The impact of plant residues on the soybean cyst nematode, *Heterodera glycines*

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Abstract: The potential of plant residues and plant root exudates, from a range of traditional and nontraditional crop species, to protect soybean (*Glycine max* (L.)) plants against *Heterodera glycines* (Ichinohe) was examined in vitro and under greenhouse conditions. Plant residues from nonhosts *Lespedeza capitata* Michx, *Lespedeza intermedia* (S. Wats.) Britt, *Lespedeza hirta* (L.) Hornem, *Lolium multiflorum* (Lam.), *Lolium perenne* (L.), *Lupinus perennis* (L.), *Melilotus officinalis* (L.) Lam., *Medicago sativa* (L.), *Trifolium pratense* (L.), Fairway B Lawngrass mixture, and *Pisum sativum* (L.) reduced the number of *H. glycines* juveniles in the soil prior to planting soybeans and subsequently in the roots of soybeans. Root exudates of nonhosts *Lespedeza capitata*, *Trifolium hybridum* (L.), *Trifolium repens* (L.), *Lolium multiflorum*, *Lupinus perennis*, *Echinochloa crusgalli* (L.) Beauv., *Vicia villosa* (Roth), *Medicago sativa*, and of the host *G. max* increased the egg hatching rate of *H. glycines* in comparison to the water control. In addition, root exudates of *Trifolium repens* and *Lolium multiflorum* increased egg hatching by 37.9 and 46.6%, respectively, compared to root exudates of soybeans. Root exudates of *Trifolium repens*, *Lolium multiflorum*, *E. crusgalli*, *Lupinus perennis*, *Trifolium hybridum*, *Medicago sativa*, and *G. max* significantly increased neutral lipid utilization of *H. glycines* juveniles in comparison to the control. Overall, *Lolium multiflorum* was the most effective of all species tested for reducing populations of *H. glycines*, by increasing egg hatching of the nematode in the absence of a host, depleting lipid reserves of the juveniles, and inducing the lowest nematode parasitism of all nonhost residues studied.

Key words: plant residues, root exudates, lipids, hatching.

Résumé : On a examiné, in vitro et en serre, la possibilité d'utilisation d'engrais verts et d'exudats de racines de plantes provenant d'un certain nombre d'espèces végétales traditionnelles et non traditionnelles pour protéger la plante de soja, *Glycine max* (L.) contre l'*Heterodera glycines* (Ichinohe). Les engrais verts provenant de plantes non-hôtes, *Lespedeza capitata* Michx, *Lespedeza intermedia* (S. Wats.) Britt, *Lespedeza hirta* (L.) Hornem, *Lolium multiflorum* (Lam.), *Lolium perenne* (L.), *Lupinus perennis* (L.), *Melilotus officinalis* (L.) Lam., *Medicago sativa* (L.), *Trifolium pratense* (L.), mélange de Fairway B Lawngrass et *Pisum sativum* (L.), ont réduit le nombre d'*H. glycines* juvéniles dans le sol avant la plantation du soja et, ultérieurement, au niveau des racines de soja. Les exudats racinaires de plantes non-hôtes, *Lespedeza capitata*, *Trifolium hybridum* (L.), *Trifolium repens* (L.), *Lolium multiflorum*, *Lupinus perennis*, *Echinochloa crusgalli* (L.) Beauv., *Vicia villosa* (Roth), *Medicago sativa* et *G. max* ont augmenté le taux d'éclosion des oeufs d'*H. glycines* par rapport à l'eau utilisée comme traitement témoin. En plus, les exudats racinaires de *Trifolium repens* et *Lolium multiflorum* ont augmenté significativement le taux d'éclosion des oeufs d'*H. glycines* par 37,9 et 46,6%, respectivement, en comparaison avec les exudats de racines de plantes de soja. Les exudats racinaires de *Trifolium repens*, *Lolium multiflorum*, *E. crusgalli*, *Lupinus perennis*, *Trifolium hybridum*, *Medicago sativa* et *G. max* ont augmenté de façon significative l'utilisation de lipides neutres par les juveniles d'*H. glycines* par rapport au traitement témoin. Parmi toutes les espèces végétales testées, le *Lolium multiflorum* s'est avéré le plus efficace pour réduire les populations d'*H. glycines* en augmentant l'éclosion des oeufs du nématode en l'absence d'hôte, en réduisant les réserves lipidiques des juvéniles et en induisant le plus faible taux de parasitisme par le nématode parmi tous les engrais verts non-hôtes étudiés.

Mots clés : engrais verts, exudat racinaire, lipides, éclosion des oeufs.

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Introduction

The recent loss of many nematicides through deregistration has increased the interest in alternative methods of nematode control, including the incorporation of plant residues into soil. Soybean (*Glycine max* (L.) Merr.) is one of the four major crops in the world, and the soybean cyst nematode (SCN; *Heterodera glycines* (Ichinohe)) is the most important cause of soybean disease in the U.S.A. and Canada (Riggs and Niblack 1993). During 1997–1998, SCN caused crop losses that amounted to $ 25 million for Ontario soybean growers (Anderson and Welacky, unpublished data). Biological and cultural approaches to managing nematodes are gaining popularity for many reasons, including cost and environmental issues associated with the use of pesticides. In Ontario, some farmers rotate soybeans with wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) in part because these are SCN nonhost crops. An alternative to rotation with nonhosts is green manuring. Some compounds such as isothiocyanates (Mojtahedi et al. 1993a) and ammoniacal nitrogen (Rodriguez-Kabana 1986) produced from decaying plant material have nematode-suppressive properties. Significant reductions in *Meloidogyne chitwoodi* Golden et al. and *Meloidogyne hapla* Chitwood populations were attained by cropping rapeseed (*Brassica napus* L. var. *napus*) and field mustard (*Brassica campestris* L.) for 2 months and then incorporating it into the soil as green manure (Mojtahedi et al. 1991) permitting production of commercially acceptable potato (*Solanum tuberosum* L.) tubers (Mojtahedi et al. 1993a). Sudan grass (*Sorghum sudanense* (Piper) Stapf) hybrids cultivars Trudan 8 and Sordan 79 also suppressed *M. chitwoodi* (Mojtahedi et al. 1993b).

The life cycle of certain species of plant parasitic nematodes, especially cyst nematodes, is synchronized closely with that of its host plant to maximize infection. Host plants produce root diffusates that induce or increase nematode hatch following a period of nematode dormancy. The hatching stimulus is necessary for nematode survival as it ensures that actively growing roots are present for nematodes to infect and feed on (Jones et al. 1998). Root exudates of neem (*Azadirachta indica* A. Juss.) and Persian lilac (*Syringa persica* L.) cause considerable nematode mortality and inhibit larval hatching of a variety of plant nematodes (Siddiqui and Alam 1989). Root exudates and extracts from in vitro grown seedlings of sesame (*Sesamum indicum* L.) also inhibit egg hatch and juvenile penetration by *Meloidogyne incognita* Chitwood (Tanda et al. 1989), while an allelopathic compound found in kidney bean (*Phaseolus vulgaris* L.) roots, glycinoeclepin A, is a natural hatching stimulus of SCN (Kraus and Vander Louw 1996). Decreased lipid reserves in starved nematodes has been correlated with decreased infectivity of many nematode species (Barrett and Wright 1998). Therefore, plant compounds that alter nematode lipid resources can lead to the development of novel control strategies against plant parasitic nematodes by suppressing hatching or by stimulating hatching under inappropriate conditions for nematode survival, such as in the absence of host plants. Our objective was to study the effect of root exudates and green manuring on hatching and survival of SCN, using a range of host and nonhost plants.

Materials and methods

Heterodera glycines (race 3) was cultured on the soybean cv. Elgin 87, in the greenhouse. Plant species used to generate green manure and root exudates are listed in Table 1.

Plant residue effect

Plants were grown for 2 months under greenhouse conditions in five replicate pots per plant species with four plants per pot. Entire plants including roots were harvested, finely chopped in 0.5-cm sections, and used immediately. Twenty grams of residue from each plant species was immediately incorporated into a plastic pot (diameter, 10 cm) containing 300 g of manufactured potting mixed soil. Potting soil consisted of approximately: 7% sand; 30% peat moss; 63% compost; magnesium sulphate, 1.81 g; calcium nitrate, 0.77 g; 10–10–10, 4.26 g ; and 0–20–0, 0.45 g). Soil containing the plant residues was kept moist for 5 days under greenhouse conditions at 25°C, then inoculated with 300 freshly hatched SCN juveniles (at a rate of 1 nematode/g soil). Five days after inoculation, 2-week-old soybean seedlings cv. Elgin 87 were transplanted into each pot. Controls consisted of: (1) soybean plant residues and SCN inoculum added to potting soil and then soybean seedlings were planted; and (2) regular potting soil in which SCN inoculum and soybean seedlings were added, in the absence of plant residues. Replicates of five pots were used for each treatment.

Plants were grown in the greenhouse at 22°C, with 16-h daylight supplemented with artificial light, high pressure sodium lamps (Philips, Eindhoven). After 56 days, nematodes were extracted from the soybean roots, using a mist extraction technique (adapted after Seinhorst 1950), and from the soil surrounding the soybean roots, using Baermann pans (adapted after Townshend 1963). The data were transformed with $\log_{10}(x + 1)$ and significance ($P < 0.05$) was tested using Kruskal–Wallis test and Tukey multiple-comparison method (Devore 1987). The experiment was repeated three times and data were combined for overall analysis.

Root exudate effect on hatching of juveniles

Root exudates were collected from *Lespedeza capitata*, *Trifolium hybridum*, *Trifolium repens*, *Lupinus perennis*, *Lolium multiflorum*, *Melilotus officinalis*, *E. crusgalli*, *Medicago sativa*, *V. villosa*, and *G. max*. Four plants of each species were grown in plastic pots (diameter, 10 cm) containing 70 g of perlite (Terra-lite 2000, W.R. Grace & Co. of Canada Ltd., Ajax, Ont.). Five pots per plant species were grown for 4 weeks under the greenhouse conditions described earlier. Root exudates were collected 4 weeks postplanting by leaching the plants: sufficient water was added to saturate the perlite, and additional water was added until a total of 30 mL of leachate was collected from all pots. For controls, water was collected from pots containing only perlite in the absence of a plant.

The leachate containing root exudates was filtered using a coarse filter paper (Whatman 54). Then 20 SCN eggs were added in a petri dish (diameter, 4 cm) containing 2.0 mL of leachate and incubated at 25°C in the dark. Egg

Table 1. Effect of plant residues incorporated into soil on *Heterodera glycines* numbers in soil and roots of greenhouse grown soybeans.

	Common name	Nematodes/g soil	Nematodes/g root
Avena sativa L.	Japanese oats cv. Saia	1.69±0.31 (17)	6.19±1.71* (13)
Brassica juncea (L.) Coss	Oriental mustard cv. Domo	9.78±0.06 (24)	18.97±4.02 (20)
Brassica napus L. var. *napus*	Rapeseed cv. Glacier	2.36±0.52 (19)	2.98±1.03* (10)
Desmodium canadense (L.) DC†	Showy tick trefoil	0.87±0.14 (12)	16.01±2.87 (19)
Echinochloa crusgalli (L.) Beauv. var. *frumenticea* (Roxb.) Link	Japanese millet	2.16±0.39 (18)	1.95±0.28* (6)
—	Fairway B Lawngrass mixture	0.41±0.04* (5)	1.93±0.31* (5)
Lespedeza capitata Michx†	Round-headed bushclover	0.42±0.06* (7)	1.30±0.45* (3)
Lespedeza hirta (L.) Hornem†	Hairy bushclover	0.51±0.07* (8)	2.35±0.59* (7)
Lespedeza intermedia (S. Wats.) Britt†	Wand-like bushclover	0.56±0.08* (9)	0.04±0.04* (1)
Lolium multiflorum (Lam.)	Annual ryegrass cv. Common No. 1	0.28±0.04* (2)	0.38±0.13* (2)
Lolium perenne (L.)	Perennial ryegrass	0.39±0.09* (4)	7.03±1.16* (15)
Lupinus perennis L.†	Perennial lupine	0.75±0.17* (11)	6.94±2.39* (14)
Medicago sativa (L.)	Alfalfa cv. Apollo Supreme	0.31±0.11* (3)	2.47±0.65* (8)
Melilotus officinalis (L.) Lam.	Yellow sweet clover	0.25±0.08* (1)	2.60±0.55* (9)
Pisum sativum L. var. *arvense* Poir	Field peas	0.62±0.08* (10)	11.60±4.38* (16)
Raphanus sativus L.	Oilseed radish	3.48±0.72 (21)	19.49±4.38 (22)
Trifolium hybridum (L.)	Alsike clover	1.39±0.43 (15)	1.56±0.49* (4)
Trifolium pratense (L.)	Red clover cv. Double Cut	0.41±0.09* (6)	13.57±3.31* (18)
Trifolium repens (L.)	White clover cv. Ladino	0.93±0.23 (13)	3.20±0.99* (11)
Triticum aestivum	Soft wheat cv. Freedom	9.24±3.02 (23)	17.67±3.89 (21)
Vicia villosa (Roth)	Hairy vetch	7.83±2.36 (22)	3.62±1.23* (12)
Zea mays	Hybrid corn BT	2.49±0.67 (20)	11.74±1.97* (17)
Control *Glycine max*	Soybean cv. Elgin 87	1.47±0.13 (16)	24.41±2.76 (23)
Control *Heterodera glycines* without plant residues	Soybean cyst nematode	1.09±0.08 (14)	29.47±3.11 (24)

Note: Data are presented as means ± standard error, followed by ranking order in parentheses. Statistical analysis was performed on transformed $\log_{10}(x + 1)$ data.

*Values significantly lower ($P < 0.05$) than values of both controls according to Kruskal–Wallis test.

†Source for seeds: Pterophylla, Walsingham, Ont.

hatching was quantified microscopically as hatched versus nonhatched eggs. For the controls, 40 SCN eggs were incubated in sterile tap dechlorinated water. Ten replicates were employed for all treatments and each treatment was repeated three times. Data were analyzed ($P < 0.05$) using Kruskal–Wallis test and Tukey multiple-comparison method (Devore 1987).

Root exudate effect on lipids in juveniles

The effect of *Lespedeza capitata*, *Trifolium hybridum*, *Trifolium repens*, *Lupinus perennis*, *Lolium multiflorum*, *Melilotus officinalis*, *E. crusgalli*, *Medicago sativa*, *V. villosa*, and *G. max* root exudates on the neutral lipid storage of SCN juveniles was determined by incubating freshly hatched juveniles in root exudates for up to 12 days. Root exudates were sampled as previously described. Freshly hatched juveniles were placed in root exudates and incubated at 25°C. The following day, and at 3-day intervals thereafter, for 12 days, SCN juveniles were sampled from the exudate and their neutral lipid content was determined by staining with Oil-Red-O dye (Croll 1972). Staining of the juveniles was recorded using a color camera (Hitachi 3CCD, Scarborough, Ont.) attached to a compound microscope (Zeiss, Jena) and quantified using the Image Capture KS400 V2.00 software package. Relative lipid quantities were expressed according to Christophers et al. (1997), where 6 represents juveniles full of lipid content (maximum) and 1 represents no lipid (minimum); a score of 3 is equivalent to about 50% lipid content. The controls were: (1) SCN juveniles incubated in root exudates collected from soybeans; and (2) SCN juveniles incubated in water collected from a pot containing perlite in the absence of a plant. Ten SCN juveniles per treatment were stained and

Table 2. Effect of root exudates originating from different plant species, on hatching of *Heterodera glycines* eggs.

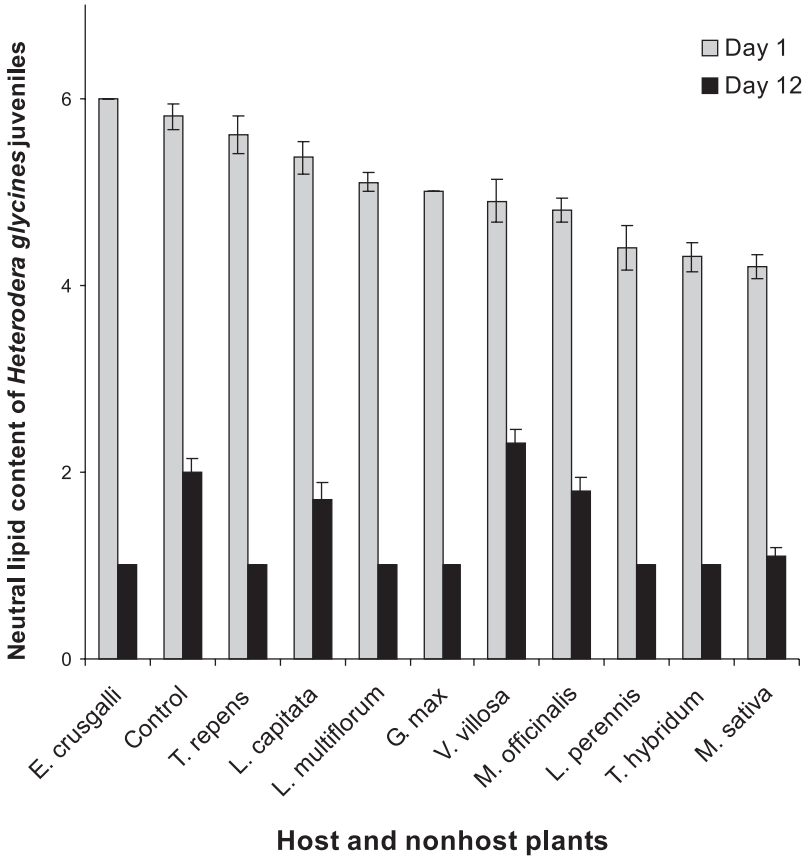
	Egg hatching (%)
Echinochloa crusgalli	17.9±1.3*
Glycine max	31.3±3.9*
Lespedeza capitata	22.9±1.4*
Lolium multiflorum	46.6±3.1*†
Lupinus perennis	16.9±1.8*
Medicago sativa	19.9±2.7*
Melilotus officinalis	18.7±1.8*
Trifolium hybridum	24.9±1.9*
Trifolium repens	37.8±2.1*†
Vicia villosa	19.0±1.7*
Control water (perlite)	7.3±1.2

Note: Data are followed by standard error.

*Values significantly higher ($P < 0.05$) than values of the control water (perlite).

†Values significantly higher ($P < 0.05$) than values of the *G. max*. root exudate treatment.

Fig. 1. Neutral lipid content of *Heterodera glycines* juveniles exposed to exudate from nonhost and host species after 1 and 12 days. Neutral lipid content of juveniles was ranked as 6 = full to 1 = depleted of lipids. Day 12 treatments: *Echinochloa crusgalli*, *Trifolium repens*, *Lolium multiflorum*, *Glycine max*, *Lupinus perennis*, *Trifolium hybridum*, and *Medicago sativa* are significantly different (Kruskal–Wallis test and Tukey multiple-comparison method, $P < 0.05$) than the control water (perlite). Error bars represent standard error.



evaluated. Data were evaluated using Kruskal–Wallis test and Tukey multiple-comparison method ($P < 0.05$) (Devore 1987).

Results and discussion

Incorporation of plant residues from *Lespedeza capitata*, *Lespedeza intermedia*, *Lespedeza hirta*, *Lolium multiflorum*, *Lolium perenne*, *Lupinus perennis*, *Melilotus officinalis*, *Medicago sativa*, *Trifolium pratense*, Fairway B Lawngrass mixture, and *P. sativum* resulted in fewer nematodes per gram of soil and per gram of root ($P < 0.05$) compared to treatments in which soybean residues had been incorporated (Table 1). In addition, *Trifolium hybridum*, *Trifolium repens*, *E. crusgalli*, *V. villosa*, *B. napus* var. *napus*, *Z. mays*, and *A. sativa* reduced the number of nematodes in the roots of soybean plants in treatments receiving no incorporated plant residues ($P < 0.05$) (Table 1). Residues of *Lolium multiflorum* were the most effective in reducing SCN in both the soil and roots of soybean plants (Table 1), suggesting that this plant species may be useful in a soybean rotation to suppress SCN. *Melilotus officinalis* was ranked lower than *Lolium multiflorum* for number of SCN/g soil but it ranked nineth for number of SCN/g root. Similarly, *Lespedeza intermedia* was ranked the lowest for number of SCN/g root but ranked nineth for number of SCN/g soil.

A range of different plant residues have been tested for their ability to manage plant parasitic nematodes. Hairy indigo (*Indigofera hirsuta* L.), Iron cowpeas (*Vigna unguiculata* (L.) Walp.), and American jointvetch (*Aeschynomene americana* L.) were effective in reducing *Meloidogyne arenaria* Neal) Chitwood, *M. incognita*, and *H. glycines* under greenhouse conditions (Rodriguez-Kabana et al. 1988). Mosjidis et al. (1993) reported that cool season annual forage legumes, *V. villosa*, common vetch (*Vicia sativa* L.), and winter pea (*Lathyrus hirsutus* L.) are not susceptible to *H. glycines*. Our results also demonstrated reduced numbers of SCN in the roots of soybean plants employing residues of a range of nonhost plants. The exact mode of action of nonhost plant residues on plant parasitic nematodes is not known. The suppressive effect of *Brassica* spp. leaves and roots on the lesion nematode (*Pratylenchus* sp.) was associated with increased levels of 2-phenylethyl glucosinolate in *Brassica* spp. (Potter et al. 1998). However, other mechanisms may be responsible for the antinematode activity of *Brassica* leaf green manure (McLeod and Steel 1999).

Root exudates of all plant species tested increased egg hatching of *H. glycines* in comparison to the water control ($P < 0.05$) (Table 2); however, root exudates of *Trifolium repens* and *Lolium multiflorum* increased egg hatch of *H. glycines* compared to the root exudates of soybeans ($P < 0.05$) (Table 2). *Lolium multiflorum* was the most effective

nonhost plant in stimulating SCN egg hatch. Field studies will be necessary to demonstrate if *Lolium multiflorum* will lead to effective decrease of SCN parasitism and lower the successful reproduction of SCN. Root exudates from fluecured tobacco (*Nicotiana tabacum* L.) stimulated hatching of juveniles of *Globodera tabacum solanacearum* (Miller and Gray) compared to deionized water (Wang et al. 1997). Root exudates from black nightshade (*Solanum nigrum* L.) stimulated greater egg hatch of *Globodera tabacum tabacum* (Lownsbery and Lownsbery) than those from broadleaf tobacco and tomato (*Lycopersicon esculentum* Miller) (LaMondia 1995). Conversely, root exudates and extracts from sesame seedlings inhibited egg hatch and juvenile penetration of *M. incognita* (Tanda et al. 1989).

Root exudates of all nonhost plants, except *L. capitata*, *V. villosa*, and *M. officinalis*, appeared equally effective in reducing neutral lipid reserves in *H. glycines* juveniles after 12 days, compared with the water control ($P < 0.05$) (Fig. 1). Neutral lipids are recognized as the main food reserve for the nonfeeding stages of certain plant parasitic nematodes (Storey 1984). The quantity of neutral lipid reserves influences the survival and infectivity of potato cyst nematode juveniles (Robinson et al. 1985; Storey 1984; Holz et al. 1999). The utilization of nematode juvenile lipids has been correlated with a reduction in infectivity in several *Meloidogyne* spp. (Balmer and Cairns 1963; Reversat 1981; Christophers et al. 1997) and *Globodera* spp. (Storey 1984; Robinson et al. 1985).

This study has shown that a range of nonhost plants can reduce the numbers of SCN both in the soil and in the roots of soybean plants under greenhouse conditions. Field studies are needed to establish the efficacy of these treatments on stimulating egg hatching, reducing lipid reserves, and reducing SCN damage to soybeans. Consequently, current agricultural practices of Ontario farmers employ *Lolium multiflorum* as a species with the greatest potential to reduce SCN populations by increasing SCN egg hatching in the absence of soybean plants and depleting SCN lipid resources, thus causing them to starve and resulting in lower levels of nematode parasitism compared with other nonhost plants. A year prior to soybeans, *Lolium multiflorum* may either be planted as a nurse crop or intercropped with corn, alfalfa, or white clover. Wheat is often seeded as a companion crop with clover to add nitrogen to the soil, and as a cover crop following wheat harvest.

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