.75 ab	5.00 a	4.00 bcd
Lectin + sugar	4.50 abc	3.75 cd	4.50 abc	3.25 de	2.50 ef
Sugar	5.00 a	3.75 cd	5.00 a	4.50 abc	2.25 f
Buffer	4.50 abc	4.00 bcd	4.75 ab	4.75 ab	4.75 ab
Distilled water	4.75 ab	4.75 ab	4.75 ab	4.50 abc	4.50 abc
EXPERIMENT 2					
Lectin	4.50 ab	4.25 bc	5.00 a	4.50 ab	4.50 ab
Lectin + sugar	5.00 a	4.75 ab	4.50 ab	4.50 ab	1.25 d
Sugar	4.75 ab	4.50 ab	5.00 a	4.75 ab	3.75 c
Buffer	5.00 a	4.75 ab	4.75 ab	5.00 a	4.50 ab
Distilled water	5.00 a	4.75 ab	5.00 a	5.00 a	5.00 a

<sup>a</sup> Scale : 0 = 0; 1 = 1-2; 2 = 3-10; 3 = 11-30; 4 = 31-100; 5 = > 100 egg masses/root system.

<sup>b</sup> Lectins and corresponding competitive sugars included soybean agglutinin (SBA) and galactose; wheat germ agglutinin (WGA) and N-acetylglucosamine; *Lotus tetragonolobus* agglutinin (LOT) and fucose; Concanavalin A (CON A) and mannose; *Limulus polyphemus* agglutinin (LPA) and sialic acid.

\* Table values are the mean of four replicates. Means followed by the same letter for each experiment are not significantly different ( $P \leq 0.05$ ) according to the Waller-Duncan k-ratio t-test.

Pickett 71 soybean was compatible with Mj, as indicated by high egg mass ratings for many lectin, sugar, and control treatments (Tab. 4). Reproduction of Mj in Pickett 71 was significantly reduced by sialic acid and sialic acid plus LPA treatment compared to all other treatments in the second experiment. Treatment with sialic acid alone and LPA plus sialic acid significantly reduced reproduction of Mj in Pickett 71 compared to all other sugar and lectin-plus-sugar treatments, respectively, in experiment 1. Ratings for sialic acid and LPA plus sialic acid, however, were not significantly lower than those for buffer and water controls of LPA in the first experiment. Relatively high egg mass ratings for many lectin, sugar, and control treatments indicated

that Centennial soybean was highly compatible with Mj (Tab. 5). Reproduction of Mj in Centennial was significantly reduced by sialic acid and LPA plus sialic acid compared to all other treatments in experiment 2. Treatment with LPA plus sialic acid significantly reduced egg mass ratings in the first experiment compared to SBA plus galactose and WGA plus N-acetylglucosamine. Reproduction of Mj in Centennial was significantly reduced by treatment with sialic acid in experiment 1, compared to egg mass ratings for galactose, N-acetylglucosamine, and fucose. Ratings for sialic acid alone and sialic acid plus LPA, however, were not significantly lower than those for buffer and water controls of LPA in the first experiment.

Table 4

Reproduction of *Meloidogyne javanica* in "Pickett 71" soybean roots after treatment of second-stage juveniles with selected lectins and their competitive sugars.

Treatment	Egg mass rating <sup>a</sup> /lectin				
	SBA <sup>b</sup>	WGA	LOT	CON A	LPA
EXPERIMENT 1					
Lectin	3.75 ab*	2.50 cdefg	3.25 abcd	2.00 efg	2.75 bcdef
Lectin + sugar	3.00 abcde	3.75 ab	4.00 a	3.00 abcde	1.50 g
Sugar	3.00 abcde	3.25 abcd	3.75 ab	3.75 ab	1.75 fg
Buffer	3.25 abcd	3.50 abc	3.00 abcde	2.25 defg	2.00 efg
Distilled water	3.25 abcd	3.50 abc	2.25 defg	3.00 abcde	1.50 g
EXPERIMENT 2					
Lectin	4.00 bcd	4.50 abc	4.50 abc	3.00 e	4.25 abcd
Lectin + sugar	3.50 de	4.75 ab	4.75 ab	4.50 abc	1.25 f
Sugar	4.00 bcd	3.75 cde	5.00 a	4.50 abc	1.00 f
Buffer	4.00 bcd	4.25 abcd	4.25 abcd	4.50 abc	4.25 abcd
Distilled water	4.75 ab	4.50 abc	4.25 abcd	4.25 abcd	4.50 abc

<sup>a</sup> Scale : 0 = 0; 1 = 1-2; 2 = 3-10; 3 = 11-30; 4 = 31-100; 5 = > 100 egg masses/root system.

<sup>b</sup> Lectins and corresponding competitive sugars included soybean agglutinin (SBA) and galactose; wheat germ agglutinin (WGA) and N-acetylglucosamine; *Lotus tetragonolobus* agglutinin (LOT) and fucose; Concanavalin A (CON A) and mannose; *Limulus polyphemus* agglutinin (LPA) and sialic acid.

\* Table values are the mean of four replicates. Means followed by the same letter for each experiment are not significantly different ( $P \leq 0.05$ ) according to the Waller-Duncan k-ratio t-test.

Table 5

Reproduction of *Meloidogyne javanica* in "Centennial" soybean roots after treatment of second-stage juveniles with selected lectins and their competitive sugars.

Treatment	Egg mass rating <sup>a</sup> /lectin				
	SBA <sup>b</sup>	WGA	LOT	CON A	LPA
EXPERIMENT 1					
Lectin	4.50 ab*	3.00 cdef	3.75 abcd	2.25 fg	4.00 abc
Lectin + sugar	3.75 abcd	4.00 abc	3.00 cdef	2.75 defg	1.75 fg
Sugar	3.50 bcde	4.00 abc	4.25 ab	3.00 cdef	2.00 fg
Buffer	4.50 ab	4.75 a	4.50 ab	2.50 efg	3.00 cdef
Distilled water	3.50 bcde	3.50 bcde	4.50 ab	3.50 bcde	2.50 efg
EXPERIMENT 2					
Lectin	4.25 abc	4.50 abc	4.75 ab	4.00 bc	4.00 bc
Lectin + sugar	4.00 bc	4.75 ab	4.50 abc	4.00 bc	1.25 d
Sugar	4.25 abc	4.75 ab	4.25 abc	3.75 c	1.75 d
Buffer	4.75 ab	5.00 a	4.50 abc	4.75 ab	4.50 abc
Distilled water	4.75 ab	4.25 abc	4.75 ab	4.25 abc	4.00 bc

<sup>a</sup> Scale : 0 = 0; 1 = 1-2; 2 = 3-10; 3 = 11-30; 4 = 31-100; 5 = > 100 egg masses/root system.

<sup>b</sup> Lectins and corresponding competitive sugars included soybean agglutinin (SBA) and galactose; wheat germ agglutinin (WGA) and N-acetylglucosamine; *Lotus tetragonolobus* agglutinin (LOT) and fucose; Concanavalin A (CON A) and mannose; *Limulus polyphemus* agglutinin (LPA) and sialic acid.

\* Table values are the mean of four replicates. Means followed by the same letter for each experiment are not significantly different ( $P \leq 0.05$ ) according to the Waller-Duncan k-ratio t-test.

## Discussion

Results from our research generally agree with observations from similar histological investigations that utilized the same populations of *Meloidogyne* spp. and soybean cultivars (Davis, 1988). The inhibition of reproduction of untreated Mi3 in Centennial soybean roots contrasts with the apparently compatible response of Centennial root tissue to untreated Mi3 observed in histological tests (Davis, 1988). Intact giant cells were associated with untreated Mi3 in Centennial soybean roots 20 days after exposure of roots to infective juveniles of Mi3. However, no gall formation or development of Mi3 past third-stage juvenile was observed 20 days after inoculation. Strong reduction in the rate of Mi3 development, or a possible nutritional deficiency that culminated in nematode death, may have occurred in this host-parasite relationship since no active plant defense (i.e. hypersensitivity) seemed to occur. The response of Centennial soybean root tissue to infection by our population of Mi3 more than 20 days postinoculation, and the potential reproduction of Mi3 in Centennial more than 60 days after infection, have yet to be determined. Differences in the degree of incompatibility of "*M. incognita*-resistant" soybean cultivars with several *M. incognita* populations have been reported (Schmitt & Noel, 1984).

Any effect of lectin or sugar on successful nematode infection of soybean roots most likely occurred at initial infection, since environmental conditions and duration of the experiment were conducive to at least two generations of root-knot nematode reproduction. One investigation has indicated that soil application of Con A significantly reduced galling of tomato roots by *M. incognita* (Marban-Mendoza *et al.*, 1987), but the activity of Con A in soil was difficult to interpret. Although moderate reduction in egg mass ratings was occasionally associated with Con A, sialic acid appeared to have the greatest and most consistent adverse effect on successful nematode infection. These results are supported by the apparent inability of several *Meloidogyne* spp. J2 to penetrate soybean roots in "unwashed" sialic acid and LFA treatments (Davis, 1988). Inaccurate quantification of initial inoculum or denaturation of sialic acid and LFA in experiment 1 may have contributed to some discrepancy in results between experiments 1 and 2 presented here. Hemagglutination tests determined that the binding capacity of LFA was relatively weak, and it was completely inhibited in the presence of 0.1 M sialic acid. This may indicate that concentrations of LFA when mixed with sialic acid were insufficient to inhibit (and may have acted in combination with) the activity of sialic acid on root-knot nematode infection of soybean roots. Threshold levels of sialic acid that significantly inhibit nematode infection need to be determined. Microscopic observation of J2 treated with sialic acid and LFA, and penetration of soybean roots by J2 treated

with sialic acid and LFA and "washed", indicated that these treatments are not lethal to J2 of *Meloidogyne* spp. (Davis, 1988; Davis *et al.*, 1988). The adverse effect of sialic acid on *Meloidogyne* spp. reproduction in soybean may be manifested in impairment of host-finding and penetration of plant roots by treated J2. This appears to be more than just an effect of low pH, since penetration of soybean roots by J2 incubated in low pH (3.0) buffer was significantly greater than nonneutralized sialic acid (0.1 M) treatments (Davis, 1988). Perhaps sialic acids act as "biological masks" similar to those found in other animal systems (Schauer, 1982). Subsequent investigations of these phenomena may provide information valuable to the development of novel means of nematode management.

## ACKNOWLEDGEMENTS

The authors would like to acknowledge Drs. A. M. Golden, Beltsville, MD, J. G. Baldwin, Riverside, CA, and J. D. Eisenback, Blacksburg, VA, for their assistance in identification of *Meloidogyne* spp. We thank Drs. K. Hinson, Gainesville, FL, and E. E. Hartwig, Stoneville, MS, for supplying soybean seed.

## NOTA

Mention of a trademark, warranty, proprietary product, or vendor does not constitute a guarantee by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

## REFERENCES

- BONE, L. W. & BOTTJER, K. P. (1985). Cuticular carbohydrates of three nematode species and chemoreception by *Trichoststrongylus columbriformis*. *J. Parasitol.*, 71 : 235-238.
- BORREBAECK, C., MATTIASSON, B. & NORDBRING-HERTZ, B. (1985). A fungal lectin and its apparent receptors on a nematode surface. *FEMS Microbiol. Lett.*, 27 : 35-39.
- CROLL, N. A. & SUKHDEO, M. V. K. (1981). Hierarchies in nematode behavior. In : Zuckerman, B. M. & Rohde, R. A. (Eds). *Plant parasitic nematodes*, Vol. 3. New York, Academic Press : 227-251.
- DAVIS, E. L. (1988). *The interactions of surface carbohydrates of Meloidogyne spp. with soybean roots*. Doct. Thesis, Univ. Florida, Gainesville, 118 p.
- DAVIS, E. L. & RICH, J. R. (1987). Nicotine content of tobacco roots and toxicity to *Meloidogyne incognita*. *J. Nematol.*, 19 : 23-29.
- DAVIS, E. L., KAPLAN, D. T., PERMAR, T. A., DICKSON, D. W., & MITCHELL, D. J. (1988). Characterization of carbohydrates on the surface of second-stage juveniles of *Meloidogyne* spp. *J. Nematol.*, 20 : 609-619.
- DUSENBERY, D. B. (1983). Chemotactic behavior of nematodes. *J. Nematol.*, 15 : 168-173.

- FORREST, J. M. S. & ROBERTSON, W. M. (1986). Characterization and localization of saccharides on the head region of four populations of the potato cyst nematode *Globodera rostochiensis* and *G. pallida*. *J. Nematol.*, 18 : 23-26.
- GREEN, C. D. (1971). Mating and host finding behavior of plant nematodes. In : Zuckerman, B. M., Mai, W. F. & Rohde, R. A. (Eds). *Plant parasitic nematodes, Vol. 2*. New York, Academic Press : 247-266.
- HUETTEL, R. N. (1986). Chemical communicators in nematodes. *J. Nematol.*, 18 : 3-8.
- HUSSEY, R. S. & BARKER, K. R. (1973). A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. *Plant Dis. Repr.*, 57 : 1025-1028.
- JANSSON, H.-B., JEYAPRAKASH, A. & ZUCKERMAN, B. M. (1985). Differential adhesion and infection of nematodes by the endoparasitic fungus *Meria coniospora* (Deuteromycetes). *Appl. Environ. Microbiol.*, 49 : 552-555.
- JANSSON, H.-B., JEYAPRAKASH, A., DAMON, R. A., Jr. & ZUCKERMAN, B. M. (1984). *Caenorhabditis elegans* and *Panagrellus redivivus* : Enzyme-mediated modification of chemotaxis. *Exp. Parasitol.*, 58 : 270-277.
- JANSSON, H.-B. & NORDBRING-HERTZ, B. (1983). The endoparasitic nematophagous fungus *Meria coniospora* infects nematodes specifically at the chemosensory organs. *J. Gen. Microbiol.*, 129 : 1121-1126.
- JANSSON, H.-B. & NORDBRING-HERTZ, B. (1984). Involvement of sialic acid in nematode chemotaxis and infection by an endoparasitic nematophagous fungus. *J. Gen. Microbiol.*, 130 : 39-43.
- JEYAPRAKASH, A., JANSSON, H.-B., MARBAN-MENDOZA, N. & ZUCKERMAN, B. M. (1985). *Caenorhabditis elegans* : Lectin-mediated modification of chemotaxis. *Exp. Parasitol.*, 59 : 90-97.
- KAPLAN, D. T., THOMASON, I. J. & VAN GUNDY, S. D. (1979). Histological studies of the compatible and incompatible interaction of soybeans and *Meloidogyne incognita*. *J. Nematol.*, 11 : 338-343.
- MARBAN-MENDOZA, N., JEYAPRAKASH, A., JANSSON, H.-B., DAMON, R. A., Jr. & ZUCKERMAN, B. M. (1987). Control of root-knot nematodes on tomato by lectins. *J. Nematol.*, 19 : 331-335.
- MCCLURE, M. A. & STYNES, B. A. (1988). Lectin binding sites on the amphidial exudates of *Meloidogyne*. *J. Nematol.*, 20 : 321-326.
- MCCLURE, M. A. & ZUCKERMAN, B. M. (1982). Localization of cuticular binding sites of Concanavalin A on *Caenorhabditis elegans* and *Meloidogyne incognita*. *J. Nematol.*, 14 : 39-44.
- NORDBRING-HERTZ, B. & MATTIASSON, B. (1979). Action of a nematode-trapping fungus shows lectin-mediated host-microorganism interaction. *Nature*, 281 : 477-479.
- PROT, J. C. (1980). Migration of plant-parasitic nematodes towards plant roots. *Revue Nématol.*, 3 : 305-318.
- ROBERTSON, W. M., SPIEGEL, Y., JANSSON, H.-B., MARBAN-MENDOZA, N. & ZUCKERMAN, B. M. (in press). Surface carbohydrates of plant parasitic nematodes. *Nematologica*.
- SASSER, J. N. & CARTER, C. C. (1985). Overview of the International *Meloidogyne* Project 1975-1984. In : Sasser, J. N. & Carter, C. C. (Eds). *An advanced treatise on Meloidogyne, Volume 1 : Biology and control*. Raleigh, North Carolina State University Graphics : 19-24.
- SCHAUER, R. (1982). Chemistry, metabolism, and biological functions of sialic acids. *Adv. Carbohydr. Chem. Biochem.*, 40 : 131-234.
- SCHMITT, D. P. & NOEL, G. R. (1984). Nematode parasites of soybeans. In : Nickle, W. R. (Ed.). *Plant and insect nematodes*. New York, Marcel Dekker : 13-59.
- SPIEGEL, Y., COHN, E. & SPIEGEL, S. (1982). Characterization of sialyl and galactosyl residues on the body wall of different plant parasitic nematodes. *J. Nematol.*, 14 : 33-39.
- SPIEGEL, Y., ROBERTSON, W. M., HIMMELHOCH, S. & ZUCKERMAN, B. M. (1983). Electron microscope characterization of carbohydrate residues on the body wall of *Xiphinema* index. *J. Nematol.*, 15 : 528-534.
- WARD, S. (1978). Nematode chemotaxis and chemoreceptors. In : Hazelbauer, G. L. (Ed.). *Receptors and recognition : Taxis and behavior, Ser. B, Vol. 5*. New York, John Wiley & Sons : 141-168.
- ZUCKERMAN, B. M. (1983). Hypotheses and possibilities of intervention in nematode chemoresponses. *J. Nematol.*, 15 : 173-182.
- ZUCKERMAN, B. M. & JANSSON, H.-B. (1984). Nematode chemotaxis and possible mechanisms of host/prey recognition. *Ann. Rev. Phytopathol.*, 22 : 95-113.

Accepté pour publication le 5 septembre 1988.