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Hatching of potato cyst nematode *Globodera rostochiensis* in host root leachates under different invasion conditions

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Summary

Results of the influence of soil-borne pathogens, heavy metal salts and wastes from logging and the wood industry on the hatching process of potato cyst nematode *Globodera rostochiensis* (PCN) were obtained. Presence of fungus *Rhizoctonia solani* in potato root leachates (PRL) affected the hatching processes. It was observed that in the treatment PRL with fungus mycelium diffuses (FD) a small volume of each component (PRL or FD) highly stimulated juveniles to hatch. When cadmium salt CdSO₄ was added to PRL the PCN hatching process was more active than in the control. The rate of hatching was significantly higher and led to a decrease in the time at which 50% of juveniles had hatched. Both fungus and heavy metal salts (without PRL) inhibited juvenile hatching. Wastes of logging and wood industries (freshly-crushed conifer bark and sodium lignosulphonates, co-products of the pulp and paper industry) independently, with or without root diffusates, reduced hatching. A delay in the onset of hatching combined with a decrease in the total juvenile abundance and the viability of eggs and juveniles inside cysts were observed. The results obtained allow a consideration of wastes of the logging and the wood industry as effective methods of *Globodera rostochiensis* control.

Key words: Potato cyst nematode, *Globodera rostochiensis*, hatching activity, host root leachates, fungus diffusates, cadmium, logging and wood industry waste

Introduction

Potato cyst nematode (PCN) is included in a list of 10 highly harmful nematode genera responsible for important yield losses in agriculture throughout the world. To manage the PCN populations effectively it is necessary to study species biology, interactions with other pathogens and investigate peculiarities of local nematode populations under specific conditions of potato growing, including the pollution of fields by heavy metals. There are some areas in Republic of Karelia where soils have increased levels of heavy metal pollution that can be caused by natural reasons (specific geological structure of underlying rocks) or due to industrial pollution. It was established that the soils with concentrations of heavy metals (Cd, Zn, Ni) greater than background values (Fedorets *et al.*, 2007) were characterized by higher infestations of PCN (Gruzdeva & Suschuk, 2008).

Crop damage by phytoparasitic nematodes is often intensified by attendant pathogens such as bacteria, viruses and fungi. These organisms form active complexes that affect the crop and each other mutually. Complex pathogenic effects of nematodes and fungi on crops under monoculture is of particular interest (Evans, 1982; Storey & Evans, 1987; Matveeva *et al.*, 2001; Back *et al.*, 2006; Romanenko *et al.*, 2008).
Potato cyst nematode is an obligatory sedentary endoparasite of the potato root system and is characterised by an almost absolute dependence on the plant host for life cycle completion. Mass juvenile emergence from cysts is possible only after stimulation with natural hatching factors. The dependence of Globodera species on root leachates produced by the host potato plants to stimulate hatch in large numbers, and the chemical composition of root leachates, is well documented and the sequence of events in the hatching process has been the subject of extensive research (Evans, 1983; Perry, 1986, 1987, 1989, 1998; Jones et al., 1998). Studies on hatching factors that cause PCN hatch showed that measures influencing nematode behaviour may eventually be used in integrated control programmes against the nematode (Devine & Jones, 2001, 2003; Devine et al., 2001). Because hatching and penetration into young host roots is the most vulnerable stage in the nematode's life cycle, it is important to target control measures at this time.

In this investigation the hatching behaviour of G. rostochiensis juveniles in root leachates under different invasion conditions has been studied in vitro. These conditions were with fungal infection, heavy metal salts and wastes of the logging and wood industry. The latter were tested in order to assess their potential for use in integrated control programmes against the nematode.

Materials and Methods

PCN inoculum

Experiments on PCN hatching were carried out in 2000–2009. A population of G. rostochiensis (pathotype Ro1) was maintained as stock cultures on potato plants, Solanum tuberosum cv. Nevsky, in closed containers (Phillips et al., 1980) and plastic pots filled with sterilised sand in growth chambers with daily 12 h light period for several years. Viability of eggs and juveniles inside cysts was checked with Meldola's blue solution (Shepherd, 1962) and was 92%.

Hatching device

A hatching device modified from that described by Been & Schomaker (1998) was used for this experiment. It consisted of a plastic disk (diameter 20 mm and volume 1.5 mL), in which nylon mesh of 20 µm were inserted. Globodera rostochiensis cysts (one cyst per one disk) were put on the mesh. Disks were fitted in plastic plates and juveniles were collected in the space between the mesh and the disk bottom. One mL of PRL was pipetted into each disk and 10 replicates were prepared simultaneously on each plate. The device was kept in the dark at 20–21°C.

Counting of hatched juveniles

Juveniles were counted in each disk at 3 day intervals for 23, 38 or 45 days depending on the treatment. For observation and counting, the nylon mesh containing cysts was taken from each disk and observed under the dissecting microscope to count the juveniles. A counting dish was used when the juveniles were too crowded to count them in the disk. Juveniles were removed with a pipette and transferred into the counting dish. At the end of the experiment cysts were crushed and the number of unhatched juveniles counted in order to determine the maximum percentage of nematode hatch.

Preparation of potato root leachates (PRL)

Chitted tubers of potato cv. Nevsky were planted in 1 L plastic pots containing sterilised sandy soil. Plants were kept in growth chambers with a daily 12 h light period and fed a complete nutrient solution. Collection of root leachates started three wks after planting. Pots were watered gradually until the water drained from the bottom of the pot when an extra 50 mL of water was added into the pot and the leachate collected in a beaker. Root leachates were collected once a week and stored at 4°C.

Treatments

Experiments on the hatching of G. rostochiensis juveniles included the study of the effects of fungal infection, heavy metal ions and wastes from logging and the wood industry on second-stage juvenile hatch. Potato root leachate as natural hatching factor for PCN and distilled water (DW) were used as controls.

As a fungal pathogen, laboratory cultures of local Rhizoctonia solani Kühn isolates were tested. Fungus mycelium was soaked in distilled water (one Petri dish of mycelium per 40 mL of water) according to Muyolo et al. (1983) and fungal diffusates (FD) were obtained. Activity of PRL and FD mixtures was assayed by preparing a dilution series from full-strength root leachates to full-strength fungus diffusates.

The study of heavy metal ions on PCN hatch was carried out with cadmium salt (CdSO₄). Concentrations of 1.5, 3 and 6 mg L⁻¹ were used based on previous laboratory experiments, (Gruzdeva et al., 2008). Mixtures with PRL (50:50% dilution) were used in the experiment.

Wastes from logging and the wood industry, particularly freshly crushed conifer bark and co-products of paper-making enterprises, sodium lignosulfonates, were tested in the experiment. As a control potato root diffusates (PRD) were used; they were obtained according to Myagi (1974), with infusion of root pieces of 3-week old plants in water (10 g of roots per 100 mL of water). The effect of bark extract and lignosulfonate solutions (SLS 1% and SLS 10%) separately and their mixtures with PRD were studied. Bark extract was obtained by the treatment of conifer bark with hot water. Five cysts per replicate were used for each treatment.

Data analysis

For the statistical analysis Statistica 5.5 was used. The effect of treatments was examined with paired t-tests (P < 0.05) and significance was checked with Tukey’s honest significant difference test (P < 0.05). To determine any influence of PRL + FD mixtures at different ratios on juvenile hatch, the data were fitted with the logistic model of one-factor analysis of variance with fixed factor levels $\gamma = \sum_{\beta} + \sum_{\beta} X_{k} + \sum_{\beta} X_{k} + e$, where $\gamma$ is power of factor, $M$ is the general mean; $\beta_1$, $\beta_2$, ..., $\beta_k$ are effects of factor levels; $\gamma$ is an equation coefficient and $e$ is the standard error. Factor levels were PRL+FD treatments. Treatments that had positive values for their effects on factor levels ($\beta > 0$) were considered as stimulating hatching, and those with negative effects ($\beta < 0$) as inhibiting hatching. Data on the influence of heavy metal salts on PCN hatching were fitted to the logistic model $y = e^{(1 + \exp(b_{-b_{0}}(t - m))}, where $y$ is the cumulative % hatch. The model is described by three parameters: the time at which 50% hatch is reached ($m$), the hatching rate ($b$) and the final hatching percentage ($c$) (Oude Voshaar, 1994; Wesemael et al., 2006).

Results

Effect of Rhizoctonia solani diffusate in natural hatching factor on the hatch of G. rostochiensis

Second-stage juveniles started to hatch quickly and were observed in the highest numbers in PRL (Table 1). Full-strength FD and DW were the worst hatching stimulants for second-stage juveniles.

The presence of Rhizoctonia solani mycelium in PRL (PRL + FD treatments) affected the hatching process. In general as PRL dilution with FD increased, hatch decreased. But some combinations, where PRL or FD occurred in very small volumes, strongly stimulated juveniles to hatch (treatments 2 and 7, Table 1).

The effect of PRL + FD treatments on the hatching process changed during the experiment (Figs 1 and 2). At the beginning (6th day) only one treatment (treatment 2) stimulated juvenile hatch. With increasing time of exposure of cysts to the test solutions (10th, 12th and 45th days) treatment 5
Table 1. The effect of *Rhizoctonia solani* diffusates on the hatching of *G. rostochiensis* second-stage juveniles J2 (mean + SE, n = 5). * Significant differences between treatments and control (PRL) at the P < 0.05 level

<table>
<thead>
<tr>
<th>N</th>
<th>Treatment</th>
<th>Start of J2 hatch (days)</th>
<th>Total number of hatched J2 absolute numbers</th>
<th>% of control</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Potato root leachates, PRL100%</td>
<td>6</td>
<td>175 ±43.13</td>
<td>100</td>
</tr>
<tr>
<td>2</td>
<td>PRL75%+ FD25%</td>
<td>4</td>
<td>188 ± 27.36</td>
<td>107.4</td>
</tr>
<tr>
<td>3</td>
<td>PRL50% + FD50%</td>
<td>6</td>
<td>130 ± 7.84*</td>
<td>74.3</td>
</tr>
<tr>
<td>4</td>
<td>PRL37% + FD63%</td>
<td>6</td>
<td>129 ± 18.40*</td>
<td>73.7</td>
</tr>
<tr>
<td>5</td>
<td>PRL25% + FD75%</td>
<td>6</td>
<td>97 ± 5.11*</td>
<td>55.4</td>
</tr>
<tr>
<td>6</td>
<td>PRL10% + FD90%</td>
<td>6</td>
<td>148 ± 6.92</td>
<td>84.6</td>
</tr>
<tr>
<td>7</td>
<td>PRL5% + FD95%</td>
<td>6</td>
<td>183 ± 11.67</td>
<td>104.6</td>
</tr>
<tr>
<td>8</td>
<td>Fungus mycelium diffusates, FD100%</td>
<td>10</td>
<td>26 ± 3.90*</td>
<td>14.8</td>
</tr>
<tr>
<td>9</td>
<td>Distilled water, DW</td>
<td>10</td>
<td>65 ± 19.85*</td>
<td>37.1</td>
</tr>
</tbody>
</table>

Fig. 1. Effect of factor levels (PRL+FD treatments) on *G. rostochiensis* second-stage juvenile hatching at 6, 10, 12 and 45 days after application. Treatments: 1 – potato root leachates PRL100%; 2 – PRL75%+ FD25%; 3 – PRL50% + FD50%; 4 – PRL37% + FD63%; 5 – PRL25% + FD75%; 6 – PRL10% + FD90%; 7 – PRL5% + FD95%; 8 – fungus mycelium diffusates, FD100%.

Fig. 2. Effect of factor levels (four PRL+FD treatments) on *G. rostochiensis* second-stage juvenile hatch over 45 days.

Table 2. The effect of CdSO₄ on the hatch of *G. rostochiensis* second-stage juveniles (mean ± SE, n = 10). * Significant differences between treatments and control (PRL) at the P < 0.05 level

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Start of J2 hatch (days)</th>
<th>Total number of hatched J2 absolute numbers</th>
<th>% of control</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRL, control</td>
<td>7</td>
<td>218L ± 20.24</td>
<td>100</td>
</tr>
<tr>
<td>PRL + 1.5 mgL⁻¹ Cd²⁺</td>
<td>7</td>
<td>160L ± 46.45</td>
<td>73.4</td>
</tr>
<tr>
<td>PRL + 3.0 mgL⁻¹ Cd²⁺</td>
<td>7</td>
<td>110L ± 39.54*</td>
<td>50.5</td>
</tr>
<tr>
<td>PRL + 6.0 mgL⁻¹ Cd²⁺</td>
<td>7</td>
<td>198L ± 51.22</td>
<td>90.8</td>
</tr>
<tr>
<td>1.5 mgL⁻¹ Cd²⁺</td>
<td>9</td>
<td>22L ± 5.28*</td>
<td>10.1</td>
</tr>
<tr>
<td>3.0 mgL⁻¹ Cd²⁺</td>
<td>10</td>
<td>30L ± 5.34*</td>
<td>13.8</td>
</tr>
<tr>
<td>6.0 mgL⁻¹ Cd²⁺</td>
<td>9</td>
<td>31L ± 13.5*</td>
<td>14.2</td>
</tr>
</tbody>
</table>

CdSO₄, without PRL, delayed the onset of hatch and the total number of hatched juveniles was only 10–14% of the control (Table 2). Parameters of the logistic model describing nematode hatching differed from the control and PRL+Cd²⁺ treatments. The final hatching (c) was very low and reached only 6–10%; the values of rate of hatch (b) was equal to control or lower than those in the treatments with PRL. Consequently the time (m) at which 50% juveniles had hatched was prolonged by 3–5 days (Table 3). The viability of the eggs and juveniles inside cysts was not affected by the heavy metal solution. At the end of the experiment the viability of eggs and juveniles was nearly 90%.

Table 3. Parameters of the logistic curve y = c/(1+ exp(-b(t-m))) describing hatching of *G. rostochiensis* second-stage juveniles from cysts in the presence of potato root leachates (PRL) and Cd²⁺ ions at concentrations of 1.5, 3.0 × 6.0 mgL⁻¹. Means ± SE of the time at which 50% hatching is reached (m), the hatching rate (b) and the maximum hatching percentage (c) are presented. Significant differences between treatments are marked with different letters (P < 0.05)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>m (days)</th>
<th>b</th>
<th>c (%)</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRL, control</td>
<td>18.6 ± 1.08*</td>
<td>0.57 ± 0.06*</td>
<td>58.8 ± 3.14*</td>
<td>0.930</td>
</tr>
<tr>
<td>PRL + 1.5 mgL⁻¹ Cd²⁺</td>
<td>13.4 ± 1.17*</td>
<td>0.64 ± 0.07*</td>
<td>57.0 ± 10.8*</td>
<td>0.933</td>
</tr>
<tr>
<td>PRL + 3.0 mgL⁻¹ Cd²⁺</td>
<td>13.5 ± 1.50*</td>
<td>0.86 ± 0.11*</td>
<td>60.7 ± 16.0*</td>
<td>0.945</td>
</tr>
<tr>
<td>PRL + 6.0 mgL⁻¹ Cd²⁺</td>
<td>13.6 ± 0.40*</td>
<td>0.80 ± 0.09*</td>
<td>60.4 ± 13.9*</td>
<td>0.966</td>
</tr>
<tr>
<td>1.5 mgL⁻¹ Cd²⁺</td>
<td>18±0.42*</td>
<td>0.37±0.02*</td>
<td>6.9±1.22*</td>
<td>0.995</td>
</tr>
<tr>
<td>3.0 mgL⁻¹ Cd²⁺</td>
<td>21±0.96*</td>
<td>0.49±0.05*</td>
<td>9.3±1.47*</td>
<td>0.988</td>
</tr>
<tr>
<td>6.0 mgL⁻¹ Cd²⁺</td>
<td>21±1.20*</td>
<td>0.37±0.01*</td>
<td>6.0±1.01*</td>
<td>0.992</td>
</tr>
</tbody>
</table>

Fig. 3. Parameters of the logistic curve y = c/(1+ exp(-b(t-m))) describing hatching of *G. rostochiensis* second-stage juveniles from cysts in the presence of potato root leachates (PRL) and Cd²⁺ ions at concentrations of 1.5, 3.0 × 6.0 mgL⁻¹. Means ± SE of the time at which 50% hatching is reached (m), the hatching rate (b) and the maximum hatching percentage (c) are presented. Significant differences between treatments are marked with different letters (P < 0.05)

Effect of heavy metal ions on the hatching of *G. rostochiensis* second-stage juveniles

The presence CdSO₄ in PRL did not significantly affect the onset of second-stage juvenile hatch. However, a decrease in hatched juvenile numbers was observed (Table 2). The final hatch (c) reached 57–61% and no differences between treatments were observed. The rate of hatching (b) was significantly higher in treatments with CdSO₄ which led to decrease in the time (m) at which 50% of total juveniles had hatched (Table 3).

Effect of bark extract and sodium lignosulphonates on the hatching of *G. rostochiensis* juveniles

Nematode hatch was greatest in PRD: the first juveniles were observed after three days and total hatch was the highest (Table 4). Bark extract (BE) and sodium lignosulphonates (SLS) delayed...
hatch; the start of hatch was delayed and the total number of hatched nematodes was reduced. Pure bark extract and SLS 10% strongly inhibited the hatching activity of second-stage juveniles with only 0.9% and 0.6% total hatch. A dilution of SLS (SLS 1%) had a weaker negative effect on hatch and a mixture of this concentration with PRD (PRD + SLS1%) stimulated hatch but the latter was not significantly different from the control (Table 4).

Table 4. The effect of conifer bark and lignosulphonates on hatching of G. rostochiensis second-stage juveniles (mean ± SE, n = 3). PRD is potato root diffusates; PRD + BE is a mixture of root diffusates and bark extract; PRD + SLS is a mixture of root diffusates and lignosulphonates; BE is bark extract; SLS is sodium lignosulphonates. Significant differences between treatments are marked with different letters (P < 0.05).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Start of J2 hatch (days)</th>
<th>Total number of hatched J2 absolute numbers</th>
<th>% of control</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRD, control</td>
<td>3</td>
<td>314 ± 61.5*</td>
<td>100</td>
</tr>
<tr>
<td>PRD + BE</td>
<td>6</td>
<td>80 ± 14.2*</td>
<td>25.5</td>
</tr>
<tr>
<td>PRD + SLS 1%</td>
<td>6</td>
<td>227 ± 49.5*</td>
<td>72.3</td>
</tr>
<tr>
<td>PRD + SLS 10%</td>
<td>6</td>
<td>27 ± 9.3*</td>
<td>8.6</td>
</tr>
<tr>
<td>Bark extract, BE</td>
<td>28</td>
<td>3 ± 0.4*</td>
<td>0.9</td>
</tr>
<tr>
<td>SLS 1%</td>
<td>6</td>
<td>90 ± 16.2*</td>
<td>28.7</td>
</tr>
<tr>
<td>SLS 10%</td>
<td>6</td>
<td>2 ± 0.8*</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Conifer bark and SLS affected the nematode eggs and juveniles inside cysts with the viability of eggs decreasing to 30% in 15 days. Almost complete death of the nematode eggs and juveniles was observed at the end of the experiment in BE treatment. In SLS solutions viability of eggs and juveniles decreased to 71%, and 52% for SLS1% and SLS10% respectively.

Discussion

Stimulation of juveniles to hatch by potato root leachates is a prerequisite for potato cyst nematode ontogeny. Hatching is the launch process during the establishment of the host-parasite interaction between potato and nematode because Globodera species are highly dependent on the host leachate to stimulate hatch and maximise invasion. Second-stage juveniles hatch in large numbers in response to hatching factors contained in host root exudates (Perry, 1987, 1989; Devine & Jones, 2001, Devine et al., 2001). The results of this investigation have showed that maximum hatch was observed in PRL. In fungus mycelium diffusates, distilled water and CaSO₄ solutions juveniles hatched inactively and mass juvenile emergence from cysts over a short period of time did not occur (Tables 1 and 2). The total numbers of hatched juveniles in general accounted for only 10–37% of control levels.

Low quantity of juveniles in the treatment with fungus mycelium diffusates without PRL indicated that Heterodera avenae inhibited the activity of G. rostochiensis juveniles. In the course of time, the negative effect of the fungus on eggs and juvenile viability became stronger. Some data on the negative effects of fungi on phytoparasitic nematodes are available for example Sunceja et al. (1984) reported that culture filtrates of the rhizosphere fungi Alternaria tenuis, Aspergillus terreus inhibited juveniles of the root-knot nematode Meloidogyne javanica.

Some treatments (where PRL or FD occurred in very small volumes) actively stimulated juveniles to hatch when compared with the control (Table 1, Figs 1 and 2). These treatments were the most optimal for nematode hatch due to the rapid stimulative effect on juvenile hatch which was maintained during experiment. Potato root leachate as natural hatching factor showed a slower stimulative effect that intensified in the course of time (Fig. 2).

In agricultural practice it can be expected that presence of Rhyzoctonia solani in the field together with Globodera rostochiensis will stimulate juveniles to hatch. But later these interactions were changing and the fungus, as a saprophytic pathogen excreting toxins to the root tissues, became antagonist to PCN which is an obligate biotrophic parasite. It was established that in presence of Rhyzoctonia solani the females of Globodera rostochiensis that developed on the potato roots were half the size of those formed without the fungal pathogen being present (Mateeva et al., 1997). A similar effect was documented by Nordmeyer et al. (1983) on the parasite complex "clover- Heterodera avenae - Fusarium avenaceum". At the establishment of host-parasite interactions Heterodera juveniles preferred clover root diffusates obtained from the roots treated by the fungal filtrate but later, when metabolic products had accumulated in root tissues, an antagonistic effect was exhibited. These results can be used as perspectives for novel biological control measures against PCN.

When CaSO₄ was added to PRL the PCN hatching process was more active than in the control; juveniles hatched quickly but for a shorter period of time. This should be taken into account by potato growers in the case of heavy metal pollution of potato fields.

The strongest inhibiting effects on potato cyst nematode were observed in treatments with conifer bark extract (BE) and a high dose of sodium lignosulphonates (SLS10%) where no spontaneous hatch of juveniles was observed. Nematocidal properties of conifer bark and sodium lignosulphonates are expressed through retarding juvenile hatching in the presence of natural hatching factors or by ceasing hatching without root diffusates (Table 4).

The mechanism of the inhibiting effect is unknown. Possibly, their components (water-releasing fractions - phenols, aromatic compounds, organic acids, tannins) affect second-stage juveniles, preventing them from hatching and destroying J2 and eggs inside cysts. Consequently, they cannot penetrate into young plant roots in time and the chance of juveniles developing into adults is diminished. Substances contained in the bark extract and SLS negatively influenced the viability of eggs and juveniles. Also, it was revealed that lignosulphonates contain many sugars that cause an adhesion of soil particles to the cyst walls, changing the natural conditions for juveniles to hatch and continue their life-cycles. As a result, the processes of maximum J2 hatch and the intensive growth of young potato roots do not coincide which decreases the opportunity for the parasite to develop inside plant roots. In early research we found that conifer bark and SLS decreased PCN populations by 3–5 fold depending upon the dose (Mateeva et al., 2002).

The results obtained allow a consideration of these substances as effective methods of Globodera rostochiensis control.

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