Phytopathologia Mediterranea (2014) 53, 3, 396–405
DOI: 10.14601/Phytopathol_Mediterr-13512

RESEARCH PAPER

Influence of soil temperature on *Globodera rostochiensis* and *Globodera pallida*

Agata KACZMAREK[1], Katrin MacKENZIE[2], Helen KETTLE[2] and Vivian C. BLOK[1]

[1] James Hutton Institute, Invergowrie, Dundee, DD2 5DA
[2] Biomathematics & Statistics Scotland, Dundee and Edinburgh, Scotland, DD2 5DA and EH9 3JZ

Summary. Relationships between soil temperatures and the potato cyst nematode (PCN) life cycle and population multiplication were investigated to understand the risks to potato crops from PCN in relation to increasing soil temperatures associated with climate change, and to support development of the United Kingdom Potato Council`s PCN management model. The initial (hatching) part of the PCN life cycle was examined for both *Globodera rostochiensis* and *G. pallida* over a range of temperatures, and the responses are then considered in relation to actual soil temperatures during the potato growing season in different sites in the United Kingdom. Hatching was stimulated by potato root diffusate over a temperature range from 5–29ºC and was monitored for 5 weeks. The greatest cumulative percentage hatch of second stage juveniles (J2) occurred between 15 and 27ºC for *G. rostochiensis* and 13–25ºC for *G. pallida. Globodera rostochiensis* hatched more quickly and had a delayed hatch at ≥25ºC while *G. pallida* was more efficient at these higher temperatures. From these observations, it is likely that climate change, and associated increases in soil temperatures, will result in increased rates and amounts of hatching for both species, leading to increased population levels on susceptible hosts and damage to potato crops. Currently, regions of the United Kingdom with warm soil temperatures are also expected to have high levels of hatching of PCN, and therefore greater multiplication resulting in greater challenges in the management of these nematodes in infested land.

Key words: climate change, modelling, population dynamics, potato cyst nematodes, *Solanum tuberosum.*

Introduction

The potato cyst nematodes (PCN) *Globodera rostochiensis* and *G. pallida* are economically important parasites of potato (*Solanum tuberosum*) and other members of the *Solanaceae* family. They are listed in the EU Plant Health Directive 2000/29/EC and are regulated by the European PCN Directive (2007/33/EC). In the United Kingdom, management of PCN relies on long rotations, nematicides and resistant cultivars, although for *G. pallida* there are few cultivars available with high levels of resistance. Climatic conditions differ around this country, and there are trends towards increasing temperatures and changes in rainfall associated with climate change (Parker *et al*. 1992; Jones *et al*. 2007) that are likely to impact on the multiplication and damage caused by soil-based plant parasitic nematodes. According to several reports (Trudgill *et al*. 2005; Kakaire *et al*. 2012; Van der Waals *et al*., 2013), one of the most influential environmental factors affecting nematode development is temperature. Nematodes, like other ectothermic animals, depend on external heat sources to maintain their body temperature. They are also poikilothermic organisms whose body temperature is almost identical to that of their environments.

During their life cycles, different nematode activities have specific temperature requirements (Franco, 1979). For example, temperature plays a very important role in embryogenesis and development

Corresponding author: A. Kaczmarek
E-mail: Agata.Kaczmarek@hutton.ac.uk

ISSN (print): 0031-9465
ISSN (online): 1593-2095
www.fupress.com/pm
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of nematodes after infection (Koenning and Sipes, 1998). Many nematodes are adapted to particular temperature ranges. These are often the most important environmental factors affecting their biology and different species have different optimum temperatures for feeding, hatching, reproduction and survival (Neilson and Boag, 1996). For example, the eggs of the root-knot nematode *Meloidogyne arenaria* in early stages of development had an optimal temperature of 15ºC (Ferris *et al.*, 1978) with an apparently better adaptation to cooler soil temperatures than *M. hispanica* which had an optimal temperature for hatching of 25°C (Maleita *et al*., 2012). Strajnar *et al*. (2011) reported that in order for *M. ethiopica* to complete its reproductive cycle, daily temperatures of 18–26ºC were required, but at 13ºC and lower it was not able to reproduce. For the cyst nematode *G. tabacum,* the most suitable temperature for reproduction and development in Italy was 26ºC (Ambrogioni *et al*., 2000). The basal threshold temperature for this nematode's biology was estimated to be 11ºC, and at 32ºC host invasion was inhibited.

The two species of PCN differ in their temperature responses. *Globodera pallida* populations generally hatch and reproduce at lower temperatures than *G. rostochiensis* populations, and *G. rostochiensis* is more successful than *G. pallida* at temperatures above 20ºC (Franco, 1979). In northern Europe, which has a temperate climate, there is usually one generation of PCN per year (Jones, 1950), although there are several studies which describe the occurrence of a partial second generation, and Jones (1950) observed that suitable soil temperatures may permit more than one generation of *Globodera* per year. Evans (1969) also reported a slight increase in *G. rostochiensis* juvenile nematodes in potato roots in Augustin Long Island, USA., which is consistent with the occurrence of a small second generation. In the Mediterranean region, Greco *et al*. (1988) recorded a completed second generation of *G. rostochiensis* at Avezzano in Italy, and Jimenez-Perez *et al.* (2009) noted the occurence of a second generation of *G. rostochiensis* at soil temperatures of 18˚C in Venezuela and also a lack of entry into diapause. The occurrence of a second generation indicates that in some conditions PCN can evade the "obligatory" diapause requirement, and thus adapt to new environmental conditions.

The aim of our research was to investigate the relationships between soil temperature and the PCN life cycle and population multiplication, to understand the risk to potato crops from PCN and to support the development of the United Kingdom Potato Council's PCN management model (Elliott *et al.*, 2004). This study focused on the hatching (initial) stage of the PCN life cycle, in relationship to temperature. The rates and amounts of hatching were determined and modelled for the two PCN species, and then examined in relation to actual soil temperatures in potato drills from different field sites in the United Kingdom. The risk to potato crops from PCN in relation to soil temperature variation is discussed.

Materials and methods

Nematode populations

Cysts from *G. rostochiensis* A (pathotype Ro1) and *G. pallida* E/Lindley (pathotype Pa2/3) populations from the James Hutton Institute PCN collection were stored at 4°C for at least 1 y prior to use. Cysts were randomly selected following sieving (250 μm) to exclude small and damaged cysts. Potato root diffusate (PRD) was produced from the susceptible cultivar 'Desirée' that had been planted 2 weeks before the experiments started. At the start of the experiments the roots were cleaned with water to remove compost, then placed in a beaker with 250 mL of sterile distilled water (SDW) for at least 4 h. The liquid was passed through Whatman filter paper No. 1 and stored at 4ºC (Rawsthorne and Brodie, 1986).

Hatching at constant temperatures

Hatching experiments were performed on a thermal gradient table (Grant GRD 1, Camlab), programmed to have a continuous temperature gradient from 5–29ºC with 11 positions across the gradient defined by a plastic grid. Ten cysts were exposed to 2 mL of PRD (five replicates) or sterile distilled water (SDW; two replicates) in a 5 cm diam. Petri dish. To determine the number of hatched second-stage juveniles (J2), the PDR or SDW was transferred into a 12 well multiwall plate. The nematodes were counted using an Olympus SZ60 stereo microscope (KeyMed). The PRD or SDW was replaced eight times during the experiment, at three to four d intervals, following the collection of J2. To determine the percentage of juveniles that had hatched, after finishing the experiment, the cysts were collected from the multiwell plates, crushed, and eggs and unhatched

J2 were counted. The percentage hatch was the total hatch/total hatch + eggs + unhatched juveniles.

Field soil temperatures

Soil temperatures were recorded during the potato growing season at 20 cm depth at 3 h intervals in potato ridges in field crops, using DS1920-F5 Temperature ibuttons (HomeChip), at The James Hutton Institute field trial site in Whitewater, Scotland (56.729023N, -2.899611) and at Harper Adams, England (52.809072N, -2.4601269). Planting and harvesting dates at these two sites were 19/5/2011 and 14/9/2011 for Whitewater, and 21/4/2011 and 21/9/2011 for Harper Adams.

Data analyses

The hatching results were analysed using the GenStat Version 14.1 and Microsoft Excel Version 14.0.4760.1000. Logistic curves were fitted to the cumulative proportions of hatched juveniles and analysis of variance (ANOVA) was carried out on the parameters of the curves to test for differences in the hatching between the two PCN species, at different temperatures, and in PRD or SDW. For samples from 5–9ºC for *G. rostochiensis*, total egg count data was not available. Data (numbers of J2 and eggs) were analysed using repeated measurements ANOVA and standard ANOVA. When required, the data were subjected to logarithmic or square root transformations to normalise the variances. The cumulative proportions of hatched nematodes were used to estimate the parameters of a logistic curve describing the hatching over time, t, for each temperature experiment separately, using the equation:

$$Y = A + C/\{1 + \exp[-B(t - M)]\} \quad (1)$$

where Y is the proportion of hatched nematodes (hatched number/total number of eggs at time t), A is the lower asymptote (an estimate of the number hatched at time zero, which is zero), C is the maximum asymptote (an estimate of the final proportion expected to hatch for any given temperature), B is the slope of the intermediate part of the curve, and M is the point of inflection (an estimate of the number of days until half of the J2s that are going to hatch have hatched, henceforth denoted HR50). The fitted curves from the logistic model were used to calculate means and standard errors for the maximum rates of hatching.

Developing a model to predict hatching based on temperature

In order to predict hatching at any temperature, equations were developed for the parameters of the logistic curve (Eq. 1). The resulting model was used to predict hatching using actual soil temperatures from Whitewater, Scotland and Harper Adams, England.

Figure 4 presents the parameters C, B and HR50 for each replicate plotted against temperature (T) for each species. Based on the shape of the curves, C and HR50 were parabolic around the optimum temperature for hatching (Topt) and B was linear for *G. rostochiensis*. The following equations were fitted to predict the logistic parameters from temperature:

$$C = C_{opt}*\{1- [(T-T_{opt})/w]^2\} \quad (2)$$
$$B = x*T+y \quad (3)$$
$$HR50 = H_{opt}+[(T-T_{opt})/w]^2 \quad (4)$$

where Topt is the optimum temperature for the given parameter (C or HR50), Copt is the final proportion that will hatch when the temperature is at its optimum, Hopt is the time taken for half of the final proportion of nematodes to hatch at Topt, w is the 'width' parameter for the response of the given variable to temperature, x determines how the hatching rate changes with temperature and y is the maximum hatching rate (since x is negative). The best root mean squared error (RMSE) fit of the data to these equations was found (Table 1 includes parameter values and model statistics), and the predicted curves (solid lines) in Figure 4 were plotted. These equations can then be used to estimate hatching (Eq. 1) for any given temperature or used on their own to describe hatching parameters.

Predicting hatching from soil temperatures

Hatching is strongly dependent on temperature (Figure 4 and Table 1). However, these experiments were performed for constant temperatures whereas field soil temperatures will fluctuate frequently. This leads to the issue of which temperature value should be used in Equations 2–4. For simplicity, we assume that the appropriate temperatures are those

Table 1. Parameters for equations 2, 3 and4 describing the relationships of the logistic parameters C, B and HR50 with temperature for *Globodera pallida* (Gpal) and *G. rostochiensis* (Gros).

C	Copt[a]	Topt[b]	w[c]	R^{2d}	Equation number
Gpal	0.88	18.4	11.7	0.86	2
Gros	0.65	19.7	11.0	0.92	2
B	**x[e]**	**y[f]**	**-**	**R^2**	**Equation number**
Gpal	-0.01	0.82	-	0.1	3
Gros	-0.06	1.87	-	0.93	3
HR50	**Hopt[g]**	**Topt**	**w**	**R^2**	**Equation number**
Gpal	9.6	18.7	3.4	0.91	4
Gros	6.5	18.8	3.6	0.79	4

[a] Final proportion that will hatch when the temperature is at its optimum.
[b] Optimum temperature for the given variable.
[c] 'Width' parameter for the response of the given variable to temperature.
[d] R-squared value for the fit of the equation to the data.
[e] Determines how the hatching rate changes with temperature.
[f] Maximum hatching rate (since x is negative).
[g] Time taken for half of the final proportion of eggs to hatch at Topt.

that occur in the period over which half of the J2 have hatched, i.e. HR50. Since HR50 depends on temperature, an average range of soil temperatures close to planting were considered, and the mean HR50 over this range for each species was computed. For example, we assume that after planting, most temperatures in the United Kingdom will fall into the range 10–15ºC and compute the mean HR50 over this range for each species (Eq. 4, Table 1). This gives HR50 values of 13 d for *G. pallida* and 10 d for *G. rostochiensis*. We then use this as the time period over which to average the soil temperatures and this is then used in Equation 4 to predict the HR50 for actual soil temperatures.

Results

Hatching at constant temperatures

Figure 1 presents the differential effect of temperature on the final percentage of J2 that have hatched for both species of PCN. The cumulative hatching analysis for *G. rostochiensis* had delayed hatch after 20 d and *G. pallida* had a delayed hatch after 30 d of incubation in PRD. These effects were particularly noticeable at temperatures >19ºC (Figures 2 and 3).

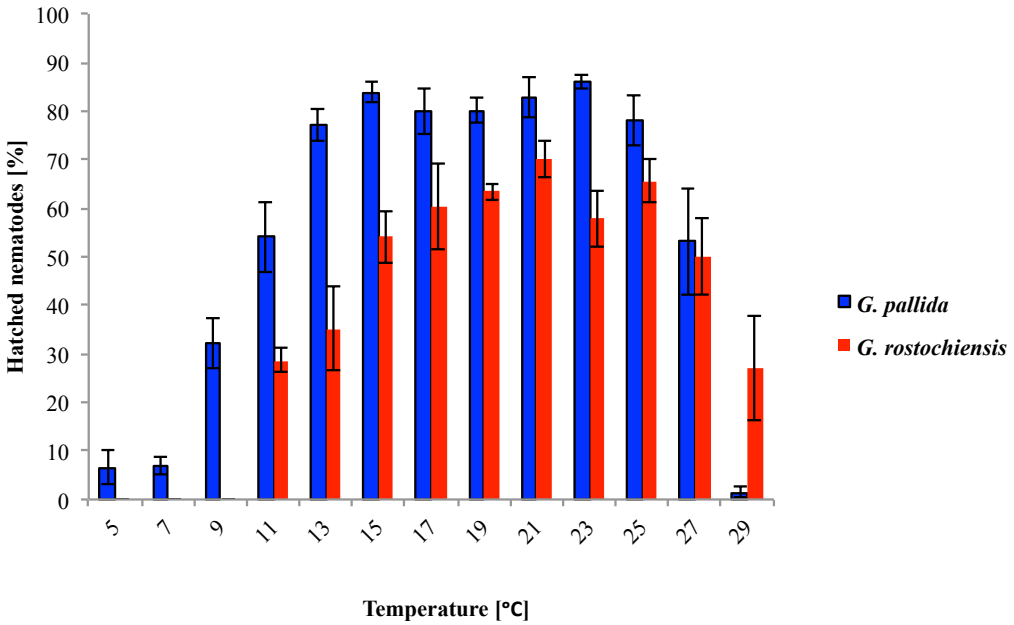

Figure 1. Mean total proportions of hatched *Globodera rostochiensis* and *G. pallida* in potato root diffusate, during 35 d incubation at different temperatures. Bars indicate standard errors of means.

For *G. pallida* there was no significant difference in the total hatching at 13–25ºC. The lowest cumulative hatch for *G. pallida* was at 29ºC followed by 5°C and 7°C, whereas for *G. rostochiensis* it was at 5°C and 7°C (Figure 2).

The hatching curves (Figures 2 and 3) revealed that most hatching took place within the first 3 weeks of incubation. *Globodera rostochiensis* hatched more rapidly than *G. pallida* with the first emergence of juveniles observed after 3 d of incubation at temperatures between 17–27°C, whereas the first appearance of *G. pallida* juveniles was recorded after 5 d in temperatures from 17–23°C. For *G. rostochiensis*, a rapid increase in hatching was recorded on day 7 (Figures 2 and 3) and hatching declined after 11 d, whereas for *G. pallida* hatching continued to increase until day 17 and then declined.

A repeated measurements ANOVA was applied to the hatching data with temperature and time of incubation in PRD as factors, to compare the impact of temperature on hatching of both species. For both species the comparison of the percentage hatch induced by PRD revealed significant differences ($P<0.001$) in the hatching at different temperatures. The greatest hatch of J2 for both species was in the intermediate temperatures. *Globodera rostochiensis* hatched more rapidly than *G. pallida*, but *G. pallida* is better adapted to low temperatures. The differences in hatching due to varying temperatures were also significant ($P<0.001$). The number of days until half

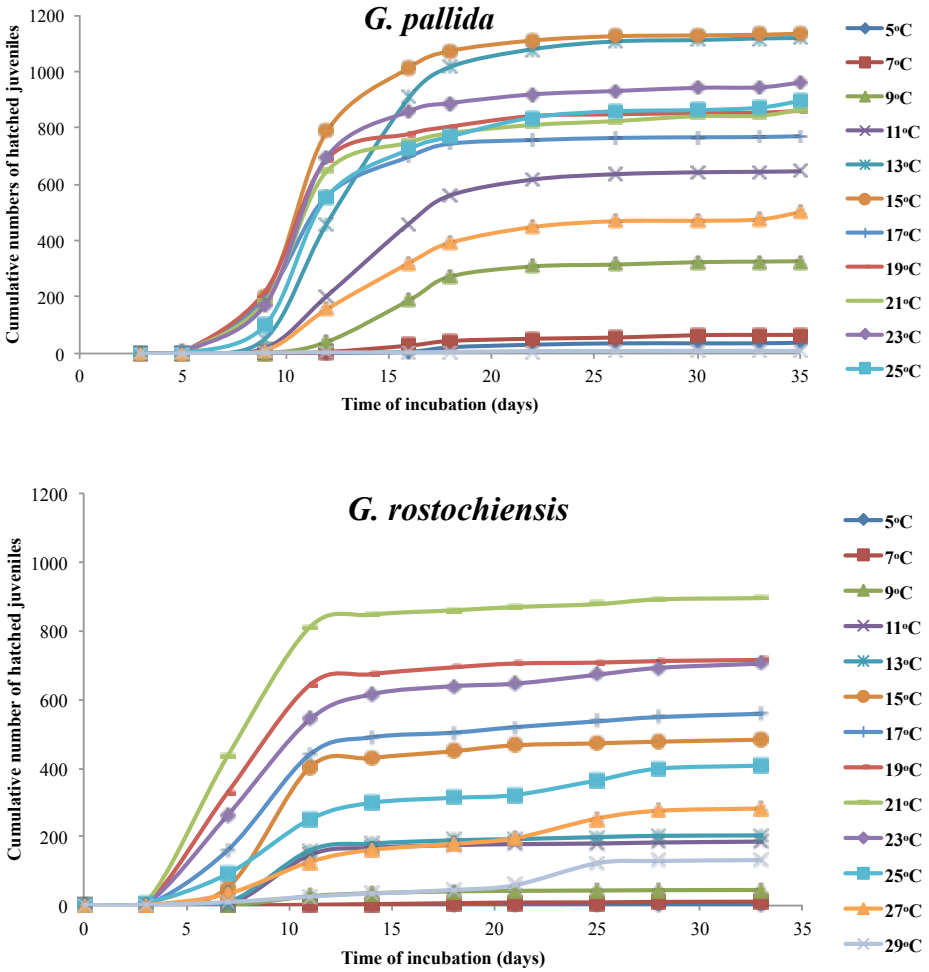

Figure 2. Mean cumulative numbers of juveniles hatched at different temperatues from ten cysts of *Globodera rostochiensis* (a) or *G. pallida* (b) in potato root diffusate during 35 d of incubation.

of the juveniles that will hatch, have hatched (HR50) was greater for *G. pallida* than for *G. rostochiensis* (Figure 2).

The percentage of total hatching for both species in SDW was <4%. There were no significant differences in relation to the amount of spontaneous hatch in SDW, temperature or species (P=0.162).

Comparison of parameters from the hatching assays

The parameters B, C and M of the logistic curve varied according to the mean temperature. The values for B showed significant differences in the rate of hatching at different temperatures (P<0.001), with no difference between the two species (P=0.449) but a significant interaction between species and temperature (P<0.001). *Globodera rostochiensis* had a greater hatching rate at lower temperatures than *G. pallida*, resulting in more rapid hatching, but at temperatures above 21ºC *G. pallida* hatched more rapidly. The parameter M indicates that *G. pallida* requires a longer period of incubation for half of the hatching to occur than *G. rostochiensis*. Significant differences between the two species were also found at different temperatures, and in the interactions between temperature and species (P<0.001). For parameter C significant differences were detected in the mean response at different temperatures (P<0.001). *Globodera pallida* had a significantly greater total percentage of hatched juveniles than *G. rostochiensis* (P=0.005), but no interaction between temperature and species in total hatching was observed (P=0.063).

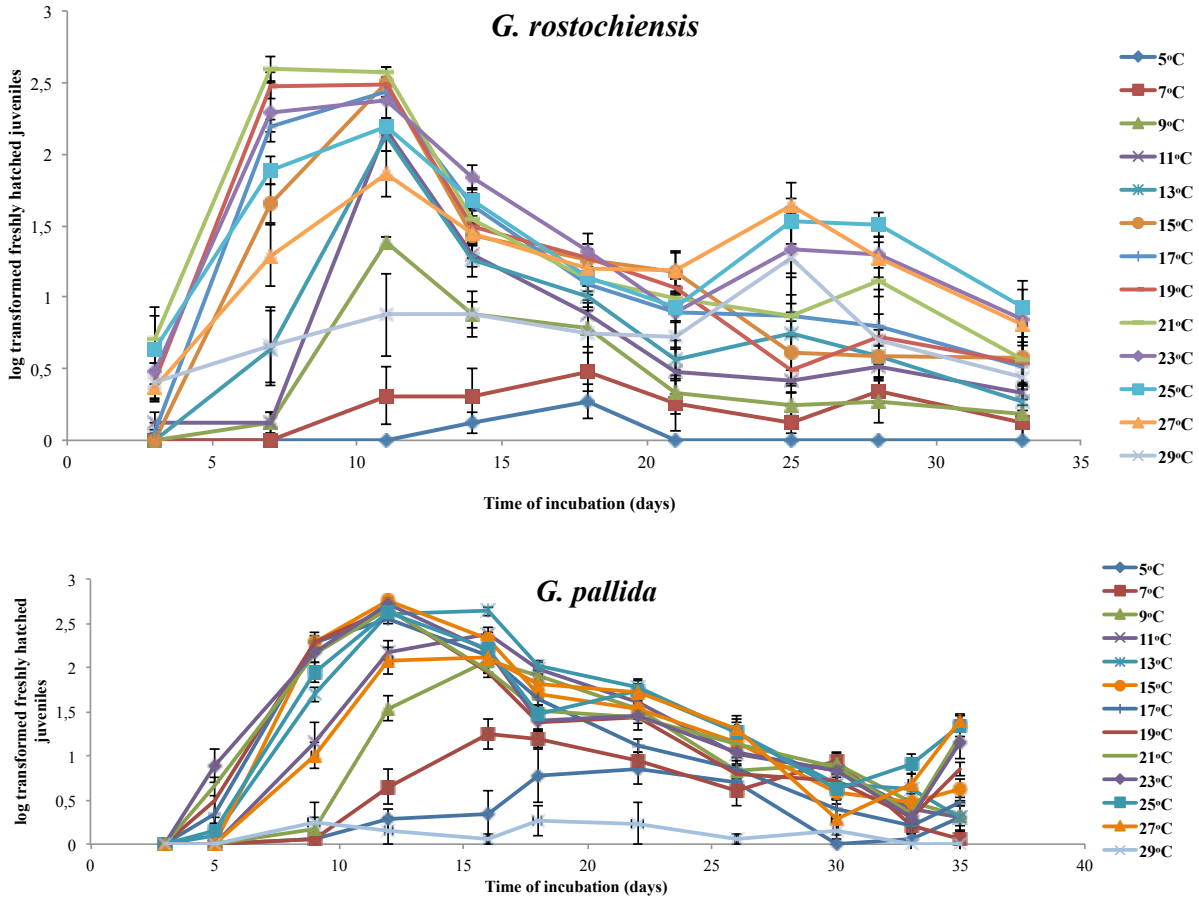

Figure 3. Mean numbers of freshly hatched juveniles of *Globodera rostochiensis* (a) and *G. pallida* (b) in potato root diffusate over 35 days of incubation over a temperature gradient from 5–29ºC. Data has been log transformed. Vertical lines indicate standard errors of means.

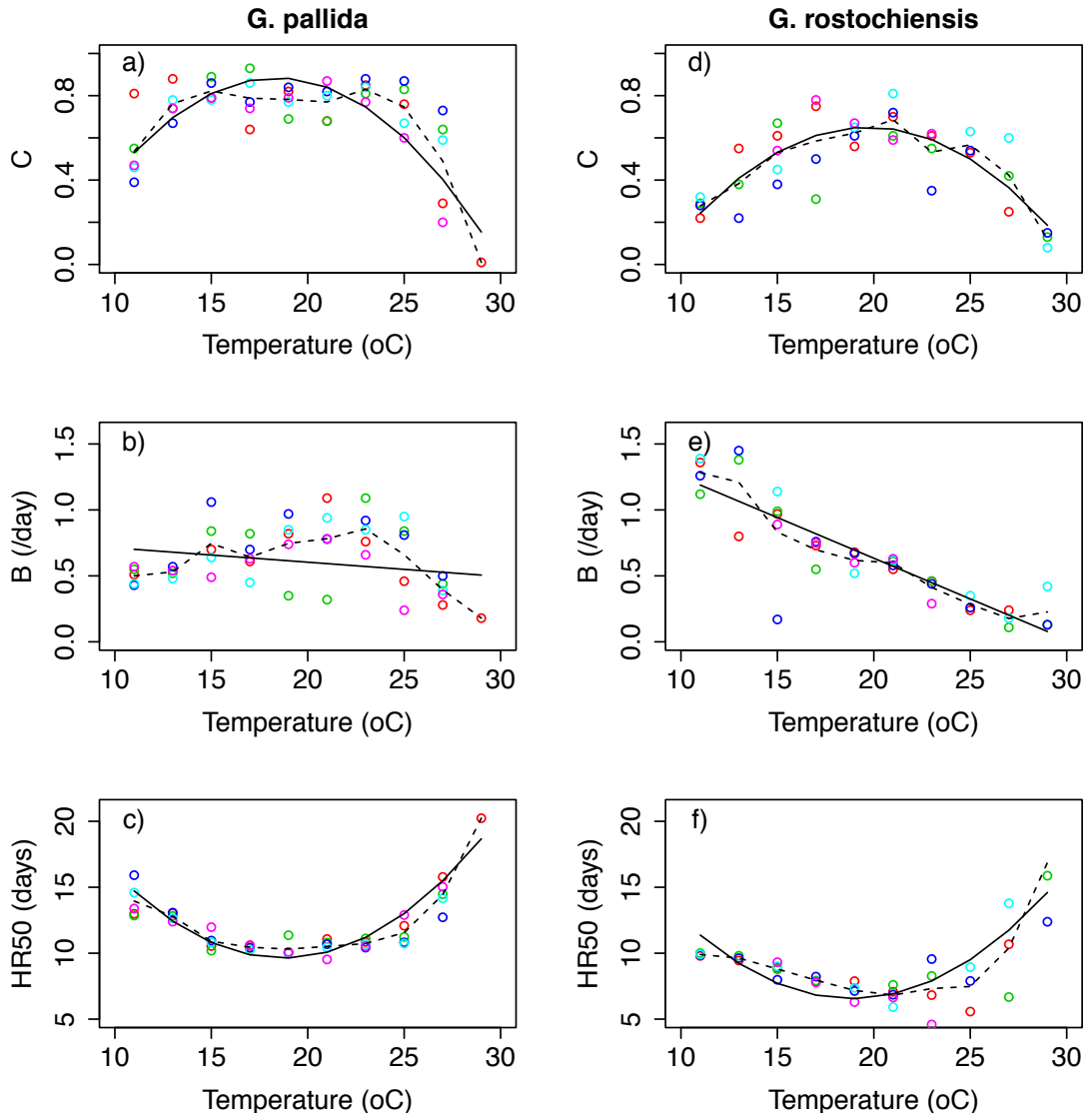

Figure 4. Parameters C, B and M (HR50) for the logistic equation (Y = A + C/(1 + exp(-B(t - M)))) as a function of temperature for *Globodera pallida* (left) and *G. rostochiensis* (right) . Each replicate is shown by the same coloured dots, the dashed line is the mean of the replicates and the solid line is the predicted curve from Equations 2, 3 and 4.

Calculating HR50 and the proportion of hatch for soil temperatures in the field

At Whitewater the soil temperatures over the potato growing season varied from 8–18.5ºC with a mean of 13.2°C. At Harper Adams the soil temperatures ranged from 9.5–22.5ºC with a mean of 15.4°C (Figure 5). The average temperature over 13 d from planting for *G. pallida* and 10 d for *G. rostochiensis* (denoted T_{av}) was used to compute HR50 (Eq. 4) for each species and at each location, resulting in the expected time required for half of the hatching to occur differing by 5 d between the two locations; for *G. pallida*, 16 d at Whitewater and 11 d at Harper Adams; and for *G. rostochiensis*, 13 d at Whitewater and 8 d at Harper Adams (Table 2). The proportion of hatch (Y) at the HR50 for *G. pallida* was 23 at Whitewater and 41 at Harper Adams, and for *G. rostochiensis* was 23 at Whitewater and 41 at Harper Adams.

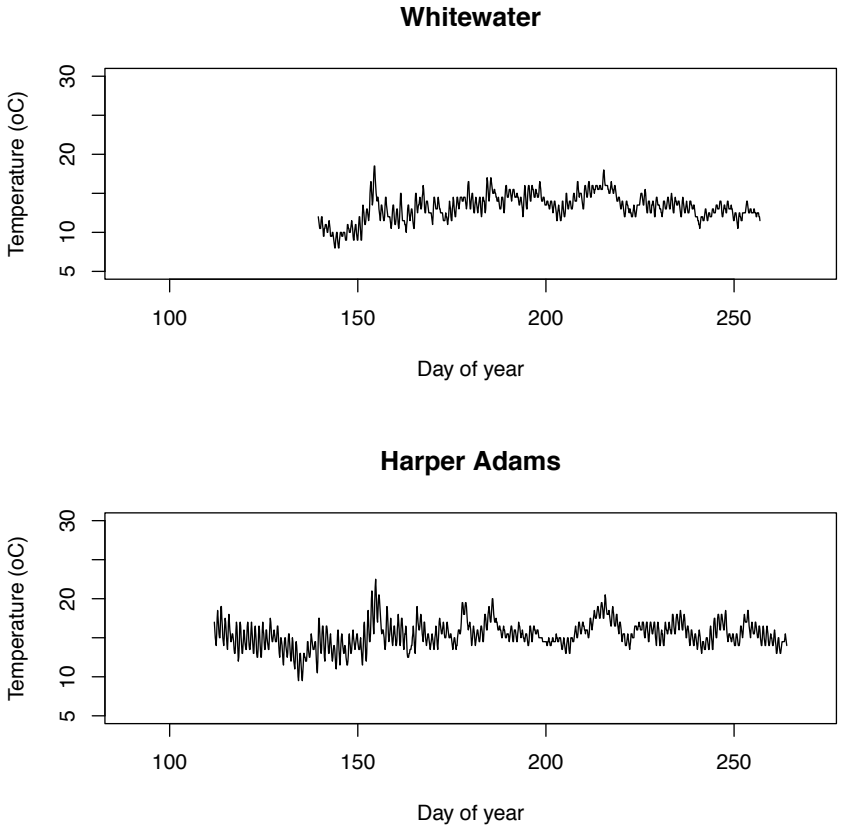

Figure 5. Soil temperatures in potato potato fields at 20 cm depth between planting and harvesting, taken at 3 h intervals at Whitewater, Scotland and Harper Adams, England for 2011.

Table 2. Predicted number of days for 50% of the hatching of *Globodera* spp. to occur (HR50), at Whitewater, Scotland and Harper Adams, England, using soil temperature data collected at 20 cm depth in potato fields.

***Globodera* species**	**Whitewater**		**Harper Adams**	
	T_{av} (ºC)[a]	**HR50 (d)**	**T_{av} (ºC)**	**HR50 (d)**
G. pallida	10.3	15.6	15.2	10.7
G. rostochiensis	10.1	12.6	15.3	7.5

[a] Average temperature during 13 d for *Globodera pallida* and 10 d for *G. rostochiensis*.

Discussion

Temperature regulates the metabolic rates of plant parasitic nematodes, and their rates of development are perturbed when the temperature drops close to the basal threshold or increases above the optimum. Temperature is therefore a key factor affecting population dynamics of PCNs, and is an important factor to take into account for pest management considerations, including potato cultivar choice and risks of more than one nematode generation occurring.

At 5ºC, the lowest temperature at which we observed hatching, the maximum hatch was ~5% in PRD and hatching below 7ºC was at the level of spontaneous hatch in SDW. This is similar to the results of Tiilikkala (1987), who noted the first J2 of *G. rostochiensis* in the soil at 4–5ºC in Finland. In contrast, Mulder (1988) reported that hatching stopped below 9ºC. However, we found ~35% hatching by *G. pallida* below 9ºC. Franco (1979) reported that *G. pallida* was better adapted to low temperatures than *G. rostochiensis*, and we also found that *G. pallida* hatched more at low temperatures than *G. rostochiensis*. The

greatest cumulative hatch for *G. rostochiensis* occurred at 21ºC, comparable to the results of Robinson *et al.* (1987) who observed a peak of newly hatched juveniles of *G. rostochiensis* at 20ºC. Our findings are also consistent with this report in that hatching by *G. rostochiensis* increased from 15 to 20ºC.

With *G. pallida* we found there was a broader temperature range over which similar amounts of hatching occurred compared to *G. rostochiensis*, in contrast to previous findings of Robinson *et al*. (1987). The greatest amount of hatching for *G. pallida* occurred between 13 and 25°C. The raw data as well as curve fitted parameters suggest that *G. rostochiensis* generally hatches more quickly than *G. pallida*. However, *G. pallida* had a significantly greater overall amount of hatching than *G. rostochiensis*. The two populations used in this study have been maintained in laboratory conditions over several generations. Differences in the hatching behaviour of our populations compared to those in other reports could be due to the adaptation of our nematode cultures to warm conditions in the glasshouses, or to intrinsic differences of the original isolates. Nevertheless, the two species were found to differ in their responses to temperature, confirming other reports (Franco, 1979). According to Hominick *et al.* (1985), environmental conditions influence the development *G. rostochiensis* females on potato roots, affecting the subsequent hatching of J2. The cysts used in our study had been multiplied and stored under well-defined conditions, and further populations will need to be tested to determine the extent of inter- and intra-specific variation in the hatching responses to temperature in field populations.

The differences in hatching expected for the two PCN species were considered in relation to soil temperature data obtained from potato fields during the crop growing period. Low soil temperatures are likely to favour *G. pallida* whereas warmer temperatures are likely to favour *G. rostochiensis* which hatches more quickly. This has implications for interspecific competition between the two species at different temperatures when they occur as mixed populations in the field, the host response to mixed infections and the composition of the final PCN populations. The two sites differed in their temperature profiles, and this had implications for which species was predicted to hatch more quickly and their respective amounts of hatching. At Harper Adams in England hatching was predicted to be more rapid for both species than at Whitewater in Scotland with *G. rostochiensis* hatching more quickly than *G. pallida*. However, the amount of hatching was predicted to be greater for *G. pallida* at both sites. Warm soil temperatures not only increase the rate of hatching for both species but also increase the amount of hatching leading to increased population densities on susceptible hosts and damage to potato crops. Regions of the United Kingdom with warm soil temperatures, or years in which crop planting coincides with warm soil temperatures, are thus more likely to have high levels of hatching of PCN, and thus greater multiplication, providing greater challenges for controlling nematode populations than where soils are cool. The potential to predict the impact of temperature on PCN population dynamics should assist growers in making appropriate pest management decisions for their particular circumstances.

The partial hatching of nematodes that was observed at non-optimal temperatures has implications for the proportion of viable eggs that remain in cysts which could hatch later, either during the growth of the same potato crop, or in the future. These differences in the proportions of unhatched juveniles are likely to affect population decline rates. The role of temperature in decline rates merits further investigation.

Acknowledgements

The assistance of Ralph Wilson, Anne Holt and Alison Paterson in this study is recognised. Funding for this work was received from the United Kingdom Potato Council, and The James Hutton Institute and Biomathematics & Statistics Scotland received funding from the Scottish Government for this research.

This paper was presented at the International Congress on "Pesticide Use and Risk Reduction for Future IPM in Europe", held in Riva del Garda, Italy, 19-21 March 2013.

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Accepted for publication: February 2, 2014

Published online: December 22, 2014